CORTICAL PROJECTION OF IMPULSES IN THE INTER-OSSEOUS NERVE OF THE CAT'S HIND LIMB

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The 'interosseous' branch of the nerve supplying flexor digitorum longus in the cat has recently been shown to contain myelinated afferent fibres supplying several different types of receptor in the deep tissues of the leg (Hunt & McIntyre, 1960). The two most frequently encountered were slowly-adapting 'tension' receptors, and rapidly-adapting receptors of remarkable sensitivity to vibration-since shown to be Pacinian corpuscles (Hunt, 1961), of which there is a dense cluster closely applied to the tibial periosteum and interosseous membrane just above the ankle joint. The author observed some years ago that electrical stimulation of the interosseous nerve yields responses in the receiving areas of the cerebral cortex, but at the time nothing was known of the receptor types served by this small afferent nerve. The present investigation was undertaken with the object of determining which of the interosseous receptor types is linked with the cerebral cortex, and by what pathways. It will be shown that the Pacinian corpuscles are the ones principally concerned, and that their impulses travel by way of the dorsal column-lemniscal system.

METHODS

The experimental animals were cats anaesthetized with pentobarbitone (Sagatal; May & Baker), given intraperitoneally in initial dosage of 30 mg/kg, followed by supplementary doses intraperitoneally or intravenously as required. In a few experiments decerebration was carried out after the initial dose of pentobarbitone, after which no further anaesthetic was given. The interosseous nerve was dissected in continuity under paraffin and identified by the absence of muscle responses upon stimulating it, together with the characteristic showers of vibration-receptor impulses recorded from it upon tapping the base plate or uprights carrying the animal. In experiments involving natural stimulation the leg and hip were extensively denervated with the object of leaving intact only the interosseous nerve. Exposure of the cerebral cortex was carried out in the usual way, and the spinal cord laid bare by laminectomy as described in previous publications (Lloyd & McIntyre, 1950; Mark & Steiner, 1958). Warmed paraffin pools covered all exposed tissues. Conventional stimulating and recording equipment was used, with the addition of an integrator (Hisey & Perl, 1958).

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and a counter-timer (Computer Measurements Corporation model 226 A) for measuring latencies, especially when volleys were fired antidromically into the leg by stimulation of the dorsal column. Input volleys in the interosseous nerve were monitored when necessary by electrodes placed centrally to the stimulating pair, in the manner described by Mark & Steiner (1958). An electromagnetic tapping device triggered from the sweep was used in some experiments; and in others tuning forks, or a Goodman vibrator (model V47) driven by a sine-wave oscillator and power stage, were used to elicit vibration of the foot or leg. Tubocurarine (Tubarine, Burroughs Wellcome) or gallamine triethyliodide (Flaxedil, American Cyanamid) was used to prevent muscle movement in some experiments, the animal being either decerebrate or anaesthetized.

RESULTS

Cortical evoked potentials

Responsive areas. Stimulation of the interosseous nerve elicited in the cerebral cortex responses of the well-known configuration for evoked potentials, a sharp surface-positivity followed by a more variable negative phase. As with cutaneous nerve volleys, the potentials were usually detectable in both the classical receiving zones for the hind limb in the contralateral cerebral hemisphere, somatic receiving areas I and II



Fig. 1. Cortical responses to electrical stimulation of the interosseous branch of flexor digitorum longus nerves. A, recorded from contralateral area I; B, from contralateral area II. Potential calibration, 100 μ V. Time marker, 10 msec.

(Woolsey, 1947). However, unlike responses to cutaneous volleys, potentials evoked by interosseous nerve stimulation were larger in amplitude and more constant in form and latency in area II than in area I. Figure 1 gives an example of the responses to interosseous nerve stimulation recorded from the two contralateral receiving zones in the same animal. The area I response in this experiment showed much less positivity and a relatively more prominent negative phase than that recorded from area II, the amplitude of which is nearly 3.5 times greater than that of the area I potential. In some preparations it was difficult to find any response in area I as a result of an interosseous nerve volley which set up a large response in area II, this despite the fact that cutaneous nerve stimulation elicited prominent potentials in both zones. For this reason attention has been focused in this investigation mainly upon cortical responses recorded from somatic area II.

