

# Functions of human muscle spindles in hand muscles as analysed with microneurography

Å. B. Vallbo\* and J. Wessberg

Department of Physiology, Göteborg University, Göteborg, Sweden

While human subjects performed voluntary movements with varying precision demands, the normal traffic of impulses originating in spindle afferents from finger muscles was recorded. Movements that demanded higher precision resulted in higher impulse rates, indicating stronger fusimotor activity. However, this was regularly associated with stronger contractions of the parent muscle, indicating joint increase of skeleto-motor and fusimotor activities. This contrasts with recordings from behaving cats where gamma independence has been emphasized. The discrepancy may be related to the different functional roles ascribed to cat hind limb muscles and human hand muscles, and related differences in neural control circuits design in the two.

NATURE has put in a lot of resources on information retrieval about mechanical events in the muscles engaged in performing work. In many of the nerves innervating the muscles, a majority of the myelinated fibres are engaged in the proprioceptive machinery, whereas the alpha fibres which directly control the muscle contraction constitute but a minority of the total, as may be inferred from counts of nerve fibres and sense organs<sup>1,2</sup>. Such considerations support the view that the sensory systems of muscles are vital for the control of motor activity.

Although there is a general agreement that muscle spindles and tendon organs are sense organs which extract information on the instantaneous state of the motor plant, nevertheless it has been difficult to define the exact role of the proprioceptive systems of striated muscles. Despite that they are considered to code for the immediate effects of self-generated movements on the moving parts of the body, their projections and effects within the central nervous system are multifarious and complex, but not very well understood in many respects.

Moreover, there is considerable disagreement on some points. Although there is agreement on the potential role of fusimotor system to set the sensitivity of muscle spindles as well as their working range in terms of muscle length, the function of the fusimotor system in the organism is still a challenge.

The present paper surveys the functions of human muscle spindles present in finger muscles include as

analysed with the microneurographic method, and a discussion on the discrepancy between cat and human data regarding the relations between fusimotor and skeleto-motor activities.

## Microneurography

Microneurography studies the normal traffic of impulses generated in human nerves<sup>3</sup>. In order to record single unit impulses from attending human subjects, a fine tungsten needle electrode, insulated till the tip, is inserted percutaneously into the nerve. Exact electrode position within the nerve is adjusted manually until impulses from a single afferent fibre can be discriminated. The microneurography procedure is usually surprisingly non-painful and comfortable for the subject although it is important to pay considerable attention to psychological factors to ensure the subject's confidence.

The present study is based on recordings of spindle afferent activity in relation to contractions of finger muscles, and movements of metacarpophalangeal joints. In addition to spindle afference, a number of associated variables were recorded as well, i.e. the EMG activity of the working muscle, the joint position, and the torque at the relevant joint.

## Response properties of human muscle spindle

Although the muscle spindle is a very complex sense organ, its basic working mode is to code length and/or length changes of the parent muscle<sup>4</sup>. This function comes out clearly when the muscle is relaxed and the joint is moved by external forces acting on the relevant joint (Figure 1).

As long as the parent muscle remains relaxed there seems to be very little or no fusimotor drive to human muscle spindles. On the other hand, there is strong evidence that the fusimotor system is generally activated along with the skeleto-motor system, during isometric contractions because they are associated with increased firing rates in most spindle afferents<sup>3</sup>. However, it is generally held that the main role of muscle spindles is in the control of movements and position holding rather than in pure isometric contractions. It is therefore of particular interest to explore their response characteristics during self-generated movements.

\*For correspondence. (e-mail: Vallbo@physiol.gu.se)

A plain stretch response usually appears in self-generated movements, i.e. the firing rate in the spindle afferent increases when the muscle is lengthening (Figure 2*b*). Figure 2*a* shows, for comparison, the response from the same spindle afferent to an imposed movement of similar speed and amplitude.

Although a stretch response as indicated in Figure 2*b* is common, it is a puzzling observation that a converse stretch response appears in many spindle afferents, particularly when the movements are slow and/or opposed by substantial external loads. Figure 3 substantiates this point and it can be observed that the impulse rate increases when the muscle is shortening. The only reasonable interpretation is that this converse stretch response is due to a strong fusimotor drive which overcompensates for the unloading effect of muscle shortening.

