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A REAPPRAISAL OF REFLEX STEPPING IN THE CAT

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SUMMARY

1. In re-evaluating Sherrington's experiment in which deafferented muscles in decerebrated cats 'stepped', we recorded from L5 ventral roots, a chief supplier of the major extensors of the hind legs, during stimulation of the common peroneal nerves. The extensor muscles had been denervated by appropriate dorsal root sections; the cats had been paralysed with a neuromuscular blocking agent.

2. Response versus interval curves were constructed using 1 Hz stimulation. When stimulation of one peroneal preceded another, the responses ipsilateral to the second stimulation were facilitated at testing intervals of −2 to 10 msec, and inhibited at intervals of 30–400 msec.

3. Responses from the L5 ventral roots mimicked 'stepping', waxing and waning at 1 Hz, only when 1 Hz was the best frequency for stimuli delivered to the two common peroneals (e.g. 24 and 25 Hz). When both sides were stimulated at the same frequency, no periodic changes in response amplitudes were seen.

4. It was concluded that the apparent 'stepping' in deafferented muscles seen by Sherrington may have been due to differences in frequency of the two inductoria he used to stimulate the peroneals. We found no evidence of central timing of a pattern corresponding to walking.

INTRODUCTION

Every behavioural act requires that a set of muscles be contracted in a particular sequence. The nervous system somehow generates an appropriate temporal sequence of activation of motor neurones. This striking property of the central nervous system has been explained in vertebrates principally in two ways (e.g. Creed, Denny-Brown, Eccles, Liddell & Sherrington, 1932; Gray, 1950; Sherrington, 1910, 1913*a*, *b*, *c*; Weiss, 1936, 1950). In one, chain reflexes produce the patterning, i.e. the motions in one part of the sequence send back proprioceptive or exteroceptive sensations which reflexly elicit the next motions of the sequence. The second explanation

emphasizes that sensory information is not necessary, and that the central nervous system can generate appropriate patterns in the absence of timing information from the periphery.

The latter explanation can be tested by intercepting all sensory pathways carrying timing information, and demonstrating that the basic behaviour pattern survives. However, in the total absence of sensory stimulation, animals are usually quiescent, hence the experimenter must find a way to stimulate the animal, being careful not to introduce any timing clues which might be capable of producing the patterned neuronal firings.

In mammals, Brown (1911*a*, *b*, 1914) and Sir Charles Sherrington (1913*c*) pioneered this approach, seemingly demonstrating that stepping in cats had a central origin. These results have been accepted in modern texts (Bullock & Horridge, 1965; Ruch & Patton, 1965). Sherrington's demonstration appeared the most convincing. He severed all the nerves in the hind limbs of decerebrate cats, except those to the vastocrureus muscles, the chief extensors of the leg. The vastocrureus muscles, though innervated, had been deafferented by appropriate dorsal-root sections. He used inductoria to stimulate the common peroneal nerves, driving the vastocrureus muscles into activity.

Upon stimulation of one common peroneal, which contains no afferents from the vastocrureus muscles, the contralateral vastocrureus went into tonic contraction. However, when both peroneals were concurrently stimulated, the deafferented muscles sometimes exhibited a rhythmic activity, contraction of the right muscle alternating with contraction of the left muscle. Sherrington called this 'reflex stepping'. As to the origin of the rhythmicity and alternation Sherrington argued as follows: because all sensory feed-back loops which could generate the pattern had been cut, and because both peroneal nerves were stimulated continuously and concurrently, the stimuli introduced no timing clues. Thus he concluded that the spinal cord, in the absence of timing information from proprio- or exteroceptors, is capable of generating the alternating pattern seen in reflex stepping.

In order to evoke reflex stepping, Sherrington found it necessary to 'balance' the *amplitudes* of stimulation to the two peroneals. To achieve this he used two separate inductoria, each delivering stimulation of a controlled amplitude. Sherrington assumed that his inductoria delivered 'continuous' stimulation in the sense of their having no rhythms with periods comparable to the stepping.

Sherrington (1910) knew, however, and by oscilloscopic examination we have confirmed, that stimuli from inductoria similar to those used by Sherrington deliver pulses at a frequency adjustable between approximately 20 and 100 Hz. However, Sherrington had no way of synchronizing

his two inductoria, and he makes no mention of trying to adjust the *frequencies* so that they would be equal. Hence, in Sherrington's experiments, the two peroneal nerves very probably received trains of pulses of at least slightly different frequencies. As these two stimulators beat against each other, the two peroneals received stimuli in virtually all possible time relations to each other. If any of these phase relations were particularly effective in evoking an augmented reflex response, then that response would be seen at the beat frequency of the stimulators. If the most effective timing was anything other than synchrony of the two pulses, then the most effective stimulation on the right would alternate with the most effective stimulation on the left, each side 'stepping' once per beat.

