

## Fusimotor and skeletomotor activities are increased with precision finger movement in man

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1. Impulses of eighteen muscle spindle afferents from finger extensor muscles were recorded from the radial nerve while subjects performed single joint finger movements of two kinds, i.e. routine and precision, which were nearly identical with regard to kinematics.
2. The firing rates of ten primary and two secondary spindle afferents were higher in the precision movements by more than 10%, although the difference reached statistical significance in only seven of them. In most cases when spindle firing was higher in precision movements the skeletomotor activity was higher as well.
3. The findings indicated that the fusimotor activity was often stronger with precision movements compared with routine movements. This result is in qualitative agreement with several studies on behaving cats, demonstrating higher fusimotor activity in more demanding motor tasks. On the other hand, the effects were much smaller in humans than in cats. Moreover, in contrast to findings from experiments in cats, no support was obtained for the hypothesis that fusimotor activity was adjusted independently of the skeletomotor activity in human finger muscles.

The  $\gamma$ -system has the potential to set the sensitivity and the working range of muscle spindles independently of the degree of contraction of the parent muscle. This potential has been explored in a number of studies on human subjects by the recording of spindle afferents (Burg, Szumski, Struppler & Velho, 1973, 1974; Burke, McKeon, Skuse & Westerman, 1980; Burke, McKeon & Westerman, 1980; Vallbo & Hulliger, 1981; Al-Falahe & Vallbo, 1988; Aniss, Gandevia & Burke, 1988; Aniss, Diener, Hore, Burke & Gandevia, 1990; Vallbo & Al-Falahe, 1990; Gandevia, Wilson, Cordo & Burke, 1994; Nielsen, Nagaoka, Kagamihara, Kakuda & Tanaka, 1994; Wessberg & Vallbo, 1995).

Although several studies in humans suggest that a small proportion of spindle endings may be subject to minor fusimotor modulations, which occur in the absence of concomitant modulations of the skeletomotor activity, it remains an enigma why substantial and consistent effects of this nature have not been found in man. On the other hand, recordings of alleged  $\gamma$ -efferents in man suggest that  $\gamma$ -activity may be readily activated while the parent muscle remains relaxed (Ribot, Roll & Vedel, 1986).

In behaving animals, on the other hand, a variable level of  $\gamma$ -activity has been inferred on the basis of recordings from spindle afferents in several studies (Prochazka, Hulliger, Zangger & Appenteng, 1985; Hulliger, Dürmüller, Prochazka & Trend, 1989). Recently, it has been claimed that a higher level of attentiveness, a higher precision requirement, or a novel motor situation is associated with an increased  $\gamma$ -drive in the cat (Prochazka, 1989).

Considering the discrepancy between findings from co-operative human subjects and behaving animals it seems pertinent to explore the issue further.

The present study examined the hypothesis that voluntary finger movements are associated with a different fusimotor drive when the precision demands are high compared with similar movements without precision demands. Although higher spindle firing was found in precision movements, the findings did not support the hypothesis of fusimotor independence because the skeletomotor activity was modulated in the same direction as the muscle spindle firing.

A preliminary report of some of this work has been published in abstract form (Kakuda, Vallbo & Wessberg, 1994).

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## METHODS

Recordings were obtained from five healthy subjects, 24–31 years old, three females and two males. All gave their informed consent according to the Declaration of Helsinki (*British Medical Journal* vol. 2, p. 177 (1964)) and the project was approved by the Ethical Committee of the Medical Faculty of Göteborg University.

Details of the experimental set-up have been given in a previous paper (Wessberg & Vallbo, 1995). Afferent activity from muscle spindles in the finger extensor muscles was studied. Single unit impulses were recorded from the radial nerve while subjects performed movements at a single metacarpophalangeal joint. With imposed movements it was assessed which finger most effectively modulated the afferent response. This finger was connected to an actuator which featured transducers for joint angle, angular velocity and angular torque as well as feedback circuits which compensated for the inertia and friction of the actuator. Hence, the finger perceived no extra load during test movements. Joint angle, angular velocity and angular torque were sampled at 400 Hz, and the nerve signal at 12.8 kHz.

EMG was recorded with surface electrodes placed on the dorsal surface of the forearm close to the optimal points for electrical stimulation of the muscle portion of the afferent unit. The EMG was root-mean-square rectified and sampled at 800 Hz. This signal was digitally low-pass filtered off-line with  $-3$  dB at 6.7 Hz and zero gain at 15.8 Hz.

### Unit identification

The unit identification procedure was based on a battery of eight discriminators which were weighted according to Bayes' decision theory (Edin & Vallbo, 1990). All individual nerve impulses were inspected off-line on an expanded time scale before the records were accepted for further data analysis. Eighteen single muscle spindle afferents were recorded. Thirteen were identified as primary and five as secondary afferents. The median probability of unit identity according to the Bayes procedure was 0.93 while the range was 0.71–0.99.

### Experimental protocol

In order to make the subject perform similar movements with two vastly different precision demands the following procedure was adopted. As soon as a muscle spindle afferent had been identified with regard to unit type and optimal finger, the subject was given a lax instruction to move the finger more or less as it pleased her/him for about 30 s. The instruction was typically 'Move your finger back and forth but avoid extreme positions and don't move too fast' (6 units, 16 pairs of trials) whereas in other experiments (11 units, 17 pairs) the subject was also shown simple line drawings on paper indicating the general pattern of movement desired, i.e. repetitive movements of either roughly uniform speed and amplitude, or movements of successively increasing amplitude or speed. However, this loose instruction did not entail any strict requirement regarding movement speed or amplitude. While the subjects performed these routine movements, the metacarpophalangeal joint angle of the moving finger was sampled by the computer at 5 Hz for a period of 18 s starting a few seconds after the onset of the free movements.