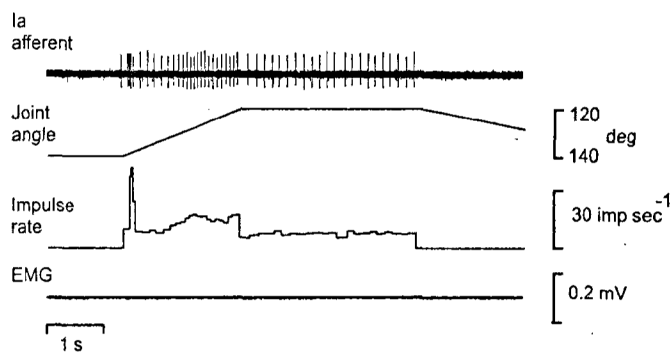
The converse stretch response poses a problem in relation to the interpretation of the afferent signal because it implies that the muscle spindle is not coding muscle length. A hypothesis put forth to explain this is that

the motor centres extract information about muscle length, and length changes by subtracting, so to speak, the outgoing fusimotor activity from the spindle afferent activity<sup>6</sup>. However, this remains to be proved and other interpretations are conceivable as well.

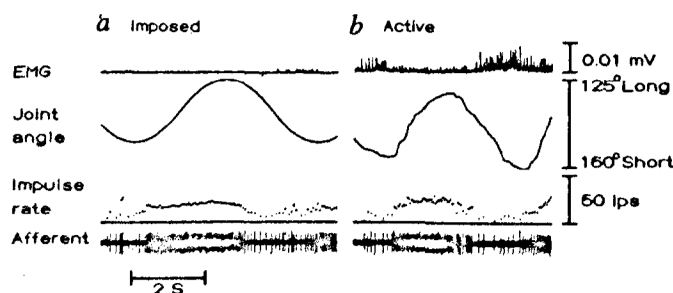
## Fusimotor dependence on precision demands

An interesting question is whether the spindle response is dependent on contextual factors which would act via higher functions, i.e. factors which might influence the subject's attention, emotional, or cognitive states. Such a role of the fusimotor system has almost been a dogma in motor control ever since the gamma system was demonstrated. It has been argued that a key feature of a separate gamma system is to allow independent settings of the intrafusal muscle fibres in order to adjust spindle sensitivity and working range differently in various motor tasks.

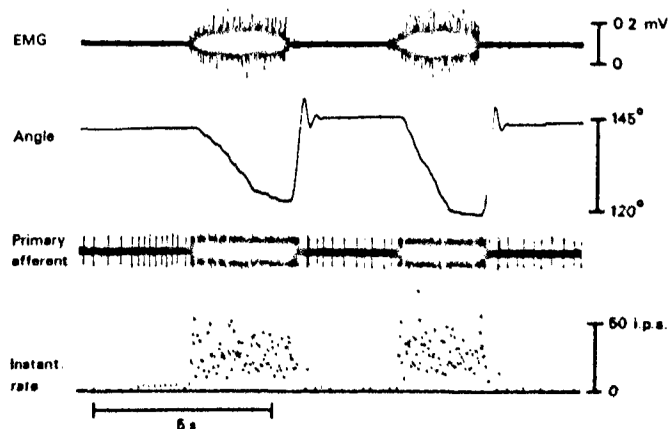
We were interested to explore whether motor tasks which require higher mental concentration are associated with higher fusimotor drive. More specifically we designed experiments to assess if firing rates of impulses are higher in muscle spindles when the subject is required to perform a movement demanding high precision compared to the firing rates in movements demanding lesser precision. To answer this question, subjects were requested to make two movements in succession which were nearly identical with regard to speed and amplitude, but which varied in requirement for precision in movement. To achieve this, the subject was instructed, first, to move his finger back and forth as it pleased him. While he performed these *routine movements*, impulses generated from a muscle spindle were recorded. Moreover, without the subject's knowledge, the joint angle



**Figure 1.** Response of a human muscle spindle primary afferent to an imposed ramp movement of the relevant metacarpophalangeal joint. The muscle spindle was located in the extensor digitorum communis muscle. Upward movement of the joint angle signal indicates stretch of the muscle, i.e. flexion at the MCP joint, in this and in all other figures. Surface EMG record (bottom) indicates that the muscle remained relaxed throughout.