The second receiving area of each hemisphere is known to receive projections from both sides of the body (Woolsey, 1947) and the interosseous nerves are no exception in that each was found to be bilaterally represented in this zone. However, the response to an ipsilateral interosseous nerve volley was much smaller than that evoked from the contralateral nerve. The region of area II responding to volleys in the nerves of the two hind limbs appeared to be the same.



Fig. 2. Responses from the same cortical point in contralateral area II set up by stimulating different nerves of the hind limb: A, interosseous nerve; B, sural nerve; C, posterior knee joint nerve. Instants of stimulation marked by white dots above stimulus artifacts. Potential calibration, 200 μ V. Time marker, 10 msec.

The maximal focus in area II for contralateral interosseous volleys was adjacent to points yielding the biggest deflexions for other nerves of the hind limb, such as the sural. Usually the sural nerve focus was about 0.5-1.0 mm lateral and caudal to the optimal point for interosseous nerve volleys, but occasionally the foci seemed identical, and in any case overlap was considerable. It appeared in some experiments that the region yielding interosseous nerve responses was rather more extensive than that for the sural, especially up towards the mid line, but systematic exploration of the whole hemisphere was not carried out as a routine. Figure 2 gives some idea of the relative amplitudes of the potentials evoked in area II by volleys in different nerves of the hind limb in the same preparation. A, B and C show respectively the responses to stimulation of the contralateral interosseous, sural and posterior knee-joint nerves, the recordings in this case all being made from the same point in area II, which appeared to be a common maximal focus. Amplitude of the response to interosseous nerve stimulation has occasionally been observed to exceed that of the potential set up from the sural nerve, as illustrated by records A and C of Fig. 3. However, records A and B of Fig. 2 represent the more usual finding.



Fig. 3. Responses, recorded from contralateral area II, to stimulation of the interosseous and sural nerves before and after infliction of a lesion on the dorsal columns: A, interosseous nerve, and C, sural nerve; stimulation with the cord intact; B and D, effects of identical stimulation of the same nerves after interruption of the dorsal columns in the 9th thoracic segment. Moments of stimulation marked by white dots above the tracings. All records taken at the same amplification. Time marker, 10 msec.

Latency and unresponsive period. In area II latency of the potential set up by contralateral interosseous nerve stimulation varied in different preparations from 9 to 13 msec. In most instances this latency exceeded by a few milliseconds that for a response to stimulation of a cutaneous nerve in the same limb with a conducting path of similar length. Latency of the response to a volley in the ipsilateral interosseous nerve was also a few milliseconds longer than for the potential evoked by stimulating its contralateral fellow. As already noted, latency of the response in contralateral area I, when responses were detectable, was more variable, and usually of longer duration than that for contralateral area II. For example, in the experiment of Fig. 1, latency of the potential in area I (A) was about 15 msec, as compared with 10.5 msec for the area II response (B).

When two successive volleys were set up in the interosseous nerve, no cortical response to the second could be seen at intervals shorter than

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40-60 msec. At longer intervals the second volley evoked a smaller response, and as in the case of cutaneous nerve stimulation (Marshall, Woolsey & Bard, 1941), recovery from this subnormality was not complete until 150-200 msec after the first volley. Somewhat similar results were obtained if the successive responses in area II were set up by stimulating first the interosseous nerve of one side, followed by stimulation of its contralateral fellow. Complete occlusion of the small potential evoked by ipsilateral nerve stimulation took place when the contralateral volley led, but only partial occlusion of the larger contralateral response occurred when the volleys arrived in reverse order. Thus many of the cortical elements taking part in the response can be activated from both hind limbs. Similar interaction between the cortical responses to interosseous and cutaneous nerve volleys was also observed.

Spinal pathways

Cortical responses to volleys in the larger myelinated afferent fibres of cutaneous nerves in the hind limb appear to travel by two principal routes, the dorsal column-lemniscal system, and a slightly more rapid pathway in the lateral column on the side of stimulation (Mark & Steiner, 1958). In the present study some experiments have been carried out to determine the pathways traversed by impulses of interosseous nerve origin en route to the cerebral cortex.