In the first set of experiments described below, we stimulated peroneal nerves at different relative times to search for particularly effective and/or ineffective timings. In the second set of experiments, we stimulated the peroneals with trains of stimuli of unequal frequency to show that, indeed, the legs 'stepped' at the beat frequency of the stimulators. Finally, when the peroneals were stimulated at exactly the same frequency, no rhythmic 'stepping' was found. We therefore conclude that Sherrington's cats may have been stepping at the beat frequency of his stimulators, and that his demonstration of a central patterning for 'reflex stepping' may no longer be acceptable. A preliminary report of these experiments has been published (Egger & Wyman, 1968).

METHODS

Cats, 2–4 kg in weight, were anaesthetized with ether or thiopental sodium (40 mg/kg I.P.), tracheostomized, and surgically decerebrated at the mid-brain–diencephalic junction. Following decerebration, the anaesthetic was discontinued. Heart rate and blood pressure were continuously monitored. More than 5 hr elapsed between discontinuation of anaesthetic and recording of electrophysiological data. Before recording, gallamine triethiodide (Flaxedil) was administered through a venous cannula (2 mg/kg). The cats were artificially respirated at rates and volumes comparable to respiration occurring before administration of the neuromuscular blocking agent.

A laminectomy was performed from L 2 to the sacrum. The spinal cord was bathed in a pool of paraffin oil continuously equilibrated with oxygen containing 5 % CO_2. The temperature of the spinal pool was maintained by heat lamps and a circulating water bath near 37° C.

The hind legs were stabilized with pins through the ankle, and the popliteal fossae opened. The nerves within each popliteal fossa were identified, ligated, and cut. The common peroneals were mounted on platinum bipolar electrodes after the fossae had been filled with paraffin oil. The peroneals on both sides were cut at approximately corresponding positions so that equal stimulation on both sides elicited simultaneous volleys at the spinal cord. In some preparations, the femoral nerves and all branches of the sciatic were also cut.

The vastocrureus muscles were deafferented by bilaterally sectioning the appropriate dorsal roots (L 4, 5, and 6) under a dissecting microscope, care being taken to preserve as much of the spinal cord's blood supply as possible. The fifth lumbar (L 5) ventral roots were carefully cut, freed from the pia-arachnoid, and mounted on platinum bipolar electrodes.

A platinum ball electrode was placed on the cord dorsum at the level of a seventh lumbar (L7) dorsal root.

The electrodes were connected to Grass P-511 preamplifiers which, in turn, were connected to the Type 3A1 plug-in of a Tektronix 565 oscilloscope. Oscilloscopic traces were photographed with a Grass C-4 kymograph camera. Stimulation pulses were programmed by Tektronix pulse and wave form generators, amplified by an ELS-2 pulse amplifier, and delivered to the stimulating electrodes through Argonaut isolation transformers.

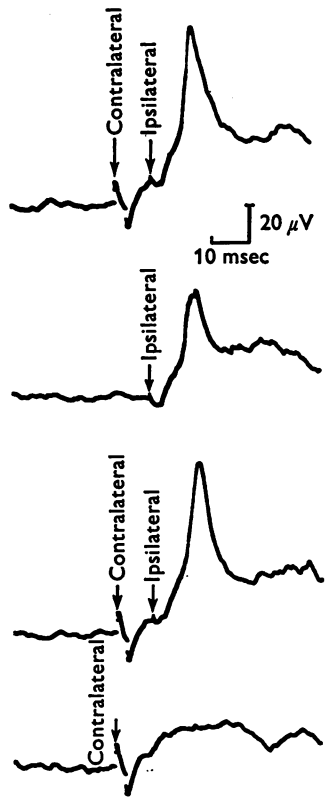

Fig. 1. Four consecutive responses recorded from L5 ventral root. In the top trace, stimulation of the contralateral peroneal preceded stimulation of the ipsilateral peroneal by 10 msec. The next trace was elicited by stimulation of the ipsilateral peroneal alone. The stimuli for the third trace are the same as for the first. The bottom trace was elicited by stimulation of the contralateral peroneal alone. Each trace was recorded 1 sec after the previous one. Stimulation pulse duration = 3 msec.

Detailed observations were made on six cats; partial observations were made on six additional cats. Responses elicited by stimulation of the common peroneal nerves were recorded from the L5 ventral roots and filmed. L5 ventral root is a chief supplier of motoneurones to the vastocrureus muscles, although it also supplies other muscles. Regardless of whether the lumbosacral plexus is prefixed or post-fixed, L5 ventral root contributes no fibres to the peroneal nerve (Romanes, 1951).

Threshold stimulation intensities were determined for responses in an L5 ventral root to

ipsilateral peroneal stimulation and to contralateral peroneal stimulation. Thresholds were also determined for inhibition of ipsilateral responses by contralateral stimulation, and for facilitation of ipsilateral responses by contralateral stimulation.

