

NERVE IMPULSES IN THE BRAINSTEM AND CORTEX OF THE GOAT. SPONTANEOUS DISCHARGES AND RESPONSES TO VISUAL AND OTHER AFFERENT STIMULI

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During investigations on the brainstem of the goat designed to trace the central responses to stretching the extrinsic eye muscles (Cooper, Daniel & Whitteridge, 1953*a, b*), other responses were often detected. These might be spontaneous, or they might be initiated by afferent stimuli. Some of them constituted useful physiological landmarks and formed a necessary adjunct to any attempt at localization by co-ordinates alone. Sometimes they were interesting enough to merit further study, and we propose to draw attention to certain outstanding features. Much spontaneous activity is found in the brainstem of an animal under light pentobarbitone anaesthesia. Certain patterns can be associated with motor-type cells, with the cerebellum and its pathways, and with parts of the superior colliculus. In addition, responses can be recorded from visual, auditory and vibrational stimuli and from the manipulation of various parts of the body. The responses from the jaw and eye muscles have already been dealt with, and only late responses from the jaw muscles will concern us here. In approaching the midbrain in intact animals the microelectrode necessarily went through the visual cortex, and a certain number of observations were made.

METHODS

The methods and materials used are fully described in the preceding papers. A microelectrode was used to explore the brain or brainstem of goats in a stereotaxic head-holder. The animals were either under pentobarbitone anaesthesia with an intact brain, or, in the later work, were decerebrated at the colliculo-pulvinar border and given small doses of pentobarbitone in an intravenous saline drip. Visual stimuli were sometimes given by a bright light flashed into the animal's eye when the contralateral side of the brain was being explored. When responses to localized visual stimuli were being studied, the eye was fixed by a wire ring sewn to the cornea. A small perimeter was then centred on the eye and a neon flash, synchronized with the sweep of the cathode-ray tube, was moved relative to the retina. The flash had an illuminated area of about 25 mm², and its diameter subtended an angle of about 1° on the eye. Auditory stimuli were given by clicking a pair of forceps, and vibrational stimuli by tapping the table or the stereotaxic framework. The body or limbs were merely touched or moved.

RESULTS

The sites from which many of the responses described in this paper were obtained are entered on the sagittal diagrams of the brainstem in text-fig. 1 a-g of our previous paper (Cooper *et al.* 1953 a).

Spontaneous discharges

Numerous patterns of spontaneous discharge can be detected in the brainstem. Many of these are random discharges associated with no particular place. Whilst some are doubtless expressions of spontaneous activity, others are injury discharges caused by damage to a cell by the advancing needle tip. These latter impulses often show very high rates of firing. The discharge is short-lasting and cannot be influenced by sensory stimuli.

In certain groups of cells a regular discharge of impulses can often be recorded, the pattern being typical for those cells. Fig. 1 shows such a regular discharge obtained with the needle tip in the nucleus of the third nerve. The single unit is firing at about 75 impulses/sec. The record shown in Fig. 2 was

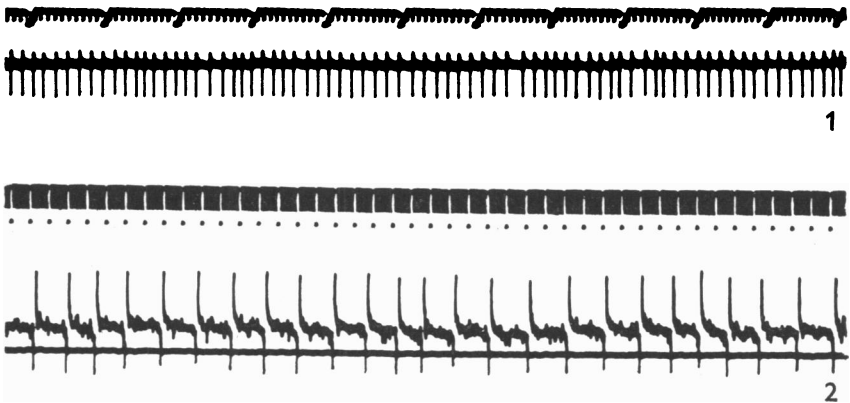


Fig. 1. Spontaneous discharge of a single unit recorded from the nucleus of the third nerve in an intact goat. Above: time in 10 msec.