Effects of spinal lesions. An obvious method of approach is to examine the effect upon the evoked cortical potentials of making partial lesions of the spinal cord, and this has been done in seven experiments of this series. Observations have been restricted to the effects of lesions on the responses in contralateral area II. Figure 3 shows cortical responses to stimulation of the interosseous nerve (A and B) and sural nerve (C and D). Those on the left of the figure (A and C) were recorded with the thoracic cord exposed but intact; B and D were photographed after a lesion had been made in the dorsal column at the 9th thoracic segment, subsequently shown by serial sections to have interrupted the whole of the medial portions of both dorsal columns down to the grey commissure. The response to interosseous nerve stimulation was abolished, whereas the sural volley still evoked a response, albeit of reduced amplitude, of the same latency as before the lesion; this has been shown to depend upon the fast lateral column pathway (Mark & Steiner, 1958). A disadvantage of such experiments with acute lesions is that compression or ischaemic damage may be inflicted on nearby cord regions which it is intended to spare; however, the persistence in this and other experiments of a substantial response to sural nerve stimulation after interruption of the dorsal column shows that conduction in the lateral column cannot have been seriously impaired. Stimulation

of the interosseous nerve at delta strength in one experiment elicited a small cortical potential of greatly increased latency even after infliction upon the dorsal column of a lesion which prevented all response to a weaker shock engaging only alpha fibres.

Section of the lateral and ventral columns on the side opposite to the nerve stimulated appeared to have no effect on the cortical response to an interosseous nerve volley. The more drastic procedure of interrupting the lateral and ventral columns of both sides, leaving the dorsal columns apparently intact, still did not abolish the response or alter its latency of onset, but did lead to a slight reduction in its amplitude. The diminution could have been a result of some unintentional impairment of dorsalcolumn conduction associated with the infliction of such extensive trauma to the spinal cord. Cortical responses to cutaneous nerve volleys are considerably reduced by such lesions of the cord, and their latency of onset is slightly increased, through loss of the lateral column path (Mark & Steiner, 1958). However, the fibres of the interosseous nerve with cortical projection to area II, at least those of lower threshold, appear from these experiments to exert their action mainly if not entirely through the dorsal column-lemniscal route.

Antidromic dorsal column volleys. That a considerable number of interosseous nerve fibres do in fact ascend the dorsal column can be shown directly by stimulating it at various levels while recording antidromically conducted impulses in the interosseous nerve itself, as in earlier experiments on the projection of muscle afferent fibres (Lloyd & McIntyre, 1950). Figure 4 gives an example of the discharge backfired into the interosseous nerve by stimulation of the dorsal column near its rostral termination. Most of this substantial but dispersed volley consists of impulses set up directly in primary afferent fibres by the stimulus; a small part of the later responses represents the 'dorsal-column relay' of Hursh (1940), the extent of which can be gauged by comparing the responses set up by two successive stimuli. The total amount of directly elicited activity reaching the interosseous nerve is, however, considerably less than that which appears when the stimulus is applied in the lumbar segments or to the L6 or L7 dorsal roots, showing that many fibres of the interosseous nerve do not ascend the whole length of the dorsal column. In view of the several receptor types known to be served by fibres in the interosseous nerve (Hunt & McIntyre, 1960), it is of particular interest to attempt identification of those with access to the cerebral cortex by way of the dorsal columnlemniscal system.

Identification of receptors

Fibres in the interosseous nerve of calculated diameter exceeding 9 μ have been subdivided into three groups on the basis of receptor behaviour

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(Hunt & McIntyre, 1960). The largest fibres, attaining diameters up to 22μ , supply slowly-adapting 'tension' receptors; fibres of medium diameter (9–16 μ) serve rapidly-adapting sense organs of two kinds, one type discharging briefly to a sharp, jarring stimulus and not to vibration ('tap' receptors), the other exquisitely sensitive to very slight mechanical shocks



Fig. 4. Antidromic volley recorded from the interosseous nerve in the leg and initiated by stimulation with fine steel needles, insulated except for the tips, inserted into the dorsal columns in the 1st cervical segment. Time marker, 1 msec.

and to vibratory stimuli. Nothing is yet known about the receptors supplied by fibres of the delta group, of which there are many in the nerve (I. A. Boyd, personal communication). Electron micrographs (kindly prepared by Dr K. Uchizono) also show the presence of numerous nonmyelinated fibres, some of which are probably afferent.