The effect of different intervals between contralateral and ipsilateral peroneal nerve stimulation on the response recorded from an L5 ventral root was then determined. To control for possible effects of long-term changes in responsiveness of the preparation, we interspersed the stimuli to the two peroneals with that to each peroneal individually. A test sequence for a given interval was of the following form: (1) stimulation of both peroneals, (2) stimulation of the peroneal ipsilateral to recording electrodes alone, (3) stimulation of both peroneals, (4) stimulation of the peroneal contralateral to recording electrodes alone.

This grouping of four sets of stimuli was repeated at least ten times for each test interval. Responses were elicited approximately once per second. All stimuli were at least 5 × threshold required for a response in L5 ventral root following stimulation of the ipsilateral common peroneal nerve. Such a group of four sets of responses is shown in Fig. 1, in which the contralateral–ipsilateral interval is 10 msec.

Response versus interval curves were constructed by comparing the heights of the responses elicited by stimulation of both peroneals to the heights of the responses to ipsilateral peroneal stimulation alone. To evaluate this, the following percentage was calculated:

$$Q = \frac{100}{2} \times \frac{T_1 + T_3}{T_2},$$

where T_1 and T_3 are the heights of the responses to stimulation of both peroneals, occurring before and after the ipsilateral stimulation alone, and T_2 the height of the response to ipsilateral stimulation alone. The mean and the estimated standard deviation of the mean (n = 10 for each interval measured for the conditioning curve) were calculated to construct these curves.

When sufficient data had been collected to construct a response versus interval curve, both peroneals were stimulated repetitively at frequencies near 25 Hz for at least 10 sec. The bouts of stimulation on both sides at exactly the same frequency were preceded and followed by bouts in which the stimuli were delivered to the two sides at different frequencies. In these cases the beat frequency was 1 Hz.

The height of each response was measured on the filmed records. These data were analysed by autocorrelation techniques to determine any periodicity within a given response train, and by cross-correlation to determine the relationship of the responses on opposite sides.

In addition, when there was a beat frequency between the two stimulations, responses were averaged according to their temporal relationship to the occurrence of simultaneous stimulation on both sides. Thus a response profile by phase of stimulation was obtained. When there was no beat frequency (both sides stimulated at the same frequency) this response profile was constructed by assuming a beat frequency of 1 Hz. All these computations were performed on an IBM 7094/7040 Direct Couple System.

RESULTS

A typical curve showing the effect of the interval between ispilateral and contralateral peroneal nerve stimulation on an L5 ventral root response is shown in Fig. 2. In general, a marked facilitation was observed for intervals of 0–10 msec, and, in some cases, facilitation was observed even when the contralateral stimulus occurred a msec or so after the ipsilateral stimulus. Figure 3 shows a curve in which facilitation occurred even when the contralateral stimulus was delivered 2 msec *following* the ipsilateral stimulus.

Inhibition occurred from about 30 msec to more than 400 msec following the contralateral stimulus.

The latency of the responses in L5 ventral root to threshold ipsilateral common peroneal stimulation was usually about 8 msec. The latency of response to threshold contralateral peroneal stimulation was 9–10 msec, and the amplitude tended to be smaller than that elicited by threshold

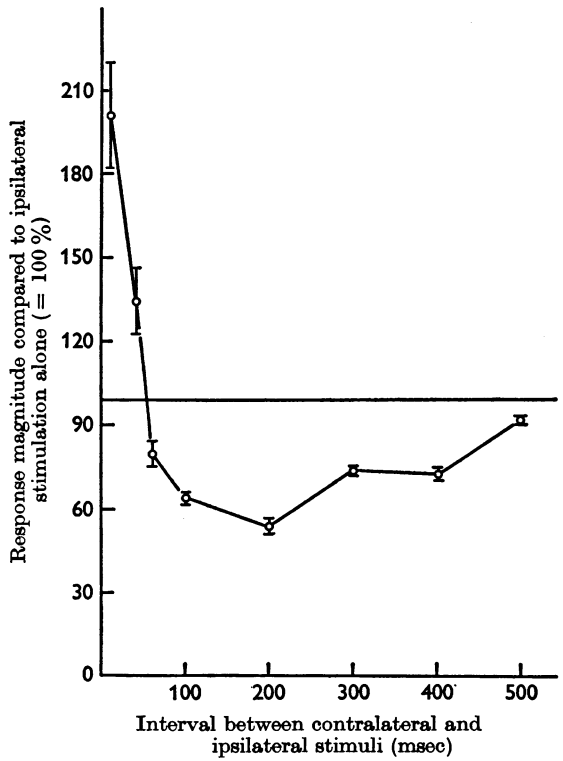

Fig. 2. Response versus interval curve: the responses were recorded from L5 ventral root. The mean size of the responses to ipsilateral stimulation alone is defined as 100 %. Each point represents an analysis of ten sets of responses. Capped vertical lines through each point depict the estimated standard deviations of the means.

ipsilateral stimulation. The thresholds for a bilateral response to stimulation of one peroneal nerve, and for inhibition of the ipsilateral response by prior stimulation of the contralateral peroneal nerve were approximately equal. This threshold was about the same as that at which it was possible to record a cord dorsum response from stimulation of the peroneal nerve. However, the facilitation threshold was generally higher than the threshold for inhibition.