Fig. 2. Spontaneous discharge of a single unit recorded from the red nucleus in an intact goat. Above: time in 10 msec.

obtained from the region of the red nucleus. We have come to associate such large diphasic responses with a nucleus composed of big motor-type cells such as are found in the red nucleus, the reticular nuclei of the midbrain and pons, and the motor nuclei of the fifth and seventh nerves.

We frequently heard the repetitive discharges from many units which we have described as 'train' noises (Cooper *et al.* 1953 b). We first heard them when the needle tip was passing through the medial longitudinal fasciculus ventral to the nucleus of the third nerve. In later experiments they were heard in other cerebellar pathways in the brainstem and also in the cerebellum itself.

It was sometimes possible to advance the needle very slowly at the edges of the fibre tracts, so that single units could be picked up. The impulses were found to occur in groups, which were repeated at a rate of 6–15/sec; within the group the rate of discharge of impulses might be very high. The record in Fig. 3 shows an example of this type of rhythm in an intact goat under pentobarbitone anaesthesia, the needle tip being in the fibres of the superior cerebellar peduncle. The discharges of the big unit form groups which recur regularly at 6/sec. Within each group the unit discharges 3 or 4 times at a rate of about 100 impulses/sec. Similar spontaneous single unit discharges were found in comparable sites in both intact and decerebrate animals, and were also recorded in the medial longitudinal fasciculus ventral to the nucleus of the third nerve and in the basilar part of the pons.

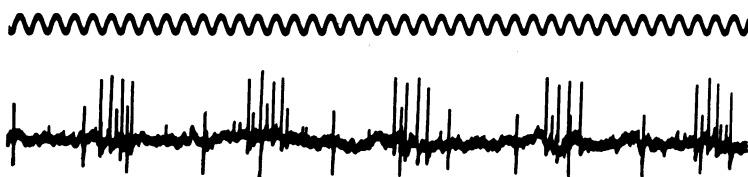


Fig. 3. Spontaneous discharge in the superior cerebellar peduncle of an intact goat. The large unit above the baseline discharges in bursts of impulses, each burst recurring at 160 msec. The diphasic impulse occurs irregularly at about 12/sec. Above: time in 50 c/s.

Spontaneous discharges were regularly obtained from the fibre layers of the superior colliculus. It was usually possible to distinguish between the stratum griseum and the stratum opticum as the needle tip passed through these layers. In complete darkness there were often other spontaneous rhythms in the superior colliculus. These were usually single unit discharges in the superficial layers. They could be abolished by light and will therefore be dealt with in the section on visual responses.

Visual responses

We found that there were well-marked and accurately localized responses in the superior colliculus of the goat to focal stimulation of the contralateral retina by a light. The superior colliculus is relatively very well developed, the stratum zonale is thin, but the stratum griseum often has a thickness of 1.5–2.0 mm in the middle of the colliculus and spreads out to form a considerable cap over the whole colliculus. Directly under the stratum griseum lie the fibre layers, and a study of horizontal sections shows how some of the optic nerve fibres sweep in from the direction of the lateral geniculate body, over the pretectal region, and into the stratum opticum of the colliculus. Below the stratum opticum lies the stratum lemniscum, with fibres coming in from the caudal end of the colliculus, and many fibres sweeping over towards the mid-line and posterior commissure. The layers of the superior colliculus are well seen in pl. 1, figs. 1–3 (Cooper *et al.* 1953*a*).

In experiments with a penetrating microelectrode the intact anaesthetized animal is very suitable for work on the localization of visual responses, since the surface of the colliculus is not subjected to exposure. As the needle tip entered the colliculus it was nearly always possible to get responses to visual stimulation. The depth of the needle for these first responses, and the ultimate depth of the run, formed one of our most reliable guides for estimating the shrinkage in the brainstem due to fixation. Localization studies on the colliculus in response to focal stimulation of the retina are also a guide to the position of the needle tip in the brainstem buried under about 2.0 cm of cerebral hemisphere. We did little exploration of the colliculus in the decerebrate animals; we had the advantage here of direct vision, so that we did not need help in finding our position in the brainstem. We took no particular precautions to protect the surface layers, which were probably inactive. We got localized responses to visual stimulation in the deeper layers in some of those decerebrate animals which still had an intact optic pathway.



