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CONVERGENCE IN A THERMAL AFFERENT PATHWAY IN THE RAT

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SUMMARY

1. In anaesthetized rats, unit activity was recorded in the afferent somatosensory pathway leading from the scrotum. Recording sites were in the dorsal horn near the entry zone of the scrotal nerve, in the ventrobasal complex of the thalamus and in the somatosensory (SI) cortex. During recording, the temperatures of the left and right sides of the scrotum were varied independently.

2. Almost all (64/67) the units in dorsal horn, thalamus and cortex responding specifically to scrotal temperature were equally affected by temperature changes on either side of the scrotum. The receptive fields of these units were bilateral and large, implying a massive convergence of fibres from thermoreceptors on to each central unit. In contrast, mechanosensitive units responded only to unilateral stimulation.

3. As a consequence of the convergence in the thermal pathway, the firing rate of each central unit was a function of an additive combination, often simply the sum, of the temperatures of the two sides of the scrotum.

4. The relationship between firing rate and the temperature of one side of the scrotum was sigmoid, the position, but not the shape, of the curve depending on the temperature at which the opposite side was maintained. An increase in the maintained temperature shifted the sigmoid response curve towards lower temperatures and vice versa.

5. The convergence which this pathway exhibits would be well suited to integration of the temperature of the scrotal skin, but not to spatial discrimination.

INTRODUCTION

This paper is concerned with the integration in afferent neural pathways of information about skin temperature. The work stems from previous observations which showed that neurones in the pathway leading from the warm and cold receptors in the rat's scrotum behave very differently from the receptors themselves (Hellon & Misra, 1973*a*, *b*; Hellon, Misra &

Provins, 1973; Hellon, Hensel & Schäfer, 1975). This contrast is illustrated in Fig. 1 which shows on the same axes the response curves for a typical warm receptor and for a typical thalamic unit excited specifically by scrotal warming. The receptor response follows a bell-shaped curve covering a temperature span of about 15° C. The thalamic unit response, however, follows a steep sigmoid curve. Its firing rate changes with scrotal temperature only over a range of 1 or 2° C; outside this range the unit is in a state

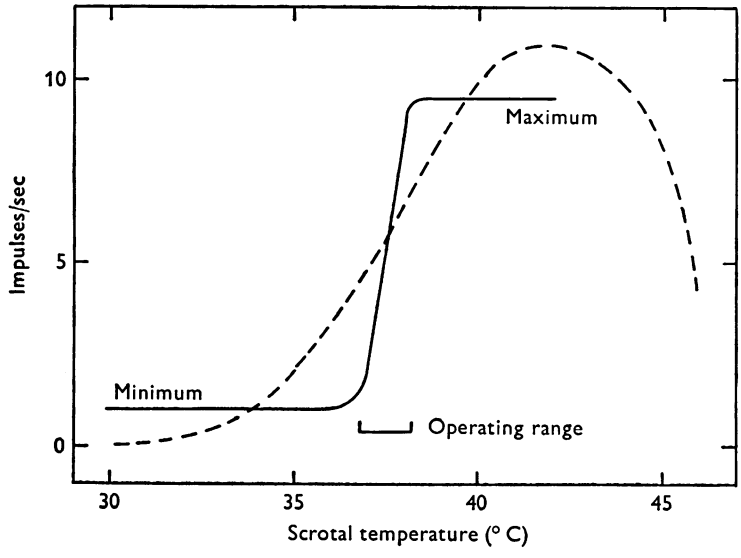

Fig. 1. Comparison between the static response of warm receptors in the rat scrotum (dashed line, taken from Hellon *et al.* 1975) and the response of a thalamic neurone (continuous line, taken from Hellon & Misra, 1973*b*) during changes in scrotal temperature. On the thalamic curve the minimum and maximum firing rates of the neurone and also the 'operating range' are marked.

of either high or low activity. Also shown in Fig. 1 is the terminology which will be used to describe various features of the sigmoid response curve: the minimum and maximum firing rates, and the operating range.

The striking contrast between the characteristics of the receptors and the characteristics of the cerebral neurones they presumably drive, indicates considerable transformation of the ascending thermal information. Contrasts of this type might result if a number of primary afferent fibres converge on to each central unit in the pathway. In the original experiments of Hellon *et al.* (1973) the whole scrotal surface was warmed or cooled so that the same stimulus must have been applied to large numbers of thermoreceptors because each receptor has a spot-like receptive field

(Hellon *et al.* 1975). In order to see whether convergence does take place in the pathway we decided to determine the size of the receptive fields of the spinal, thalamic and cortical neurones sensitive to scrotal temperature.

Pilot experiments were carried out using a small perfused capsule applied to various sites on the scrotum. The main experiments employed two capsules, each of which covered one entire half of the scrotal area.

A short account of some of the results has already been published (Hellon & Mitchell, 1974).

METHODS

Animal preparation

Male albino rats weighing between 250 and 350 g were anaesthetized with urethane given intraperitoneally in doses sufficient to induce and maintain areflexia (1·0–1·5 mg/g body wt). Deep body temperature was maintained near normal (38° C) using a heating pad controlled from a rectal thermistor. All fur was shaved from the scrotum and surrounding area.