When one side was stimulated repetitively at 25 Hz and the other side at 24 Hz, a marked waxing and waning of the responses was observed (Figs. 4 and 5). The autocorrelogram of these responses revealed marked periodicity at the beat frequency of 1 Hz (Fig. 6). Cross-correlating the responses of one side with those of the other (Fig. 7) showed that the oscillations on the two sides occurred out of phase. However, when the two

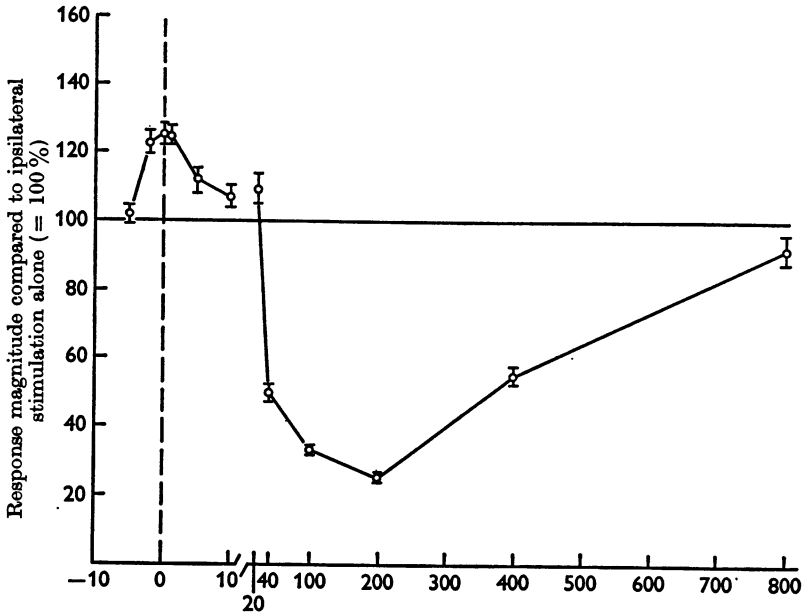

Fig. 3. Data similar to that depicted in Fig. 2, but from another cat. Note the marked facilitation produced when the contralateral stimulation was delivered two msec following ipsilateral stimulation (interval = −2 msec).

peroneals were both stimulated at 25 Hz (Fig. 8) the size of the responses first declined, then increased, but did not show any periodicity (Fig. 9). An autocorrelogram showed no evidence of rhythmicity (Fig. 10). A cross-correlogram of the two sides also showed no evidence of rhythmicity.

During repetitive stimulation of the two peroneals at different frequencies, the timing between the pulses is continually changing. Any particular interval between right and left stimulation occurs once in each beat cycle. The effect of these changes on the responses can be determined by averaging those responses which occurred when the stimulating pulses were separated by a given interval. A graph of these averages is shown in Fig. 11. The shape, however, is not what would be expected from the responses versus interval curves of Figs. 2 and 3, in which maximum

responses occurred when the contralateral stimulation pulse was delivered 0–10 msec *before* the ipsilateral pulse. In the curves of which Fig. 11 is an example, the maximum response was quite consistently found to occur when the contralateral pulse arrived about 30 msec before the ipsilateral pulse. The curves of Figs. 2 and 3 were taken with stimuli delivered at 1 Hz,

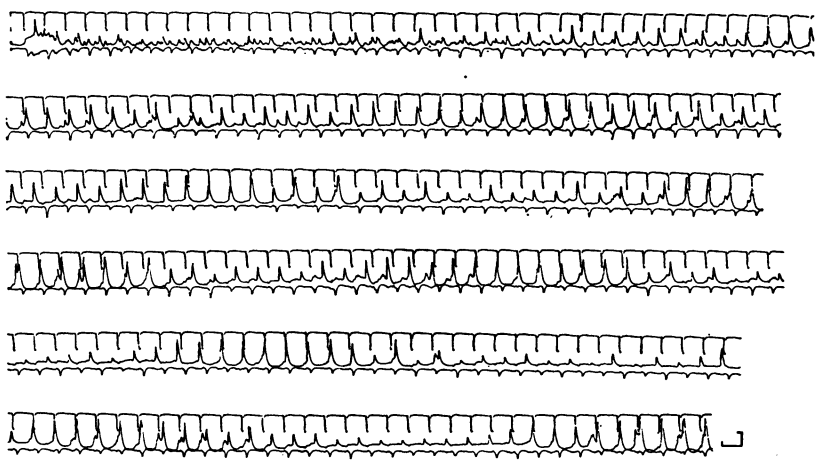

Fig. 4. The two lower traces are a continuous record of the responses recorded from the right and left L 5 ventral roots during 25 Hz stimulation of one common peroneal and 24 Hz stimulation of the other common peroneal. The top trace was recorded from a monopolar electrode near the entry zone of dorsal root L 7, ipsilateral to electrodes recording bottom trace. Electrical stimuli were 3 msec/pulse. Responses were filtered at both high and low frequencies, to $\frac{1}{2}$ amplitude at 0·15 Hz at the low frequency end of the spectrum and to $\frac{1}{2}$ amplitude at 100 Hz at the high frequency end. Horizontal calibration: 40 msec. Vertical calibration: top trace 1·5 mV; middle trace 150 μV; bottom trace 300 μV. Traces retouched. Data in this and all subsequent Figs. are taken from the cat whose conditioning curve is shown in Fig. 3.

