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THE DEGREE OF SHORT-TERM SYNCHRONY BETWEEN α- AND γ-MOTONEURONES COACTIVATED DURING THE FLEXION REFLEX IN THE CAT

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SUMMARY

1. Cross-correlation analysis of unitary neuronal discharges has been used to study the linkage between α- and γ-motoneurones coactivated during the flexion reflex of the semitendinosus muscle in the decerebrated spinal cat.

2. A flexion reflex was elicited by firm grip or squeeze of the ipsilateral heel, shank or foot. The stimulus excited the discharges of both α- and γ-motoneurones and increased the frequency of discharge of those γ-motoneurones that had shown a background discharge prior to intentional stimulation.

3. Short-term synchrony was present between a high proportion of semitendinosus γ-motoneurones both for background discharges (sixteen out of nineteen pairs) and during the flexion reflex (thirteen out of fifteen pairs). All nineteen pairs of α-motoneurones examined during the flexion reflex showed short-term synchrony of discharge. Few α-motoneurones displayed background discharges but synchrony was observed in the two instances studied.

4. The degree of synchrony was measured as the ratio (k') of the total counts contributing to the peak of the correlogram over the number expected by chance alone. The ratio was higher when the average frequency of motoneurone discharge was low. k' was generally higher for α-motoneurone pairs than for γ-motoneurone pairs. The higher degree of synchrony for α-motoneurones reflected their lower discharge rates.

5. During the flexion reflex the degree of synchrony between γ-motoneurones was greater than expected for that same discharge rate in the absence of intentional stimulation.

6. Only twenty-seven out of forty pairings of an α- with a γ-motoneurone showed a significant degree of synchrony of discharge. On average, the degree of synchrony for α/γ pairs was lower than that for either α/α or γ/γ pairings at the equivalent discharge rate.

7. The results support the conclusion that coactivation of α- and γ-motoneurones during the flexion reflex occurs largely through independent sets of interneurones.

8. The possibility is discussed that those α-motoneurones which showed short-term synchrony with γ-motoneurones were skeleto-fusimotor (β-motoneurones) in nature.

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INTRODUCTION

The intrafusal muscle fibres of muscle spindles in the mammal are innervated largely by γ-motoneurones, the function of these being purely fusimotor (Hunt & Kuffler, 1951). Skeletal muscle fibres are innervated independently by α-motoneurones although some of these are mixed skeleto-fusimotor (or β) motoneurones that provide a degree of motor innervation of muscle spindles (Laporte, Emonet-Denand & Jami, 1981). There are no exclusively fusimotor α-motoneurones (Ellaway, Emonet-Denand, Joffroy & Laporte, 1972). This paper is concerned with the continuing debate over the degree to which the central nervous system can produce independent activation of α- and γ-motoneurones. There is direct evidence from animal studies that the brain controls γ-motoneurones through routes that are independent of those controlling α-motoneurones (Jansen & Matthews, 1962; Appelberg & Emonet-Denand, 1965). Separate reflex control of α- and γ-motoneurones is also evident at the segmental level. The most notable example is that homonymous I a (spindle primary) afferents provide monosynaptic connexions to α-motoneurones but not to γ-motoneurones (Ellaway & Trott, 1978; Appelberg, Hulliger, Johansson & Sojka, 1983; Noth, 1983). Differences between the reflex connexions to α- and γ-motoneurones have been established for a number of other afferent systems. These have been reviewed several times (Murthy, 1978; Ellaway, Murphy & Trott, 1981; Hulliger, 1984).

Despite the availability of independent central nervous routes to α- and γ-motoneurones the two types of motoneurones are seen to be coactivated in many motor acts, both in lower mammals (Sears, 1963; Severin, Orlovsky & Shik, 1967; Appenteng, Morimoto & Taylor, 1980), and in man (Vallbo, 1970). The question arises as to whether coactivation in these motor acts represents tight α/γ linkage, consisting of a common final input to the two species of motoneurone (Granit, 1955), or independent, but parallel, pathways to α- and γ-motoneurones. The latter would seem desirable since it allows for the separate central nervous control of α- and γ-motoneurones.

Our study makes use of the fact that neurones which share synaptic inputs may show a degree of synchrony in their discharges as a result of near simultaneous synaptic events (Perkel, Gerstein & Moore, 1967; Sears & Stagg, 1976). We have found that short-term synchrony occurs between γ-motoneurones in the spinal cat (Ellaway & Murthy, 1985*a*, *b*). Also, α- and γ-motoneurones are coactivated in the spinal cat during the flexion reflex (Hunt & Paintal, 1958). We therefore chose the flexion reflex to assess the extent of shared inputs between α- and γ-motoneurones by measuring the incidence and degree of their synchronized firing. The preparation is suitable since it was a study of the flexion reflex which led to the original idea of tight α/γ linkage (Granit, 1955).

