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ACTIONS ON γ-MOTONEURONES ELICITED BY ELECTRICAL STIMULATION OF GROUP III MUSCLE AFFERENT FIBRES IN THE HIND LIMB OF THE CAT

BY B. APPELBERG, M. HULLIGER*, H. JOHANSSON AND P. SOJKA

From the Department of Physiology, Umeå University, S-901 87 Umeå, Sweden†, and the Brain Research Institute, University of Zürich, CH-8029 Zürich, Switzerland

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SUMMARY

1. The reflex actions evoked by electrical stimulation of group III muscle afferent fibres were investigated with micro-electrode recordings from ninety-three γ-motoneurones projecting to hind-limb muscles of cats anaesthetized with chloralose. For seventy-eight of the ninety-three γ-cells the frequency of occurrence and types of effects mediated via group II and group III muscle fibres were compared.

2. Seventy-seven of the cells tested at intensities which excited group III and seventy-five of the cells tested at intensities which excited both group II and group III afferent fibres were classified as either static or dynamic, using the method of mesencephalic stimulation (Appelberg, 1981).

3. The responsiveness of the whole sample of γ-motoneurones to inputs from group III muscle fibres was high and comparable to that found with group II fibres.

4. It was found that group III muscle fibres acted preferentially on static γ-motoneurones. In contrast, group II fibres acted preferentially on dynamic γ-motoneurones.

5. Both excitatory and inhibitory effects were provoked by stimulation of group III fibres. Generally excitation was more frequent than inhibition.

6. A strong dominance of excitation over inhibition was found in flexor muscles, and a weaker prevalence of excitation was also encountered in extensor muscles. This prevalence of excitation in extensor γ-motoneurones is in contrast to the striking predominance of group III-evoked inhibition of extensor α-motoneurones as described by the flexion reflex afferents concept.

7. A comparative survey is also given of the patterns of responses elicited in individual posterior biceps–semitendinosus and gastrocnemius–soleus γ-cells by stimulation of group II and group III fibres. These data further corroborate the view that reflexes from high-threshold muscle afferent fibres to γ-motoneurones are organized differently from those to α-motoneurones.

8. The functional implications of these findings are discussed. It is proposed that the pools of γ-motoneurones should be considered as integrative systems intercalated

* Present address: Brain Research Institute, University of Zürich, August-Forel-Strasse 1, CH-8029 Zürich, Switzerland.

† Where all the experimental work was done.

between descending and reflex pathways on the one hand and the skeletomotor neurones on the other. The descending messages and the multisensory peripheral information, integrated in the fusimotor neurones, undergo final adjustment in the muscle spindle. The link to the skeletomotor neurones is formed by the primary spindle afferents. These constitute a final common input, conveying integrated detailed polymodal feed-back, to the central nervous system. This new concept is referred to as the 'final common input' hypothesis.

INTRODUCTION

The pattern of oligosynaptic reflexes evoked in α-motoneurones of spinal preparations by electrical stimulation of group II and group III muscle afferent fibres, and of high-threshold cutaneous and joint afferent fibres, is remarkably simple. It does not conform to the refined organization which is known for the Ia, Ib and Renshaw pathways converging onto agonist and antagonist α-motoneurones (for reviews see Lundberg, 1972, 1979*b*; Matthews, 1972; Lindström, 1973). Thus flexor α-motoneurones are normally excited and extensor α-motoneurones are inhibited by the activity in high-threshold afferent fibres (Eccles & Lundberg, 1959). Holmqvist & Lundberg (1961) coined the term flexion reflex afferents (f.r.a.), which includes all high-threshold afferent fibres that tend to evoke such a stereotyped pattern of excitation and inhibition in flexor and extensor motoneurones.

Comparatively little was known previously about the reflex control of γ-motoneurones from high-threshold afferent fibres. Grillner, Hongo & Lund (1969) found, in a rather small sample ($n = 5$) of γ-cells, that their responses to stimulation of high-threshold afferents from muscle, skin and joint nerves conformed to the f.r.a. pattern of α-motoneurones. We have re-investigated this aspect in the course of a study on the reflex control of γ-motoneurones, in which a large sample of cells ($n = 120$) was included.

The results of the present study on the reflex actions of group III muscle afferent fibres on γ-motoneurones are suported by those of the accompanying report on group II-evoked reflexes (Appelberg, Hulliger, Johansson & Sojka, 1983*b*). They clearly show, that the organization of γ-cell reflexes cannot be described adequately by the f.r.a. concept. Instead, a considerably more refined pattern of reflex organization was found. This indicates that there may be a considerable degree of independence between the control of dynamic and static fusimotor activity on the one hand, and fusimotor and skeletomotor activity on the other hand.

METHODS

Reflex effects from muscle, skin and joint afferent fibres were investigated in hind-limb γ-motoneurones of cats anaesthetized with chloralose. Intra- or extracellular micro-electrode single-unit recordings and electrical stimulation of dissected hind-limb nerves were used. Each cell was first identified as a γ-motoneurone on the basis of its conduction velocity (below 55 m/sec). Most of the γ-cells were then classified as static or dynamic by the indirect method of classification by stimulation in the mesencephalic area previously demonstrated to influence dynamic γ-cells (Appelberg, 1981). The responses elicited by electrical stimulation of the nerves were stored on magnetic tape. Excitatory and inhibitory effects were assessed using conventional criteria.

A full account of the general methods and of the criteria of differentiation between group II and group III fibre reflex effects has been given in the accompanying papers (Appelberg, Hulliger, Johansson & Sojka, 1983*a*, *b*). Reflex effects elicited by electrical stimulation of hind-limb muscle nerves were allocated, according to the relative contributions of group II and group III fibres, to one of the following five categories: pure group III action, predominant group III action, undecided group II/III dominance, predominant group II action and pure group II action. Thus unambiguous group III reflex actions were allocated to one of the first three categories, where established group II effects were assigned to one of the last four categories.

Group IV effects, mediated via slowly conducting non-myelinated fibres, were not included in the present material. Even the effects with the longest latencies occurred, at least with their principal components, well below the minimal group IV latency of the nerve from which they were elicited. The minimal group IV latencies for each nerve were calculated in the same way as the group III latencies (see Appelberg *et al.* 1983*b*). Thus the latency values were derived using the mean values of the measured conduction distances, a maximum group IV conduction velocity of 2 m/sec (see e.g. Matthews, 1972) and assuming a central delay for group IV fibres of 2 msec. Since most of the group IV fibres obviously conduct at velocities slower than the maximum for group IV, the working figures for group IV latencies were, if anything, too short, precluding the possibility that significant group IV actions could be mistaken for slow group III reflex effects. The figures obtained were 25 msec for quadriceps, i.e. the nerve with by far the shortest conduction distance, and 50–100 msec for the remaining nerves.