whereas the 'stepping curves' such as Fig. 11 were taken from responses elicited during 25 Hz stimulation. This discrepancy in the timing of the peaks must be attributed to an altered time course of facilitation and inhibition at these higher stimulus frequencies. The origin of this altered time course is unknown.

As expected, a similar analysis of the data during simultaneous 25 Hz stimulation of both peroneals, averaged by assuming a 1 Hz beat frequency, showed no evidence of 1 Hz rhythmicity (Fig. 12).

DISCUSSION

We have demonstrated that the motor response in ventral root L 5 can vary rhythmically at the beat frequency of the stimulators. Since the

vastocrureus muscles cannot contract fast enough to follow the fundamental frequency of the responses (25 Hz), its motions, if unparalysed, would represent some sort of a time-average of the motoneuronal responses. This time-average should also vary at the best frequency of the stimulators, as is the case in Fig. 5. The peak in this time-average can be called a step. What should the phase of these steps be with respect to the beat cycle of the stimulators? We should expect the step to occur when the timing of the pulses to both peroneals elicits maximally facilitated responses.

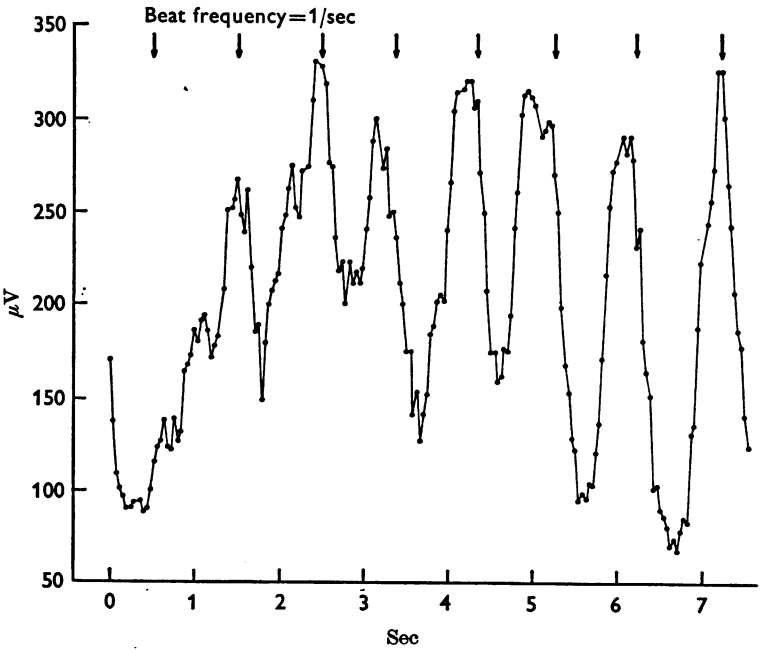

Fig. 5. Mean heights of responses recorded from an L 5 ventral root when the contralateral common peroneal was stimulated at 25 Hz, the ipsilateral at 24 Hz, as shown in middle trace of Fig. 4. Each point is the average of four consecutive responses, averaged in sliding blocks. The arrows indicate occurrence of stimulation simultaneously on both sides.

Consider the case where the left peroneal is stimulated every 40 msec (25 Hz) and the right peroneal every 41·67 msec (24 Hz). The interval between the pulses to both peroneals changes by 1·67 msec at each stimulus repetition. Thus, six 'right peroneal' pulses after a synchrony, the right pulse lags the left by 10 msec; eighteen pulses after a synchrony it lags by 30 msec, but is occurring 10 msec before the next left pulse. The 24th pulse to the right peroneal is back in phase, being synchronous with the 25th to the left peroneal. Thus, in a cat where the peak of facilitation is at an interval of 10 msec, we should expect a right leg step near pulse no. 6

and a left leg step near pulse no. 18, on each cycle of twenty-four pulses. In this situation a step should occur every twelve pulses, right leg alternating evenly with the left.

However, if the maximum facilitation is at -2 msec, we should, by the same analysis, expect the left leg to step one pulse after a synchrony and the right leg to step twenty-three pulses after a synchrony or one pulse before the next synchrony. In this case, the steps do not evenly divide the cycle, but occur in this pattern: step, step, pause, step, step, pause, etc.

