SOMATOSENSORY PROJECTIONS TO THE SUPERIOR COLLICULUS OF THE ANAESTHETIZED CAT

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SUMMARY

1. Experiments in anaesthetized cats have shown that the superior colliculus receives deep afferent input from the forelimb and hindlimb, but not from the large superficial neck muscles.

2. Neuronal activity in the superior colliculus is readily elicited by electrical stimulation of C2 and C3 cutaneous nerves. A significant proportion of neurones so activated have multiple receptive fields and some with no identifiable receptive fields in regions innervated by C2 and C3 nerves have receptive fields elsewhere on the body surface. Many collicular neurones activated by C2 and C3 stimulation had no identifiable receptive fields.

3. Natural stimuli to the limbs, hitherto believed to activate only cutaneous receptors, are sufficient to activate deep receptors which contribute to the neuronal responses in the superior colliculus elicited by the natural stimulus. These same natural stimuli set up transmitted vibration adequate to excite receptors some distance from the applied stimulus.

4. No evidence was found for a rigorous somatotopy in the superior colliculus. The great majority of neurones received trigeminal input which is widely distributed throughout the superior colliculus.

5. Tactile stimuli to the face are most effective in eliciting unit activity in the superior colliculus and many neurones activated by these stimuli were shown to be tectospinal neurones. In particular, the specialized receptors of the face, including the glabrous skin of the snout (the planum nasale) and the vibrissae, are major sources of input to collicular neurones including tectospinal neurones.

6. It is suggested that a major role of the superior colliculus is in the organization of head movements associated with the use of the specialized receptor organs of the face in exploratory behaviours. The superior colliculus may also be involved in the organization of aversion movements of the head.

INTRODUCTION

It is well established that the superior colliculus of the cat receives a somatic input. Electrical stimulation of nerves and skin, natural stimuli including hair movement, skin displacement and joint movement all have been shown to activate

neurones in the superior colliculus of both non-anaesthetized and anaesthetized animals (Jassik-Gerschenfeld, 1965; Stein & Arigbede, 1972; Gordon, 1973; Abrahams & Rose, 1975a, b; Stein, Magalhães-Castro & Kruger, 1976; Rose & Abrahams, 1978; Nagata & Kruger, 1979; Clemo & Stein, 1986; Meredith & Stein, 1986). Most of this input is believed to originate from cutaneous receptors (Nagata & Kruger, 1979), but studies using natural stimuli have shown that 17–24% of unit activity could be elicited by the stimulation of deep receptors (Stein et al. 1976; Clemo & Stein, 1986). Further, electrical stimulation of muscle nerves is very effective in eliciting unit discharge in the superior colliculus (Abrahams & Rose, 1975a, b).

The somatosensory input to the superior colliculus exhibits a number of unusual features. Although responses can be evoked by small movements of one or a few hairs, most accounts report that the most consistently effective natural somatic stimuli are fast movement of hair or high-velocity displacements of the skin (Stein et al. 1976; Nagata & Kruger, 1979). The most common pattern of neurone response to such stimuli is one or a few impulses (Stein et al. 1976; Nagata & Kruger, 1979) and the units receiving somatosensory input are frequently also activated from other sensory systems (Jassik-Gerschenfeld, 1965; Abrahams & Falchetto, 1966; Stein & Arigbede, 1972; Meredith & Stein, 1986).

The characteristics of the somatosensory input to the superior colliculus of the cat have led to the hypothesis that this is a system concerned with the spatial origin of the stimulus and which uses that information to initiate attentional and alerting behaviour including appropriate head and eye movements (Stein et al. 1976). There is considerable physiological and anatomical evidence that the superior colliculus plays a role in the organization of head and eye movement (Apter, 1946; Hess, Bürgi & Bucher, 1946; Anderson, Yoshida & Wilson, 1971; Abrahams & Rose, 1975a; Harris, 1980; Roucoux, Guitton & Crommelink, 1980; Meredith & Stein, 1986), which makes such hypotheses of collicular function plausible. However, the significance of the input to the superior colliculus from deep receptors has not been explained, nor have some unusual aspects of the somatosensory input to the superior colliculus. Apart from the nature of the adequate stimulus, these include a mixture of large and small discrete receptive fields and the large representation from the face (Gordon, 1973; Stein et al. 1976).

In the present work, a study of the somatotopy within the superior colliculus has been made. The receptive fields of cutaneously activated units have been examined, and the potential contributions to these receptive fields from deep receptors analysed. As part of that examination the ability of adequate stimuli to set up transmitted vibration has been measured. The effectiveness of a number of stimuli, including natural stimuli to activate output neurones of the superior colliculus has also been investigated and the nature of input from neck muscle receptors has also been re-examined. These latter studies were prompted by recent findings (Abrahams & Turner, 1981; Abrahams, Lynn & Richmond, 1984) which suggested that the extensive nuchal input to the superior colliculus arises not from neck muscle as originally supposed (Abrahams & Rose, 1975a), but from cutaneous receptors. Some preliminary accounts of this work have appeared (Abrahams & Clinton, 1986; Abrahams, Clinton & Downey, 1986).

METHODS

Two anaesthetic regimens were used. In one the cats were anaesthetized with chloralose (60 mg/kg) after the induction of anaesthesia with ethyl chloride and ether. In the second, the cats were first anaesthetized with ketamine (33 mg/kg I.M.). Because of the prolonged persistence of ketamine in the body, a significantly lower dose of chloralose (usually 30 mg/kg) was sufficient to provide ten or more hours of deep anaesthesia. The initial injection of chloralose was supplemented as necessary during the course of the experiment by the I.V. administration of 5 mg sodium pentobarbitone/kg (Somnitol M.T.C.). To prevent movements initiated by stimulation of nerves the animals were immobilized by 20 mg I.V. gallamine triethiodide (Flaxedil, Poulenc). Each dose of the neuromuscular blocking agent was allowed to wear off before more was administered to ensure that the animal was areflexic and adequately anaesthetized.