Immediately following the free movements, the subject was requested to perform a visual tracking with high precision. The

sampled signal previously recorded during the free movement was replayed as a command signal in an indirect tracking task, i.e. the difference between the actual finger position and the demanded position was presented as an error signal on an oscilloscope in front of the subject. The beam was swept vertically and split into an upper half, which was permanently kept in the middle of the screen, and a lower half, which indicated the error. The subject was continually urged to minimize the error. Hence, he produced a replica of part of his previous free movements, although he was not aware of the relation between the two kinds of movements. On the oscilloscope screen, one degree of joint angle corresponded to 2.8 mm on the screen, while the width of the beam was 0.6 mm.

### Data analysis

The individual trial of precision movement yielded an 18 s recording, which included a series of flexion and extension movements, the number being dependent on the speed of movement the subject decided to use. Data from the corresponding 18 s of free movements, which formed the template of the precision tracking task, constituted the reference to be compared with the data from the precision trial, the two constituting a pair of trials. The individual flexion or extension movement, in turn, constituted a segment which was analysed separately for most purposes. In addition, all data, from either flexions or extensions, or from flexions as well as extensions, of the individual unit were pooled prior to analysis.

Mean discharge rates of spindle afferents were computed for each movement segment, while the mean EMG activity during the same periods was computed from the rectified and low-pass filtered EMG signal. The values of corresponding segments from routine and precision movements were paired and the set of segment data collected from the unit was tested for significance of difference using Wilcoxon ranked sign test ( $P < 0.05$ ). When the subject chose a low angular speed only a few segments were obtained and statistical tests could not be employed, while a difference was often obvious to the eye. In addition to the analysis of intra-unit data, the grand means of the firing rates in routine and precision movements from individual units were calculated, and the means from the eighteen units were tested for differences between the two tasks (Wilcoxon). Linear-regression analysis was used to explore the correlation between EMG activity and the mean discharge rate.

## RESULTS

Eighteen spindle afferents were analysed for difference in firing rates between routine movements and precision movements. The tests were designed to generate similar kinematics and identical external loading conditions in the two tasks in order to ensure the relevance of a direct comparison. Altogether, thirty-three pairs of trials were collected, twenty-three with thirteen units classified as muscle spindle primary afferents, and ten pairs with five units classified as muscle spindle secondary afferents. The number of trials was one to six with individual primary afferents and one to three with secondary afferents.

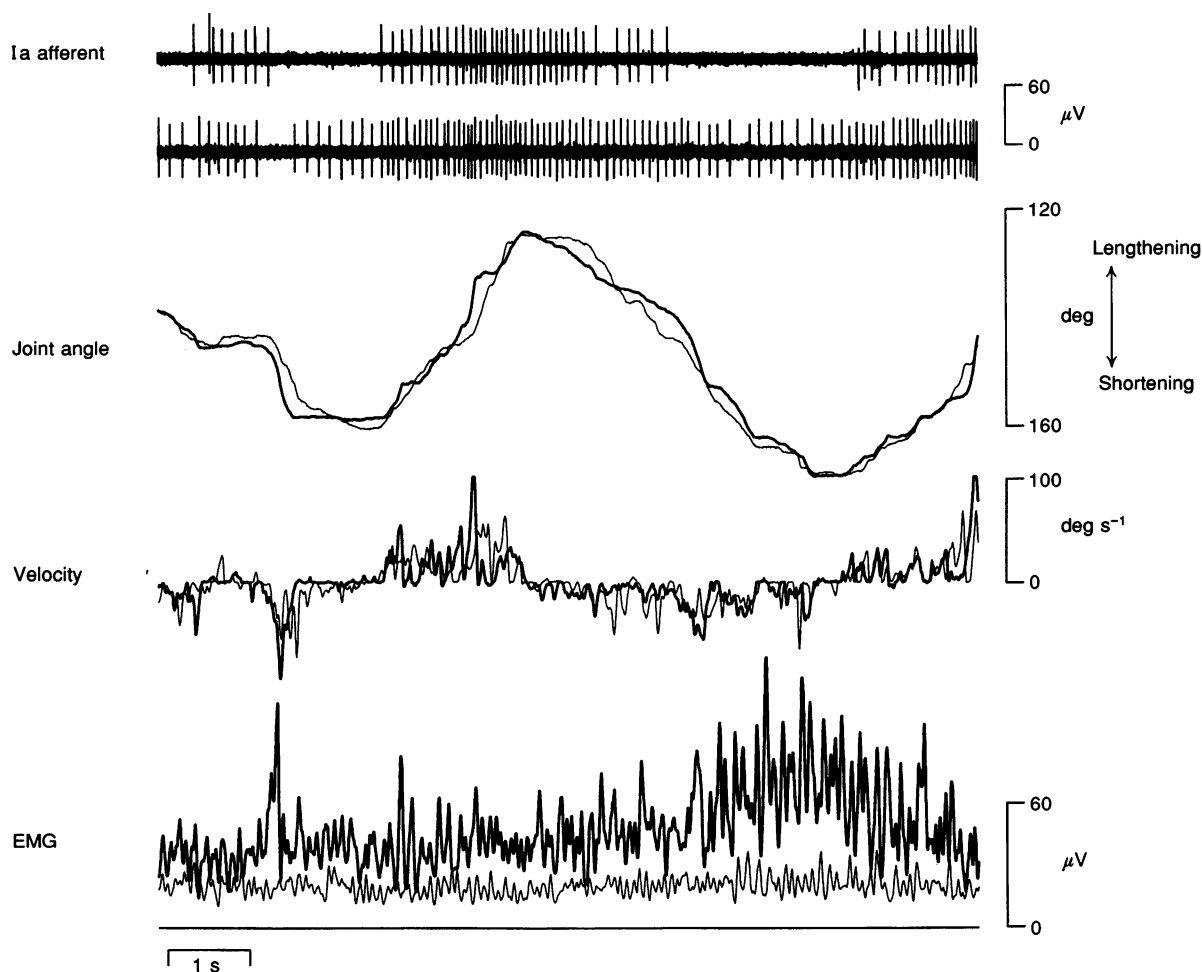
### Afferent response in precision and routine movements