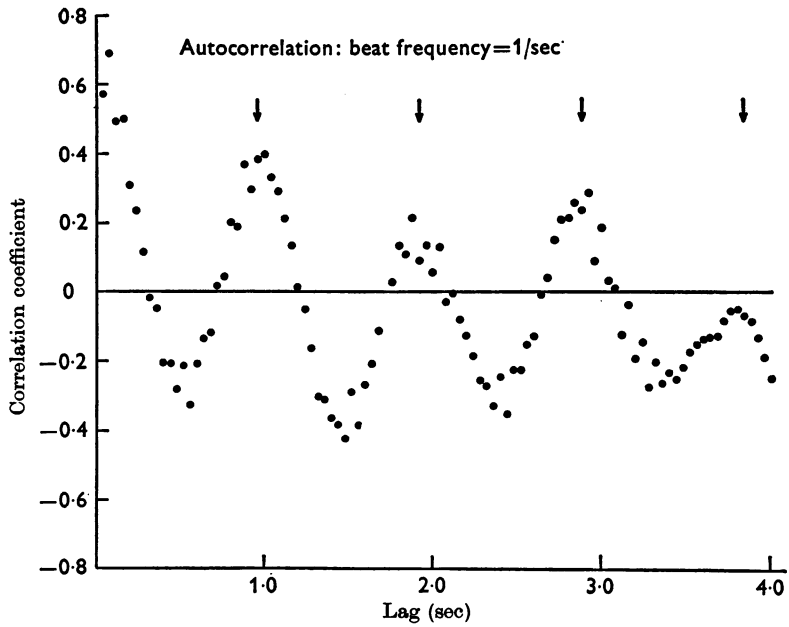

Fig. 6. Autocorrelogram of the responses of middle trace of Fig. 4. This form of averaging brings out repetitive features of the responses. The sinusoidal shape of the correlogram reflects the rhythmic nature of the response variations. The recurrence of correlogram peaks at 1, 2, 3, and 4 sec indicates that peaks and troughs in the responses recurred every second. The stimulator beat frequency was 1 Hz, hence any stimulus configuration recurs at 1 Hz. The arrows mark the lags at which identical stimulus configurations recur. 168 responses were used to compute the correlogram.

This is, in fact, what was seen in most of our preparations. Apparently this was also what Sherrington observed: 'It was not rarely seen that instead of the two phases of the step succeeding each other without pause between them, a brief pause occurred either at end of the relaxation phase or, less often, at end of the contraction phase' (1913*c*).

In some of our preparations, the phases of maximum responses on both sides were the same. In other preparations, the response in one L5 ventral

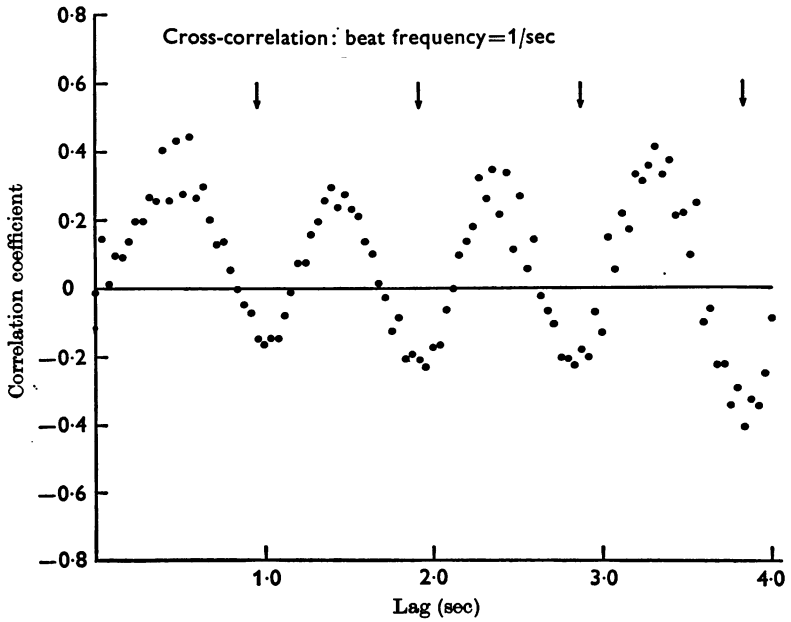

Fig. 7. Cross-correlogram of responses on opposite sides, comparing the height of responses of middle and lower traces of Fig. 4. The occurrence of the first peak at a lag of about 0·5 sec indicates that variations in the magnitude of responses in one L 5 ventral root occurred 0·5 sec after similar variations of the responses in the other L 5 ventral root. This is an example of alternating 'stepping'. The peaks recur at 1 sec intervals, following the beat. Arrows mark lags corresponding to integral numbers of beats.