In experiments concerned primarily with input to the superior colliculus from the face and neck the animals were placed in a stereotaxic machine (La Précision Cinématographique, Asnièrs, France) designed to permit visual stimulation and easy access to the face. The recording microelectrodes were then introduced into the brain using stereotaxic technique. Identification of the collicular surface in the course of the penetrations was aided by the response to a flash stimulus delivered every 4 s. In all other experiments the animals were placed in a Transvertex stereotaxic machine and the microelectrode was introduced into the superior colliculus under direct vision. In these experiments, a wide craniotomy was made, one occipital lobe partially aspirated and the remaining tissue displaced laterally to expose the surface of the superior colliculus. If necessary, windows were made in the mesh of blood vessels and pia overlying the collicular surface to facilitate the introduction of microelectrodes. Recordings were made from well-isolated single units, which because of spike configuration were usually judged to be generated by cell bodies and not from axons.

Paired platinum electrodes were used for electrical stimulation of nerves which were left intact. The nerves included the great auricular nerve branch of the C2 dorsal ramus (which supplies the skin of the occiput and pinna), the C2 muscle branches supplying complexus and biventer cervicis muscles, the cutaneous components of the rostral division of the C3 dorsal ramus supplying neck skin (Abrahams *et al.* 1984), the C3 muscle nerves to complexus and biventer cervicis, the deep radial nerve in the forelimb, and the flexor digitorum longus nerve and its interosseus branch in the hindlimb. The afferent volley in neck nerves was monitored by paired recording electrodes placed on the C2 and C3 dorsal rami close to the spinal cord. Afferent volleys in limb nerves were monitored by paired recording electrodes placed proximally. All electrodes were secured in place using paraffin wax which also served to reduce current escape from the electrodes. Electrical stimuli to nerves consisted of single 50 μs pulses or trains of three 50 μs pulses at a frequency of 300 Hz. To excite tectospinal cells antidromically, a bipolar stimulating electrode (SNEX 100, Rhodes) was introduced into the contralateral ventral quadrant of the C1 spinal segment. 100 μs pulses were delivered through this electrode at 1 s intervals. The position of the electrode within the cord was adjusted while recording from the superior colliculus so that the minimum stimulating current (usually less than 250 μA) was needed. Cells were regarded as activated antidromically if they responded at consistent short latencies (usually 0·4–1·4 ms), responded to paired stimuli at appropriately (approximately 2 ms) short intervals and had clearly distinguishable IS and SD segments. When a neurone appeared to be activated by both spinal and sensory stimulation, collision extinction within the critical interval had to be demonstrated for that neurone to be accepted as a tectospinal neurone.

Either varnished or glass-coated tungsten microelectrodes were used for unit recording. Cutaneous receptive fields were examined by natural stimuli including hair and skin movement and pinching the skin with nylon or toothed metal forceps. When precise timing of a mechanical stimulus to the skin was necessary, a vibration exciter (B&K type 4810 or Ling type 203) was used to produce a movement of either a metal probe with a 1 mm diameter tip or calibrated von Frey hairs. Ramp and hold waveforms for controlled movements of the vibrators were generated by a specially constructed function generator and sine waves by a standard laboratory function generator (Krohn-hite, Type 5100A). Sine waves were amplified by an AC power amplifier (B&K type 2706). A DC power amplifier (Aim Electronics, Cambridge) with a feed-back system ensured accurate following of ramp and hold waveforms. Probe movements were measured by a sensitive strain gauge or a calibrated light-weight accelerometer (B&K type 4344 or 4375) attached to the

moving element of the vibrator. In experiments in which tissue vibration was measured, the light-weight accelerometer was attached to the shaved skin or to bone using sealing wax. The axis of movement measured was in the same direction as the imposed displacement. The accelerometer output was fed to a double-integrating charge amplifier (B&K type 2635) which permitted recording either of acceleration, velocity, or displacement. Many units in the superior colliculus excited by somatic input also have an auditory input. To ensure that the noises associated with movements of the vibrator were not the adequate stimulus, control observations were made with the vibrator running, but with the probe moved away from the skin.

Unit activity, timing pulses, transducer outputs and a voice track were recorded on an instrumentation tape-recorder (Racal Store 4). Records were subsequently photographed if necessary and post-stimulus histograms were constructed using an Apple IIe microcomputer equipped with an APL-D2 system or a Zenith 158 microcomputer equipped with an ISC-16 system (RC Electronics, Santa Barbara, CA, U.S.A.).

Two or three recording sites in each experiment were marked by passing 5 μA for 10 s through the electrode (electrode cathode). At the end of each experiment the animals were given an additional dose of anaesthetic and then perfused transcardiacally, first with saline and then with a 25% solution of formalin at about 60 kPa pressure. A brain slice containing the superior colliculus was removed and immersed in formalin. Serial sections of the superior colliculus were cut at 30 μm several days later and stained with luxol fast blue and cresyl violet (Klüver & Barrera, 1953) or neutral red.

It is a common finding that neurone responses in the superior colliculus can be erratic, especially when latencies are long, but become more consistent when the interval between stimuli is long (Abrahams & Rose, 1975a, b; Stein et al. 1976; Nagata & Kruger, 1979). To ensure reasonable consistency of response therefore, the interval between stimuli was rarely less than 4 s and often 16 s or more. The ability to demonstrate afferent input to the superior colliculus was also dependent on the level of anaesthesia and responses were abolished or sharply reduced immediately after anaesthetic administration. In the experiments reported here recording commenced no earlier than 6 h after the induction of chloralose anaesthesia and was suspended for about 30 min after each subsequent dose of pentobarbitone.