Fig. 4. Discharge from a point 0.4 mm below the surface of the superior colliculus of an intact goat during complete darkness. About 40 msec after the light is turned off a unit begins to discharge and continues to do so throughout the period of darkness. When a light is shone into the contralateral eye there is a wave 'on' effect and the unit stops discharging. Many of the units are double. Above: time in 50 c/s; light signalled by photocell, up indicates light off.

Responses to stimulation of the contralateral retina by light can be obtained from the whole surface of the colliculus as well as from the underlying layers and also from that superficial part of the pretectum composed of optic tract fibres on their way to the colliculus. The sites of responses to visual stimuli may be seen in text-fig. 1*b-f* (Cooper *et al.* 1953*a*). Text-fig. 1*e* and *f* show the sites of the responses that were obtained in the pretectal region. No responses were found in the mid-line. The responses to visual stimuli are entered as diamonds; when we got sharply localized responses to focal retinal stimulation the diamonds have been filled in, \blacklozenge .

During periods of complete darkness there were sometimes marked spontaneous discharges in the colliculus. If the animal's contralateral eye was illuminated for short periods, both 'on' and 'off' effects were clearly heard. In the record in Fig. 4, when the light goes off, the needle records the discharge

of a single unit firing at a rate of about 50 impulses/sec after a latency of 40 msec. This unit stops discharging when the light is turned on, and the wave which follows may well be an 'on' effect. A record from another animal is shown in Fig. 5. About 70 msec after the light is turned off there is a series of waves at a rate of about 25/sec. There is a tendency for these waves to be in groups at about 3.5/sec. They were abolished by even a feeble light.

When the retinal illumination was by means of a small neon flash and was focal in character, the responses could only be obtained from small restricted areas of the colliculus. Once the collicular response had been detected, a movement of the light, greater than 10–15° on the perimeter, immediately abolished it. The localization results are not sufficiently numerous for us to attempt to

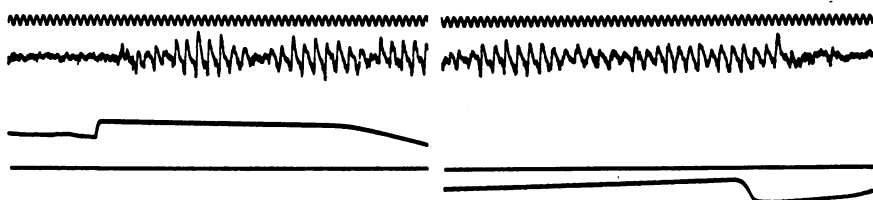


Fig. 5. Discharge obtained from a point 0.4 mm below the surface of the superior colliculus of an intact goat during complete darkness. About 70 msec after the light on the contralateral eye is turned off a wave discharge begins. The waves recur at about 25/sec and tend to be grouped in spindles at about 3.5/sec. The gap indicates an interval of 1.5 sec. The waves outlast the period of darkness by about 150 msec. Above: time in 50 c/s; below: light signalled by photocell, up indicates light off.

give a map of the colliculus, but we found that the horizontal meridian is strongly represented on an oblique antero-posterior strip of the contralateral colliculus, the caudal end of this strip being closer to the midline than the rostral end. Responses at the caudal end are from the nasal part of the retina; those at the rostral end are from the temporal part. The lower part of the retina is represented medial to the antero-posterior strip of the contralateral colliculus, while the upper part is represented laterally. Both the retina and pupil of the goat are better adapted for lateral than for vertical vision.

The more dorsal and the deep lateral sites on the colliculus usually gave wave responses to a localized neon flash. Sometimes it was possible to detect single units superimposed on these waves. Responses in the form of single units were most commonly found in the middle layers. The wave response shown in Fig. 6 came from a site in a deep lateral layer; there is a latency of 25 msec, and there are three main waves occurring at intervals of about 70 msec. The record in Fig. 7 is from one of the fibre layers of the colliculus; the noise level is high, due to much spontaneous discharge, but the single units are none the less clear, following the flash with a latency of 30 msec.