Establishment of lack of effect. If (from a certain muscle nerve input) a cell was not studied throughout the whole range of stimulation intensities required for a comprehensive assessment of group II and group III effects, the classification of the reflex effects involved certain problems (see Appelberg *et al.* 1983*b*, Methods). In cases where apparently 'pure' group II effects were encountered but where only the lower group III intensity range was thoroughly tested, this was entered in the chequer-board diagrams of group III effects as 'no observation' (open squares in Figs. 5, 6 and 7). Similarly, when group III effects were classified as 'pure' but when there remained a risk of contamination by high-threshold and long-latency group II effects, this was entered in the chequer-board diagrams of group II as 'no observation' (open squares in Figs. 5, 6 and 7). Thus, the number of 'no effects' was probably underestimated. However, had the less reliable 'no effect' observations been included in the material, this in fact would only have accentuated the reflex pattern described here.

Abbreviations used in the text

A.b.s.m., anterior biceps and semimembranosus (nerves or muscles); D, dynamic γ-cell; d.p., deep peroneal nerve (pure muscle nerve supplying extensor digitorum longus and tibialis anterior); s.d.p., deep peroneal nerve with small cutaneous admixture (comprising d.p., the branches to peroneus brevis, to peroneus tertius, to extensor digitorum brevis and the deep peroneal cutaneous branch); f.d.l., flexor digitorum et hallucis longus (nerve or muscle); f.r.a., flexion reflex afferents; g.s., gastrocnemius and soleus (triceps) (nerve or muscle); N, non-classified γ-cell; p.b.s.t., posterior biceps and semitendinosus (nerve or muscle); Q., quadriceps (nerve or muscle); S, static γ-cell; *T*, threshold.

RESULTS

Electrical stimulation of hind-limb muscle nerves within the range of intensities that excited group II and III afferent fibres elicited potent and widespread reflex actions in lumbar γ-motoneurones (Figs. 2, 3 and 4). As is explained in the Methods, it turned out to be impossible to ascribe every single reflex action provoked by graded stimulation of a muscle nerve to either group II or group III fibres only (see Methods and Appelberg *et al.* 1983*b*). Therefore, transsynaptic responses with an established or suspected group III contribution were allocated to one of the following four categories. (1) Pure group III action, with no evidence for any group II admixture, as illustrated in Fig. 1 for a non-classified g.s. γ-cell. For this cell, stimulation of f.d.l. at 10 *T* was without effect (Fig. 1*B*), whereas stimulation at 50 *T* elicited an

excitatory response (synchronized spike discharge in Fig. 1*C*, with a latency of 11·8 msec, which was above the minimal latency for group III (8·5 msec) and below that for group IV (90 msec). (2) Predominant group III action (for this and the following two categories see Appelberg *et al.* 1983*b*, Fig. 1), with the group III contribution clearly outweighing the group II effect. (3) Undecided group II/III dominance, with group III and group II contributions of about the same size.

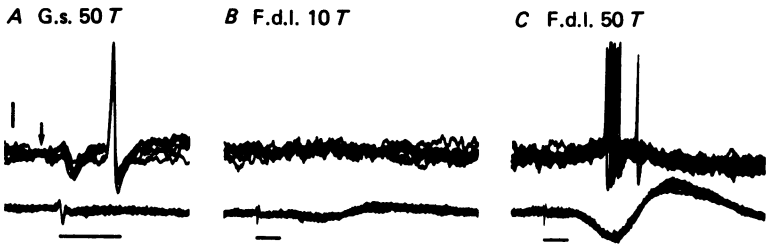

Fig. 1. Pure group III action on a non-classified g.s. γ-motoneurone. *A*, antidromic identification (arrow indicates stimulus shock; cell no. 111; conduction velocity 26 m/sec). *B*, absence of effect with stimulation of the f.d.l. nerve at 10 times Ia threshold (*T*). *C*, stimulus-locked discharges of spikes (latency 11·8 msec from earliest positive deflexion in the volley recording) with stimulation of f.d.l. at 50 *T*. Upper traces: juxtacellularly recorded cell responses. Lower traces: records of incoming volley at dorsal root entry zone. Vertical calibrations: bar in *A* (applicable to all recordings) = 1 mV. Horizontal calibrations: all bars = 5 msec.

(4) Predominant group II action, with responses which might have been pure group II effects, but for which a suspected and weak group III contribution could not be wholly excluded (see Figs. 2, 3 and 4). It bears emphasis that none of the effects described here could be attributed to group IV fibre activity, since they all occurred below the minimum group IV latency (see Methods).

Trends of group III reflex action

Of the total sample of 120 γ-cells of the present series of investigations (Appelberg, Hulliger, Johansson & Sojka, 1982*a–d*) ninety-three cells were studied with stimulation of group III muscle afferent fibres, and out of these, seventy-eight were examined in both the group II and group III range (Figs. 5–7). Of the group III-tested sample (ninety-three), thirty-four cells projected to p.b.s.t. (13 D, 16 S and 5 N cells), forty-two projected to g.s. (22 D, 13 S, 7 N), nine to a.b.s.m. (2 D, 6 S, 1 N), five to d.p. (1 D, 2 S, 2 N), two to tibial muscle (1 D, 1 S), and one cell (N) projected to f.d.l. Seventy-five (97·4 %) of the cells tested within the stimulation intensity range for both group II and III were classified as either dynamic or static. In the chequer-board diagrams of Figs. 5–7 some cells (4 S and 2 D p.b.s.t. cells, and 2 S and 5 D g.s. cells), which were merely tested with stimulation of skin and joint afferents or of descending pathways, were also included for cross-reference with the accompanying papers (Appelberg *et al.* 1982*a*, 1983*a–c*).

Fig. 2 shows the general trends for the reflex actions elicited in p.b.s.t. and g.s. γ-motoneurones by stimulation of group III muscle afferent fibres. The upper part

of the diagram shows, separately for dynamic and static cells, the frequency of occurrence of group III excitation (▲) and of group III inhibition (○). The lower part shows the frequency of negative observations. The Figure gives a summary of all the observations made with the p.b.s.t. and g.s. cell populations, irrespective of