RESULTS

Unit discharge in the superior colliculus after electrical stimulation of limb and neck nerves

Nuchal input from the cervical dorsal rami originates mainly from the skin and stimulation of nerves supplying neck muscles was largely ineffective except at high stimulus strengths. In three animals, electrical stimuli were delivered to branches of the dorsal rami of C2 and C3 which served only muscle or only skin (Abrahams et al. 1984). In these experiments sixty-one units were found in the superior colliculus and underlying tegmentum which could be excited only by cutaneous nerve stimulation. A further six units were found which responded to stimulation both of cutaneous and muscle nerves. Unit activity could usually be evoked in cutaneous nerves at 2 T (threshold) or below, but muscle nerve stimulation required stimulus strengths of 15–64 T (Fig. 1).

The existence of an input to the superior colliculus from forelimb and hindlimb muscle nerves was readily confirmed. Unit discharge was evoked in the superior colliculus in seven of eight experiments in which the deep branch of the radial nerve was stimulated electrically. In a further three experiments, stimulation of the hindleg deep nerve, flexor digitorum longus or its interosseus branch at 2–10 T was also found to be effective in eliciting unit discharge.
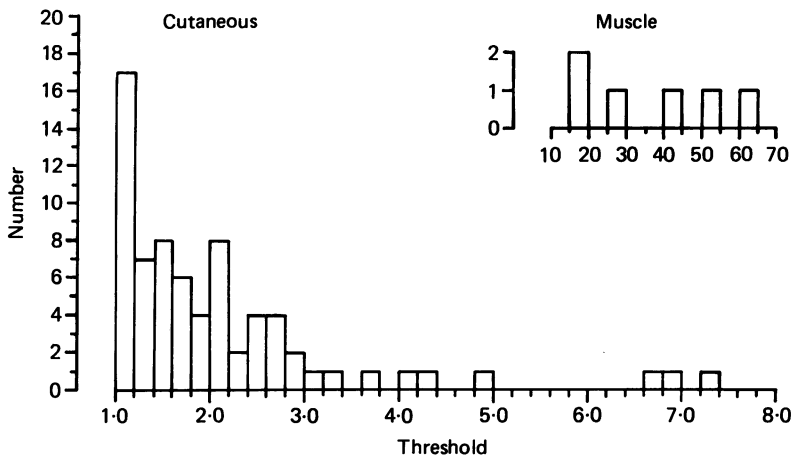
Fig. 1. Strength of stimuli to C2 and C3 dorsal rami nerves necessary to evoke neuronal activity in the superior colliculus and underlying tegmentum.

Receptive fields of units responding to C2 and C3 cutaneous nerve stimulation

Although electrical stimulation of C2 and C3 cutaneous nerves was effective in eliciting unit discharge in the superior colliculus, natural stimulation was less effective. Only thirty-two of 124 units (26 %) tested in ten animals had circumscribed cutaneous nuchal receptive fields in the regions known to be served by C2 and C3 dorsal rami (Abrahams *et al.* 1984). These receptive fields on the head, neck or pinna were about 1–3 cm in diameter, and the collicular units responded to fast brushing of hairs or a light tap to the skin. Movements of only a few hairs on the inner surface of the pinna were particularly effective in eliciting unit discharge. Seven units that did not respond to hair movement could be activated by applying firm pressure applied to the base of the ear and one unit responded to pinching of the temporal muscle. No units were found in these or later explorations which responded to nociceptive stimulation.

Twenty-seven of the thirty-two units which were activated by electrical stimulation of C2 or C3 cutaneous nerves and which had receptive fields in C2 and C3 regions had additional receptive fields located outside regions supplied by C2 and C3 nerves (Table 1). Most commonly these receptive fields were located on the face and forepaw. A further forty-three units which were activated by C2 or C3 nerve stimulation, but which did not have C2 or C3 receptive fields were found to have receptive fields elsewhere on the body (Table 2). Nineteen of these forty-three units had trigeminal receptive fields and were responsive to movement of one or more vibrissae, light taps to the planum nasale, or had small receptive fields on the face activated by tap or by brushing hair. Most units, however, were sensitive to tactile stimulation of one or both forepaws. Although hair movement and air puffs were sometimes effective stimuli at this site a tap was usually the effective tactile stimulus. As Tables 1 and 2 show, multiple separate receptive fields were common. Regardless of the location of the receptive field the response to almost all stimuli

TABLE 1. Receptive fields of neurones in the superior colliculus. C2 or C3 plus other discrete areas

One other		Two other		Three or more other areas	
Pinna and forepaw	3	Pinna, nose, vibrissae	1	Pinna, nose, maxillary skin, vibrissae	1
Pinna and face	1	Pinna, nose, periorbital skin	1	Pinna, nose, forepaw, frame tap	1
Pinna and frame tap	1	Pinna, nose, maxillary skin	1	Pinna, nose, forepaw, vibrissae	1
Occiput and nose	2	Pinna, nose, forepaw	2	Pinna, occiput, nose, forepaw	1
Occiput and forepaw	2	Pinna, forepaw, vibrissae	1	Occiput, nose, maxillary skin, forepaw	1
		Pinna, forepaw, frame tap	2	Occiput, nose, vibrissae, forepaw	1
		Pinna, occiput, frame tap	1	Occiput, pinna, nose, vibrissae, forepaw and stereotaxic frame tap	1
		Occiput, nose, frame tap	1		
		Occiput, nose, face	1		
Totals	9		11		7

The neurones listed here were responsive to electrical stimulation of C2 or C3 cutaneous nerves, had receptive fields in skin areas served by C2 and C3 cutaneous nerves and had additional receptive fields elsewhere on the body surface. Neurone responses to light tap of the stereotaxic machine or ear bars are indicated.