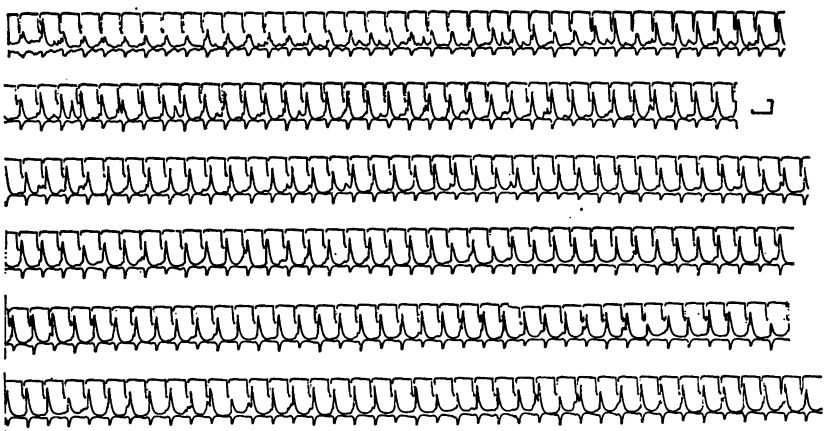

Fig. 8. Identical to Fig. 4 with the exception that stimulation of both common peroneal nerves was at 25 Hz. Other parameters of stimulation and recording calibrations are the same as Fig. 4. Traces retouched.

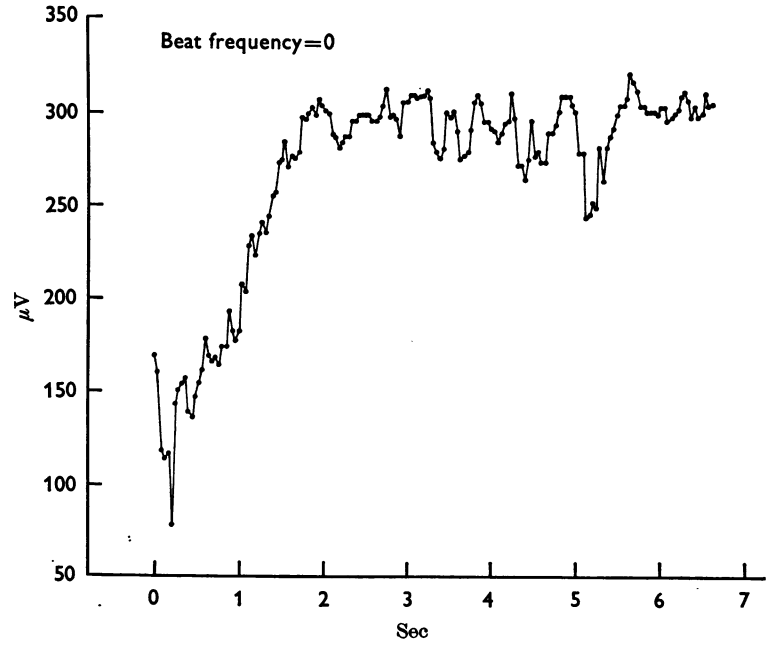

Fig. 9. Same as in Fig. 5, except that both common peroneals were stimulated at 25 Hz.

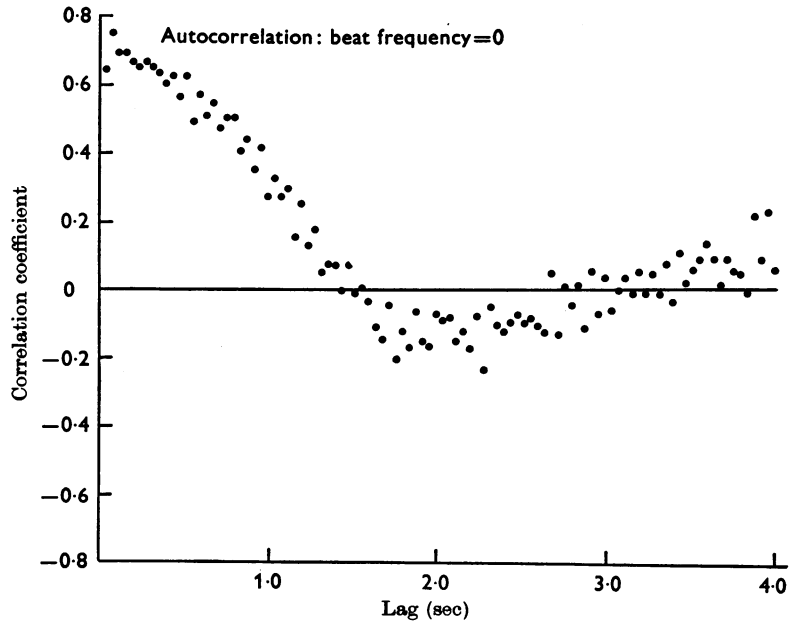

Fig. 10. Autocorrelogram of the height of responses shown in the middle trace of Fig. 8. Note the lack of rhythmicity indicating an absence of rhythmicity in the responses.