Three approaches have been adopted in attempting to identify the receptors with access to the cerebral cortex through the fasciculus gracilis and medial lemniscus. The first is to compare the threshold of the nerve to stimulation with the threshold for the appearance of a cortical response, and this has been done by constructing input-output curves. Secondly, the conduction velocity of antidromically conducted impulses, set up by stimulating the dorsal column near its rostral termination (Fig. 4), has been examined in the interosseous nerve. The third method was to observe the type of natural stimulus which sets up cortical responses by way of interosseous nerve fibres.

Input-output curves. By using finely graded strengths of stimulation and measuring the amplitude of cortical response at each input level, some idea can be gained as to the threshold of the executant fibres in relation to that of the most excitable fibres of the whole nerve, in addition to information about the properties of the synaptic relays in the pathway. An inputoutput curve which rises very steeply from zero obviously means that impulses in the fibres of lowest threshold are effective in eliciting some cortical output, and this in fact is the kind of relationship found by Mark & Steiner (1958) for cutaneous nerve volleys. With interosseous nerve fibres providing the input, curves of similar shape were obtained, but some differences were apparent. Usually quite small volleys elicited some cortical output, and with increasing strength of stimulation the amplitude of the evoked potential rose very steeply and, as with cutaneous nerves, tended to reach a plateau with the input volley only 30-50 % of maximum. However, unlike curves for cutaneous nerves, the very smallest volleys were ineffective, as shown by the left-hand curve (filled circles) in Fig. 5, in which no output was detectable unless the input exceeded 3 % of maximum. Such a curve suggests that the fibres of very lowest threshold (supplying tension receptors in this instance) are not concerned, and is consistent with the view that the group of fibres of slightly higher threshold (supplying tap or vibration receptors) are the ones responsible for cortical effects by way of a pathway with very powerful synaptic linkages of the usual afferent type, with a high safety factor for transmission and minimal need of summation (McIntyre & Mark, 1960).

However, the relationship in some preparations was different, a larger volley being necessary to secure a cortical response, so displacing the curve to the right. The curve denoted by open circles in Fig. 5 is an example, and it can be seen that it also rises less steeply and shows less of a plateau than does the other curve. The response nevertheless approaches 80 % of its maximum with volleys only half-maximal. Such a curve could mean that the threshold of fibres constituting the effective input in these instances is higher than usual with respect to others in the nerve, their recruitment to the input volley thus being shifted to the right on the abscissa. Alternatively, its displacement and change in shape could be the result of a relatively depressed state of the synapses on the pathway, so that more summation is required in these cases to secure transmission than

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is usual in afferent synapses. The second of these suggestions is regarded as the more likely explanation, because in one experiment with the inputoutput curve showing this displacement to the right, the delivery of two small volleys in rapid succession, each alone subthreshold for cortical response, was observed to evoke a small potential. Furthermore, in another preparation, the input-output relationship changed during the



Fig. 5. Input-output curves for cortical response to stimulation of the interosseous nerve. Abscissa, amplitude of volley recorded diphasically from the interosseous nerve central to the stimulating electrodes and expressed as percentage of maximum. Ordinate, magnitude of evoked cortical surface-positive wave also expressed as percentage of maximum. Each point the average of nine or more observations. Filled and open circles show the relationship obtained in two different preparations.

course of the experiment from one in which a volley about 30% of maximum was required to elicit a response to one in which much smaller single volleys were effective. It may be that differences in depth of anaesthesia are at least in part responsible for the variations observed.

Conduction velocity of antidromic impulses. If the largest fibres in the interosseous nerve, supplying 'tension' receptors, were included amongst the ones which transmit impulses by the dorsal column to the cerebral cortex, stimulation of their central terminations in the nucleus gracilis should lead to antidromic impulses travelling in the leg at rates exceeding 100 m/sec. In six experiments a sufficient length of the interosseous nerve was dissected to permit recording from it at three different points, so making it possible to determine the conduction velocity of impulses travelling along it. Antidromic volleys elicited by stimulation of the L7

dorsal root, or the dorsal column in nearby segments, travelled as expected at velocities between 101 and 120 (average 109) m/sec. However, the conduction velocity of antidromic volleys such as the one illustrated in Fig. 4, set up by stimulating the dorsal columns high up, in no instance attained 100 m/sec, the range being 54-83 (average 71) m/sec. Figure 6 illustrates the difference observed in one of these experiments, latency (ordinate) being plotted against distance along the nerve (abscissa). The line drawn through the upper three points (filled circles) has a slope of



Fig. 6. Plots of latency against conduction distance along the interosseous nerve of the initial deflexion of antidromic volleys set up by stimulation of primary afferent fibres. Abscissa, distance in millimetres distal to the most proximal of four electrodes on the interosseous nerve, the most distal being on the cut end. Ordinate, time from the instant of stimulation (note discontinuity). Filled circles, latency of volley initiated in the first cervical segment and recorded from three points along the nerve. Open circles, latency of volley recorded from the same three points but set up by stimulation of the L7 dorsal root.