TABLE 2. Receptive fields of neurones in the superior colliculus

Single receptive fields		Two receptive fields		Three receptive fields	
Forelimb	21	Nose and vibrissae	3	Nose, upper lip, vibrissae	1
Trunk and limbs	3	Nose and maxillary regions	1	Nose, forepaw, frame tap	3
Vibrissae	2	Nose and forepaw	2		
Nose	1	Nose and stereotaxic frame tap	1		
Stereotaxic frame tap	2	Periorbital area and vibrissae	1		
		Face and frame tap	1		
		Forepaw and frame tap	1		
Totals	29		10		4

These neurones could be activated by electrical stimulation of C2 and C3 cutaneous nerves, had no receptive fields in skin regions supplied by these nerves, but had receptive fields elsewhere. Neurone responses to light tap of the stereotaxic machine or ear bars are indicated.

recorded in the superior colliculus consisted of one or a few nerve impulses (Fig. 2).

In a number of instances, units activated by C2 or C3 nerve stimulation were also activated by taps to the ear bars or the stereotaxic frame. This response was not due to the activation of receptors with afferent fibres travelling in cervical nerves. In
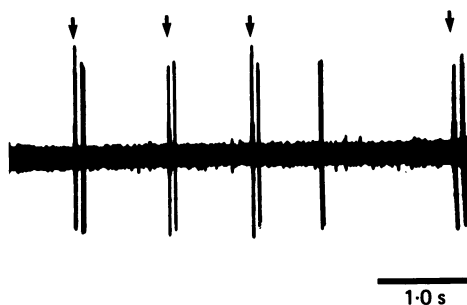

Fig. 2. Characteristic neuronal response in the superior colliculus. At each arrow a neuronal response has occurred as a result of a light tap to the planum nasale.

three experiments, the C2 cutaneous nerve occipitalis major (Elliott, 1961) was dissected into small bundles each containing one or a few axons so that the receptive fields and adequate stimulus for these axons could be examined. All commonly reported cutaneous receptor types (including those served by group IV axons) were present in these axons and had appropriately located receptive fields. In no instance was an axon in a C2 nerve excited by a tap to the ear bars or the stereotaxic machine.

No adequate stimulus of any kind could be found for the remaining twenty-two units in the superior colliculus that responded to electrical stimulation of C2 or C3 nerves.

Organization of the somatic input to the superior colliculus

In the course of examining the receptive fields of collicular neurones excited by C2 or C3 nerve stimulation, it became clear that a number of observations were inconsistent with existing accounts of somatotopy in the cat superior colliculus (Stein *et al.* 1976). Accordingly a more systematic examination of receptive fields, adequate stimuli and somatotopy was made in a series of experiments in which a systematic series of penetrations were made into the superior colliculus on a 1 mm grid. In the course of these experiments fifty-six well-isolated neurones were examined. Forty-eight of the fifty-six neurones (86 %) had facial receptive fields either alone or in combination with other receptive fields. The receptive fields on the face were often in specialized receptor regions, and thirty neurones were activated by light mechanical stimulation of the planum nasale with a von Frey hair. Twenty-seven of these neurones were also activated by small movements of one or a few vibrissae. Elsewhere on the face receptive fields were usually small and the adequate stimulus was the movement of a few hairs or a light finger tap. Of thirty neurones that only had receptive fields on the face, twenty had contralateral receptive fields

and ten bilateral receptive fields. This finding is in agreement with that of Gordon (1973), but in contrast to that of Stein *et al.* (1976). Ten neurones with contralateral facial receptive fields also had forelimb receptive fields; seven of these receptive fields were contralateral, and three bilateral. Three neurones had forelimb and hindlimb receptive fields as well as facial receptive fields and a further three neurones could be activated by taps delivered to any part of the body surface. A single neurone was found with contralateral facial and hindlimb receptive fields.
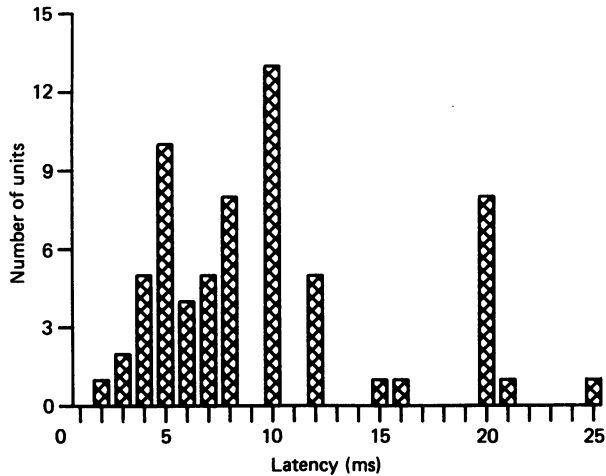

Fig. 3. Latency of onset of neuronal response in the superior colliculus following stimulation of infraorbital nerve. Mean latency 9·7 ms (s.e.m. 0·7 ms).

Only eight neurones had no facial receptive fields. Of these, five had forelimb receptive fields, three contralaterally, one ipsilaterally and one bilaterally. Two neurones had bilateral forelimb and chest receptive fields, and one neurone could be activated from any part of the body except the face.

No evidence for precise somatotopy within the superior colliculus was found, but there were twice as many neurones with facial receptive fields present in the rostral half of the superior colliculus as in the caudal half.