**Figure 2.** Responses of a human muscle spindle primary afferent to one imposed movement (*a*) and one self-generated movement (*b*). The muscle spindle was located in the extensor digitorum communis muscle and movements engaged the relevant metacarpophalangeal joint. A small constant torque load opposed the active movement (from ref. 5).



**Figure 3.** Responses of a human muscle spindle primary afferent to self-generated movements involving active shortening of the parent muscle under isotonic conditions. The muscle spindle was located in one of the flexor digitorum muscles and movements engaged the relevant metacarpophalangeal joint.

signal was sampled to a computer during a period of his routine movements. The sampled signal was subsequently used as a command signal in an indirect tracking task. Indirect visual tracking implies that the error between the desired and the actual joint position was displayed on an oscilloscope screen in front of the subject. In this part of the experiment, subjects were requested to perform very *precision movements*, i.e. they were encouraged to minimize the error on the screen. Since the routine and the precision movements had almost identical kinematics, a direct comparison between spindle response in the two would reveal whether the fusimotor drive was substantially different between the routine and precision movements.

Figure 4 shows that the impulse rates from muscle spindles were higher in precision movements (lower record of nerve impulses) than in routine movements, although the difference was not very large. Actually, the difference in impulse rate was smaller in most afferents than in this example, but the difference in the total sample was statistically significant. Figure 4 also shows a fundamental role of the fusimotor system in active movements, i.e. to counteract the effect of shortening, which tends to silence the spindle. Hence fusimotor activity may guarantee spindle firing throughout the movement providing a more complete coding of the self-generated movement. This role to counteract the unloading effect of self-generated movements was postulated long ago by Kuffler and co-workers<sup>8</sup>.

Although stronger fusimotor drive may tend to provide a more complete coding of the active movement from the individual spindle, it entails a potential complication. The afferent signal might become ambiguous in that two

different muscle lengths or opposite directions of movement might be coded for by the same impulse rate.

### Lack of fusimotor independence

Another difference between the two movements is shown in Figure 4. Not only spindle firing rate, but the amount of EMG activity as well is larger in the precision movements, as shown in the bottom records. The higher EMG activity in the precision movements indicates that the subject produced stronger co-contraction of agonists and antagonists when high precision was demanded.

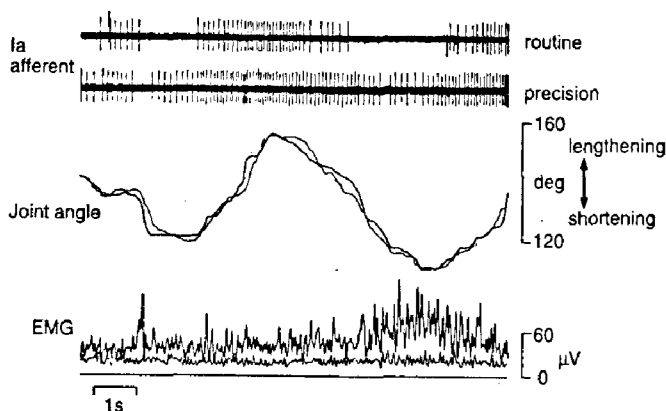
From this finding, it must be concluded that, although the fusimotor drive was higher with the more demanding task, the higher fusimotor drive was part of a general increase of the motor output to the muscle, which involved the fusimotor as well as the skeletomotor systems. Hence the findings give no support for an independent gamma control in these tests.

These findings are consistent with a large number of previous studies in humans, which have failed to demonstrate that major modulations of gamma activity occur independently of modulations of parent muscle contractions<sup>3,9,10</sup>. In contrast, many investigations with behaving animals have reported evidence of pronounced gamma independence<sup>11-14</sup>.

Speculations regarding which factors might account for this discrepancy have been advanced in a number of reports. Particularly, differences have been emphasized with regard to experimental design, including difference in freedom to move the limb, the size and speed of movements, as well as assumptions regarding degree of vigilance<sup>15</sup>.