A localized response to the flash found in the surface layers of the colliculus was sometimes lost as the needle tip passed deeper, but by moving the light

a new position on the retina could be found giving a good collicular response. Text-fig. 1*b-f* (Cooper *et al.* 1953*a*) gives some idea of the depths from which the responses to visual stimulation could be obtained. Visual responses at depths of up to 8 mm were found in the more lateral regions. In one experiment (text-fig. 1*d*) a clear-cut visual response was picked up in the fibres just rostral to the central grey matter of the midbrain. The record showed an 'off' effect in which the first burst appeared after a latency of 180 msec, and was followed

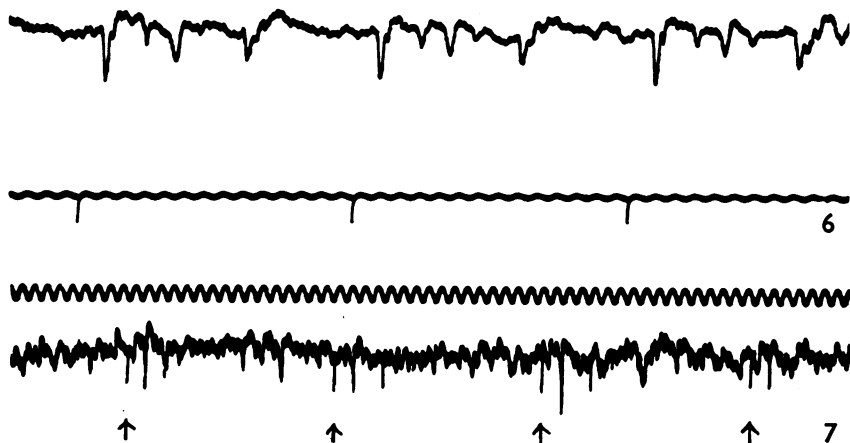


Fig. 6. Responses to localized flashes on the retina of the contralateral eye recorded from a deep lateral region of the superior colliculus, 4.0 mm below the surface, in an intact goat. Wave responses only are seen, starting 25 msec after the flash and continuing for 150 msec. Below: time in 50 c/s, with the neon flash signalled on the time trace.

Fig. 7. Responses to a neon flash localized on the fixation point of the contralateral eye. Recorded from the fibre layer of the superior colliculus, 2.0 mm below the surface, in an intact goat. The background is noisy, but each flash is followed after 30 msec by a single unit. A second impulse is usually seen about 40 msec later. The neon flash is signalled on the recording trace itself as shown by the arrows. Above: time in 50 c/s.

by a second burst 140 msec later. At a site 0.03 mm more ventral there were responses to pulling on the ipsilateral eye muscles. At several sites in the stratum opticum, and in the fibres connected with this stratum in the pretectal region, responses to pulling on ipsilateral eye muscles were obtained (Cooper *et al.* 1953*b*). At some of these sites responses to contralateral visual stimulation could also be picked up.

Cortical responses

Since our approach to the midbrain lay through the occipital lobe, we often tested for the visual area of the cortex and were interested to see if we could get any responses to pulling on eye muscles from the adjacent areas of the cortex. We had no difficulty in getting responses to visual stimuli, and found that the upper part of the contralateral retina was represented farther forward

in the cortex than the lower part. The best surface responses were obtained from a strip of cortex about 1.0 cm wide running forward from the occipital pole. As the needle tip advanced, other parts of the visual cortex were detected deep in sulci or on the ventral surface of the hemisphere. This ventral surface overlies the dorsal surface of the superior colliculus, but there was always a period of silence as the needle tip passed from one structure to the other. In the course of some runs, in experiments in which the anaesthesia was light, stretching ipsilateral eye muscles gave responses at sites in the cortex near to, but not coincident with, those that gave visual responses. These eye-muscle responses were heard on the loud-speaker, but were not suitable for photography.