It will be shown that short-term synchrony between α- and γ-motoneurones is found both less frequently and at a lower magnitude than that between like motoneurones. A preliminary report of some of the findings has been made (Connell, Davey & Ellaway, 1985).

METHODS

The preparation

The experiments were carried out on decerebrated cats. Decerebration was performed at an intercollicular level under halothane in oxygen anaesthesia. The spinal cord was transected at the T9–10 vertebrae. The anaesthetic was discontinued after these procedures and the cats were paralysed with gallamine triethiodide (Flaxedil) and artificially respired. The left hind limb was fixed to a myograph stand by a steel pin placed in the base of the femur and by a retort clamp supporting the foot. The supports allowed manual stimulation of the heel and toes. The innervation of the limbs was left largely intact except for the muscle nerve fascicles dissected for peripheral recording.

Blood pressure, heart rate and rectal temperature were monitored and maintained within physiologically desirable ranges.

Peripheral nerve recording

The discharges of single α- and γ-motoneurones were recorded from dissected, cut filaments of part of the nerve supply to the semitendinosus muscle. The axonal conduction velocities of the motoneurones were established by measuring the conduction delay over a known length of the nerve. A time-delayed average of whole nerve activity was triggered by the single unit recorded at a more peripheral site in order to make this measurement. γ-Motoneurones were identified as having axonal conduction velocities below 50 m/s and α-motoneurones above 50 m/s. The range of axonal conduction velocities was 79–102 m/s for α-motoneurones and 14–41 m/s for γ-motoneurones.

Cross-correlation analysis of motoneuronal impulses

An RML380Z microcomputer was programmed to compute the degree to which spike discharges were correlated in the time domain (Ellaway, Murthy & Pascoe, 1982). The program measured and stored the times of occurrence of all spike discharges in two separate recording channels for a period of 10 s. Cross-correlation and autocorrelation functions were computed for these time series from zero time shift up to ± 128 ms in 1 ms steps. The correlation computation could then be extended by sampling further 10 s periods of discharge. An 80 s period was usually sufficient to obtain a reasonable estimate of the form and degree of any peak in the correlogram.

The location and extent of the primary peak in a correlogram was judged by eye with the aid of a cumulative sum product of the correlogram bin counts. The cusum technique had previously been developed for use with peristimulus time histograms (Ellaway, 1978; Ellaway, Gardner-Medwin & Pascoe, 1983). Cross-correlograms were repeated, whenever possible, to confirm the position of a peak. The degree of synchrony, represented by a peak in the correlogram, was measured as follows. The mean count (m) expected by chance in any single bin was estimated from ninety consecutive bins in a control region of the correlogram which did not form part of any primary peak or secondary feature in the correlogram. A ratio k' was calculated as the sum of the counts (Σx), in the n bins constituting the peak, divided by the number of counts expected in that period by chance alone ($n \times m$). The test of whether a particular value of k' represented a significant degree of synchrony depended upon our observation that the counts in control regions of the correlogram (outside the peak) always had a Poisson distribution. A significant correlation was taken as one where the integrated counts in the peak exceeded the counts expected by chance alone ($n \times m$) by more than $3{\cdot}29 \sqrt{(n \times m)}$ (see also, Ellaway & Murthy, 1985*a*, *b*). Finally, when no primary peak was evident to the eye, k' was assessed for a set of bins spanning the expected position of synchrony. Since this last point is crucial to any conclusion that synchrony is absent the procedure is expanded upon in the Results section.

RESULTS

The flexion reflex

Eight decerebrated cats with complete spinal cord transections at T9–10 were studied. Recordings from peripheral axons of the nerve to the semitendinosus muscle showed that the majority of γ-motoneurones exhibited background discharges in the absence of intentional stimulation. In contrast, α-motoneurones rarely showed background discharges. Lightly gripping or rubbing the ipsilateral shank, toes or heel evoked an increase in the discharge rate of those γ-motoneurones that were already firing and recruited α-motoneurones and some other γ-motoneurones. Stronger stimulation, such as pinching the foot, raised the discharge frequency of the motoneurones previously recruited by non-noxious stimulation and could recruit further α-motoneurones. Stimulation did not result in muscle contraction since the cats were paralysed (see Methods). Fig. 1 illustrates the nature of the reflex discharge of α- and γ-motoneurones in response to innocuous gripping of the foot. The frequency of discharges elicited by stimulation fluctuates during each period of continuous stimulation but the increased rates, compared with the control periods, are maintained throughout. Repeated periods of stimulation, lasting at least 10 s each (see Methods and Fig. 1), formed the basis of the experimental protocol for assessing the degree of correlation between discharges of motoneurones during the flexion reflex.