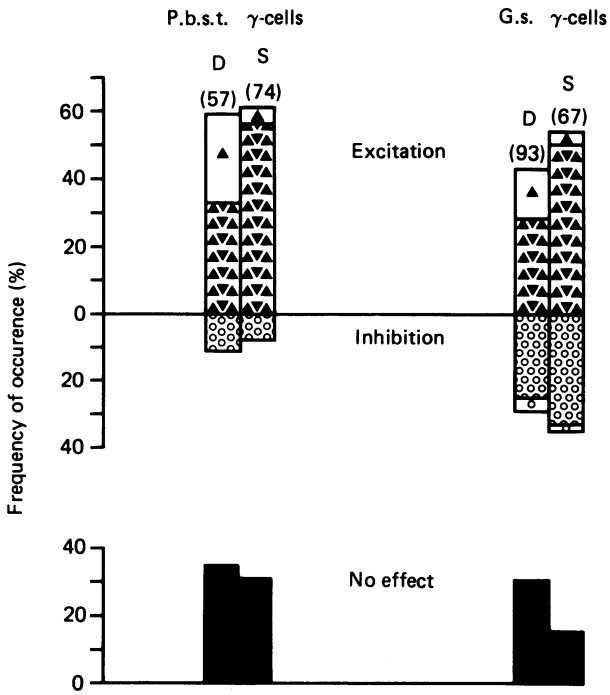

Fig. 2. Type and incidence of group III muscle reflex action elicited in p.b.s.t. and g.s. γ-motoneurones by electrical single-shock stimulation of hind-limb muscle nerves. The frequency of occurrence is expressed as percent of the total number of observations (given above each column) within each of the four populations illustrated. Excitation (plotted upwards, triangle pattern), inhibitions (plotted downwards, circle pattern) and absence of group III reflex action (black columns in the lower part plotted upwards). Multi-symbol filling: unambiguous group III effects (i.e. pure and predominant group III action and undecided group II/III dominance). Single-symbol filling: ambiguous group III effects (i.e. predominant group II action where contribution from group III fibres could not wholly be excluded; see also text). Pooled data from 29 p.b.s.t. γ-cells (13 D and 16 S) and from 35 g.s. γ-cells (22 D and 13 S). Every single cell may be represented by up to seven observations (each from a different muscle nerve input) (see Figs. 5–7). Since individual observations (i.e. one cell tested from one muscle nerve input within group III range) may consist of blends of excitations and inhibitions (see e.g. Fig. 6, cell 28), the percentage figures for each population of γ-cells may add up to more than 100%. Same cells as in Figs. 4–7. Note the close parallelism in the representation technique between this Figure and Fig. 2 in Appelberg *et al.* (1983*b*).

the particular muscle nerve from which they were elicited. The frequencies are expressed as percent of the number of observations within each of the four populations of cells. As before (Appelberg *et al.* 1983*b*) the term 'observation' refers to the final assessment of all the tests with graded stimulation within the group III (or group II) range, which were made on a single cell from a particular muscle nerve.

Since the reflex effects summarized in Fig. 2 were elicited from a range of functionally quite heterogenous nerves (including synergists and antagonists), the same data as in Fig. 2 are also shown as a set of histograms constructed separately for each nerve tested, both for p.b.s.t. cells (Fig. 4*A*) and for g.s. cells (Fig. 4*B*). In this Figure the frequencies of observations are given for each input nerve and for dynamic and static cells separately, and they are expressed as percent of the total number of observations

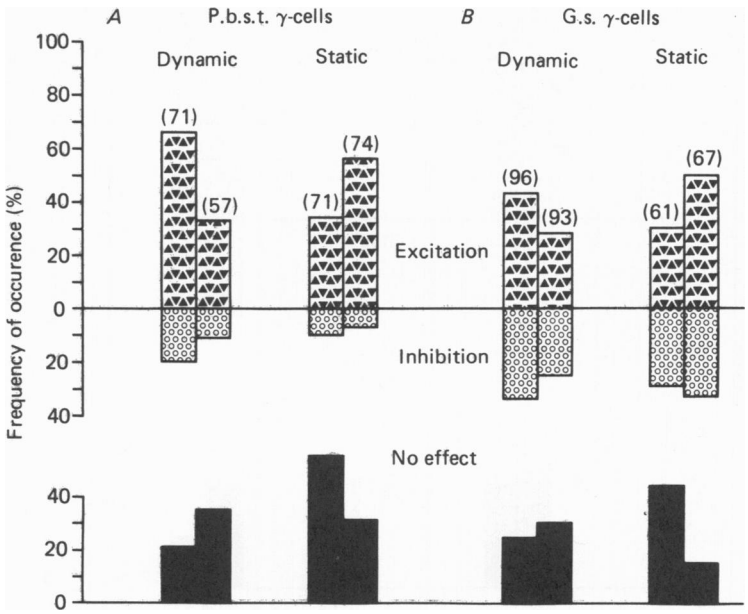

Fig. 3. Comparison of frequencies of group III and group II muscle reflex action on dynamic and static p.b.s.t. and g.s. γ-motoneurones (see also Figs. 5–7). Left-hand columns: group II action. Right-hand columns: group III action. The frequencies of occurrence for each group, are expressed as percent of the total number of observations within the range for that group. The total number of observations (i.e. 100 %) indicated above each column. Excitations: plotted upwards, triangle pattern. Inhibitions: plotted downwards, circle pattern. Absence of effect: lower part, black columns plotted upwards. Only reliable group III effects (i.e. pure group III action, predominant group III action and undecided group II/III dominance; see also Methods and text) are included in the columns for group III action. This explains why the columns for group III action do not add up to 100 %. Since individual observations (i.e. one cell tested from one muscle nerve input within group III range) may consist of blends of excitations and inhibitions (e.g. see Fig. 6, cell 28), the percentage figures for each population of γ-cells may add up to more than 100 %. Same cells as in Figs. 5–7.

for all p.b.s.t. cells (see Figs. 5*B* and 6*B*) and for all g.s. cells (see also Fig. 7*B*) respectively. Given the difficulties in estimating the contribution by group II and group III afferent fibres to a certain reflex effect, the risk had to be avoided that pure group II effects, falsely classified as predominant group II effects (with a small group III admixture) unduly increased the estimated incidence of group III reflex actions. Therefore the display of Figs. 2 and 4 differentiates between *unambiguous* group III effects (pure group III action, predominant group III action and undecided group II/III dominance) and *ambiguous* group III effects.

An important feature of Fig. 2 is that group III reflex actions on γ-motoneurones were *frequent*, both with p.b.s.t. (Figs. 2*A* and 4*A*) and g.s. γ-cells (Figs. 2*B* and 4*B*). Thus, for p.b.s.t. cells (both dynamic and static) and for dynamic g.s. cells positive observations (including both excitatory and inhibitory reflex effects) were about twice as frequent as negative observations (lower half of Fig. 2), whereas with static g.s. cells positive observations were about six times more frequent than negative findings. However, this holds true only when all effects, including the uncertain group III