In one experiment we explored a small part of the sensory cortex. There was an area that gave good responses to stroking the dorsum of the contralateral forelimb. About 2.0 mm rostral to this area responses could be obtained from touching the ipsilateral upper lip; more rostral still was the area for the ipsilateral lower lip. These results agree exactly with the representation of the somatic receiving area in the goat given by Adrian (1943*a*).

Auditory responses

Our animals, with fixation plugs in their auditory meati, were not ideal preparations for investigating auditory responses. Nevertheless, responses were very easily detected in any part of the auditory system that the needle traversed. They were picked up in the inferior colliculus and its commissure, and also in the lateral lemniscus, the superior olive and the trapezoid body. The click from a pair of forceps was sufficient stimulus, and the best responses were obtained when the stimuli were applied to the contralateral ear. These responses formed a good physiological landmark for the boundary between the caudal end of the superior colliculus and the rostral end of the inferior colliculus. Associated with the auditory effects were responses to vibrational stimuli. On the pathway between the inferior colliculus and the nuclei of the eighth nerve, responses could be picked up to any touch of the animal, stereotaxic framework, or table.

Responses from various parts of the body

Limbs and trunk. Sometimes stimuli were applied to the limbs or body and the effects either noted or recorded. The sites of these responses have been entered as crosses, +, in text-fig. 1*b-d* and *f* (Cooper *et al.* 1953*a*). Responses obtained by tapping or flexing the contralateral limbs were picked up in the rostral end of the medial longitudinal fasciculus (text-fig. 1*b*) and, slightly more laterally, in the central tegmental tract (text-fig. 1*c, d*). In this tract the responses to stimulating the fore-limb tended to be picked up at a more dorsal level than the responses from the hind-limb. Fig. 8 shows a response to

flexing the opposite ankle when the needle tip was in the tegmental tract. There are spontaneous units firing at slow rates; the stimulus causes repetitive bursts. The latency of the first burst is long, the discharge rate during the burst is high, and the bursts recur at 7.5/sec. The discharges probably bear no relation to the duration of the stimulus. Sometimes in these regions very slight peripheral stimuli produced responses. In one experiment, when the needle tip was in the medial longitudinal fasciculus ventral to the nucleus of the third nerve, very light pressure on the pad of the contralateral hind-hoof gave a single burst of up to a dozen rapid impulses.

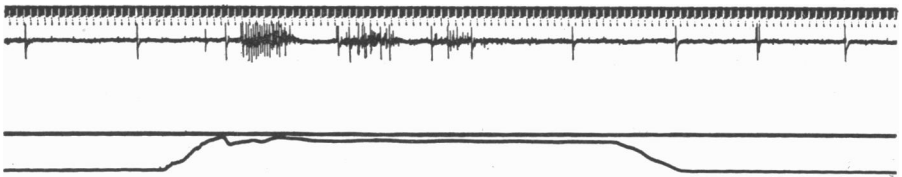


Fig. 8. Response to flexing the contralateral ankle recorded from the central tegmental tract in the midbrain of an intact goat. The large unit responds with repetitive bursts after a latency of 120 msec. A rate of 400 impulses/sec is reached in the first burst. Above: time in 10 msec; below: flexion signalled by condenser system.

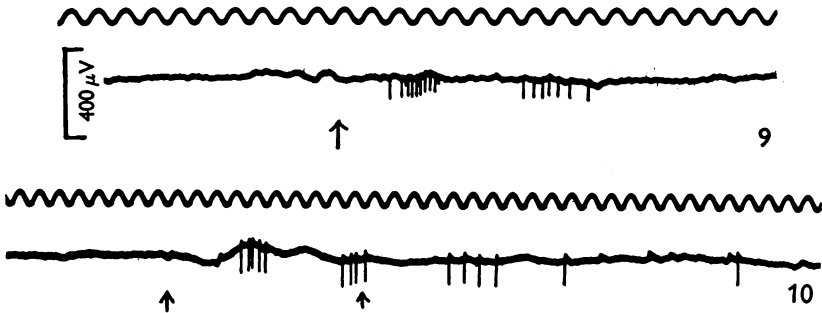


Fig. 9. Response to tapping the contralateral foreleg recorded from longitudinal fibres immediately dorsal to the red nucleus in an intact goat. After a latency of about 35 msec there are two bursts of impulses. Amplification greatly reduced. Above: time in 50 c/s; tap indicated by arrow.