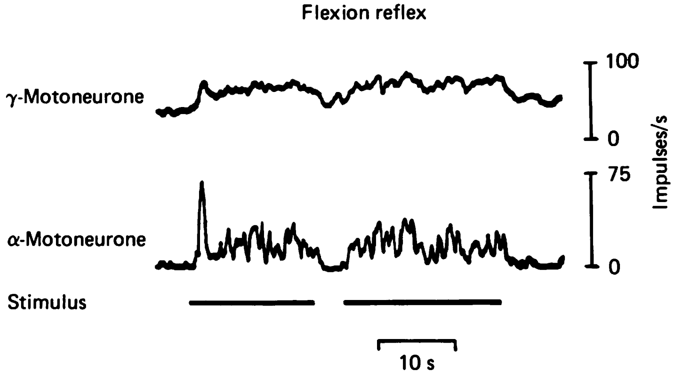

Fig. 1. Semitendinosus α- and γ-motoneurones coactivated during the flexion reflex. The reflex was elicited by gripping the ipsilateral foot. Above: discharge of a single γ-motoneurone, axon conduction velocity 41 m/s. Middle: the summed discharges of two α-motoneurones, conduction velocities 90–92 m/s. Frequency of motoneurone discharge is displayed on linear scales. Below: bars indicating the durations of two periods of stimulation of the foot. Note that, typically, the γ-motoneurone displayed a background discharge prior to intentional stimulation.

Short-term synchrony between γ-motoneurones

The background discharges of a small sample (three pairs) of semitendinosus γ-efferents studied previously (Ellaway & Murthy, 1985*b*) all showed a tendency to synchronized firing in the absence of intentional stimulation. In the present study, sixteen out of nineteen pairs of semitendinosus γ-efferents showed synchrony in their background discharges. A typical example is shown in Fig. 2*A*. The width of the peak was gauged from the cumulative sum in Fig. 2*B* and measured ±10 ms. Note, however, that the steepest slope of the cusum lasts only 8 ms and represents an accentuated central peak of synchrony with a half-width of 4 ms. In this correlogram

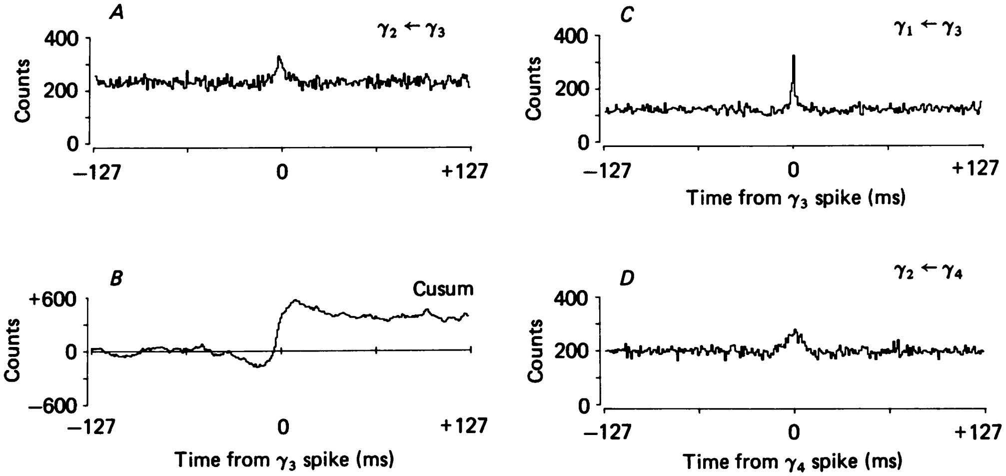

Fig. 2. Short-term synchrony between the background discharges of semitendinosus γ-motoneurones in the spinal cat. *A*, cross-correlogram computed from 80 s of discharge in the absence of intentional stimulation. *B*, cumulative sum (cusum) of the cross-correlogram in *A*. The degree of synchrony in correlogram *A*, as expressed by k', is 1·14 and the average rate of discharge was 39 impulses/s.

the peak is centred approximately 3 ms to the left of time zero. When the position of the peak was corrected for the peripheral conduction times of the γ-motoneurone axons the peak became centred on time zero. This indicates that the tendency to synchrony was indeed being created at the level of the spinal cord.

It would be misleading to quote the range of widths and amplitudes of the central peaks of synchrony since, in a previous study (Ellaway & Murthy, 1985*a*), these parameters were found to depend upon the frequency of γ-motoneurone discharge. Both the relative size (k') and width of the peak in the correlogram became smaller at higher frequencies. It is possible, however, to make a general qualitative statement about the range of shapes of correlogram peaks. As mentioned above, the peak can appear to have two components consisting of a broad base (± 10 ms) and a narrow central region (± 3–4 ms). Both are present, for example, in the correlogram of Fig. 2*A*. The characteristics of short-term synchrony exhibited by semitendinosus γ-motoneurones were found to be similar in all respects to those reported previously for gastrocnemius γ-motoneurones (Ellaway & Murthy, 1985*a*).