Access to the zone of the spinal cord at which the scrotal nerves enter was provided by laminectomy at T13 and L1 using techniques described previously (Hellon & Misra, 1973*a*). When spinalized animals were required a laminectomy was also performed at T7 or T8. A ligature was placed around the cord without rupturing the membrane, knotted and then pulled tight. Access to the thalamus and cortex was provided by a suitable craniotomy. The atlanto-occipital membrane was routinely opened following craniotomy to provide cisternal drainage. Exposed nervous tissue of the brain and cord was bathed in mineral oil.

Stimulation

Thermal stimulation of the scrotal skin was provided by perfused thermodes: hollow brass capsules through which water could be circulated. The water was derived by mixing streams from two constant temperature baths, one at 10° C and the other at 46° C. Each thermode had its own supply. Manual control of the mixing allowed step changes or slow ramp changes in temperature to be made.

The thermode used in the pilot experiments had a circular contact area with 10 mm diameter. The two thermodes used in the main experiments were rectangular. The contact surface of each measured 30 mm × 12 mm. These rectangular thermodes were mounted rigidly on a non-metallic frame and separated from each other by a 2 mm air gap. Preliminary experiments showed that the temperature of the skin under one capsule was not affected by changes within the physiological range of the temperature of the other capsule. The pair of capsules was placed lightly against the scrotum with the scrotal mid line lying along the air gap separating the individual capsules. A thin film of oil was used to enhance contact betweeen the skin and the capsule surface.

Recording

Scrotal skin temperature was measured using miniature thermistor beads cemented to the surface of each capsule in contact with the skin. The thermistors were incorporated in standard bridge circuits, the outputs of which were amplified and recorded simultaneously on magnetic tape and on a chart recorder. The thermistors were calibrated in a water-bath to an accuracy of about 0·2° C.

The activity of neurones in the pathway leading from the scrotum to the

somatosensory cortex was recorded at three anatomical levels: the dorsal horn of the spinal cord in the entry zone of the scrotal nerves, the ventrobasal complex of the thalamus, and the *SI* somatosensory area of the cortex. The location of the three sites has been described in detail previously (Hellon & Misra, 1973*a*, *b*; Hellon *et al.* 1973). Unit activity was recorded extracellularly using glass micro-electrodes broken to a tip diameter of 1–2 μm and filled either with 5 M sodium chloride solution, 0·5 M sodium acetate solution containing Pontamine sky blue dye (Hellon, 1971), or with a low melting point metallic alloy (Cerrolow 136) plated with platinum black (Chung, Raymond & Lettvin, 1970; Dowben & Rose, 1953). After conventional impedance matching, amplification, and filtering using a band-pass of 0·2–3·0 kHz, unit activity was recorded on another channel of the same magnetic tape on which the scrotal temperatures were recorded. On-line assessment of unit firing rates was made using the window discriminator and counter described by Lewin (1972) and the same equipment was used for more careful analysis during playback of the tape. A recording showing typical signal-to-noise ratio is shown in Fig. 2.

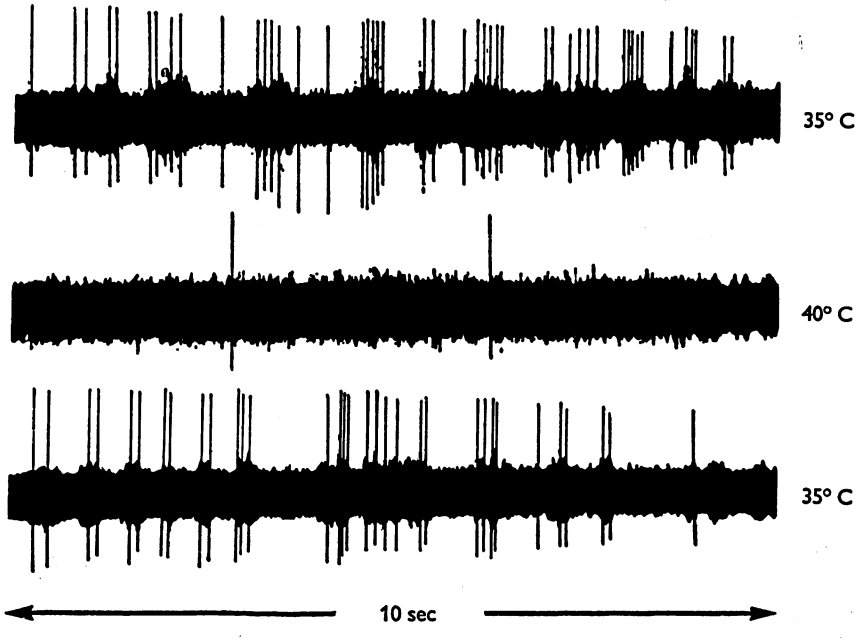

Fig. 2. Activity of a cortical neurone before, during, and after scrotal warming from 35 to 40° C. The signal-to-noise ratio is typical of that obtained for cortical and cord recordings, thalamic recordings tended to have lower noise.