Figure 1 shows sample records of spindle firing, motor performance and EMG activity in precision and routine movements. The figure illustrates the main findings of the investigation, namely that spindle firing as well as EMG activity were often higher in precision movements than in routine movements in spite of almost identical trajectories.

The unit of Fig. 1 is not representative of the whole sample, however, because spindle response was not consistently higher with precision movements. Generally, the inter-unit variability was considerably higher than the intra-unit variability.

Figure 2 illustrates the variation between units in a display designed to facilitate a comparison of afferent firing between the two tasks. In the unit of Fig. 2A the impulse rate was considerably stronger in the precision movements compared with routine movements. The increase was particularly pronounced in the phases when the muscle was relatively short, which resulted in a reversal of the stretch response present with the routine movement. A similar shift of response pattern from a stretch response to an inverse stretch response has previously been described when the parent muscle contraction is increased (Burke, Hagbarth & Löfstedt, 1978; Al-Falahe, Nagaoka & Vallbo, 1990).

The unit of Fig. 2B also exhibited a clear and consistent increase of spindle firing in precision movements, although



**Figure 1. Differences between routine and precision movements**

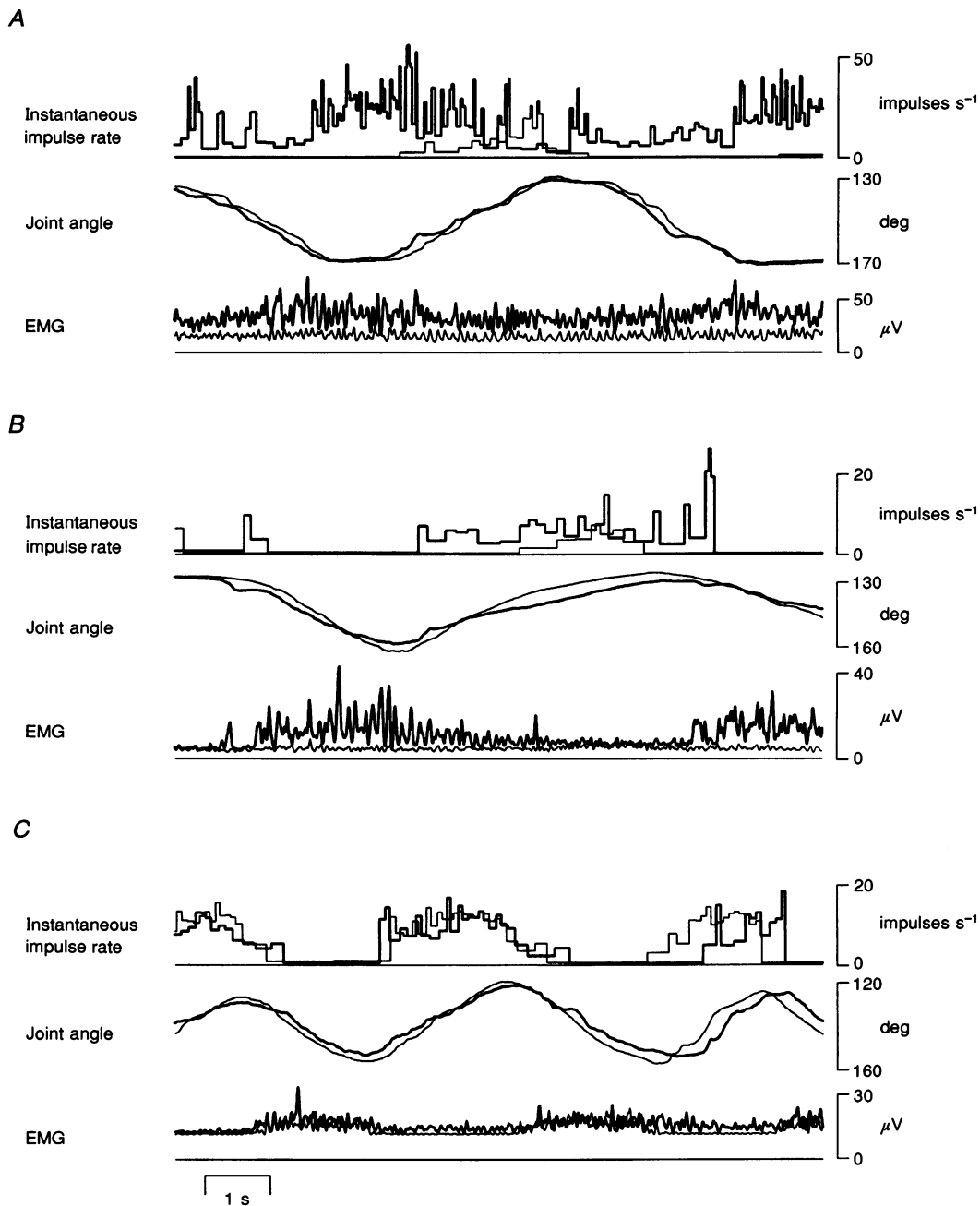
Upper nerve record and thin lines refer to routine movements, while lower nerve record and thick lines refer to precision movements. Upward deflections in the joint angle signal represent lengthening of the parent muscle. Unit number 4.

it was smaller in absolute figures. On the other hand, in relative figures the difference was quite pronounced.