In Fig. 3 the degree of synchrony between γ-efferent discharges is shown to be greater during the flexion reflex than for the background discharges alone. To arrive at this conclusion it was necessary, first, to establish whether the degree of short-term synchrony between pairs of semitendinosus γ-motoneurones depended upon their frequency of firing in the manner previously established for gastrocnemius γ-efferents (Ellaway & Murthy, 1985*a*). This is examined in Fig. 4. In this experiment the background discharges of two γ-efferents in the spinal cat had mean rates of 86 and 105 impulses/s. At these frequencies there was a small but significant ($P < 0{\cdot}001$) degree of synchrony with k' values in the range 1·03–1·05. To assess the degree of synchrony at different discharge rates the cat was given intravenous injections of

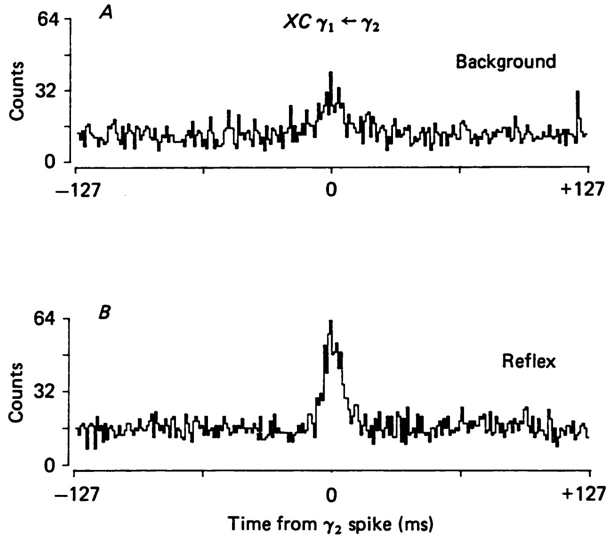

Fig. 3. The difference in the degree of synchrony between the background and the reflex discharges of semitendinosus γ-motoneurones. *A*, correlogram constructed from 80 s background discharge. *B*, correlogram constructed from 80 s discharge recorded from the same neurones during a flexion reflex elicited by gripping the ipsilateral heel. The degree of short-term synchrony (peak width ±8 ms) was 2·03 in *A* and 2·60 in *B*.

sodium methohexitone (Brietal) 4 mg/kg until the mean discharge rate had dropped to less than 10 impulses/s. On discontinuing administration of the barbiturate, the mean frequency rose to about 30 impulses/s. The degree of synchrony was assessed at different discharge rates during the time course of action of the anaesthetic. Fig. 4 shows that k' increased with decreasing discharge rates. The implication of this relationship when studying the behaviour of motoneurones during the flexion reflex is that, if the frequency of discharge is raised by an excitatory stimulus, the relative size of a peak in the cross-correlogram might be expected to fall. The degree of synchrony between the two γ-motoneurones in Fig. 4 was also assessed during the flexion reflex. In this case the reflex increase in discharge was produced by firm stroking of the ipsilateral heel. Correlograms were constructed both before and during administration of the barbiturate sodium methohexitone (see above). Fig. 4 shows that, at any particular mean frequency of γ-motoneurone discharge, the value of k' was greater during the flexion reflex than for the equivalent background discharge rate. In the Discussion we argue that the act of eliciting the flexion reflex increased the degree of synchrony in the discharge of the neurones if examined at a particular frequency of firing. This difference is normally obscured by the fact that the increase in discharge rate during the reflex response results in a reduction in the value of k'.

Not all stimuli that caused reflex excitation of γ-motoneurones had the effect of increasing their degree of synchrony above that expected for the equivalent background discharge rates. Squeezing the ipsilateral toes, rather than the heel, evoked a strong reflex increase in discharge rates but, having allowed for the tendency for k' to fall with increasing rate of firing, the degree of synchrony remained unchanged. It was the skin of the heel in particular that provided a source of additional synchrony when stimulated.

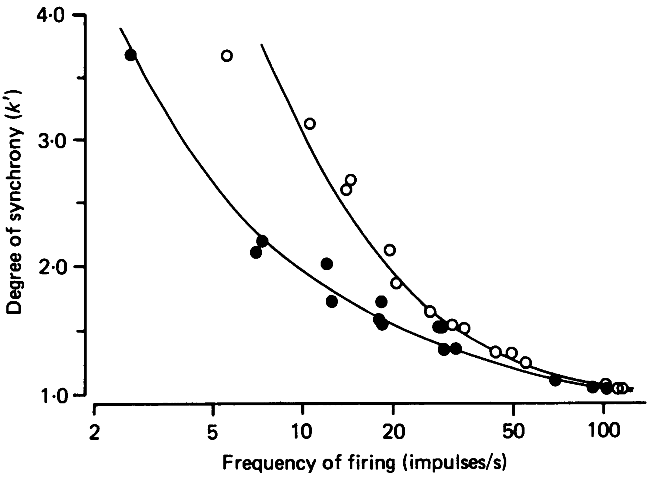

Fig. 4. The relationship between degree of synchrony and frequency of firing for a single pair of semitendinosus γ-motoneurones. Degree of synchrony (k') is plotted against the geometric mean frequency (logarithmic scale) of the two neurones. Each point is calculated from 80 s of recording. The continuous curves have been drawn freehand to link points obtained either in the absence of intentional stimulation (●, background) or during the flexion reflex (○, reflex). Correlograms from Fig. 3 provided points at mean frequencies of 12 (●) and 14 (○) impulses/s.