Procedure

The animal's head was clamped in a head holder (Baltimore Instrument Co., U.S.A.) attached to the precision stereotaxic apparatus developed by Lister & Woodget (1972). In those experiments requiring access to the spinal cord the vertebral column was clamped above and below the laminectomy. The regions of scrotal representation in the cortex, thalamus, or cord were mapped by defining the area of maximum evoked response to repeated electrical stimulation of the scrotal

skin (Hellon & Misra, 1973*a*, *b*; Hellon *et al.* 1973). A micro-electrode was then driven through a series of vertical penetrations in the target area. Each spontaneously active neurone which could be isolated was tested for sensitivity to scrotal skin temperature changes. Those that were not sensitive were ignored or sometimes tested for sensitivity to mechanical stimuli. Neurones which were sensitive to scrotal temperature changes were also routinely subjected to a repertoire of tests for mechanosensitivity: the skin of the scrotum, the base of the tail and the thighs were stroked with a camel hair brush, or a single vibrissa, poked with a blunt rod, and sometimes squeezed with forceps.

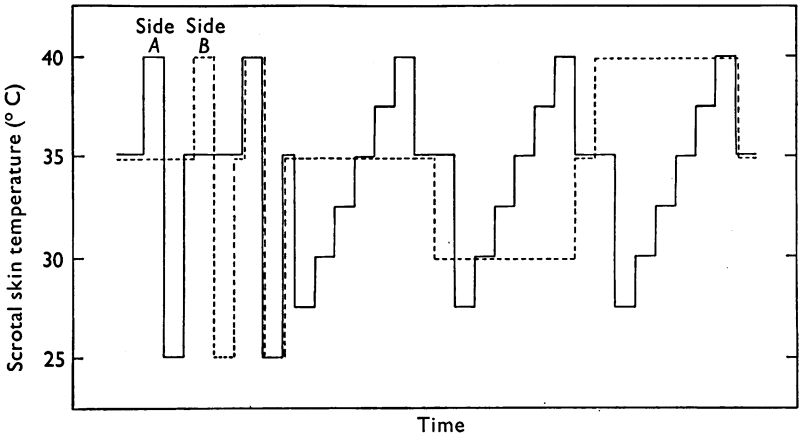

Fig. 3. Programme of temperature changes applied to the two halves of the scrotum, *A* and *B*. The duration of the full programme was 30 to 60 min. and depended on the number of plateau levels used on side *B* while side *A* was raised in steps.

Since only those cells spontaneously active during the search were investigated further, statistics about the distribution of units between various sensory modalities are of little meaning. Under the conditions of the search many mechanosensitive units would not have been spontaneously active. The nature of the temperature senstive units encountered would have depended on the temperature at which the scrotal skin was maintained during search. This temperature was always maintained in the physiological range, but was more often in the warm region ($> 35°$ C) than in the cool (< 30 °C).

In the pilot experiments the test for sensitivity to scrotal temperature changes was conducted with the small thermode positioned at a number of sites on the scrotum. In the main experiments, where the thermodes covered the entire scrotum, after a unit had been shown to respond to temperature changes of the scrotal skin, it was subjected to a test profile such as that shown schematically in Fig. 3. The unit was first tested for sensitivity to large temperature changes of the skin on each side of the scrotum. Next, the sensitivity to changes of temperature of the whole scrotum was tested. Finally, the temperature of one side was held at a series of constant levels while at each level the temperature of the other side was increased (or decreased) in a stepwise fashion. The side held at the series of constant temperatures was sometimes contralateral to the site of the neurone under investigation and sometimes ipsilateral.

The idealized profile of Fig. 3 could not be applied rigorously to all units. To

complete a profile such as that shown required 30–60 min, a period for which only a small proportion of units could be held. Each combination of temperatures was applied for just sufficient time to produce a steady level of activity. The actual levels of temperature which were applied depended on the results of initial testing, which indicated the range of temperatures over which the unit was sensitive. Units which did not return to the same firing rate when the base temperatures were re-established were rejected.

RESULTS

Pilot experiments

In the pilot experiments four thalamic cells sensitive to scrotal temperature changes were investigated in three rats. In every case, changes in unit activity could be elicited from sites widely distributed on both sides of the mid line. The receptive fields were therefore much larger than those of the primary fibres, indicating that convergence occurs. However, it was extremely difficult to obtain consistent results with the small thermode, presumably because only part of the receptive field was under close thermal control. It was for this reason that we resorted to the stratagem of using two thermodes, each of which covered one entire half of the scrotal area. This technique did not permit the exact definition of receptive field size, but did allow us to examine the consequences of convergence of input from thermoreceptors in two parts of the same field.

Main experiments

Thirteen units sensitive specifically to temperature changes of the scrotum were investigated in the spinal cords of ten rats. A full test profile was completed on five of these units. In the thalamus, thirty-four units were investigated in twelve rats and ten profiles were completed. In the cortex, twenty units were investigated in ten animals: five profiles were completed. Other units were encountered which responded specifically to a mechanical stimulus of the scrotum, to both mechanical and thermal stimuli, and some which could not be characterized.