64 m/sec, and shows the conduction velocity of impulses backfired from the first cervical segment. The lower three points show the latencies at the same three recording stations of a volley set up in the L7 dorsal root; the slope of this line is 114 m/sec. There is considerable inaccuracy in this method because of the necessarily short conduction distances over which to measure latency increments. Also, measurements have been limited to the wave-front, or to the first two or three deflexions if characteristic enough to be recognized clearly, so that impulses of more rapid conduction velocity in the leg might be submerged in the later part of the discharge. Nevertheless, the results do suggest that fibres in the interosseous nerve of conduction velocity greater than about 85 m/sec do not ascend in the fasciculus gracilis. This is consistent with the notion that the fibres which do so belong to the 'tap' or vibration category.

Natural stimulation. Of the receptors supplied by the larger myelinated fibres of the interosseous nerve, the vibration-sensitive Pacinian corpuscles have such low thresholds that they can be readily made to discharge by extremely small mechanical changes, provided they are sudden enough



Fig. 7. Potentials recorded from the same point in contralateral area II and evoked either by electrical stimulation of the interosseous nerve or by a very weak mechanical pulse triggered from the sweep and applied to the lateral malleolus. A, response to electrical stimulation; B, to the mechanical pulse. In C the mechanical pulse is followed by the same electrical stimulation as in A. In D the electrical stimulus precedes the mechanical pulse. White dots mark the instants of stimulation. Time marker, 10 msec.

(Hunt, 1961). Such weak stimuli are quite inadequate to fire either the 'tension' or the 'tap' receptors, of which the latter may in fact be simply high-threshold Pacinian corpuscles. Very weak mechanical pulses applied to a foot or leg denervated except for the interosseous nerve are indeed effective in eliciting prominent cortical responses of very similar form to those set up by electrical stimulation of the nerve. The records in Fig. 7 illustrate this, A being evoked by electrical stimulation, B by a brief and very weak mechanical pulse applied to the lateral malleolus. Another stimulus which was also effective in such a preparation was very light brushing of the hairs over the same region, a manoeuvre known to set up impulses in the most sensitive deep Pacinian corpuscles in the interosseous

region (Hunt & McIntyre, 1960). C and D (Fig. 7) show the additional point that the response to either mechanical or electrical stimulation is subnormal if it follows by less than 150 msec or so a potential set up by the other method; complete occlusion takes place at intervals of less than about 60 msec.

In such experiments it may be necessary to isolate mechanically the skeletal structures of the leg below the knee in order to prevent the stimulus spreading to other receptors of very low mechanical threshold,



Fig. 8. Responses of the same point in contralateral area II to stimulation of interosseous receptors or nerve. A shows the response to a weak mechanical pulse applied to the lateral malleolus with the nerve intact. In B the same pulse was applied at the same instant during the sweep, but after severing the nerve. Cshows the response to electrical stimulation of the central end of the cut nerve. As in other figures, white dots mark the instants of stimulation. Leg and foot in this preparation largely isolated mechanically by removal of a section of femur and suspension from a mechanically insulated stand. Time marker, 10 msec.

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presumably also Pacinian corpuscles, in other parts of the body. This can be done by removing a section of the femur and supporting the foot and leg from a stand insulated by sponge rubber from the main base plate carrying the animal. Figure 8 consists of records obtained from such a preparation, and demonstrates that the cortical response to a weak mechanical pulse applied to the malleolus does indeed depend upon stimulation of receptors with fibres running in the interosseous nerve. A was recorded before, and B immediately after, cutting the interosseous nerve, the same mechanical pulse being applied where indicated in each case. That the abolition of response in B was really the result of interruption of nerve fibres and not of fortuitous failure of the cortical mechanisms or central pathways is proved by the large response still elicited by stimulation of the central end of the severed nerve, as shown in C. There can thus be no doubt, in view of the properties of the various receptors concerned, that the cortical responses to weak mechanical pulses applied in this way are brought about by impulses arising in Pacinian corpuscles, and that at least the major part of the response to electrical stimulation of the interosseous nerve is also a result of impulses set up in the fibres serving these receptors.