Facial and nuchal cutaneous input to tectospinal neurones

A significant proportion of tectospinal cells receive input from trigeminal and nuchal afferent fibres. Nineteen (37%) of fifty-two tectospinal cells tested showed collision extinction when a neurone discharge was elicited by stimulation of the infraorbital nerve as did twenty-six of 124 tectospinal (21%) cells tested against discharges elicited by stimulation of the C2 cutaneous nerve. Thirty tectospinal units were tested against both nerves, and seven (23%) were found to have both infraorbital and cervical input. The typical pattern of unit discharge elicited in a neurone of the superior colliculus following electrical stimulation of the infraorbital nerves was a train of five to seven impulses. Latencies of these responses ranged from 2–25 ms, the majority being below 10 ms (Fig. 3). Consistent with the evidence from the retrograde transport of horseradish peroxidase (Coulter, Bowker, Wise, Murray,
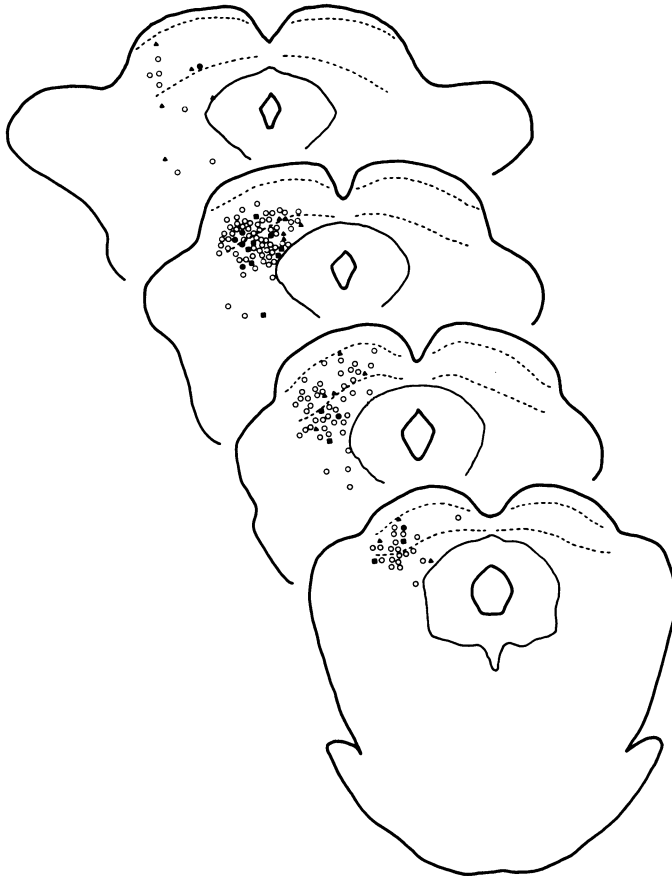
Fig. 4. Series of diagrammatic sections through the brain stem to show the distribution of tectospinal neurones. Top section, most rostral, bottom section, most caudal. ■, tectospinal neurones with input from infraorbital nerve. ▲, tectospinal neurones with C2 cutaneous nerve input. ●, units with input from both nerves. ○, neurones not activated by either nerve. The dashed lines indicate the boundaries of the superficial, intermediate and deep layers of the superior colliculus. A number of recording sites were found which were outside the boundaries of the superior colliculus.

Castiglioni & Westlund, 1979), tectospinal cells in these recording experiments were located in the intermediate and deep layers of the superior colliculus and were most common in the caudal parts of the superior colliculus (Fig. 4).

Planum nasale and input to the tectospinal tract

The glabrous skin of the cat nose (the planum nasale), like the planum nasale of most fur-bearing animals, is richly endowed with sensory receptors in a manner resembling the digits of a primate, and is believed therefore to be able to execute detailed sensory analyses (Montagna, Roman & MacPherson, 1975; Abrahams, Hodgins & Downey, 1987). The planum nasale contributes a significant proportion of the facial input to tectospinal cells. Fifty-eight neurones in the superior colliculus were found that could be excited by the controlled application of a von Frey hair to

the planum nasale. Of the fifty-eight neurones, twenty-one (36%) were shown to be tectospinal neurones by the collision technique (Fig. 5), a proportion of tectospinal neurones very similar to that excited by electrical stimulation of the infraorbital nerve.
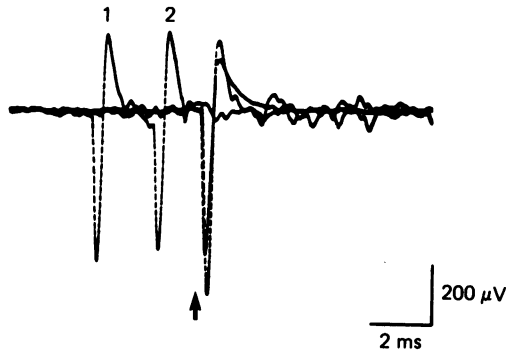

Fig. 5. Three superimposed traces of action potentials recorded from the superior colliculus. The arrow indicates antidromic potentials recorded from a tectospinal neurone. The spinal cord was stimulated during each sweep. In two sweeps an action potential was also elicited by the application of a von Frey hair to the planum nasale. One sweep contained two orthodromic impulses, numbered 1 and 2: the second of these (2) fell in the critical interval, causing collision and extinguishing the antidromic action potential. This experiment demonstrates that the neurone activated by tactile stimulation was a tectospinal neurone.

Contribution of deep receptors to somatic input to the superior colliculus

As pointed out earlier, the adequate stimulus commonly needed to elicit unit discharge from the trunk and limbs was a tap. The possibility that such stimuli activate deep receptors as well as cutaneous receptors was tested in six experiments. The skin of one forelimb below the elbow was first denervated by section of the superficial radial, medial, ulnar and musculo-cutaneous nerves (Kitchell, Canton, Johnson & Maxwell, 1982). The superior colliculus was then explored with a micro-electrode until a unit was identified that responded to electrical stimulation of the deep radial nerve. The surface of the forelimb over the distal part of the ulnar was then subjected to ramp displacements by a probe with a 1 mm diameter tip. The amplitudes and velocities of the displacements were similar to those used by Stein *et al.* (1976) and Nagata & Kruger (1979) in their experiments to characterize the cutaneous receptors initiating responses in the superior colliculus. Fourteen units were found in these experiments which were responsive to deep radial nerve stimulation and all fourteen units could also be activated by controlled displacements of the forelimb. The displacement parameters needed to activate the neurones were similar to those used by Nagata & Kruger (1979). The lowest velocity of displacement needed was 30 μm/ms, the smallest displacement, 10 μm. However, as Fig. 6 shows, the responses recorded in the superior colliculus from deep receptors were less velocity dependent than those reported by Nagata & Kruger (1979).