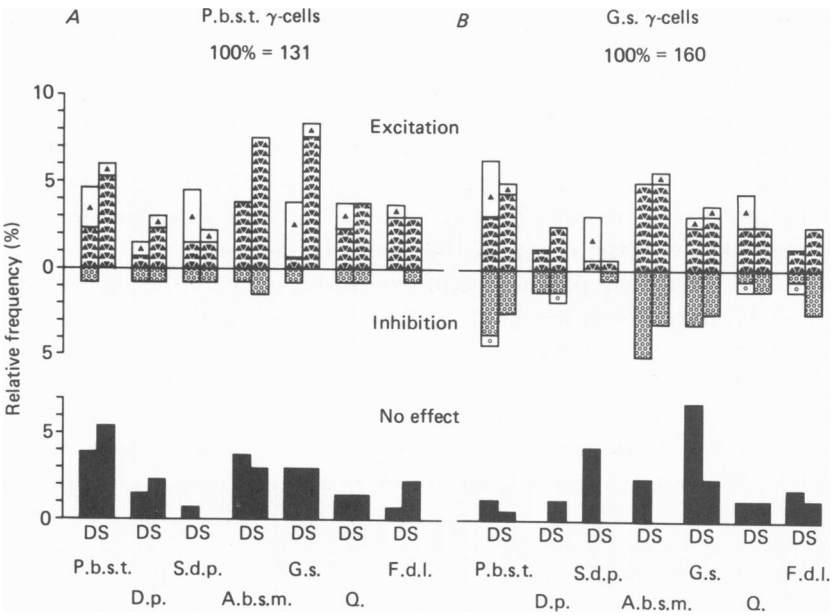

Fig. 4. Relative frequency of group III reflex action from various muscle nerves on p.b.s.t. γ-cells (*A*) and g.s. γ-cells (*B*). In order to facilitate comparison between the effects on dynamic and static cells here and in Fig. 3 in the accompanying paper on reflex actions from group II muscle afferents (Appelberg *et al.* 1983*b*) the frequencies of occurrence are expressed as percent of total number of observations (see text) within the populations of all p.b.s.t. γ-cells (131 observations) and of all g.s. γ-cells (160 observations). Upper part, excitation (plotted upwards, triangle pattern), inhibition (plotted downwards, circle pattern); lower part, absence of effects (plotted upwards, black columns). Multi-symbol filling: unambiguous group III effects; single-symbol filling: ambiguous group III action (see text and legend to Fig. 2). Same cells as in Figs. 2 and 5–7.

effects (with a dominant group II admixture) are considered. These weak and/or ambiguous group III effects were largely confined to dynamic γ-cells, as may be seen from Figs. 2 and 4.

However, since a high proportion of the predominant group II effects (weak and/or ambiguous group III effects) were probably pure group II effects, only the unambiguous group III responses can safely be taken into consideration. Then the *static γ-cells* stand out as the *predominant recipients of group III action*. This was, in fact, the main finding of this investigation, and it stands in clear contrast to the considerably smaller incidence of group II action on static cells. Conversely, *dynamic γ-cells* were *the predominant recipients of group II action* and were less responsive to

group III inputs. This is illustrated in Fig. 3 for the p.b.s.t. (*A*) and g.s. (*B*) γ-cell populations, where the responses (or lack of responses) to stimulation of group II fibres (left-hand columns) and group III fibres (right-hand columns) are given separately for dynamic and static cells. In this Figure a frequency of 100 % is equal to the number of observations given above each column. It should be observed that, since the less reliable (i.e. the ambiguous) group III effects have been excluded without being added to the 'no-effect' columns, the columns for group III effects add up to less than 100 %.

On the whole, *excitation was more frequent than inhibition* for unambiguous as well as for uncertain group III reflex action (Fig. 2). This was true both in p.b.s.t. (i.e. flexor γ-cells) and in g.s. (extensor γ-cells), although it was more pronounced in the former. This prevalence of excitation from group III afferents was especially salient in *static γ-cells* projecting to p.b.s.t., whereas in static g.s. cells excitation and inhibition were more balanced, although the former was still more frequent than the latter. The input specific display of Fig. 4 shows that this was a general feature, no matter which nerve was the origin of the group III action.

With *dynamic γ-cells* the prevalence of excitation over inhibition was distinct in p.b.s.t. but only marginal in g.s. (Fig. 2). However, when the actions elicited from individual nerves are considered, some exceptions to this rule may be recognized. Thus with dynamic p.b.s.t. cells unambiguous excitation and inhibition were evenly balanced on stimulation of the d.p. and g.s. nerves. With dynamic g.s. cells, unambiguous group III inhibition was slightly more prominent than excitation on stimulation of the p.b.s.t. and a.b.s.m. nerves, whereas excitation prevailed from quadriceps.

Reflex patterns of individual γ-cells

The summarizing diagrams of Figs. 2 and 4 bring into prominence the main features of group III reflex action, but they mask the considerable *variability* that was present between individual cells. The responses of individual γ-motoneurones are therefore shown in the chequer-board diagrams of Fig. 5 (for the static cells projecting to p.b.s.t.) and of Figs. 6 and 7 (for the dynamic cells projecting to p.b.s.t. and g.s.). As in the preceding paper (Appelberg *et al.* 1983*b*) each square in these diagrams summarizes the findings of all tests with graded stimulation that were performed on a single cell from an individual nerve. These results are shown separately for tests within each of the group II and group III muscle ranges, and for tests with stimulation of skin and joint nerves. The skin and join responses are presented without subdivision into 'activation-threshold' categories, in order to further emphasize the high over-all responsiveness. The reflex effects elicited from muscle nerves, on the other hand, are classified according to the degree of group II or group III prevalence (see Methods and legend to Fig. 5).

The cell-by-cell comparison of group II and group III reflex action (Figs. 5–7) demonstrates that the general trend in the cell populations of a preference by group III for static and by group II for dynamic γ-cells was also present at the level of individual cells. Moreover, there was a greater tendency for individual cells to be predominant recipients of either excitation or inhibition than for individual nerves to be exclusive sources of either one or the other. However, perhaps the most