### Functional roles of cat hind limb muscles vs human hand muscles

It seems reasonable to ask if part of the difference in spindle response between the two sets of experiments is authentic, and a reflection of functional differences between neural control circuits. Spindle recordings in behaving animals have been mostly concerned with the hind limb muscles of the cat, whereas many micro-neurography studies have been concerned with human hand muscles. These two muscle groups have vastly different roles in behaviour. The main roles of the cat hind limb are in posture and locomotion, i.e. innate, relatively stereotyped and automatic motor activities serving to support the body weight and transport the animal. In contrast, the human hand is mostly engaged in motor activities which are learnt during development rather than innately present. Hand movements often require considerable attention, not only during the learning phase, but later when we practice learnt movements



**Figure 4.** Responses of a human muscle spindle primary afferent during two self-generated finger movements, one *routine movement* performed without precision demands (upper nerve record), and one *precision movement* when the subject was requested to be very exact (lower nerve record). Thin and thick lines of joint angle and EMG records represent routine and precision movements respectively. The muscle spindle was located in the extensor digitorum communis muscle and movements engaged the relevant metacarpophalangeal joint. The movements were unopposed by external load (from ref. 7).

as well. Moreover, hand and finger movements often involve finer motor synergies than leg movements<sup>16,17</sup>. Thus cat hind limb movements and human finger movements are probably close to extremes on the scale between most automatic and least automatic movements<sup>18</sup>.

## Response to imposed movements

Responses of the motor systems to imposed movements might serve to illustrate differences of this nature. When a flexion movement is imposed on the cat hind limb by applying a force to the plantar aspect of the foot, the cat usually contracts its extensor muscles, producing an elastic resistance during the whole movement. Moreover, muscle spindle primary afferents fire at high rates, often at rates of several hundred impulses per second. Incidentally, this test manoeuvre has been presented as a very reliable and efficient means to activate the dynamic fusimotor system in the cat hind limb<sup>19</sup>. It seems likely that the muscular response is, at least partly, a tonic spinal stretch reflex—considering the high impulse rate in the spindle afferents and the established fact that the stretch reflexes are very strong in hind limb extensor muscles. Anyway, the cat produces a stereotyped motor response of a kind which would help support the body if the cat were freely moving on the ground.

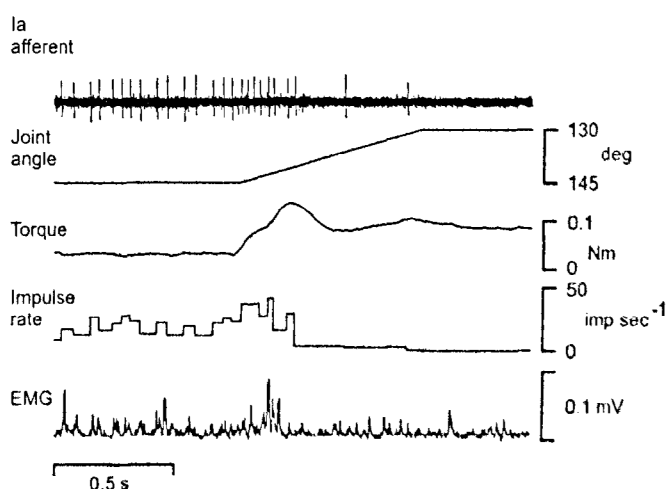
In contrast, when an imposed movement is applied to a human finger, a stereotyped response of this kind is not elicited. If the human subject is initially relaxed, there is usually absence of any muscular response, but the spindle impulse rate usually increases with the stretch of the muscle (Figure 1). The response is very similar to that of a de-efferented cat muscle spindle. On the other hand, if the human subject is initially contracting his muscles, e.g. by carrying a load, when the imposed movement is applied, interesting reactions are observed (Figure 5). For the first few tens of a second, responses appear which show some resemblance to those of the cat, i.e. an increased EMG activity and an increased impulse rate from the muscle spindle. In Figure 5, the contraction is also visible in the torque record as a second increase after onset of stretch. However, after a few tens of a second the muscular response diminishes substantially. Apparently, a decision, presumably at a higher level within the central nervous system, abruptly alters the set of the motor system. What is particularly interesting is that this resetting includes the fusimotor system, as evident from the dramatic drop of spindle impulse rate in spite of the muscle being continuously stretched. This finding again suggests close coactivation between the fusimotor and the skeletomotor systems. It should be added that the responses of human muscles to imposed stretch during position holding may vary a lot depending on the instruction to the subject. In the

experiment of Figure 5, the human subject was not given any particular instruction.