Bilateral response

A striking and unexpected result of the present experiments was the observation that almost all the specifically temperature sensitive units encountered could be stimulated from either side of the scrotal mid line. Table 1 shows the numbers of thermosensitive, thermo- plus mechanosensitive, and mechanosensitive units which could be stimulated from the ipsilateral scrotum only, from the contralateral scrotum only and bilaterally. Mechanical stimulation of the scrotum affected units only on the ipsilateral side of the cord and the contralateral side of the thalamus and cortex. Similar geometry applied to units which were both thermo- and

TABLE 1. Total numbers of neurones in three modality groupings and in sub-groups according to the relationship of the receptive field and the recording site

	Thermosensitive			Thermo- + mechanosensitive			Mechanosensitive		
	Ipsi-	Contra-	Bilateral	Ipsi-	Contra-	Bilateral	Ipsi-	Contra-	Bilateral
Cord	1	0	12	10	0	0	26	0	0
Thalamus	2	0	32	0	3	0	0	3	0
Cortex	0	0	20	0	0	0	0	22	0

mechanosensitive, but sixty-four of the sixty-seven specifically thermosensitive units encountered were affected by temperature changes on either side of the scrotum.

The bilateral temperature sensitivity encompassed units the activity of which was enhanced both by warming and by cooling of the scrotal skin. The two thalamic ipsilateral units were warm sensitive. The ten spinal bimodal units showed no response at high temperatures, and only a phasic

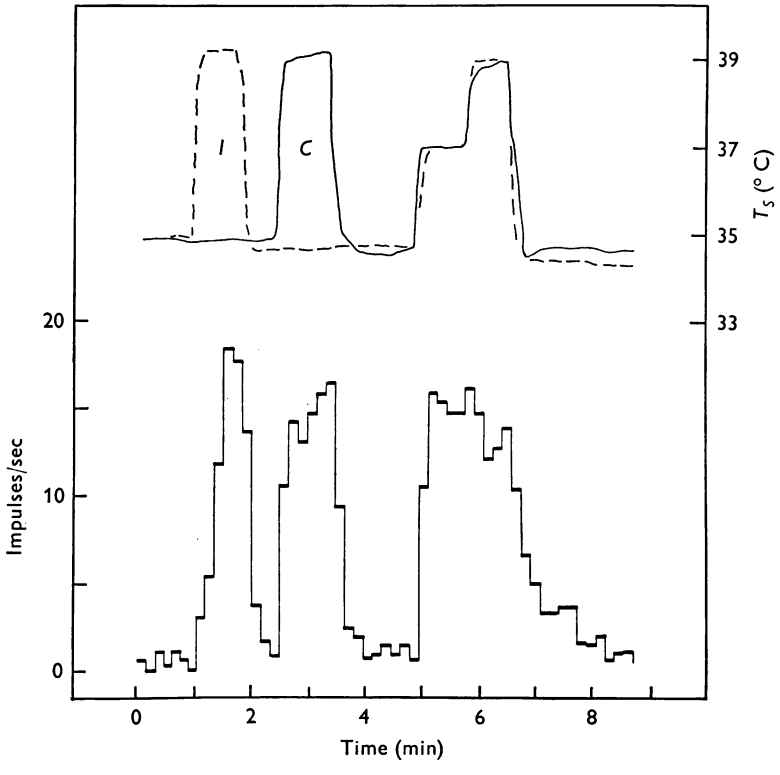

Fig. 4. Firing rate of a thalamic cell (lower trace) in response to unilateral and bilateral changes in scrotal temperature, T_s (upper trace). *I* and *C* indicate temperatures on the ipsilateral and contralateral sides of the scrotum respectively.

response to falling scrotal temperature. Such behaviour is typical of what Iggo calls 'spurious thermoreceptors' (Iggo, 1969; Duclaux & Kenshalo, 1972; Burton, Forbes & Benjamin, 1970; Burton, Terashima & Clark, 1972). The three thalamic bimodal units showed only very weak responses to scrotal temperature; two were warm sensitive and one cold sensitive. The single ipsilateral thermosensitive unit in the spinal cord showed no