Finally, the unit of Fig. 2C produced the same or nearly the same firing rates in routine and precision movements, although a difference might be fallaciously suggested due to a poor tracking in the last cycle.

The whole sample is presented in Fig. 3, where the height of the individual bars gives the mean difference in firing

rate between precision and routine movements for the individual afferents. The diagram is based on all available recordings, i.e. flexion movements as well as extension movements. Figure 3A shows the difference in absolute figures, i.e. impulses per second, whereas Fig. 3B demonstrates the difference in relative figures, i.e. as a percentage of the mean firing rate during the routine movements.

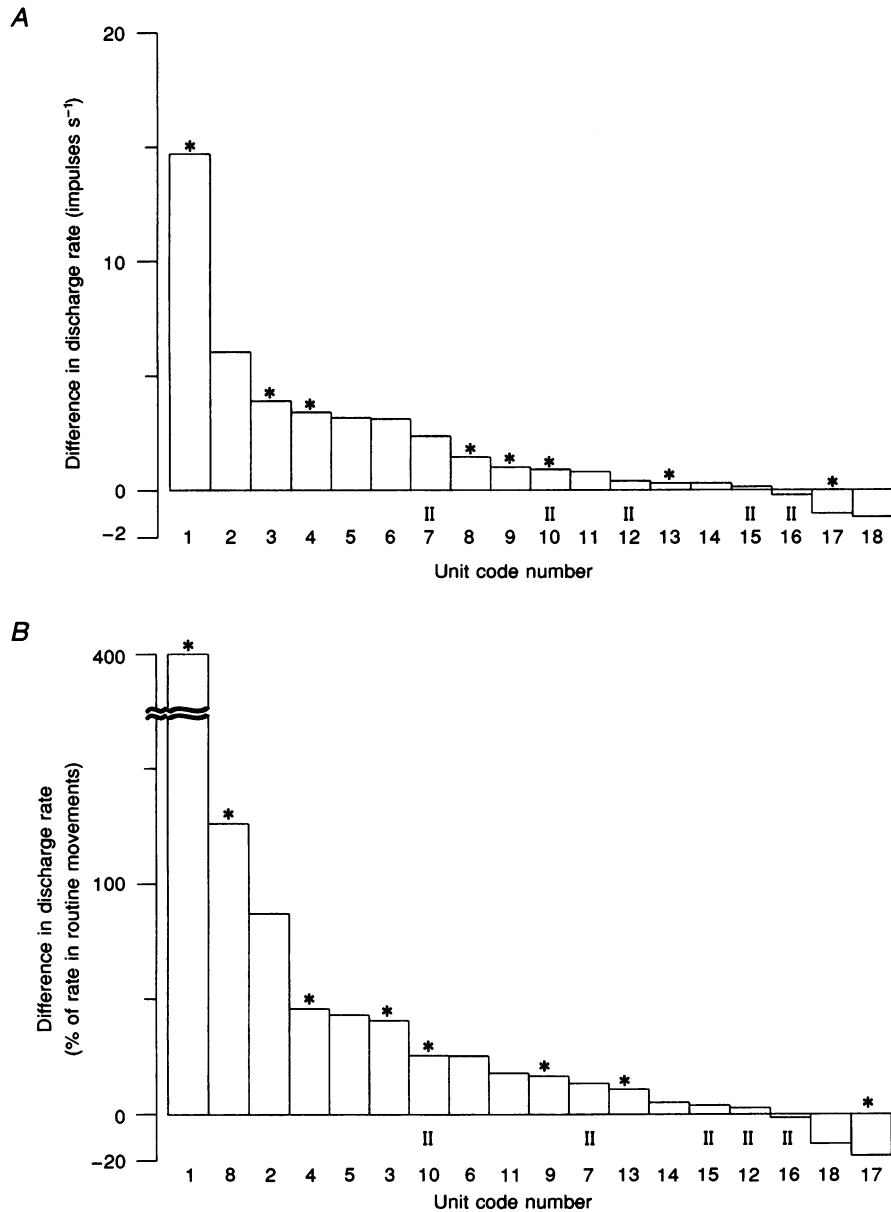


**Figure 2.** Differences between routine and precision movements with three Ia afferents (*A*, *B* and *C*)

Thin lines refer to routine movements, while thick lines refer to precision movements. Upward deflections in the joint angle signal represent lengthening of the parent muscle. Units number 1, 8 and 17.