Fig. 10. Response to pressing the contralateral thigh recorded from longitudinal fibres along the lateral border of the red nucleus in an intact goat. The latency is about 70 msec and repetitive bursts of impulses are seen. Amplification greatly reduced. Above: time in 50 c/s; pressure applied between arrows.

Another group of responses to body stimulation was found in the neighbourhood of the red nucleus (text-fig. 1 *c, d*). The record in Fig. 9 was obtained when the contralateral fore-leg was tapped. The latency is about 35 msec and there are again two bursts of impulses, the first showing a discharge of up to 400 impulses/sec, while the discharge in the second is about half this rate. The bursts recur at 10/sec. The record in Fig. 10 is from a similar site, the stimulus

being a tap to the contralateral thigh. There is a repetitive discharge of bursts at about 10/sec, each burst having fewer impulses than its predecessor.

Occasional responses were noted in the deeper layers of the superior colliculus. Other responses, entered in text-fig. 1*f*, were obtained when the needle tip was just caudal to the thalamus and fairly well lateral. The more dorsal response was elicited by touching the thigh and base of the tail; the ventral one by tapping the Achilles tendon. Both responses were contralateral.

Jaw muscles. In addition to the short latency responses to stretching the jaw muscles already reported (Cooper *et al.* 1953*a*), we obtained many late responses to stretching these muscles. The sites were identified histologically and entered as open triangles in text-fig. 1*a-g* (Cooper *et al.* 1953*a*). These responses were found in the medial longitudinal fasciculus, the tegmental tract, and on the outskirts of the mesencephalic nucleus of the fifth nerve, especially near its more caudal end. A group of late jaw responses was also found near the head of the spinal nucleus of the fifth nerve. A record of a response to

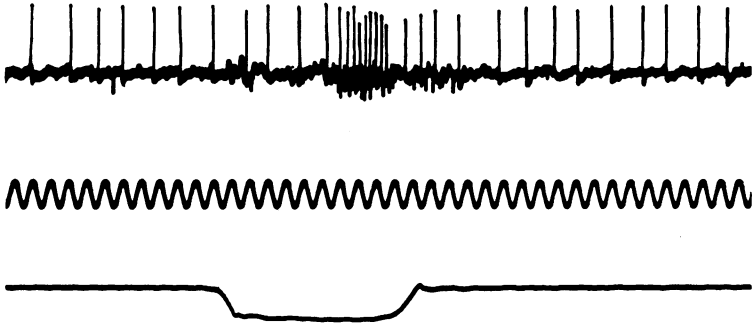


Fig. 11. Response to stretch of the jaw muscles. Afferent discharges from a single unit in a decerebrate goat recorded from fibres ventral to the medial longitudinal fasciculus and medial to the red nucleus. There is a spontaneous discharge, and 140 msec after opening the jaw there is a burst of impulses reaching a rate of about 150/sec. Amplification reduced. Below: time in 50 c/s; stretch signalled by a condenser system.

stretching the jaw muscles, when the needle tip was in the ventral aspect of the medial longitudinal fasciculus near the red nucleus, is given in Fig. 11. This response consists of a single burst of impulses. Other responses were often repetitive in character. No systematic work was done on these late jaw responses, but the stimulus of stretching the jaw muscles was very frequently given and any response was noted. In the region of the medial longitudinal fasciculus and the tegmental tract in the midbrain, responses from the proprioceptors of the eye muscles, jaw muscles and body were frequently noted in sites that were in close proximity, but good responses were rarely obtained in identical sites. More caudally in the pontine regions the sites of the responses to stretching the jaw muscles were much more separated from the sites of the eye muscle responses, thus pointing to quite distinct pathways.

Face. Ipsilateral responses were obtained from tactile stimuli to the face, especially in the main sensory nucleus of the fifth nerve. As the needle tip advanced through the nucleus, responses were obtained successively from the lower jaw, the base of the ear, the upper lip and, finally, the nose. Thus, the sensory representation of the face appears to be upside-down in the nucleus. This is perhaps interesting when compared with observations on the rotation of the sensory root between the Gasserian ganglion and the pons (Davis & Haven, 1933).