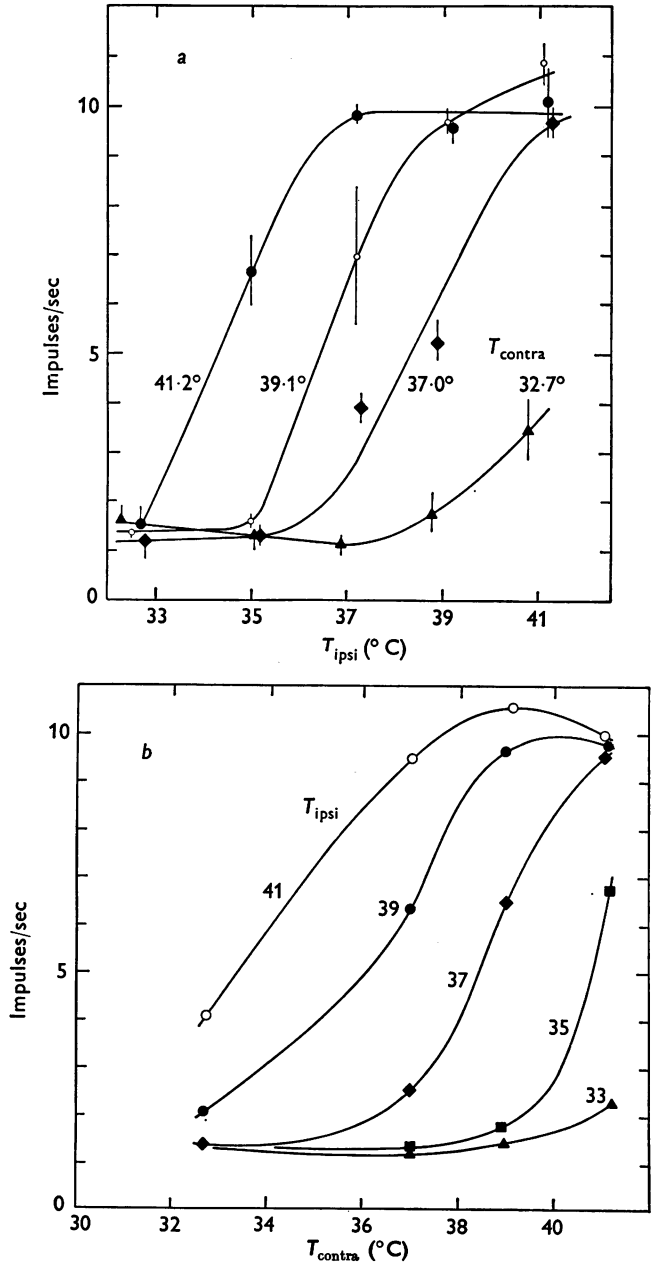

Fig. 5. Firing rate of a thalamic cell in response to independent temperature changes on the ipsilateral (T_{ipsi}) and contralateral (T_{contra}) sides of the scrotum. (*a*) Measured firing rates (mean ± S.E. of mean over three or four successive 10 sec periods) during warming of the ipsilateral side with the four indicated fixed temperatures on the contralateral side. (*b*) Curves derived by making vertical cuts through the curves of (*a*) at five ipsilateral temperatures to show firing rates during warming of the contralateral side .

response to warming and only a phasic response to cooling: it may well have had a 'spurious thermoreceptor' afferent input, the mechanosensitivity of which was not detected in the experiment.

Fig. 4 shows a typical example of the bilateral response. It depicts the response of a specifically thermosensitive unit in the thalamus to the initial stages of the test profile (Fig. 3). The unit was virtually silent at scrotal temperatures less than 34° C. Warming either the ipsilateral or the contralateral side separately from 35 to 39° C increased the firing rate to about 15 impulses/sec. Warming both sides simultaneously did not elicit a larger response than could be elicited from either side separately.

Summation of input

Because the thermoreceptors in the rat's scrotum have small receptive fields, the observation that most specifically thermosensitive units in pathways driven by these receptors can be stimulated from either side of the scrotal mid line must mean that each central unit receives input from receptors distributed on both sides of the mid line. The consequences of this convergence on the responses of central units to separate stimulation of the two sides of the scrotum were investigated in more detail using the full test profile (Fig. 3). Because more test profiles were completed for thalamic units, their responses will be described first.

Thalamic neurones

The quantitative consequences of the convergence in a thalamic unit are illustrated in Fig. 5 which shows the response of a typical unit which increased activity during scrotal warming. The temperature of the side of the scrotum contralateral to the unit was held at four different levels between 32 and 42° C, and at each level the temperature of the ipsilateral side was raised in steps from 32 to 41° C. Figure 5*a* shows the activity of the unit as a function of ipsilateral and contralateral temperature. Curves were fitted by eye to the data points corresponding to each contralateral temperature. Fig. 5*b*, derived by taking vertical cuts through the curves in Fig. 5*a*, shows a similar family of curves depicting the effect on activity of warming the contralateral scrotum while holding the ipsilateral scrotum at a series of steady temperatures. Clearly, increasing the temperature of one side displaces the operating range of the unit in response to temperature changes on the other side towards lower temperatures. However the maximum and minimum firing rates achieved during heating and cooling one side do not depend to any great extent on the temperature of the opposite side. The effectiveness of the steady contralateral (Fig. 5*a*) and ipsilateral (Fig. 5*b*) temperatures in displacing the operating range appear to be approximately equal.

If a unit is equally responsive to temperature changes on either side of the scrotum then its firing rate should be a function of the mean temperature of the scrotum. Fig. 6 shows this to be the case for the thalamic unit whose properties are given in Fig. 5. The activity of the unit is now plotted against the arithmetic average of the temperatures of the two sides of the scrotum. The four separate curves in Fig. 5*a* collapse on to one curve in Fig. 6. Since averaging is an equivalent operation to simple summation, the activity of this unit is just a function of the sum of the inputs from the two sides of the scrotum.