It is obvious that most units ( $n = 15$ ) fired at higher rates in precision movements (positive difference). In eight units (44%) the firing rate was 25% higher or more with the precision movements (Fig. 3*B*), and in twelve units (67%) it was 10% higher or more. The positive difference was statistically significant with seven units, which are indicated by asterisks in the diagrams of Fig. 3. Even though a significant difference was found in less than half of the units, the increase in the mean discharge rate with

precision movements was highly significant in the group data, i.e. when means from individual units were tested (Wilcoxon ranked sign test,  $P < 0.005$ ). It can be seen that lower rates with precision movements were found in only three units. The differences were small but statistically significant with one of them. It is also clear from Fig. 3*A* and *B* that there is a continuum within the sample with regard to dependence on precision requirement with no clear grouping of units.



**Figure 3. Difference in muscle spindle firing rates between routine and precision movements in the entire sample**

Positive values indicate higher firing rates in precision movements. Individual columns represent individual afferents. *A*, difference expressed as mean impulse rate. Unit code number assigned according to size of difference. *B*, difference expressed as a percentage of the firing rate in routine movements. Unit code numbers as in *A*. Asterisks indicate statistical significance (Wilcoxon ranked sign test;  $P < 0.05$ ). The symbol II under some columns indicates muscle spindle afferents classified as group II afferents. The order is dissimilar in *A* and *B*, because the bars are consistently arranged according to their difference in size, while the individual unit may be identified by its code number.

### Movement trajectories in routine and precision movements

In order to identify the mechanisms behind the difference in spindle firing rates between routine and precision movements it is pertinent to consider the movement trajectories as well as the EMG activity.

In most pairs of trials, the trajectories of joint angle exhibited only minor differences, as was obvious from mere inspection of the records (cf. Figs 1 and 2). This impression was substantiated by assessing the means of three kinematic variables, i.e. joint angle, velocity and standard deviation of velocity. Differences were usually less than 10% and not systematic for any of these parameters in paired segments, i.e. individual phases of flexion or extension movements. Thus, it seemed unlikely that the differences in spindle firing rate were due to differences in kinematics.

### EMG activity in routine and precision movements

As pointed out above, the EMG activity was often stronger in precision movements, as was obvious from mere inspection of the records (Figs 1 and 2). Particularly, it was stronger in the phase of muscle shortening and/or while the muscle was in the short length range.

Figure 4 presents data from all recordings in a plot of mean difference in spindle firing rate against mean difference in EMG activity. Individual data points represent individual units and are based on all recordings with the unit.

Considering EMG alone, the sample was uniform in that EMG activity was larger in the precision movements for all

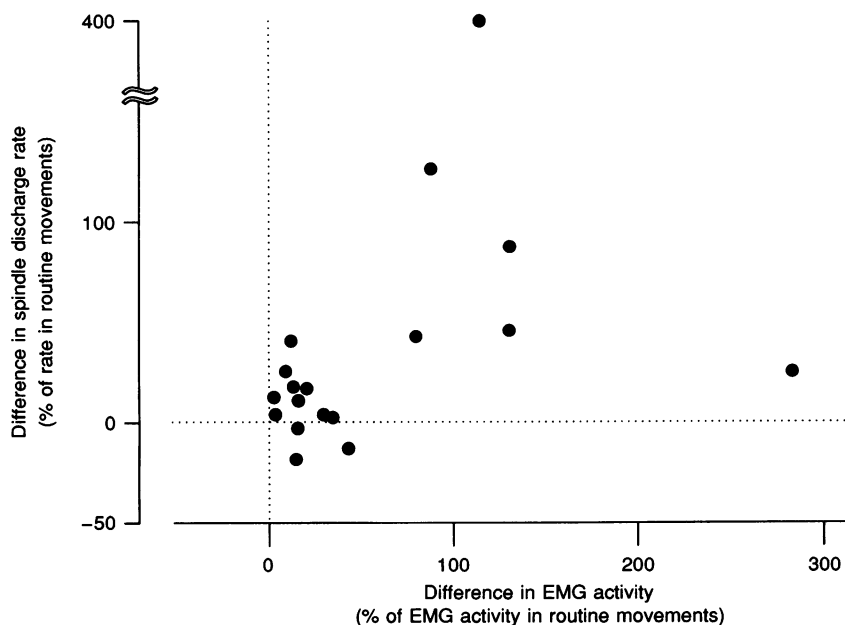
units, although the difference was small or moderate in many cases. The difference was statistically significant in eleven units. With an additional four units the difference was clear, as in Figs 1 and 2A, but failed to reach statistical significance because the number of segments was small ( $n = 2-4$ ).

The finding that the EMG activity was consistently higher in precision movements indicated that subjects relied more on co-contraction when the task was more demanding (Smith, 1981). However, the strength of the effect varied between subjects and, importantly, four of the six units which were associated with a large difference in EMG (more than 50%) were recorded from one single subject.

### Spindle firing versus EMG activity in precision and routine movements

In order to explore the issue of fusimotor independence it is particularly relevant to consider to what extent higher firing rates in muscle spindle afferents occurred in precision movements without concomitant increases of skeletomotor activity. The scatter plot of Fig. 4 does not support such an independence because whenever spindle firing increased, the EMG activity increased as well, yielding a positive correlation between the two variables, although it failed to reach statistical significance (correlation coefficient, 0.29;  $P = 0.24$  by linear-regression analysis).

In order to exemplify the inter-test variability Fig. 5 was constructed. It shows data from lengthening movements of six sample units. Lines connect data pairs from individual tests.