In a further series of four experiments the effects of progressive cutaneous denervation was examined. In all four experiments the 1 mm diameter probe was placed on the skin over the ulnar at a site where the onset of a 300 Hz oscillation of 100–200 μm led to unit response in the superior colliculus. The four nerves supplying
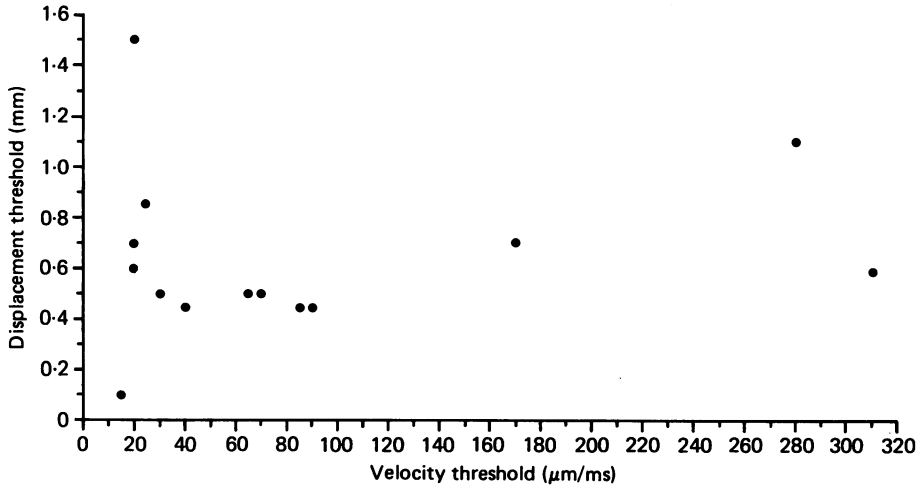
Fig. 6. Each circle gives the displacement and velocity thresholds of skin displacements which led to neuronal discharge in a neurone of the superior colliculus. The displacements were applied to the distal skin of a cutaneously denervated forelimb. Displacement thresholds were estimated at velocities 6–10 times the velocity threshold. Velocity thresholds were measured for displacements of about 2 mm.
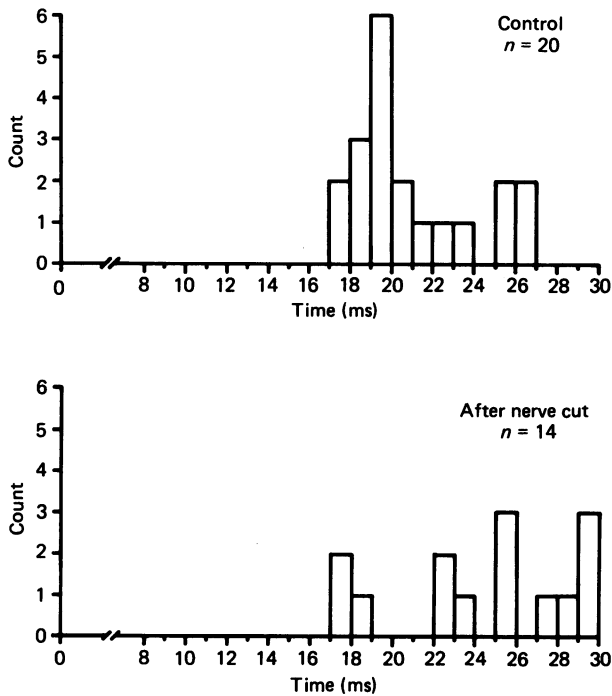

Fig. 7. Effects of cutaneous denervation on responses initiated in the superior colliculus by a 10 ms 300 Hz oscillation applied to the dorsal surface of the distal forelimb. Top, post-stimulus histogram from ten sweeps prior to denervation. Bottom, post-stimulus histogram from ten sweeps after cutaneous denervation.

Shoulder

Elbow

100 ms
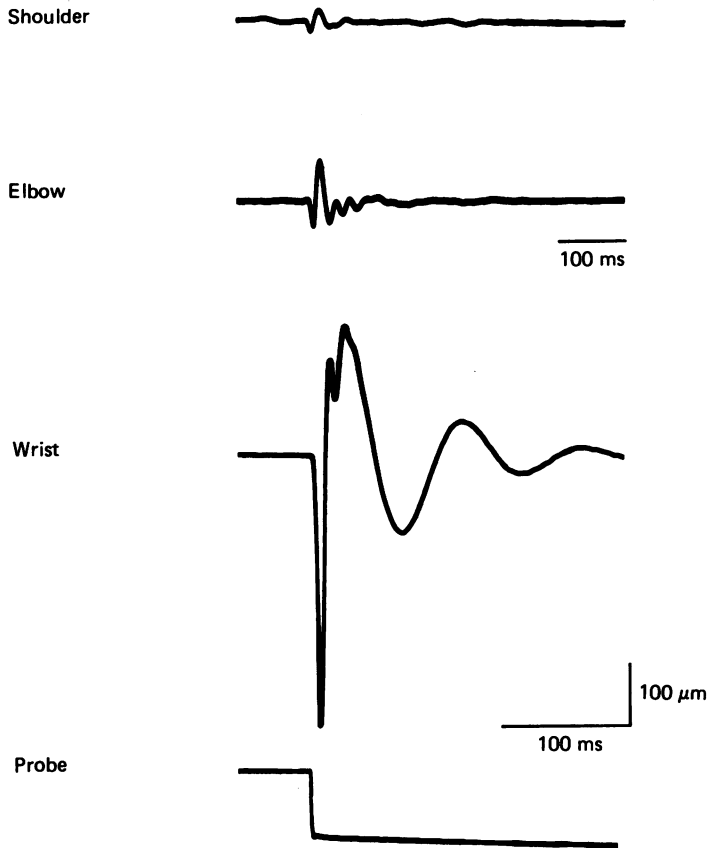
Wrist

100 μm

100 ms

Probe

Fig. 8. Records of displacements recorded by an accelerometer cemented to the skin over the shoulder, elbow and close to the wrist following an abrupt displacement of approximately 1·8 mm to the skin over the wrist. Lowest record shows output from transducer monitoring probe movement. Note the different time scale used in the bottom accelerometer record.

the forepaw skin were then sectioned in turn. In three experiments, unit response to vibration was reduced, but still present after cutting all four nerves (Fig. 7). In the remaining experiment the response was lost immediately after section of the median nerve.