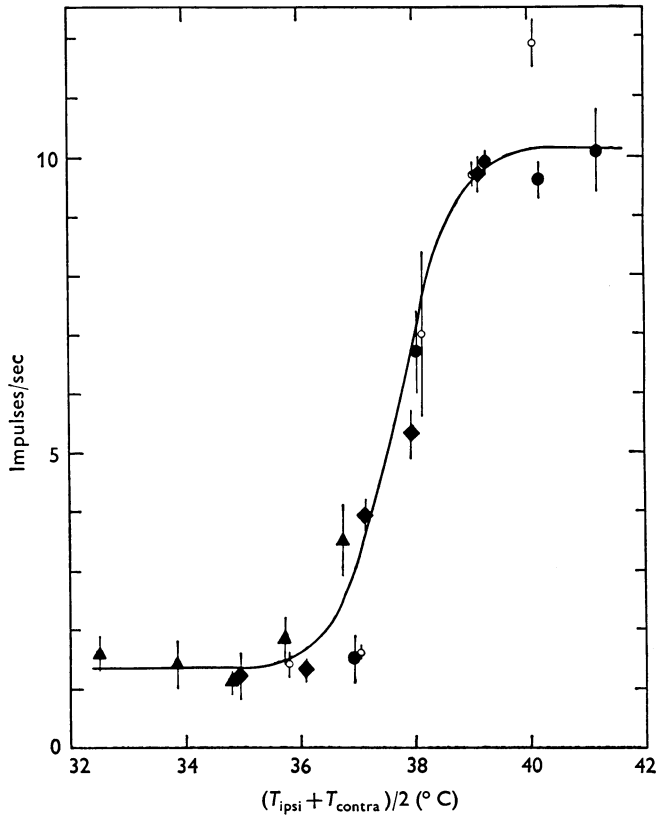

Fig. 6. Firing rate (mean ± S.E. of mean) of the thalamic cell activity shown in Fig. 5 as a function of the mean temperature of the two sides of the scrotum. Symbols denote the four contralateral temperatures of Fig. 5*a*.

Eight of the ten thalamic units on which it was possible to complete test profiles showed increased activity during scrotal warming: their response curves had a positive slope. Two units showed reduced activity: their response curves had negative slope. The responses of all ten to

independent temperature changes on the two sides of the scrotum could be represented by families of displaced sigmoid curves. The inputs from the two sides of the scrotum interacted synergistically on the activity of each thalamic unit. Holding the temperature of one side at a series of increasing temperature levels successively displaced towards lower temperatures the operating range in response to the temperature of the other side, as may be seen in the example of Fig. 5. The direction of displacement was the same for the two units showing reduced activity during warming.

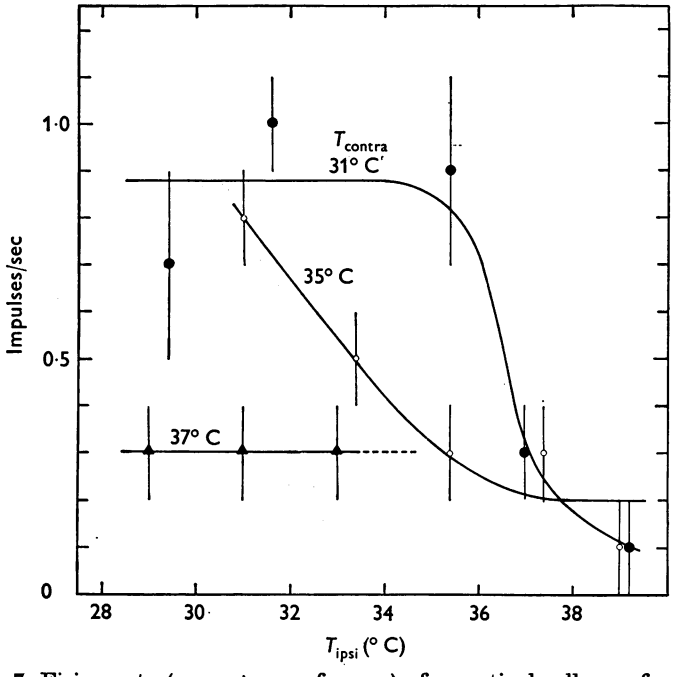

Fig. 7. Firing rate (mean ± S.E. of mean) of a cortical cell as a function of T_{ipsi} at three steady levels of T_{contra}.

In all ten thalamic cells, firing rate was a function of an additive combination of the inputs from the two sides of the scrotum. In nine cells, the rule of addition was that of simple summation: the activity could be expressed as a single-valued function of mean temperature of the scrotum (cf. Fig. 6). In the remaining unit, changes in temperature on the contralateral side of the scrotum had a greater effect than changes on the ipsilateral side.

Cortical neurones

Hellon *et al.* (1973), in their paper on the responses of units in the somatosensory cortex to scrotal heating, pointed out the similarity between the responses of cortical units and thalamic units. The only out-

standing difference was that the majority of cortical units showed reduced activity during scrotal warming whereas the majority of thalamic units showed enhanced activity. They suggested a simple inhibitory link between relay units in the thalamus and units in the somatosensory cortex. The results of the present experiments support their suggestion. Fig. 7 shows the responses of one of the five cortical units on which it was possible to complete a full test profile. The responses resemble a mirror image of the responses of thalamic units which increase activity on scrotal warming (cf. Fig. 5). The switch-like characteristics were retained. Temperature sensitivity was confined to the scrotal temperature range 30–42° C. Input from both sides of the mid line converged on the cortical unit with a synergistic effect on its activity: warming one side shifted the range of sensitivity to warming the other side towards lower temperatures. In all, the unit seemed to follow faithfully the response of thalamic relay units but with suppression rather than excitation. The other four units in the somatosensory cortex on which tests were completed had very similar characteristics to those of the unit in Fig. 7. All showed reduced activity during scrotal warming.