The responses described in this section were merely the result of sporadic testing. No note has been made of the many negative results. Most of our responses appeared to come from the stimulation of proprioceptors rather than from exteroceptors. A study of the horizontal diagram in text-fig. 2 (Cooper *et al.* 1953*a*) shows that by chance the main line of the medial lemniscus was missed in the exploration. It is of interest that responses from the body proprioceptors can be detected in various sites in the brainstem, while most of the responses from the exteroceptors presumably run through this region in a restricted pathway on their way to the thalamus and cerebrum.

DISCUSSION

It is well known that considerable spontaneous electrical activity goes on in the nervous system, even under quite deep anaesthesia. In the course of our exploration we met with some of this activity. We only wish here to comment on those patterns of discharge that come from identifiable sites. It was usually possible to recognize the impulses in the main motor nuclei. There was much spontaneous activity, and if a single unit was picked up it was usually found to be discharging at a regular rate of 50 impulses/sec or more; this rate might be maintained for an indefinite period. The assumptions are that some of the activity is from cells engaged in maintaining the tone of the muscles; some may be from cells of origin of the small nerve fibres to the muscle spindles; some again may be from the pre-motoneurones whose discharge is not sufficient to stimulate the final motoneurones and so set up a contraction. In those experiments in which we had recording needles in the extrinsic eye muscles for recording the threshold for motor discharge we sometimes found small units discharging spontaneously. There was certainly tone in the animal's muscles, and this would demand discharges from a number of units. The intra-fusal muscle fibres would, in these conditions, also be activated (Hunt, 1951). We found that nuclei composed of large motor-type cells, such as the red nucleus, were in a constant state of activity.

We made little direct study of cerebellar activity, but no doubt it plays a significant part in modifying proprioceptive messages at some stage in their passage through the nervous system. According to Grundfest & Campbell (1942), proprioceptive discharges from the limbs travel more rapidly in the

spino-cerebellar pathways than do the discharges which travel in the fasciculus gracilis. If this is the case, then the cerebellum is in a position to modify the later messages to other places. Knowledge of the complexity of cerebellar pathways is increasing (Snider, 1950); the inferior olive, for example, is assuming greater importance in relation to the cerebellum (Brodal, Walberg & Blackstad, 1950). The spontaneous activity of the latter organ is not fully understood (Adrian, 1943*b*; Brookhart, Moruzzi & Snider, 1950, 1951). Rhythms of 10–15/sec are reported by these authors; some of these may be intrinsic, others may be imposed by structures such as the cerebral hemispheres or the thalamus. We did not obtain records from the cerebellum itself, but we obtained many records from pathways, such as the superior cerebellar peduncle, which are supposed to be exclusively cerebellar, or from the medial longitudinal fasciculus which has a strong cerebellar element. We were impressed by the prevalence of a 7–15/sec rhythm in these pathways, in spite of the fact that a number of the animals were decerebrate. It seems likely that this rhythm may have affected some of the late repetitive responses discussed in these papers.

Stimulation of small areas of the goat's retina by a light has shown that there is a point-to-point localization between the retina and the contralateral superior colliculus. This finding amplifies and confirms the work done with surface electrodes on the rabbit (Wang, 1934) and cat (Apter, 1945), and also the degeneration studies by Bodian in the opossum (1937). In experiments on monkeys we obtained comparable results, and this leads us to suppose that such localization is a feature common to all mammals. The advantages of a fine microelectrode are that the responses are picked up from a very small area, not only close to the surface, but also in the deeper layers. On exploring the deeper layers of the colliculus with the needle tip, point-to-point localization was still found, but one point on the retina might be related to various points in the deeper layers. This localization could be found throughout a considerable depth of colliculus, as indicated in the diagrams of text-fig. 1 (Cooper *et al.* 1953*a*). Probably with different, or lighter, anaesthesia localization could be found even deeper, since there is a close relation between the superior colliculi and the oculomotor nuclei (Apter, 1946). It should be emphasized that it is the responses from the surface that have hitherto provided the material for evidence of retinal projection on the colliculus. The responses from the deeper strata need to be investigated further.