**Figure 4.** Difference in spindle firing rate and EMG activity between routine and precision movements in the entire sample

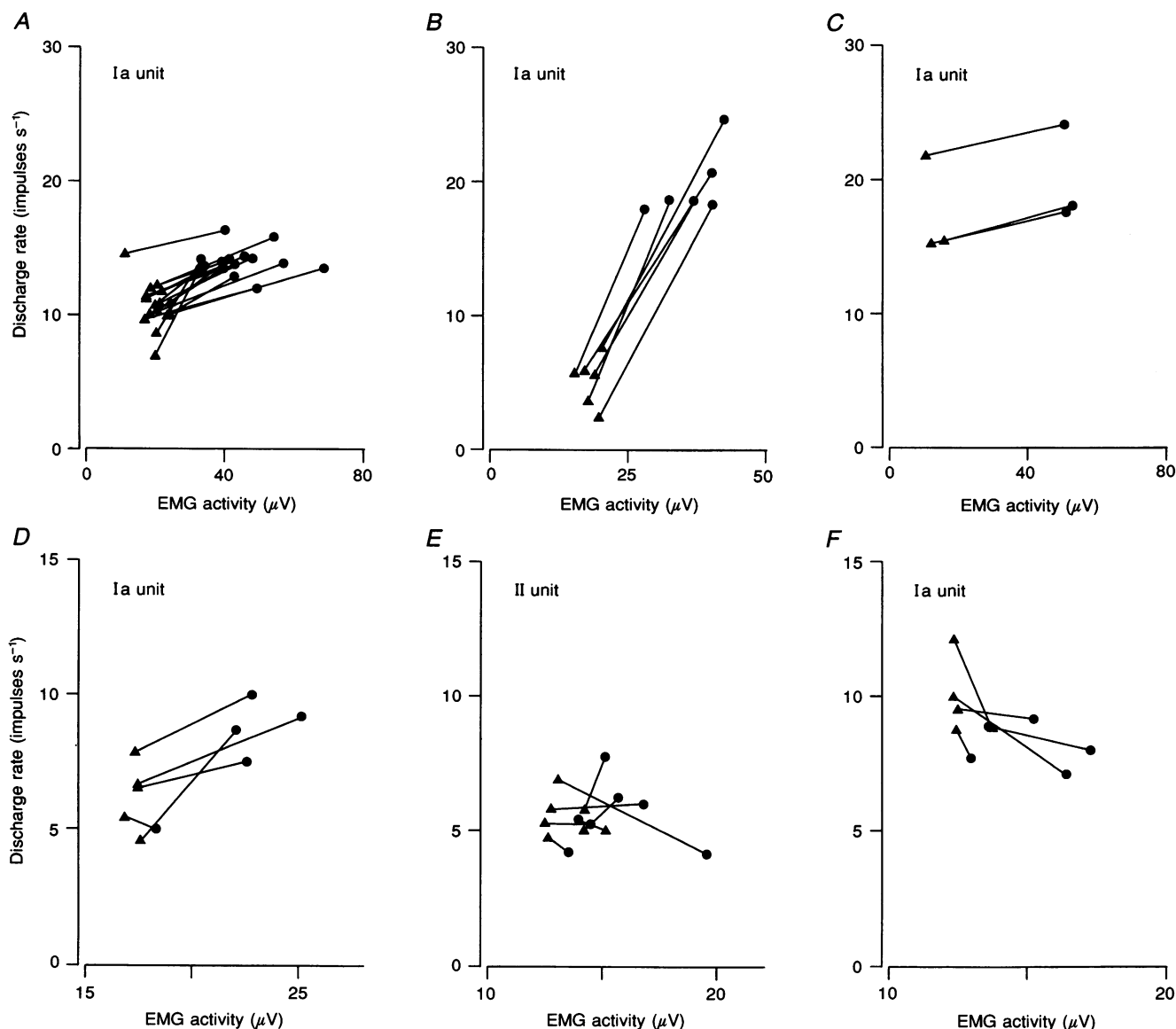
Points represent individual units and are based on all recordings from the unit. Differences are expressed as a percentage of firing rate and EMG activity in routine movements.

Figure 5 illustrates that many units yielded consistent findings in the sense that all or most tests demonstrated an increase of both spindle firing rate and EMG activity in precision movements (Fig. 5*A, B, C* and *D*). A similar pattern was seen in twelve units (units 1–6 and 8–13 of Fig. 3).

With another five units there was a considerable variation between tests in that some provided an increase of both variables, while others provided a slight decrease in spindle firing with an increase in EMG activity (Fig. 5*E*). In most units with the latter pattern the difference in spindle firing was quite small, i.e. the mean difference was often less than 1 impulse  $s^{-1}$ . In one unit the spindle firing decreased

systematically while the EMG activity increased in the precision movements (Fig. 5*F*, unit 17). It seems reasonable that decreases in spindle firing rate with stronger EMG activity might be due to mechanical unloading.

During shortening movements the pattern was similar, although it differed in details. Spindle firing and EMG increased with precision movements in nine units (units 1–4, 6–9 and 12). With another eight units, spindle firing rate remained the same during precision movement. EMG activity increased in five of these units but was largely unchanged in the other three. With one afferent (unit 18), the spindle firing decreased while the EMG activity increased in precision movements.



**Figure 5. Inter-test variability with regard to difference in spindle firing rate and EMG activity between precision and routine movements**

Data from 6 sample units during flexion movements demonstrating various patterns of variability. ●, precision movement; ▲, routine movement. Plots are based on absolute figures of impulse rate and EMG activity, rather than relative figures. Note the difference in *y*-scales in *A, B* and *C* versus *D, E* and *F*. Units number 4, 1, 6, 11, 15 and 17 in *A–F*, respectively.