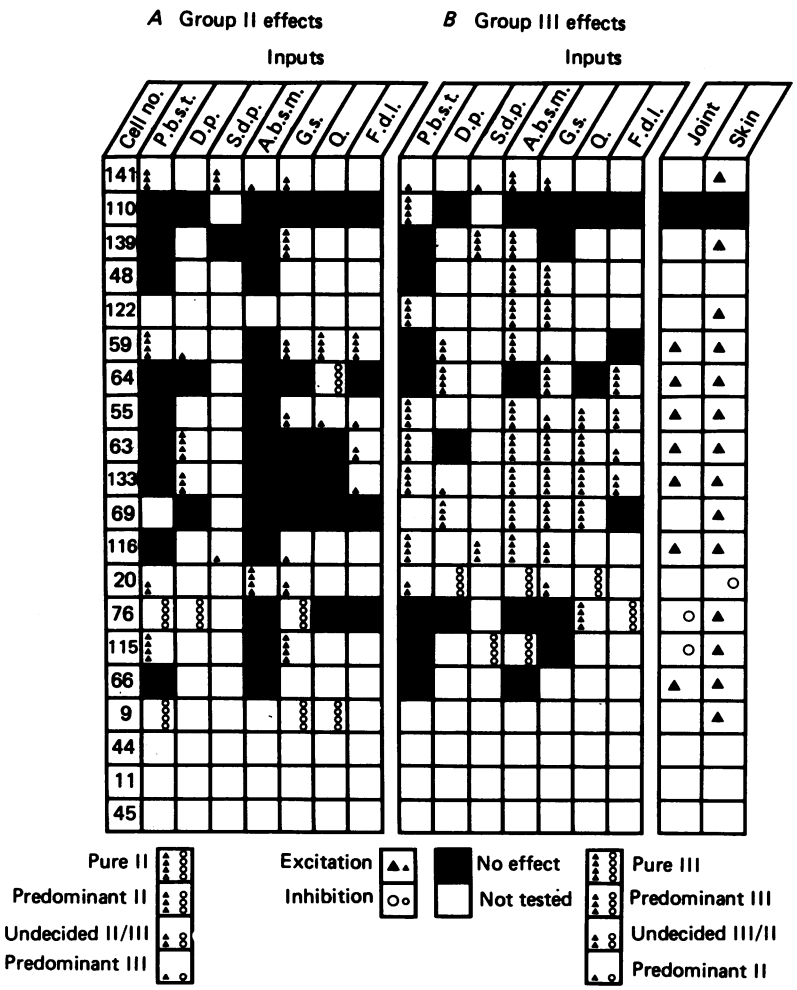

Fig. 5. Static p.b.s.t. γ-cells. Comparison of reflex actions from muscle group II (*A*), muscle group III (*B*) and skin and joint receptor afferent fibres. For details about the different categories of group II and group III effects, see text (see also Appelberg *et al.* 1983*b*). In order to illustrate the general responsiveness of the cells, the actions from skin and joint afferent fibres are presented, without subdivision (see text), in the two columns at the far right. In *A* (group II) four triangles or circles indicate pure group II excitation or inhibition, respectively. In *B*, four symbols indicate pure group III action. In both *A* and *B* (in Figs. 5–7) two symbols indicate undecided group II/III dominance. In *A*, three symbols indicate group II and one symbol group III dominance, whilst in *B* three symbols indicate group III and one symbol group II dominance. Note that the group II data shown in Figs. 5*A*, 6*A* and 7*A* are the same as in Figs. 4 and 5 of Appelberg *et al.* (1983*b*). However, the order in which individual cells are displayed is different, since in the present context the cells were grouped so as to focus attention onto particular aspects of group III reflex action. Cells 9, 11, 64, 76 were also influenced by group I muscle afferent fibres (see Appelberg *et al.* 1983*a*, Figs. 4 and 5). Cells 11, 44 and 45 were included merely to facilitate cross-reference with the related reports (Appelberg *et al.* 1982*a*, 1983*a*, *b*).

conspicuous feature of Figs. 5–7 is the intricacy and non-uniformity of the reflex pattern found from high-threshold muscle afferents on γ-cells.

Static p.b.s.t. cells. It is seen in Fig. 5 that for these cells, pure or predominant group III excitations (four or three triangles) were much more frequent in *B* than the corresponding group II effects in *A* (same symbols), (see especially cells

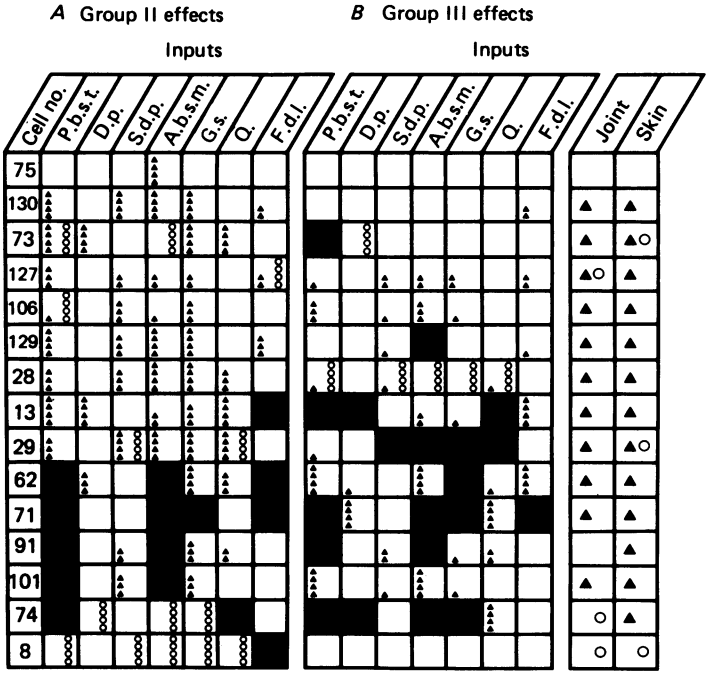

Fig. 6. Dynamic p.b.s.t. γ-cells. Comparison of reflex actions from muscle group II (*A*), muscle group III (*B*) and skin and joint receptor afferent fibres. In cells 73 and 74 effects were elicited also by stimulation of group I muscle afferents (see Appelberg *et al.* 1981*a*, Figs. 2 and 3). For account of symbols see Fig. 5.

no. 64, 55, 63, 133, 69 and 116 in Fig. 5). That is reflects a genuinely higher probability of occurrence of group III excitations is further borne out by the much higher incidence of negative observations (black squares, no effects) in the group II range (*A*) and by the approximately equal frequency of observed inhibitory group II and group III effects.

In the Methods we called attention to the fact that the number of 'no-effect' observations was probably underestimated. If every observation of a 'pure' effect in the group II or the group III halves of the chequer-board diagrams had its counterpart (i.e. a no effect, black square) in the other half of the diagram, then the group II part of Fig. 5 would contain seven more and the group III part four more black squares. It should be observed that all inhibitions are either of 'pure' group II nature (four circles in *A*) or of 'pure' group III nature (four circles in *B*).

Static g.s. cells. For these cells, Group III reflex action was also much more frequent than group II action, yet for the g.s. cells this came about by a roughly proportional increase in the frequency of occurrence of both excitatory and inhibitory effects. In accordance with the higher frequency