Spinal cord neurones

Of the five units in the intact spinal cord which were specifically sensitive to scrotal temperature and on which it was possible to complete tests, four showed increased activity to scrotal warming and one reduced activity. Their characteristics were remarkably similar to the characteristics of thalamic units, a surprising result since it implies not only that the spinal units receive input from receptors on both sides of the scrotal mid line but also that sufficient processing takes place at the level of the entry zone to produce the switch-like characteristics and the synergistic integration of activity. Figure 8*a* shows a unit with similar characteristics to those found in thalamic and cortical units. At each of the three contralateral temperature levels the unit had an operating range of about 2° C, only a fraction of the operating range of the receptors presumably driving it.

The particular unit shown in Fig. 8*a* was much more strongly affected by temperature changes on the ipsilateral side of the scrotum than by changes on the contralateral side. This bias was not typical. On average, as was the case with thalamic units, the spinal units were about equally responsive to stimulation from either side of mid line.

A feature of the response shown in Fig. 8*a* which was not observed in any thalamic or cortical units is the evidence of sensitivity to temperature changes below 30° C, that is into the range of the scrotal cold receptors (Iggo, 1969; Hellon *et al.* 1975). Cooling the contralateral scrotum from 30·7 to 25° C shifted the curve of response to ipsilateral temperature

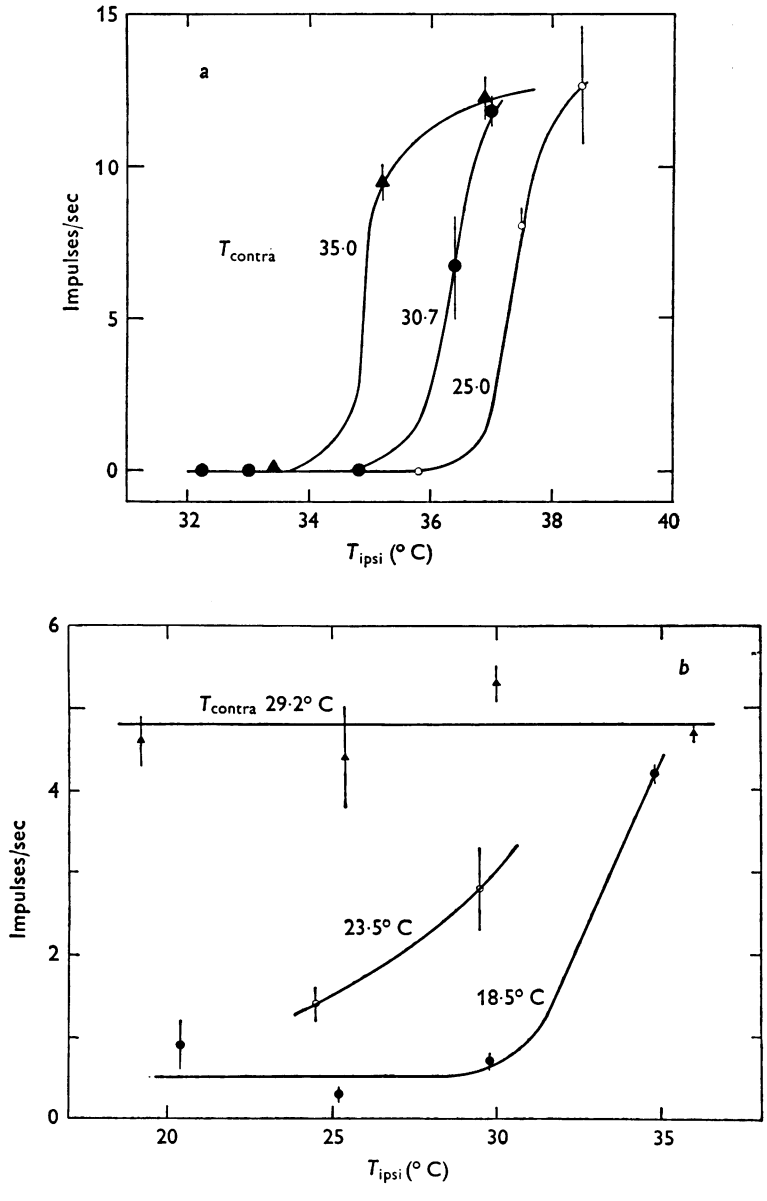

Fig. 8. Firing rates (mean ± S.E. of mean) of two dorsal horn cells as a function of T_{ipsi} at three steady levels of T_{contra}. Note that in (*a*) the firing rate is more strongly affected by T_{ipsi} than T_{contra}, and in (*b*) the firing rate is influenced by temperature changes in the range of the cold receptors.

towards higher temperatures. The sensitivity of some spinal units to temperature changes in the region below 30° C is illustrated more forcibly in the responses of the unit shown in Fig. 8*b*. At a contralateral temperature of 29·2° C the unit maintained its maximum activity as ipsilateral temperature was lowered to 19° C, while at contralateral temperatures of 23·5 and 18·5° C, the activity decreased with decreasing ipsilateral temperature.