DISCUSSION

The most striking feature of the cortical responses evoked in area II by stimulating the interosseous nerve is their large amplitude in relation to the small size of the nerve. Similarly prominent responses appear when small joint nerves are stimulated (Skoglund, 1956), as seen in Fig. 2, which also shows for comparison a response to sural nerve stimulation. The relatively large potentials elicited by volleys in these small deep nerves suggest that the afferent impulses normally traversing them must constitute information of considerable importance to activities and adjustments mediated by higher levels.

In view of the properties of the receptors supplied by the interosseous nerve and the type of stimulus effective in setting up cortical responses, there can be little doubt that much of the potential evoked by stimulating the nerve results from the engagement of fibres belonging to Pacinian corpuscles. Presumably the responses studied in the present work represent a particular example of those described by Mountcastle, Covian & Harrison (1952) and Mountcastle & Powell (1959), whose experiments demonstrated the effectiveness of very weak mechanical stimulation of deep structures in eliciting cortical potentials. Their responses were probably also largely brought about by impulses from Pacinian corpuscles. It seems very likely that impulses from these receptors located in many different regions of the body, including the mesentery (Amassian, 1951; Downman, 1951), not only fulfil proprioceptive function, contributing

information about active bodily movements, but in addition serve as detectors of very slight passive movements of suitable frequency characteristics, such as ground-borne vibrations. For such seismographic function the corpuscles supplied by the interosseous nerve would, in the standing or crouching animal, be very favourably placed for responding to ground tremors transmitted through skeletal structures of the foot. Similar arrangements probably obtain in the forelimb (Skoglund, 1960; Hunt, personal communication). When the animal's belly is in contact with the ground, mesenteric Pacinian corpuscles might also respond to such vibrations transmitted as pressure waves through the abdominal contents. Such a system could act as a device for giving warning of the approach of danger, or as a means of helping to locate moving prey. It is interesting that the cortical potentials observed by Mountcastle et al. (1952) and in this work tended to spread from area II into regions also receiving projections from vestibular or auditory receptors.

No conclusions can be drawn from these experiments as to the interosseous receptor types and fibres responsible for the smaller and less constant responses in area I, but the impression was gained that the potentials in this region depended more on the input of impulses in the smaller fibres of the nerve. Impulses in fibres of the delta group appear to have access both to areas I and II, probably by pathways not involving the dorsal column, and may subserve nociceptive function. The possibility that the group of fastest fibres, serving 'tension' receptors, also have cortical projection cannot be rigidly excluded by these experiments. However, the input-output relation (Fig. 5) weighs against this, and they do not appear to enter the dorsal column-lemniscal pathway. Should the 'tension' receptors prove simply to be unusually-sited tendon organs, as suggested by Barker (1962), they would presumably have the same central projection as other Group I fibres of this type, which does not appear to include access to the cerebral cortex by simple routes (Mountcastle et al. 1952; McIntyre, 1953). The findings in this investigation are consistent with this interpretation of the nature of the 'tension' receptors.

SUMMARY

1. Stimulation of the interosseous branch of the nerves of flexor digitorum longus sets up potentials in the cerebral cortex, especially contralateral area II. Responses are smaller and more variable in contralateral area I and ipsilateral area II.

2. The pathway for the major part of the response in contralateral area II is by way of the dorsal column-lemniscal route. Other pathways to the cortex may be available for impulses in delta fibres of the interosseous nerve, possibly nociceptive in function.

3. Impulses conducting antidromically from high up in the dorsal column travel in the interosseous nerve at velocities of less than 85 m/sec, probably in fibres belonging to the group of Pacinian corpuscles supplied by the nerve.

4. Stimuli known to cause firing of the most excitable of these Pacinian corpuscles elicit prominent cortical responses especially in contralateral area II.

5. It is concluded that the Pacinian corpuscles are the principal receptors served by the larger fibres of the interosseous nerve with cortical projection, and that one of their functions may be the detection of ground-borne vibration.

6. The 'tension' receptors (possibly aberrant tendon organs) supplied by the group of largest fibres in the interosseous nerve do not appear to have cortical projection.

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