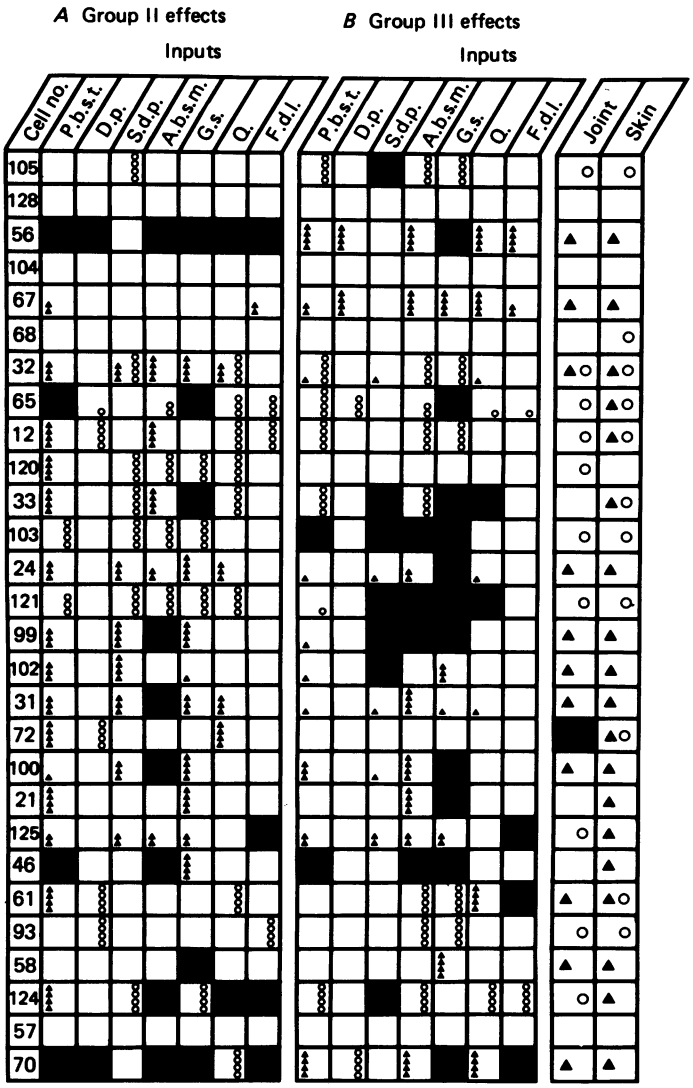

Fig. 7. Dynamic g.s. γ-cells. Comparison of reflex actions from muscle group II (*A*), muscle group III (*B*) and skin and joint receptor afferent fibres. Note that cells 58, 61, 65, 102 and 121 were influenced also by stimulation of muscle afferent fibres in the group I range of intensities (see Appelberg *et al.* 1983*a*, Figs. 2, 3 and 4). Cell 128, 104 and 57, which were not tested with the inputs listed in the diagram, were included for cross-reference with the related reports (Appelberg *et al.* 1982*a*, 1983*a–c*). For account of symbols see Fig. 5.

of group III reflex actions is the higher number of negative observations within the group II range of stimulation intensities.

As regards the relationship, for individual cells, between the types of effects elicited in the group II and group III range, weak tendencies, already present with group II, could be further enhanced in the group III response pattern (Fig. 5, cells no. 55, 63, 133 and 116). Reflex actions could also be completely restricted to the group III range of muscle afferents, whereas group II fibres were ineffective, as in the particularly striking example of cell no. 69 (Fig. 5). Yet a preference for

excitation in the group II range could also be contrasted by a prevalence of inhibition in the group III range (or vice versa), sometimes even with stimulation of the same nerve (see cell no. 20 in Fig. 5). These examples merely emphasize the rather high variability of single-cell responses compared with the general trends.

Dynamic p.b.s.t. cells. For these cells (Fig. 6), unambiguous group III effects (two or more symbols in Fig. 6*B*), i.e. effects which do not include the group II-dominated effects (one symbol in *B*, see also Methods), were considerably less frequent than unambiguous group II effects (Fig. 6*A*); the latter comprised all group II-influenced actions, including the group III-dominated effects (one symbol in *A*; see also Methods). Excitatory actions (triangles) clearly prevailed over inhibitory effects (circles), not only in the group II but also in the group III range. It is noteworthy, however, that for individual cells the balance between excitation and inhibition was not necessarily the same in the group II and group III range. Thus, group II excitation could be accompanied by group III inhibition or vice versa, even with tests from one and the same nerve (see Fig. 6, cells no. 73, 28 and 74).

Dynamic GS cells. Similar findings were obtained for these cells (Fig. 7), apart from the virtually even balance between excitation (triangles) and inhibition (circles) in both the group II range (Fig. 7*A*) and the group III range (Fig. 7*B*). Thus, unambiguous group III effects were less frequent than established group II effects (forty-nine observations in Fig. 7*B*, as opposed to seventy-two in Fig. 7*A*). Moreover, inversion of reflex effects (group II responses compared with group III responses) were also found, even with tests from the same muscle nerve. Thus group II excitation could be contrasted by group III inhibition (see cells 32, 12, 33, and 124) or vice versa (cells 61 and 70).

It should be noted that also for dynamic cells the number of negative observations (black squares) were probably underestimated (see Methods: *Establishment of lack of effects*). This is particularly prominent in Fig. 6 (dynamic p.b.s.t. γ-cells). In Fig. 6*A* there would have been two more black squares and in Fig. 6*B* fifteen more, if every 'pure' group III effect had been matched by a black square in the group II part of the diagram and if every 'pure' group II effect had corresponded to a 'lack of effect' in the group III part of the diagram. Obviously this would further crystallize the differences between group II and group III effects on dynamic and static γ-cells.

Other populations of γ-cells. In the populations of p.b.s.t. and g.s. γ-motoneurones which were not further classified as dynamic or static, some of the general features found in the samples of classified cells were re-encountered. Thus, excitatory as well as inhibitory responses were found on stimulation of group III muscle fibres, group III effects were elicited from all hind-limb muscle nerves and the cells tended to be rather specific recipients of either excitation or inhibition. As with muscle group I, muscle group II, skin and joint fibre stimulation (muscle group I: see Appelberg *et al.* 1983*a*, Figs. 3 and 5), the static a.b.s.m. γ-motoneurones received inhibition preferentially from muscle nerves stimulated within the group III range of intensities. The only conspicuous feature among the small samples of d.p. and tibial neurones was, that the two tibial γ-cells (1 D, 1 S) were massively excited from all muscle nerve group III inputs and from skin and joint nerves as well.

DISCUSSION

Descending pathways to fusimotor neurones have been investigated extensively, but there are few conclusive experimental studies on the reflex control of fusimotor neurones (for a review see Matthews, 1972). Owing to this and perhaps also to the protracted debate on whether or not fusimotor neurones are part of a follow-up servo

system (Eldred, Granit & Merton, 1953; Merton, 1953; Matthews, 1972), one may have been inclined to consider fusimotor neurones mainly as targets of descending pathways conveying direct command signals and to underestimate the significance of segmental reflex inputs.

The present series of experiments was undertaken in order to assess the relative contribution of muscle, skin and joint afferent fibres to the reflex control of γ-motoneurones by studying a large sample of lumbar γ-cells (see also Appelberg *et al.* 1983*a*, *b*; Johansson, 1981). The results allow us to rectify the balance between the views on the significance of descending and reflex inputs to γ-motoneurones. They also revealed that segmental reflexes to γ-motoneurones differ considerably from those to α-motoneurones, and thus that the γ-reflex pattern is not compatible with a rigid linkage between α- and γ-motoneurones. We should therefore like to introduce a working hypothesis in which the pools of fusimotor neurones are regarded as integrative neuronal systems intercalated between descending and reflex pathways on the one hand and the skeletomotor neurones on the other hand, the link to the latter being formed by the primary spindle afferents. The primaries are looked upon as conveying a final and polymodal feed-back signal to the central nervous system. This is referred to as the 'final common input' hypothesis (see below).