Passive spread of vibration following ramp displacement applied to the skin

The large somatic receptive fields seen in the present experiments resemble those reported in previous experiments (Stein & Arigbede, 1972; Stein *et al.* 1976). Since an effective stimulus in these receptive fields is a high-velocity movement such as a tap (Stein & Arigbede, 1972; Stein *et al.* 1976; Nagata & Kruger, 1979), the possibility was explored that the stimulus caused a transmitted vibration sufficient to excite receptors distant from the stimulus. This hypothesis was tested in three experiments in which ramp displacements of the forepaw skin were applied at velocities similar to those used in the experiments of Stein *et al.* (1976) and Nagata & Kruger (1979).

Light-weight sensitive accelerometers were cemented in various positions on the forelimb and shoulder skin.

Displacements of 1·85 mm applied to the wrist at a velocity of 15 μm/ms led to a 75 μm vibration 17 mm from the probe. No transmitted vibration could be measured at the elbow at this low velocity. When the skin was displaced at higher velocities (30–400 μm/ms) vibrations travelled considerable distances and the peak displacement measured at the elbow ranged from 30 to 80 μm. In some instances the transmitted vibration was sufficiently great so that vibration could be measured at the shoulder (Fig. 8). Taps delivered over the vertebrae were found to cause transmitted vibrations which travelled for long distances over the spine. A skin displacement of 1·5 mm delivered over the lower thoracic vertebrae set up vibration with peak displacements of 300 μm close to the base of the tail.

Measurements were also made of skull vibrations elicited by taps to the stereotaxic machine or ear bar. Taps similar to those which elicited unit discharge in the superior colliculus led to a damped oscillation of the skull with a peak displacement of about 70 μm at frequencies of 125–250 Hz. This raises the possibility that neuronal responses to taps could have been bone-conducted auditory or vestibular responses in animals whose response to air conduction was impaired due to ear bar damage.

DISCUSSION

The organization of somatosensory input to the superior colliculus

It is commonly accepted that a somatotopy exists within the superior colliculus of the cat. Input to the rostral half of the structure is thought to derive from the face and occiput, that in the caudolateral region is from the contralateral forepaw and that from the remainder of the body is in the caudomedial superior colliculus (Gordon, 1973; Stein *et al.* 1976). The results presented here do not wholly support that concept. The dominant input to the superior colliculus is unquestionably from the face and although this input is most prominent rostrally, there is also input from the face to more caudal regions. There are a number of other aspects of collicular receptive fields that make it virtually impossible to construct a simple somatotopic map. These include the blend of contralateral, ipsilateral and bilateral receptive fields sometimes recorded from the same unit, the mixture of discrete and large receptive fields, the presence of neurones with input from separated body sites and the participation of deep receptors in neuronal responses to somatic stimulation. It may therefore be more useful to consider the somatosensory input to the superior colliculus on the basis of functional distinctions rather than on a somatotopic order.

The superior colliculus receives most of its input from the face and occiput and much of that input comes from two groups of specialized receptors, the planum nasale and the vibrissae. The planum nasale of the cat, like the planum nasale of all fur-bearing animals contains a wealth of receptors (Montagna *et al.* 1975; Abrahams *et al.* 1987). The structure is composed of an array of rete pegs, each of which is raised so that microscopic examination of the surface of the planum nasale shows it to be pebbled. Surrounding each peg are many encapsulated receptors, a row of Meissner's corpuscles lies at the base of the peg and free nerve endings ascend through the peg

to end in the superficial layers of the skin. Apart from the absence of Ruffini corpuscles the receptor organization of the planum nasale closely resembles that of the digital skin of the primates and thus must be considered as a major tactile organ capable of high resolution of cutaneous stimuli. The vibrissae too contain a complex array of receptors at their base and are important receptor organs (Gottschaldt, Iggo & Young, 1973). Any hypotheses which seek to explain the role of the sensory input to the superior colliculus from the face must consider the input from these specialized receptor organs and the fact that many neurones activated by that stimulus are output neurones with access to neck motoneurones.

In contrast to the receptive fields on the face, the present experiments, like many other studies, show that receptive fields on the limbs and trunk (with the exception of some on the contralateral forepaw) are usually large, sometimes discontinuous, and the adequate stimulus needs to be relatively vigorous, usually a tap (Stein & Arigbede, 1972; Gordon, 1973; Stein *et al.* 1976; Nagata & Kruger, 1979; Clemo & Stein, 1986). These characteristics cannot be attributed solely to the use of chloralose as an anaesthetic in the present experiments. Similar observations have been made in non-anaesthetized animals (Stein & Arigbede, 1972; Gordon, 1973) and in animals anaesthetized with nitrous oxide, or barbiturates (Stein & Arigbede, 1972; Stein *et al.* 1976; Meredith & Stein, 1986). This input stands in sharp contrast to that from the face and may have a separate functional role. The adequate stimulus usually excites both deep and superficial receptors over a wide area. It is the kind of stimulus that would initiate general orienting reactions, a motor role that has been proposed for the superior colliculus (Stein *et al.* 1976).