Short-term synchrony between α-motoneurones

In most cats there was no evidence of a background discharge in the α-motoneurone population. In only two instances (different cats) was it possible to isolate two α-motoneurones with background discharges. Fig. 5*A* shows the cross-correlogram ($k' = 3{\cdot}2$) for the discharges of one of these pairs. In the other case a weaker ($k' = 1{\cdot}16$), although significant, peak ($P = 0{\cdot}001$) was evident. It was not possible to examine the way in which degree of synchrony of a particular pair of α-motoneurones changed with discharge rate. However, it was observed for all cats that, during the flexion reflex, there was a tendency for the degree of synchrony to be greater for those α-motoneurones having the lower discharge rates (e.g. see Fig. 7).

Synchrony between coactivated α- and γ-motoneurones

All nineteen pairs of α-motoneurones (six cats) examined during the flexion reflex showed a significant degree of short-term synchrony. The form of the synchrony for α-motoneurones was similar to that seen between γ-motoneurones but the degree of synchrony was generally greater. The higher values of k' may be related to the lower rates of discharge of the α-motoneurones. In one instance the degree of correlation between α-motoneurone discharges was examined both for a period of background discharge and during the flexion reflex. The correlogram peak during the reflex (Fig. 5*B*) was typical of that seen for other α-motoneurone pairs that were recruited during the flexion reflex.

The incidence of correlations between the discharges of α- and γ-motoneurones coactivated during the flexion reflex varied from cat to cat. A substantial number of α/γ pairs (a single α- and a single γ-motoneurone) showed evidence of short-term synchrony between their discharges. However, for the eight cats studied, the

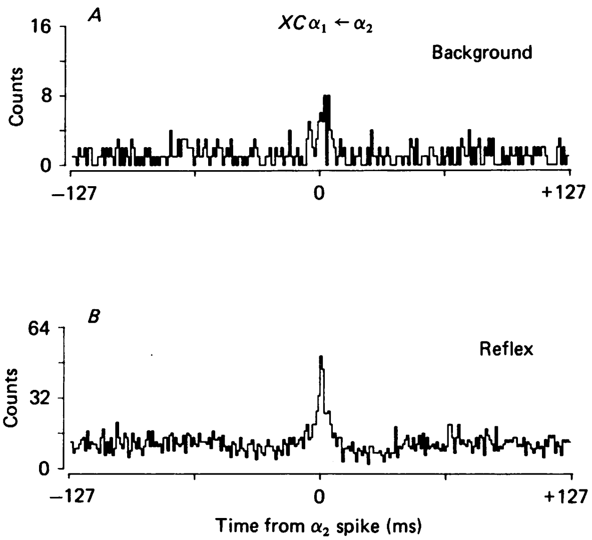

Fig. 5. Short-term synchrony between semitendinosus α-motoneurones. *A* and *B*, correlograms constructed from 80 s discharge of two α-motoneurones with axonal conduction velocities of 79·5 m/s (α_1) and 91·2 m/s (α_2). *A*, background discharges. $k' = 3{\cdot}22$, width ±7 ms. *B*, flexion reflex discharge elicited by squeezing the ipsilateral shank close to the heel. $k' = 1{\cdot}97$, width ±9 ms.

incidence of synchrony between α/γ pairings (twenty-seven out of forty) was lower than for γ/γ pairings (thirteen out of fifteen) or α/α pairings (nineteen out of nineteen).

The results in Fig. 6 were chosen for presentation because it proved possible to pair α- and γ-motoneurones for correlation analysis as α/γ combinations and as component neurones of α/α and γ/γ pairings. Synchrony of discharge during the reflex was evident for the α/α ($k' = 1{\cdot}82$) and γ/γ ($k' = 1{\cdot}08$) pair (Fig. 6*A* and *B*) but was present for only one of two α/γ pairings (Fig. 6*C* and *D*). Furthermore, the significant degree of synchrony for the α/γ pair ($k' = 1{\cdot}12$) in Fig. 6*D* is weak for an average discharge rate of 42 impulses/s. Synchrony was also present between the background discharges of the γ-motoneurones featured in Fig. 6 ($k' = 1{\cdot}24$, mean frequency = 52 impulses/s).