Reflexes from high-threshold muscle afferents

The great majority of the cells of the present sample was readily influenced from both low- and high-threshold skin and joint afferent fibres as well as from high-threshold muscle afferents and was thus highly responsive (see also Appelberg *et al.* 1983*a*, *b*). In γ-motoneurones projecting to p.b.s.t. (i.e. flexor muscles) the stimulation of group III muscle afferent fibres of both flexor and extensor nerves provoked excitatory effects which clearly outweighed inhibitory actions. This conforms with the reflexes which are elicited in flexor α-motoneurones of spinal preparations by stimulation of high-threshold afferents so-called flexion reflex afferents (f.r.a.; Holmqvist & Lundberg, 1961). However, whereas the predominant action on extensor α-motoneurones is inhibition, the group III reflex effects on the present sample of γ-motoneurones of extensor muscles (g.s. and a.b.s.m.) studied in anaesthetized preparations with partly intact spinal cord did not conform to this f.r.a. pattern. Excitation and inhibition occurred with equal frequency on stimulation of the group III muscle afferents to those γ-cells. A similar prevalence of excitation in flexor γ-motoneurones and an approximately even blend of excitation and inhibition in extensor γ-motoneurones was also found on stimulation of group II muscle afferent fibres (which were also counted amongst the f.r.a. fibres; see Introduction; Eccles & Lundberg, 1959; Holmqvist & Lundberg, 1961). Moreover, in other respects there were clear-cut differences between group II and group III muscle reflex action on γ-motoneurones (below).

The majority of the γ-motoneurones of the present sample were classified as static or dynamic γ-cells, using the indirect method of mesencephalic stimulation (Appelberg *et al.* 1982*a*; Appelberg, 1981). It is of particular interest that the relative contributions of group II and group III muscle reflex action was not the same for the two types of γ-motoneurones. Group II reflexes were considerably more frequent with dynamic γ-cells, whereas group III reflexes were more frequent with static cells (see Fig. 3).

Also with regard to the balance between excitatory and inhibitory effects on the different populations of γ-motoneurones there were differences between group II and group III muscle afferents. Although excitation generally prevailed over inhibition, this was more pronounced with group II reflex action on dynamic γ-cells and group III reflex action on static cells (Fig. 3).

As already emphasized, such contrasts between group II and group III reflex effects do not conform to the pattern of f.r.a. reflexes as it was described for α-motoneurones in spinal preparations (Eccles & Lundberg, 1959; Holmqvist & Lundberg, 1961; Lundberg, Malmgren & Schomburg, 1975, 1977). Also the differences between the group II and group III reflex effects were not the same for all muscle nerves (compare Fig. 4 with Appelberg *et al.* 1983*b*, Fig. 3). This is again in contrast to the uniformity of the f.r.a. pattern. Thus, for example: p.b.s.t. and g.s. group II inputs on dynamic g.s. cells gave a very pronounced predominance for excitation, while this was turned into a slight dominance for inhibition from group III fibres of the same input nerves. When, with the same population of dynamic g.s. γ-cells, quadriceps, d.p. or s.d.p. were used as inputs, the excitation/inhibition ratio changed in the opposite direction. A third alternative could be seen with a.b.s.m. used as input, for which no difference in the excitation/inhibition ratio could be seen between group II and group III reflexes.

The general trends could be detected also in the reflex patterns of individual γ-cells. Thus, in static p.b.s.t. γ-cells, group II reflex action could be absent or scarce, whereas group III effects were readily elicited from the same nerves. With dynamic g.s. cells, group II excitation could be accompanied by group III inhibition, even on stimulation of the same muscle nerves.

In view also of the scarcity of group I reflex action on γ-motoneurones (Appelberg *et al.* 1983*a*) it stands out quite clearly, that the organization of reflexes to γ-motoneurones from muscle afferent fibres differs considerably from the pattern of muscle afferent reflexes to α-motoneurones.

Differences between reflexes to α-motoneurones and to γ-motoneurones

It is well known that α-motoneurones are the final targets of a wide range of both descending and reflex inputs. A similar degree of widespread convergence is encountered with dynamic as well as static γ-motoneurones (Fig. 8). Of course this similarity by no means implies that the skeletomotor and fusimotor systems will show identical patterns of activity. As is shown in Fig. 8, the details of each system's wiring diagram are already sufficiently different to preclude the generation of rigidly parallel patterns of activity. The differences between α- and γ-motoneurones and between dynamic and static γ-motoneurones can be summarized as follows:

(1) Powerful inputs from both autogenetic and heteronymous Ia and Ib fibres are a prerogative of α-motoneurones (Appelberg *et al.* 1983*a*).

(2) Group II muscle afferent input to α-motoneurones conforms to the f.r.a. concept, which, however, does not apply to γ-motoneurones. Also, group II fibres act preferentially on dynamic γ-motoneurones (Appelberg *et al.* 1983*b*).

(3) Group III muscle afferent inputs to γ-motoneurones do not conform to the group III (f.r.a.) pattern to α-motoneurones. Also, group III fibres exert a more potent influence on static than on dynamic γ-motoneurones (see above, *Reflexes from high-threshold muscle afferents*).

(4) High-threshold recurrent inhibition of γ-motoneurones has been demonstrated (Appelberg *et al.* 1983*c*), whereas it seems to be absent in α-motoneurones (Westbury, 1980; Ellaway & Murphy, 1981).

(5) Dynamic γ-motoneurones receive a specific descending pathway from the mesencephalon (see review by Appelberg, 1981).