With regard to the absolute firing rate in relation to EMG activity, Fig. 5 demonstrates a considerable inter-test variation with some units, e.g. Fig. 5C. At first sight this might suggest an independence between fusimotor and skeletomotor activity. However, such a conclusion is not justified because the movement parameters were not standardized, implying that starting positions as well as the speed of movement varied between tests.

## DISCUSSION

The purpose of the present study was to explore whether fusimotor activity was different in precision movements compared with routine movements when subjects voluntarily moved a single finger. The approach was to measure impulse rates of individual muscle spindle afferents in free movements and movements when subjects were encouraged to perform with maximal precision. Data indicated consistently higher spindle firing in the precision movements with 67% of the units, although the difference was significant in only 39% of them, largely due to the small number of observations. On the other hand, in group data, when means from all units were tested, the difference between precision and routine movements was highly significant. The effect was mostly seen in primary but also in a small percentage of the secondary muscle spindle afferents.

An inference of stronger fusimotor activity on the basis of a higher afferent impulse rate can only be justified, however, if the movements are identical with regard to time course, angular range and amplitude. If not, a higher spindle firing might be due to a more efficient mechanical stimulus in terms of muscle length and changes in length. Considerable measures were taken in the present study to ensure that the tests involved similar movement trajectories in the two tasks of a pair. Analyses of kinematic data from the two kinds of movements indicated that the discrepancies were small and non-systematic and they were considered trivial. Therefore, it seemed likely that fusimotor activity was higher in precision movements than in routine movements in about half of the muscle spindle afferents.

The experimental procedure involved visual tracking with the precision movements, but not with the routine movements. It may be argued that visual information, rather than precision requirement, was the essential factor to reset the fusimotor drive. However, a previous study demonstrated that access to visual information in tests of this nature has a negligible effect on the fusimotor activity (Wessberg & Vallbo, 1995). It seemed, therefore, justified to conclude that the precision requirement was an essential factor to reset the fusimotor drive to a higher level in precision movements than in routine movements.

The present experiments were designed to involve a minimum of assumptions for testing the core hypothesis.

Simply, a direct comparison between pairs of numerical data was required. On the other hand, rather few data points were available from the individual afferent because the experimental protocol prevented many data points being collected from the single unit. Hence, levels of statistical significance were generally moderate, and with many afferents higher firing rates in precision movements failed to reach significance. On the other hand, the finding that most units exhibited higher, albeit non-significant, firing rates in precision movement adds further support to the conclusion that precision movements were associated with stronger fusimotor drive. Moreover, the difference was highly significant in the group data.

The present data have a bearing on another issue that has attracted a lot of interest in relation to natural movements in man and behaving animals, i.e. whether the fusimotor activity is modified independently of the skeletomotor output or not (Prochazka, Gorassini & Taylor, 1992). Several studies in behaving cats indicate that the fusimotor activity is increased in more demanding motor tasks which involve high attention or vigilance (Prochazka *et al.* 1985; Prochazka, Hulliger, Trend & Dürmüller, 1988; Hulliger *et al.* 1989; Prochazka *et al.* 1992). It is interesting that this was also true in the present study as spindle firing was often higher in precision movements. However, EMG recordings from the parent muscle revealed that the higher afferent impulse rates were regularly associated with stronger muscle contraction. Hence, the findings do not allow the conclusion that fusimotor activity was adjusted independently of the skeletomotor activity.

An additional difference between the present findings and those from behaving cats is that the size of the fusimotor effects induced by the more demanding motor task was considerably smaller in human finger muscles than those found in cat hindlimb muscles (Prochazka *et al.* 1985, 1988, 1992; Hulliger *et al.* 1989).

It should be emphasized that the present study was qualitative in the sense that only the occurrence and the direction of fusimotor changes were examined, whereas no attempt was made to assess the amount or the type of fusimotor modulation. Hence, changes in the quantitative relationships between fusimotor and skeletomotor activities were not explored. On the other hand, since spindle primary afferents were studied during voluntary movements, and not only during position holding, it seems obvious that dynamic fusimotor effects would not escape attention.

Clearly, the present findings do not allow any conclusions to be drawn with regard to the neural mechanisms which account for the association between increases of fusimotor and skeletomotor activities in precision movements, e.g. to what extent it is due to co-activation of the  $\alpha$ - and  $\gamma$ -systems or  $\beta$ -activation (Emonet-Dénand, Jami & Laporte, 1975; Emonet-Dénand & Laporte, 1975; Jami, Murthy & Petit, 1982). However, it may be relevant that



morphological analyses for plate-1 endings on intrafusal muscle fibres, which implicate  $\beta$ -innervation (Scott, Kümmel & Illert, 1995), suggest that  $\beta$ -innervation is common in human finger extensor muscles (J. J. A. Scott, Å. B. Vallbo & A. Ejeskär, unpublished observations).