Fig. 7 shows the degree of synchrony plotted against the average frequency of discharge for all pairs of motoneurones in a single cat. Each different pair of motoneurones is represented by a single point. In those correlograms where no peak was evident to the eye the following procedure was used for the assessment of k'. The procedure was based on observations in both this and a previous study (Ellaway & Murthy, 1985*b*) that the peak of synchrony occurs at time zero with reference to firing at the level of the spinal cord rather than the peripheral recording site. The correlogram in Fig. 6*C* features a γ- and α-motoneurone with axon conduction velocities of 35 and 86 m/s respectively. The conduction distance from the spinal cord to the peripheral recording site was approximately 160 mm, giving a difference in conduction time between the two neurones of 2·7 ms. The centre of the expected peak

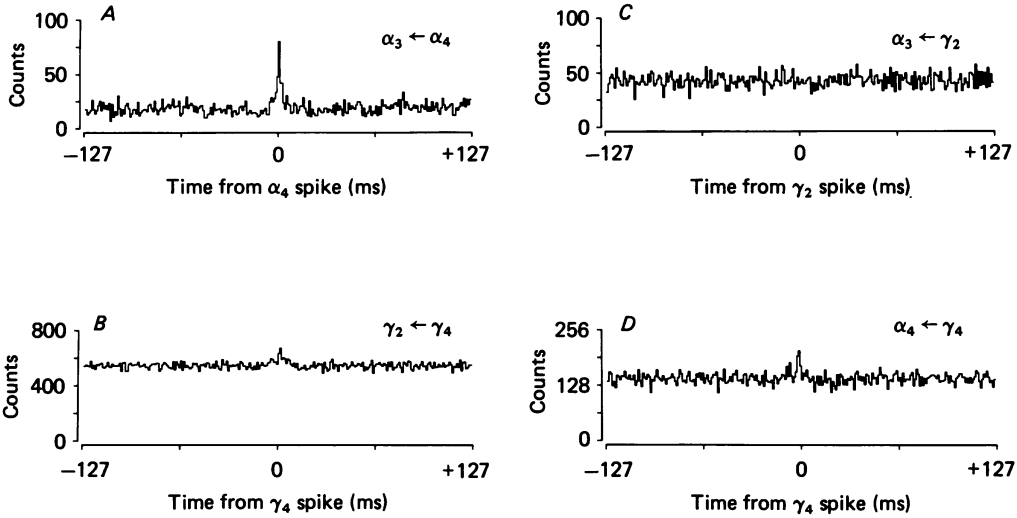

Fig. 6. Synchrony of discharge between α- and γ-motoneurones coactivated during the flexion reflex. *A–D*, cross-correlograms constructed from 80 s periods of discharge of motoneurones during stimulation of the ipsilateral foot. All motoneurones were recorded in the same cat. *A*, α-motoneurone pair. *B*, γ-motoneurone pair. *C* and *D*, α/γ pairs. NB each motoneurone is featured in both a homologous and a heterologous pairing. The degree of synchrony and the average discharge rates were: *A*, $k' = 1{\cdot}82$, 15 impulses/s; *B*, $k' = 1{\cdot}08$, 85 impulses/s; *C*, $k' = 1{\cdot}01$ (insignificant $P > 0{\cdot}01$), 23 impulses/s; *D*, $k' = 1{\cdot}12$, 42 impulses/s.

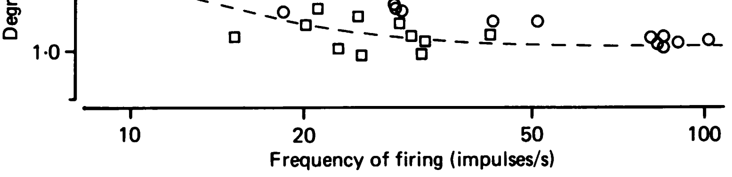

Fig. 7. Short-term synchrony between α- and γ-motoneurones and its relation to mean frequency of discharge. Each point represents the degree of synchrony between an individual pair of motoneurones. Discharge frequency is calculated as the geometric mean of the two rates and is plotted on a logarithmic scale. Each γ/γ pairing (○) is featured twice: one value of k' assesses synchrony for the background discharge (frequencies all < 75 impulses/s) and another for the flexion reflex (frequencies all > 75 impulses/s). k' for all α/α (△) and α/γ (□) pairs was assessed during the flexion reflex. The dashed line separates those points that represent a statistically significant value of k' ($P < 0{\cdot}001$) from those that are insignificant. All neurones were recorded in the same cat.

of short-term synchrony was therefore predicted to occur 2·7 ms from bin zero (to the left in this case) of the correlogram. Since the narrowest peaks have a half-width of 3–4 ms, a value for k' was calculated over seven bins centred 3 ms to the left of time zero on the abscissa of the correlogram. The value of k' was 1·01 which represented an insignificant degree of synchrony ($P > 0{\cdot}01$). In Fig. 7 a curved line has been drawn to divide those points (above) which represent a significant degree of synchrony ($P < 0{\cdot}001$) from those (below) showing no synchrony between motoneurones. Inspection of the Figure shows that a number of α/γ pairs have no short-term synchrony. Furthermore, it appears that even those α/γ pairs with a significant peak exhibit less synchrony (lower k') than either α/α or γ/γ pairings. Because of the dependency of k' on frequency of firing, the comparable set of points to the α/γ pairs, in that frequency range, are the pairings for γ-motoneurones showing a background discharge rather than α or γ pairings assessed during the flexion reflex. Nevertheless, there was sufficient overlap of discharge rates for the different pairings in this and other experiments to support the conclusion that α/γ pairings showed the least synchrony of discharge.