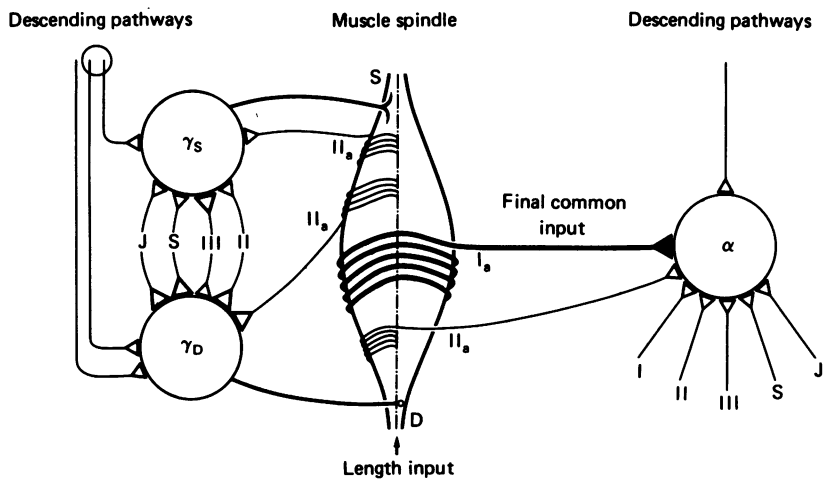

Fig. 8. The final common input hypothesis. To the left, the scheme portrays the multisensory convergence onto static (γ_S) and dynamic (γ_D) γ-motoneurones from descending pathways (those acting in parallel on both classes of γ-motoneurones are encircled), autogenetic (II_a) and heteronymous (II) muscle group II, muscle group III (III), skin (S) and joint (J) afferent pathways. The size of the diagrammatic synaptic boutons illustrating the afferent projections to the γ-cells is intended to represent the relative size of the effects on dynamic and static cells. The information processed in the fusimotor neurones is transmitted to the spindle (in the middle), where it undergoes a final adjustment according to the length and length changes of the muscle fibres. The primary muscle spindle afferents (final common input) then convey the polymodal feed-back message to the central nervous system and the α-motoneurones (α) (to the right). The secondary spindle afferents constitute a link between the two types of γ-cells, although they also influence α-motoneurones to some extent. For primary spindle afferents only the dominant projection to α-motoneurones is shown. Note that each input category (illustrating the convergence onto the three types of motoneurones) is represented by a single channel which may stand for a number of parallel pathways and for both excitatory and inhibitory connexions.

(6) High-threshold skin afferent inputs to γ-motoneurones do not conform to the f.r.a. pattern to α-motoneurones. Low-threshold cutaneous afferents seemed to act more powerfully on dynamic γ-motoneurones than on static γ-cells (H. Johansson & P. Sojka, unpublished results).

(7) Joint receptor afferents act more potently on γ-cells than on α-cells. The pattern of effects on γ-motoneurones does not conform to the corresponding pattern on α-motoneurones (f.r.a.) (H. Johansson & P. Sojka).

On account of these differences between α- and γ-motoneurones and between dynamic and static γ-cells, α–γ linkage is likely to be no more than a special case among all possible functional variations in motor output. Therefore we would like to propose a more general concept for the function of fusimotor activity.

The final common input hypothesis

Pools of fusimotor neurones act as integrative neuronal systems intercalated between descending and reflex pathways on the one hand and the skeletomotor neurones on the other hand. The descending messages and the receptor information from individual group II and III muscle, skin and joint afferents, integrated in the fusimotor neurones, undergo final adjustment in the muscle spindle. The link to the skeletomotor neurones is formed by the primary spindle afferents. Thus these constitute a final common input, conveying integrated detailed polymodal feed-back to the central nervous system (see Fig. 8).

The integrative function of fusimotor neurones

α-motoneurones receive a potent input from homonymous primary spindle afferents. The signals carried in these Ia fibres have long been known to be of complex nature, since they are shaped not only by variations in muscle length but also by activity in both static and dynamic fusimotor neurones. The present view of fusimotor neurones as an intercalated integrative system adds an extra dimension of complexity, and of significance. Clearly, any motor act, although initiated and sustained by central commands, is bound to be continuously adjusted by feed-back from peripheral receptors. The feed-back from primary spindle afferents to α-motoneurones has particular characteristics. The signals are continuously shaped by fusimotor activity which, in turn, is the result of ongoing integrative processing of movement-related inputs from joint, skin and muscle afferents.

What is meant by *integration*? The lack of quantitative studies of the interaction of the various pathways converging onto γ-motoneurones precludes the use of the term 'integrative' in any other than a qualitative sense. In particular, we do not wish to claim that γ-motoneurones behave like linear integrators in the mathematical sense. The connotations we should like to emphasize, though, are the interaction and summation (no matter how non-linear) of a wide range of inputs which are connected in a functional context, such as with natural movements. Under these conditions co-ordinated information from descending as well as from proprioceptive, skin and join afferent pathways are likely to reach the fusimotor neurones. There they are bound to interact and thus to form a highly processed polymodal message.

The projection of Ia fibres onto α-motoneurones should not be considered as a rigid monosynaptic connexion, but rather as the final link of an integrative premotoneuronal system. The spindle should be seen as the point of final adjustment of the integrated descending and peripheral message according to the actual length and the ongoing length changes of the muscle fibres, so that primary afferents provide *a polymodal final common input* to α-motoneurones.

The type of interaction which takes place in the primary ending is likely to be quite different for static and dynamic fusimotor activity. Normally static action should reduce and dynamic action should increase the afferent's dynamic sensitivity for length changes, even if fusimotor activity varies with time. Further, the direct excitatory action of static fibres is known to be considerably stronger than that of dynamic fibres (Hulliger, 1979). Hence, when *static action* prevails, the spindle is likely to act as a *summer* of reflex-shaped fusimotor and external length signals, with more

weight being given to the neural input. When *dynamic fusimotor action* dominates, the spindle is likely to act like a *gate*, since the activity in the dynamic neurones would only be brought into prominence by concomitant and ongoing dynamic changes in muscle length. Thus the dynamic fusimotor neurones continuously adjust the spindle so that, on a change in muscle length, the central nervous system immediately receives up-to-date integrated information from a wide range of peripheral receptors via the primary muscle spindle afferents.

The signals carried in secondary spindle afferents should be similarly polymodal and not unlike the primary afferent's signal when dominated by static fusimotor activity, although the external length component is likely to be more strongly influenced by muscle position than by dynamic length changes. However, with respect to their central action the secondary afferents differ significantly from the primary afferents. The main targets of the latter are the homonymous α-motoneurones, whereas the former project widely to dynamic fusimotor neurones. Thus, secondary afferent fibres constitute a link between static and dynamic fusimotor neurones. However, it has to be borne in mind, that this link is not rigid since, at the level of the muscle spindle, its transmission gain may be strongly modulated by external length signals.

The concepts of fusimotor neurones as integrative systems with wide receptive territories and of the Ia afferent fibres as constituting a channel conveying a polymodal final common input to α-motoneurones may be seen in relation to other integrative systems of the central nervous system, such as the multisensory f.r.a. interneurones (Lundberg, 1979*b*) or the cervical propriospinal neurones (Lundberg, 1979*a*). They all have in common, the fact that they are intercalated integrative systems which provide highly processed input signals to the same target, the skeletomotor neurones.

Using natural stimulation of muscle receptor afferents Appelberg, Hulliger, Johansson & Sojka (1979, 1981, 1982*b*) have shown that the fusimotor reflexes which so far have only been demonstrated by electrical stimulation, can also operate under more natural conditions. Particularly relevant in the present context is the finding that the reflex activation of triceps fusimotor neurones was sufficiently powerful to drastically alter the responses of triceps primary afferent units to stretching of the parent muscle.

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