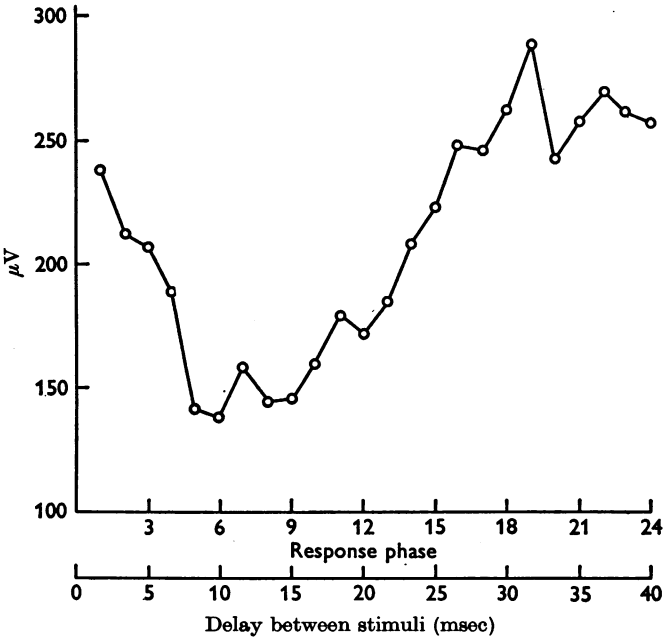

Fig. 11. Average shape of a step. Data taken from middle trace of Fig. 4. The stimulator for the middle trace was set at 24 Hz, the other at 25 Hz. The record was cut into segments one beat (twenty-four responses) long, each segment starting at a point of synchronous stimuli to both legs. Each point in this Figure is the average of the corresponding points in all the segments.

Fig. 12. Data from middle trace of Fig. 8. The stimulators were both set at 25 Hz. The record was cut into segments twenty-four responses long, starting at the first response. Each point in this Fig. is the average of the corresponding points in all the segments.

root waxed and waned, while those in the opposite were small and variable. Sherrington also saw both of these phenomena; he called the first 'galloping' and the latter a 'unilateral rhythmic reaction' (Sherrington, 1913*c*).

These congruences with Sherrington's results strongly suggest that we are working with the same phenomena that Sherrington was. In this same vein, Sherrington noted that the rate of stepping was variable 'from more than two steps per sec to one step in 1·4 sec'. We would attribute this to a change in the beat frequency of his stimulators (the frequency of Sherrington-type inductoria is adjustable by a screw). He also noted that he had 'usually not found it possible to maintain the rhythmic reflex for more than about twenty or thirty steps in succession' (Sherrington, 1913*c*). We have had the same experience, both the response and the facilitation of the response decline after a score or so of 'steps'.

In addition, in control preparations in which all ventral roots were intact, we observed 'stepping' i.e., rhythmical muscular contractions, only when the peroneal nerves were stimulated at slightly different frequencies. This 'stepping' followed the beat. Similarly, Brücke (1922) observed in decerebrate cats that when one sciatic nerve was stimulated at 50 Hz, the other at 51 Hz, the quadriceps muscles contracted rhythmically at 1 Hz following the beat of the stimulators. The direct observation of this 'stepping' with the beat demonstrates that we introduced no fundamental error by recording from L5 ventral roots, which innervate muscles in addition to the vastrocrureus, rather than directly from the vastocrureus muscles themselves.

In order to produce the rhythmical stepping, Sherrington (1913*b*) usually balanced the intensity of stimulation to the peroneals. Although we did not balance our stimulation intensities in exactly the same way that Sherrington did, we did not find any evidence of central rhythmicity over a wide range of intensities. In addition, Sherrington (1913*c*) noted that in the deafferented preparation such as we used, 'the rhythmic reflex was in some experiments obtained by combinations of opposed stimuli in strengths ranging over a long portion of the inductorium scale'.

Finally, the possibility remains that the rhythmicity Sherrington observed might have been related to the fact that the muscles studied were deafferented several weeks before the 'stepping' experiments were performed (Sherrington, 1913*c*). This possibility is rendered less likely by Sherrington's observation of identical 'stepping' in preparations with all afferents intact (Sherrington, 1913*b*).

CONCLUSION

The response versus interval curves of Figs. 2 and 3 demonstrate that the responses in a ventral root on one side are not independent of the timing of stimulus pulses on the other side. The results of repetitive stimulation to the two peroneals at different frequencies, in which we found that rhythmic and alternating responses appeared in the two ventral roots, suggest that Sherrington's 'stepping' may have been due to beating between his stimulators. We found no evidence for central rhythmicity in our preparations. When the peroneals were stimulated at equal frequencies, no rhythmic output was observed.

At this stage we have no way of knowing whether any of the observed phenomena are related to walking as a natural behavioural act, and we certainly cannot say that there is no centrally timed rhythm involved in walking. The strongest conclusion we can make is that Sherrington's apparent demonstration of central rhythmicity in 'stepping' is now open to question.

Thanks are due to Mr Leslie R. V. Kerby, a one time technician of Sir Charles Sherrington, who helped us perform the decerebrations, and to Walter Gezari and Elizabeth Clark for technical assistance.

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