DISCUSSION

In this investigation we have used the incidence and degree of synchrony of motoneurone discharge to assess the neural basis of coactivation of α- and γ-motoneurones. Synchrony of discharge may arise through impulses in common presynaptic axons which will tend to synchronize motoneurones as a result of the near simultaneous production of post-synaptic potentials (Perkel *et al.* 1967; Sears & Stagg, 1976). Synchrony of motoneurone discharge may also result from synchronized discharges in anatomically separate presynaptic axons (Kirkwood & Sears, 1982; Hamm, Reinking, Roscoe & Stuart, 1985). In the present study the preponderance of narrow peaks in the correlograms, or of an accentuated central region to the peak with half-widths in the range 3–4 ms, suggests that a major component of the synchronized discharges arises from activity in common presynaptic stem fibres (Knox & Poppele, 1977; Kirkwood, 1979). Some correlogram peaks were wider, which could indicate an element of synchrony between different presynaptic axons. However, since the entire time course of the post-synaptic potential can influence the time of firing of an action potential (Knox & Poppele, 1977), and not just the rising phase (Knox, 1974; Kirkwood, 1979), a broad correlogram peak may simply reflect shared inputs from common stem fibres. Direct investigation of the influence of synaptic potential shape on the time course of spike discharge has been attempted only for α-motoneurones with muscle afferent inputs (Fetz & Gustafsson, 1983; Gustafsson & McCrea, 1984). It is therefore premature to speculate on that relation for γ-motoneurones excited by different segmental inputs. However, if synchrony between individual input neurones does contribute to motoneurone synchrony then we suggest that it is likely to be synchrony between the interneurones involved in the flexion reflex rather than the primary afferents themselves. In a preliminary study (Davey & Ellaway, 1985) we have found no evidence for tight synchrony of discharge between primary afferents of either hair or pressure receptors excited by stimulation of the skin of the foot. The receptors tested were known, from the conduction velocities of their axons, to be among the population in the sural nerve field that cause powerful excitation of γ-motoneurones in the spinal state (Catley & Pascoe, 1977).

Irrespective of the mechanism of motoneurone synchrony, comparison of the incidence and degree of synchrony can be used to assess the extent to which there is tight coupling between α- and γ-motoneurones when they are coactivated. Such a comparison is complicated by the previous finding (Ellaway & Murthy, 1985*a*) that the relative size of a peak in the correlogram is dependent upon the mean discharge rate of the neurones. This implies that the correlogram peak may be affected by the average rate of depolarization of the constituent neurones as well as their particular synaptic inputs. A mechanism to account for this effect has already been proposed (Ellaway & Murthy, 1985*a*). Thus, when comparing different pairs of neurones a larger correlogram peak does not necessarily indicate a stronger projection of certain inputs. Another factor to consider in our analysis is the use of a barbiturate anaesthetic to examine synchrony between the same pair of γ-motoneurones at different mean rates of discharge. The barbiturate may well have altered either the balance of synaptic inputs to the neurones or the rise times of post-synaptic potentials (cf. Kirkwood, Sears, Tuck & Westgaard, 1982). Our conclusion that synchrony between γ-motoneurones is increased by stimulation of cutaneous afferents from the heel is thus tentative because the control discharges are recorded at different levels of barbiturate anaesthesia. However, the conclusion is supported by the finding that, under the same conditions of partial barbiturate anaesthesia, other afferent inputs such as cutaneous receptors of the toes (this study) or glabrous skin (Ellaway & Murthy, 1985*b*) did not alter the relationship between k' and rate of discharge.

In this study we have shown that γ-motoneurones have a tendency to synchronized firing during stimulation of the skin of the ipsilateral foot and that this may represent an increase in synchrony over that seen between the background discharges prior to stimulation (Figs. 3 and 4). α-Motoneurones invariably showed a marked degree of synchrony during the flexion reflex elicited by the same stimulus. In contrast, heterologous (α/γ) pairings of motoneurones were much less likely to show synchrony, or had a weaker degree of synchrony, compared with either type of homologous pairing, i.e. α/α or γ/γ. There is no reason to suggest that the excitation of α- and γ-motoneurones during the flexion reflex has origins in different sensory receptors (Hunt & Paintal, 1958) and we propose, therefore, that the final connexions to the two types of motoneurone may, for the most part, be segregated. That is, the afferent input excited during the flexion reflex is routed to α- and γ-motoneurones largely through different sets of interneurones.