## Differences between neural circuits controlling cat hind limb and human hand muscles

It seems likely that the difference in response to imposed movements is a result of differences in neuronal organization. It is becoming increasingly obvious that neural control circuits are not uniform but vary between motor nuclei of separate muscle groups, justifying some caution in interpreting human data on the basis of findings from the cat hind limb. Interesting differences have been identified, though not specifically between cat hind limb circuits and human hand circuits, but generally between cat and primates, and between hind limb and forelimb in the cat, and finally between proximal and distal muscles in the cat forelimb. From these findings it seems reasonable to assume that there might be substantial differences between neural circuits which control cat hind limb muscles and those controlling human hand muscles. Moreover, it seems reasonable to raise the question if the discrepancy with regard to fusimotor independence in the two muscle groups might just be one aspect of differences in neural circuits, rather than a result of differences in experimental design.

*Cortico-motoneuronal connections.* It is well known that the pyramidal tract in primates contains numerous monosynaptic projections from motor cortex to spinal motoneurons which innervate distal limb muscles. 'This cortico-motoneuronal component is a major characteristic of the primates ... it increases in bulk as one ascends



**Figure 5.** Response of a human muscle spindle primary afferent to imposed stretch applied while the parent muscle is working against a small force. The muscle spindle was located in the extensor digitorum communis muscle and movements engaged the relevant metacarpophalangeal joint.

the scale of living primates<sup>20</sup>. Such connections are not present on motoneurons innervating cat hind limb muscles.

**Stretch reflex mechanisms.** A number of differences have been identified with regard to stretch reflex mechanisms. The reflexes are particularly strong in the triceps surae. This is true for cat as well as man. On the other hand, stretch reflexes are weak in many human hand and finger muscles, particularly the finger extensor muscles, which have been extensively studied by micro-neurography experiments.

Looking at the cellular level, the monosynaptic potentials in the spinal motoneurons elicited from muscle spindles differ in size: (i) There are general species differences because comparative studies have demonstrated that these potentials are universally smaller in primates (baboon) than in cats<sup>21</sup>. (ii) There is a gradient from proximal to distal muscles in the cat forelimb<sup>22</sup>. (iii) It has been shown that the synaptic potentials are particularly small in extrinsic finger muscles in forelimbs of monkeys<sup>23</sup>, whereas they are particularly large in cat hind limb motoneurons<sup>21</sup>.

It has also been demonstrated, in the cat, that there are considerable differences with regard to distribution of heteronymous Ia projections, because they are more widespread in proximal than in distal forelimb muscles<sup>22</sup>.

In addition to the difference in synaptic connections, impulse rates generated in spindle afferents suggest that the stretch reflexes play a smaller role in the human hand muscles than in the cat hind limb. It has been consistently found that the generated impulse rates are considerably higher in the behaving cat than in the human subjects. During normal walking, cat spindles usually fire up to 100 impulses per second and, in response to imposed stretch, rates may go up to several hundred impulses per second<sup>24,19</sup>. In contrast, in humans impulse rates are considerably lower in natural movements (Figure 4).

These observations support the interpretation that contractions of cat hind limb muscles are determined by the stretch reflex to a greater extent than the human hand muscles. In contrast, human hand muscles seem to be more under the control of cutaneous afferents<sup>17,25</sup>. **Recurrent inhibition.** That the differences are not limited to corticospinal projections and stretch reflex mechanisms have been substantiated by the observation that recurrent inhibition varies widely between motor nuclei in the spinal cord. While in the cat forelimb segments, recurrent inhibition is prominent in proximal muscles whereas, it is virtually absent in nuclei of many distal muscles<sup>26</sup>. A similar gradient also seems to be present in humans<sup>27</sup>.