We pointed out in our previous paper (Cooper *et al.* 1953*b*) that responses to stretching the ipsilateral eye muscles were also found in the fibre layers of the superior colliculus at sites closely adjacent to the sites from which responses to contralateral visual stimuli were obtained. This juxtaposition of visual and eye-muscle responses suggests that the proprioceptors of the eye muscles are of importance in any relationship between the colliculi and the eye

muscles. For instance messages from the proprioceptors of the eye muscles may play a part in the visual grasp reflex (Hess, Bürgi & Bucher, 1946).

The records of the visual responses show a few points that are worth further comment. Figs. 4 and 5 show latencies of 40 and 80 msec for the 'off' effect. The latencies for the responses to flashes shown in Figs. 6 and 7 are 25 and 30 msec. These are of the same order as those found for visual responses in the optic nerve and the visual cortex, and must be almost entirely due to retinal delay. If the impulses travel in fibres of similar size, the latency of the collicular response should be slightly less than that of the cortical response, since the impulses to the cortex have a cell station in the lateral geniculate body and a slightly longer pathway.

Wave responses to visual stimuli of the retina have previously been recorded from the superior colliculus, but we are unaware of records showing single units. Well-defined single units are seen in Figs. 4 and 7. The waves seen in Fig. 5 are interesting in that they are occurring when the retina is not being stimulated and are reminiscent of, but much faster than, the cortical waves which can be recorded when the eyes are closed (Adrian & Matthews, 1934). Similar phenomena have been observed in rabbits (Hamdi & Whitteridge, in preparation).

Our observations on cortical localization to contralateral visual stimuli were few, but they did confirm that the antero-posterior representation was similar to that in other mammals. Since sites for responses to eye-muscle pulls were found adjacent to sites for responses to retinal stimulation in the superior colliculus, and since stimulation experiments have shown that there is a close connexion between the colliculus and the oculomotor nuclei, we looked for similar conditions in the cortex. The areas adjacent to the visual cortex are known to be concerned with eye movements, and we did find here faint responses to ipsilateral eye-muscle pulls, particularly in animals in which the anaesthesia was light. We see no reason to doubt that a similar state of affairs exists in the higher mammals and man. Considerable integration between proprioceptive responses from the eye muscles and visual responses may well take place in the cortex.

Exploration of the auditory and vestibular pathways by a needle electrode technique has been carried out on the cat by Ades & Brookhart (1950) and Gernandt (1950). We obtained single unit responses to click stimuli from all parts of the brainstem auditory pathways central to the nucleus of the eighth nerve.

The main features of the body and limb responses picked up in the course of our work were their repetitive character and long latency. To some extent they resemble the late repetitive response to stretching an eye muscle described in a previous paper (Cooper *et al.* 1953*b*), and were detected in similar pathways. They were mostly from intact animals, so that we have no means of

knowing the direction in which they were travelling. We are inclined to believe that some form of cerebellar influence has been impressed on the primary messages, since the spacing of the repetitive bursts was similar to the rhythms which we recorded in cerebellar pathways. Our results are too few to confirm this. The presence of localized responses to limb stimulation in the tegmental tract of the midbrain suggests that there is an organized pathway for proprioceptive impulses in this region. The number of responses to stimulation of the proprioceptors of the eye muscles, body muscles and jaw muscles in the tegmental tract and in and near the medial longitudinal fasciculus certainly suggests that this tegmental region of the midbrain is of importance for the transmitting of messages and perhaps for the full functioning of the proprioceptive system.

SUMMARY

1. Patterns of spontaneous discharge recorded with a microelectrode in the brainstem of the goat are described and discussed.
2. Localized responses to focal stimulation of the contralateral retina with a light were recorded from the surface and deeper layers of the superior colliculus. The significance of these in relation to eye movements is discussed.
3. Faint responses to pulling on an eye muscle were obtained from areas of the cortex adjacent to the visual cortex.
4. Discharges in the brainstem were obtained in response to auditory and body stimulation.

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