The effectiveness of synchronous receptor activation may explain why electrical stimulation of nerves (an extreme form of synchronous activation) is particularly effective in eliciting collicular discharge. In the present experiments and those of Daniellson & Norrsell (1986) electrical stimulation of nerves could excite many more units in the superior colliculus than could be excited by natural stimulation. This implies widespread subthreshold effects to natural stimuli and would be consistent with the finding that coterminous multimodal input to collicular cells can greatly facilitate or inhibit the responses observed by unimodal stimulation (Meredith & Stein, 1986). Sensory input can have prolonged effects on the excitability of both tectospinal and tectoreticular neurones (Rose & Abrahams, 1978). Once orthodromically excited, these neurones cannot be antidromically invaded for 50–600 ms.

Deep receptors and the superior colliculus

The large dorsal neck muscles contain an unusually high density of muscle spindles and other receptors (Richmond & Abrahams, 1975). They were believed to participate in the role of the superior colliculus in the execution of head movement. That hypothesis is no longer tenable since there is little if any input from neck muscle receptors. There is, however, no doubt that deep receptors in the limbs project to the superior colliculus. Earlier experiments (Abrahams & Rose, 1975*b*) based on electrical stimulation of forelimb nerves showed that virtually all receptors served by myelinated fibres may contribute to the input. The same series of experiments showed that hindlimb input to the superior colliculus comes from receptors supplied by the smaller myelinated fibres. Both muscle spindles and Pacinian corpuscles are

very likely to be activated by a tap to a limb for they are both exquisitely sensitive receptors (Hunt & McIntyre, 1960; Matthews & Stein, 1969) and they must be considered as likely sources of the input. This possibility is supported by the effectiveness of interosseus nerve stimulation, a nerve known to innervate many muscle spindles and Pacinian corpuscles (Hunt & McIntyre, 1960; Barker, 1962).

Somatosensory somatotopy and motor output from the superior colliculus to the head

Most recent theories of collicular function rely on the existence of sensory maps within the superior colliculus and have placed importance on a perceived registration between the sensory map and a motor map that has also been thought to be located within the superior colliculus (Stein *et al.* 1976; Stein, 1984). The data presented here are not consistent with the existence of a simple somatotopic map. The evidence for a head motor map in the superior colliculus is also somewhat questionable.

Early experiments (e.g. Hess *et al.* 1946) cannot, on their own, be used to define a head motor map. The experiments of Apter (1946) were based on the effects of crystals of strychnine placed on the exposed surface of the superior colliculus. The application of the strychnine initially enhanced visual-evoked potentials and after some time, visual stimuli led to appropriate eye movements to foveate the stimulus. Longer periods of contact with strychnine led to neck muscle contractions, but these were not well organized and were also associated with movements of other muscles. These experiments do not permit the construction of a motor map. Electrical microstimulation experiments (Harris, 1980; Roucoux *et al.* 1980) support the view that there is a separation of collicular regions controlling eye and head movements and that head movements are most readily obtained by stimulation of caudal collicular regions. The nature and extent of the head movements that were observed were related to the duration of the stimulus as well as the stimulus site. None the less, Roucoux *et al.* (1980) describe the head movements that they observed as goal directed, that is the movements always brought the head to a particular position in space regardless of the initial position of the head. Harris (1980) was not able to confirm the observations of goal-directed movements, but found that the duration of stimulation determined the size of a stimulus-induced head movement. These results are sufficiently contradictory that they are not sufficient to support the notion of a head motor map located in the superior colliculus.

Facial input to the superior colliculus and the foveation hypothesis

Most experiments on the motor role of the superior colliculus have been concerned with the organization of gaze movements (Harris, 1980; Roucoux *et al.* 1980), that is co-ordinated movements of both head and eyes which lead to foveation of a target. It is widely presumed that the organization of gaze movements is a major collicular function. However, foveation is only one of a number of head motor tasks that should be considered in any functional analysis of the superior colliculus of the cat. Sensory organs of the head include those used for olfactory and tactile exploration. The use of these systems will require head movements not necessarily related to foveation; nor do many of the movements associated with feeding and grooming. In particular, the effective use of the planum nasale as an organ of tactile exploration will require tight integration of the input from this structure with the neural

elements controlling head movements. One other motor act of the head which must be of overriding importance is the execution of aversive movements. There is an imperative need for a system capable of removing the head and its receptor organs quickly from potentially harmful situations. Tactile input from wide regions of the face must be able to initiate such movements and the connections exist within the superior colliculus for tectospinal neurones to provide a suitable output. There is, however, evidence that tectospinal neurones only exert weak effects on neck motoneurones (Anderson *et al.* 1971). These experiments suggested that the tectospinal pathway has only weak synaptic effects on neck motoneurones and reticulospinal pathways are far more effective. However, both indirect (Rose & Abrahams, 1978) and direct (Grantyn & Grantyn, 1982) experiments show that tectospinal axons collateralize extensively among reticulospinal neurones and that by activating those neurones, tectospinal neurones can exert powerful effects on neck motoneurones.

Considerable evidence already exists for an oligosynaptic pathway from trigeminal receptors to neck motoneurones that could underly a wide range of head motor activity including aversion (Manni, Palmieri, Marini & Pettorossi, 1975; Sumino & Nozaki, 1977; Abrahams, Anstee, Richmond & Rose, 1979). Whether aversive movements utilize a collicular loop or a more direct pathway from the trigeminal system to neck motoneurones is as yet unknown. Electrophysiological and anatomical experiments have shown that trigeminal primary afferent fibres project to the upper cervical cord (Kerr & Olafsson, 1961; Kerr, 1972) and it was suggested by those authors that this is a pathway for eliciting aversive reflexes. However, neck motoneurones are mostly activated 7–20 ms after electrical stimulation of branches of the trigeminal nerve (Sumino & Nozaki, 1977; Abrahams *et al.* 1979). These latencies are sufficiently long for a trigemino-cervical reflex pathway involving the superior colliculus.

The data presented here reinforce the importance of the input from the face to the superior colliculus. The nature of these connections and the origin of many of the afferent fibres in specialized receptors of the face make it plausible that the superior colliculus participates in many motor acts as well as those of foveation.

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