However, the role of recurrent feedback is far from settled. It has been discussed in relation to the finding that the number of recurrent collaterals is highly variable in forelimb segments<sup>26-28</sup>. One of the theories is that

the recurrent inhibition is essential to focus the motor command to a limited number of muscles and motor units. If this is true, it is reasonable to suggest that recurrent feedback may be superfluous for the control of distal forelimb muscles because they are mostly executing fine motor synergies, which are probably defined already by higher motor levels.

Another hypothesis for the role of recurrent feedback is that it is essential to keep the firing rate low. If this is the case, it is reasonable that recurrent inhibition plays a larger role for postural muscles, whose motor units often fire at low rates during long periods than for human hand muscles which are active for short periods as well as fire at higher impulse rates in manipulative movements.

Anyway, these observations on pyramidal tract connections, stretch reflex mechanisms, impulse rate in proprioceptors, and recurrent inhibition suggest that there are substantial differences between neural circuits controlling human hand muscles and those controlling cat hind limb muscles. Thus, it is uncertain if the functions of the two muscle groups are based on the same principles. Moreover, it seems reasonable to raise the question if the observed discrepancy with regard to fusimotor independence between cat and man, might be one of the aspects of functional differences between the neural organizations controlling the two muscle groups.

**Beta innervation.** Particularly pertinent in relation to the microneurography data presented above are recent findings with regard to fusimotor innervation. For a long time, the fusimotor control was assumed to be exerted exclusively by a gamma system in higher animals and by a beta system in many lower animals, for example in the frog. Beta innervation implies that the intrafusal muscle fibres are controlled by branches of alpha motoneurons.

However, about 20 years ago Laporte and his co-workers<sup>29</sup> demonstrated that in addition to the ordinary gamma fibres, many muscles in the cat hind limb have beta innervation as well.

The role of the beta system in mammals is difficult to ascertain. However, the system has the interesting implication that any contraction of the main muscle leads to an obligate co-activation of the intrafusal fibres in muscle spindles. The canonical view is that the beta system is vestigial residue and represents a more primitive mode of controlling muscle spindles. Moreover, it is generally assumed that such a system is well suited to lower animals showing a more stereotyped motor repertoire. In contrast, the gamma system has been regarded as a more sophisticated system for it involves a potential flexibility between intra- and extrafusal contractions. It seems to be generally held that this flexibility is essential for more advanced motor activities.

However, a couple of recent observations seem to militate against this view. Illert *et al.*<sup>28</sup> demonstrated that beta innervation is, in fact, more pronounced in distal muscles of the cat's forelimb than in proximal muscles. Moreover, morphological observations suggest that beta innervation is very common in the human finger extensor muscles because the characteristic beta terminals (plate-1 endings)<sup>30</sup> seems to be present in most muscle spindles (Scott, Vallbo and Ejekskar, unpublished).

The above two observations that (i) beta innervation is more common in distal than in proximal forelimb muscles in the cat; and that (ii) beta innervation seems to be prominent in human finger muscles, suggest that the canonical view of the role of beta system might not be all that solid. The recent findings actually suggest a relation which is almost the opposite to the canonical view, namely that muscles which are more involved in manipulative movements, more voluntary and less automatic motor tasks have a particularly rich beta innervation.

One might speculate that a certain amount of beta innervation of muscle spindles is for some reason acceptable, maybe even advantageous, when the control of a muscle group is shifted to higher levels in the central nervous system; while a number of spinal mechanisms, such as the stretch reflex and recurrent inhibition, come to play a smaller role.

Although the functional significance of beta innervation in higher animals is difficult to ascertain at present, it is clear that beta innervation is more compatible with weak stretch reflexes. On the other hand, strong beta innervation and powerful stretch reflexes is a combination that could give problems because of positive feedback effects.

A caveat should be added in relation to the reasoning above. Although a beta system is present in the distal limb muscles of higher animals, it should be emphasized that gamma innervation is the dominating fusimotor system even in these muscles. On the whole, the beta system still seems to be the minor partner. However, the fact that the beta system is more prominent in the muscles which perform the most flexible motor tasks is an observation which might justify some caution in regarding a close coactivation of the intrafusal and extrafusal systems as incompatible with advanced motor systems, such as fine manipulative movements.

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