It is worth noting that cutaneous input from the heel has the same effect on semitendinosus and gastrocnemius γ-motoneurones. Innocuous stimulation raises the discharge rate of both types of efferent and appears to increase the degree of synchronized firing within each population. The common excitation may be related to the fact that the muscles are not true antagonists since, although gastrocnemius extends the ankle joint, both muscles tend to flex the knee. Alternatively it may reflect a local sign of reflex movement: simultaneous knee flexion and ankle extension. Notwithstanding the common excitatory effect of heel stimulation, the afferent inputs leading to synchronized firing may not necessarily be the same as those eliciting the reflex discharge. A number of different receptor types would have been stimulated by grasping or squeezing the foot.

Previous studies have not generally addressed the basis of α/γ linkage in the direct manner used here. The exception is the respiratory system where Kirkwood, Sears & Stagg (1974) could not demonstrate short-term synchronization between α- and fusimotor discharges. Using a more sensitive test of interaction Kirkwood & Sears (1978) have reported synaptic depolarization of respiratory α-motoneurones that was correlated with discharges of γ-motoneurones in the anaesthetized cat. Because of this Kirkwood (1979) raised the question of whether the cross-correlation technique might be insufficiently sensitive to detect shared inputs. If, for example, the rise times of post-synaptic potentials were slower for γ- than for α-motoneurones they would be less likely to influence the precise time of spike discharge and short-term synchrony might be absent. This argument is not likely to account for the relative lack of α/γ interactions in the present study since it would, presumably, also apply to γ/γ correlations. Synchrony between γ-motoneurones has been observed for a large proportion of both semitendinosus (this study) and gastrocnemius efferents (Ellaway & Murthy, 1985*a*).

One reason why synchrony of discharge occurred between certain α/γ pairs, and not others, could relate to the fact that neither α- nor γ-motoneurones are homogeneous populations. α-Motoneurones have been classified as fast fatigable, fast fatigue resistant or slow (Burke, Levine, Tsairis & Zajac, 1973) and γ-motoneurones as static or dynamic (Emonet-Denand, Laporte, Matthews & Petit, 1977). It has also been demonstrated in the human that motoneurones with similar recruitment thresholds to voluntary contraction show greater tendency to synchronized firing than those with dissimilar thresholds (Datta & Stephens, 1980; Datta, Fleming, Hortobagyi & Stephens, 1985). We had no means of ascertaining the type of either α- or γ-motoneurone excited during the flexion reflex. However, there is some evidence that the semitendinosus γ-motoneurones that have a background discharge in the spinal cat are of the static variety (Alnaes, Jansen & Rudjord, 1965). Despite the possibility that the present study dealt with a uniform population of static γ-motoneurones, the argument that it is a particular type of α-motoneurone that shows synchrony with the γ-motoneurone population, and that another does not, is not supported by the observation that all α/α motoneurone pairings studied during the flexion reflex showed a pronounced synchrony of discharge. There was no evidence that the α-motoneurones which showed synchrony with γ-motoneurones also correlated more strongly between themselves than with the α-motoneurones that lacked synchrony with γ-motoneurones.

A substantial proportion of α-motoneurones in the cat are mixed skeleto-fusimotor (β motoneurones) (Bessou, Emonet-Denand & Laporte, 1965; Laporte *et al.* 1981). They are of two types: β-motoneurones innervating the slow type of skeletal muscle fibre exert a dynamic action on muscle spindles (Emonet-Denand & Laporte, 1975) whereas those innervating fast units have a static fusimotor action (Jami, Murthy & Petit, 1982). It is to be expected that the fusimotor action of β-motoneurones would require them to receive the same synaptic inputs as the γ-motoneurones having the same function (static or dynamic). We expect such shared inputs in the spinal animal to result in synchrony of discharge. It is thus possible that those α-motoneurones showing short-term synchrony with γ-motoneurones are, in fact, β-motoneurones.

These same β-motoneurones might also be expected to show synchrony with the purely skeletomotor α-motoneurones for the same reason, i.e. that they would share inputs involved in the direct activation of skeletal muscle motor units.

If the limited degree of synchrony between α/γ pairings is not due to the presence of β-motoneurones in the sample then an alternative interpretation of the results is that a number of shared inputs do exist between α- and γ-motoneurones. Thus the incidence of α/γ synchrony may represent a genuine degree of tight α/γ linkage through common interneurones.

Finally we consider the implications of α- and γ-motoneurones receiving independent inputs in a motor act such as the flexion reflex. Our results suggest that, when certain α- and γ-motoneurones are coactivated during the flexion reflex, the two types of motoneurone are excited via separate sets of interneurones. We know that there exists central nervous control over both the α (Holmqvist & Lundberg, 1961) and γ (Bergmans & Grillner, 1968; Grillner, 1969) components of the flexion reflex. The advantage of having separate interneurone links to α- and γ-motoneurones in the flexion reflex, over one of linkage through common interneurones, is that the central nervous system may exercise independent control over the reflex activation of α- and γ-motoneurones. If the final separate interneurone connexions to α- and γ-motoneurones are themselves shared by other afferent sources, which are peculiar either to α- or γ-motoneurones, then this differential control would undoubtedly be appropriate.

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