- AL-FALAHE, N. L., NAGAOKA, M. & VALLBO, Å. B. (1990). Response profiles of human muscle afferents during active finger movements. *Brain* **113**, 325–346.
- AL-FALAHE, N. L. & VALLBO, Å. B. (1988). Role of the human fusimotor system in a motor adaptation task. *Journal of Physiology* **401**, 77–95.
- ANISS, A. M., DIENER, H. C., HORE, J., BURKE, D. & GANDEVIA, S. C. (1990). Reflex activation of muscle spindles in human pretibial muscles during standing. *Journal of Neurophysiology* **64**, 671–679.
- ANISS, A. M., GANDEVIA, S. C. & BURKE, D. (1988). Reflex changes in muscle spindle discharge during a voluntary contraction. *Journal of Neurophysiology* **59**, 908–921.
- BURG, D., SZUMSKI, A. J., STRUPPLER, A. & VELHO, F. (1973). Afferent and efferent activation of human muscle receptors involved in reflex and voluntary contraction. *Experimental Neurology* **41**, 754–768.
- BURG, D., SZUMSKI, A. J., STRUPPLER, A. & VELHO, F. (1974). Assessment of fusimotor contribution to reflex reinforcement in humans. *Journal of Neurology, Neurosurgery and Psychiatry* **37**, 1012–1021.
- BURKE, D., HAGBARTH, K.-E. & LÖFSTEDT, L. (1978). Muscle spindle activity in man during shortening and lengthening contractions. *Journal of Physiology* **277**, 131–142.
- BURKE, D., MCKEON, B., SKUSE, N. F. & WESTERMAN, R. A. (1980). Anticipation and fusimotor activity in preparation for a voluntary contraction. *Journal of Physiology* **306**, 337–348.
- BURKE, D., MCKEON, B. & WESTERMAN, R. A. (1980). Induced changes in the thresholds for voluntary activation of human spindle endings. *Journal of Physiology* **392**, 171–181.
- EDIN, B. B. & VALLBO, Å. B. (1990). Classification of human muscle stretch receptor afferent: A Bayesian approach. *Journal of Neurophysiology* **63**, 1314–1322.
- EMONET-DÉNAND, F., JAMI, L. & LAPORTE, Y. (1975). Skeleto-fusimotor axons in hind-limb muscles of the cat. *Journal of Physiology* **249**, 153–166.
- EMONET-DÉNAND, F. & LAPORTE, Y. (1975). Proportion of muscle spindles supplied by skeletofusimotor axons ( $\beta$ -axons) in peroneus brevis muscle of the cat. *Journal of Neurophysiology* **38**, 1390–1394.
- GANDEVIA, S. C., WILSON, L., CORDO, P. J. & BURKE, D. (1994). Fusimotor reflexes in relaxed forearm muscles produced by cutaneous afferents from the human hand. *Journal of Physiology* **479**, 499–508.
- HULLIGER, M., DÜRMÜLLER, N., PROCHAZKA, A. & TREND, P. (1989). Flexible fusimotor control of muscle spindle feedback during a variety of natural movements. *Progress in Brain Research* **80**, 87–101.
- JAMI, L., MURTHY, K. S. K. & PETIT, J. (1982). A quantitative study of skeletofusimotor innervation of the cat peroneus tertius muscle. *Journal of Physiology* **325**, 125–144.
- KAKUDA, N., VALLBO, Å. B. & WESSBERG, J. (1994). Activity of human muscle spindle afferents during high precision movements. *Acta Physiologica Scandinavica* **151**, 21A.
- NIELSEN, J., NAGAOKA, M., KAGAMIHARA, Y., KAKUDA, N. & TANAKA, R. (1994). Discharge of muscle afferents during voluntary co-contraction of antagonistic ankle muscles in man. *Neuroscience Letters* **170**, 277–280.
- PROCHAZKA, A. (1989). Sensorimotor gain control: a basic strategy for motor control? *Progress in Neurobiology* **33**, 281–307.
- PROCHAZKA, A., GORASSINI, M. & TAYLOR, J. (1992). Adaptive control of proprioception. In *Muscle Afferents and Spinal Control of Movement*, ed. JAMI, L., PIERROT-DESEILLIGNY, E. & ZYTNIICKI, D., pp. 129–141. Pergamon Press, Oxford.
- PROCHAZKA, A., HULLIGER, M., TREND, P. & DÜRMÜLLER, N. (1988). Dynamic and static fusimotor set in various behavioural contexts. In *Mechanoreceptors*, ed. HNIK, P., SOUKUP, T., VEJSADA, R. & ZELENKA, J., pp. 417–430. Plenum Press, New York.
- PROCHAZKA, A., HULLIGER, M., ZANGGER, P. & APPENTENG, K. (1985). 'Fusimotor set': new evidence for  $\alpha$ -independent control of  $\gamma$ -motoneurons during movement in the awake cat. *Brain Research* **339**, 136–140.
- RIBOT, E., ROLL, J.-P. & VEDEL, J.-P. (1986). Efferent discharges recorded from single skeleto-motor and fusimotor fibres in man. *Journal of Physiology* **375**, 251–268.
- SCOTT, J. J. A., KÜMMEL, H. & ILLERT, M. (1995). Skeletofusimotor ( $\beta$ ) innervation of proximal and distal forelimb muscles of the cat. *Neuroscience Letters* **190**, 1–4.
- SMITH, A. M. (1981). The coactivation of antagonistic muscles. *Canadian Journal of Physiology and Pharmacology* **59**, 733–747.
- VALLBO, Å. B. & AL-FALAHE, N. L. (1990). Human muscle spindle response in a motor learning task. *Journal of Physiology* **421**, 553–568.
- VALLBO, Å. B. & HULLIGER, M. (1981). Independence of skeleto-motor and fusimotor activity in man? *Brain Research* **223**, 176–180.
- WESSBERG, J. & VALLBO, Å. B. (1995). Human muscle spindle afferent activity in relation to visual control in precision finger movement. *Journal of Physiology* **482**, 225–233.

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