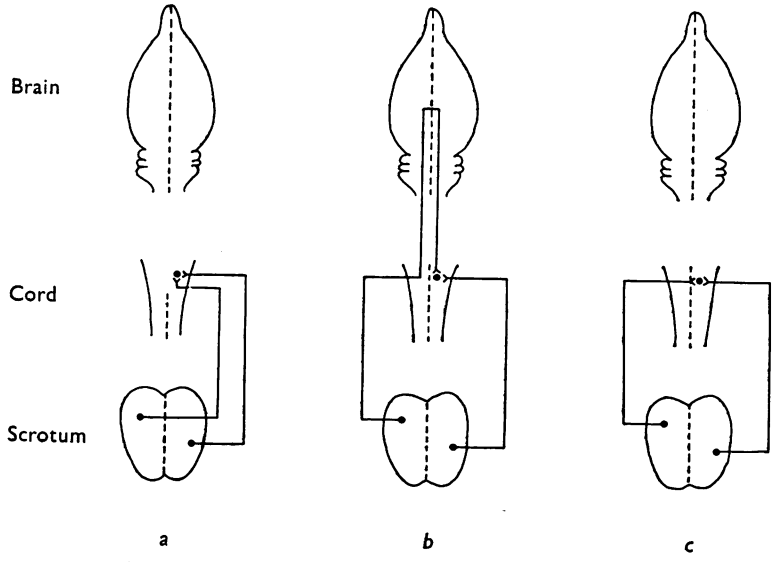

Fig. 9. Diagram of three hypothetical routes through which a bilateral response could arise by convergence at a dorsal horn cell in the entry zone. (*a*) Primary fibres cross the scrotal mid line; (*b*) interneurones cross proximal to the entry zone; (*c*) interneurones cross at the entry zone.

There are three possible anatomical routes, illustrated in Fig. 9, by means of which a bilateral response could arise at a dorsal horn neurone. The first possibility, that afferent fibres cross the scrotal mid line, was tested in two rats by surgically separating the two halves of the scrotum. The bilateral response was left intact. The second possibility, that the bilateral response depends on ascending and descending fibres in the cord, was examined by performing complete spinal sections at T7 or T8 in four rats. In these rats seven cord units were encountered which responded to scrotal temperature changes: all seven had bilateral fields. Thus the bilateral response must arise through the transfer of information across the mid line of the cord in the entry zone.

DISCUSSION

Sensory information arising from thermoreceptors in the skin is commonly believed to travel to the somatosensory cortex via a crossed pathway, ipsilateral to the dorsal horn but with a contralateral destination in the brain. The belief stems largely from clinical experience of the effects of cord lesions on temperature sensation in man. We have demonstrated in the present experiments that the input from thermoreceptors in the rat scrotal skin is not confined to a crossed unilateral pathway. The pathway is to all intents and purposes fully bilateral: of the sixty-seven specifically thermosensitive units investigated at the levels of cord, thalamus, and cortex, sixty-four responded to changes in temperature on either side of the scrotal mid line.

Furthermore, the bilateral response is established at the level of the entry zone in the spinal cord, and must arise from interneurones crossing the mid line of the cord near the entry zone. The neuroanatomical machinery capable of such transfer remains uncertain. However, dorsal commissural fibres such as those described by Ramón y Cajal (1909), Scheibel & Scheibel (1968) and Réthelyi & Szentágothai (1973) might well serve this function. The bilateral responses observed in thalamus and cortex could be the direct consequence of the crossover in the entry zone in the cord, but we cannot at the moment rule out the possibility of additional higher commissural connexions.

In the pilot experiments in which we attempted to measure receptive field sizes with a small thermode, central unit activity could be elicited from sites widely distributed over the scrotum. Thus the receptive fields are not bilateral and small but bilateral and large.

To the best of our knowledge, three other tests of receptive field location for central units responding specifically to skin temperature have been reported. Poulos and Benjamin (1968) described cells in the thalamus of the monkey which responded to temperature changes of the tongue. In most cases the receptive fields were contralaterally situated, but in some cases they were ipsilateral. No bilateral fields were reported. Fruhstorfer & Hensel (1973) briefly described the responses of neurones in the cat trigeminal nucleus to temperature changes of the perinasal skin; all fields were apparently ipsilateral. The tongue and nose share with the scrotum the property of being mid line organs. Iggo & Ramsey (1974) have observed dorsal horn cells which respond to temperature changes on the hind foot of the monkey; receptor fields were all ipsilateral. Thus only in the case of the rat scrotum have bilateral receptor fields been observed, although the ipsilateral fields reported by Poulus & Benjamin (1968) in the monkey

require the existence of a pathway other than the conventional crossed pathway.

The fields of central units responding to temperature changes of the monkey tongue (Poulos & Benjamin 1968) and hind foot (Iggo & Ramsey 1974), the cat nose (Fruhstorfer & Hensel 1973) and now the rat scrotum have in common the feature that in all cases the field size is much larger than the field size for a primary afferent fibre. Thus convergence may well be a general feature of thermosensitive pathways. The organized behavioural responses of animals in disparate thermal environments certainly require that integration must take place of neural information arising from thermal receptors in different skin areas. If thermosensitive pathways generally do exhibit convergence, then localization of pure thermal stimuli must necessarily be poor: spatial integration and spatial discrimination are mutually exclusive.

Whether the integrating mechanisms exhibited by the rat scrotal pathway are to be found in other pathways remains to be explored. Only in the case of this pathway have the consequences of applying different thermal stimuli in the same field been pursued. In addition, this pathway appears to be the only one responding specifically to warming of the skin in which receptive fields have been investigated. There is no doubt that the investigation of the integration of the information arising from thermoreceptors needs to be extended to other pathways and other animals.

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