Interaction between Cortico-tectal and Retino-tectal Inputs as Revealed by Analysis of Field Potentials of the Cat's Superior Colliculus

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Tamai, M. and Ogawa, T. Interaction between Cortico-tectal and Retino-tectal Inputs as Revealed by Analysis of Field Potentials of the Cat's Superior Colliculus. Tohoku J. exp. Med., 1972, 107 (2), 127–142 — In chloralose-anesthetized cats, electrical stimulation of the optic tract evoked a negative-positive field potential wave at the surface of the ipsilateral superior colliculus which reversed to a positive-negative wave at the deeper part of the superficial gray layer. The maximal amplitude of the deep positivity was reached at the optic layer. Cortical stimulation of visual and surrounding areas elicited similar field potentials in the ipsilateral superior colliculus. Reversal in polarity occurred at the same depth as did for the tract-evoked field potential. In general, stimulation of cortical areas surrounding the visual cortex, for example, the posterior suprasylvian gyrus, gave rise to a larger response than stimulation of the visual cortex. Reversible inactivation of the cortical visual and adjacent areas by cooling resulted in a reduction of the tract-evoked field potential with a gradual recovery to the initial amplitude after removal of the cooling agent. This finding indicates that the geniculo-cortico-tectal pathway contributes the generation of collicular response to stimulation of the retinotectal pathway. Topographical interrelationships between the effective cortical area and the superior colliculus were examined with the amplitude of cortically evoked collicular responses as an index. It was revealed that the junctional part between the lateral and postlateral gyri was related to the posterior part of the superior colliculus and that the upper part of the post-suprasylvian gyrus was associated with the anterior part of the superior colliculus. As to interaction between cortico-tectal and retino-tectal inputs, it was found that preceding stimulation of the effective cortical areas produced an initial facilitation from 50 to 200 msec followed by a depression of collicular response to optic tract stimulation lasting for as long as 500 msec. —— cat's superior colliculus; visual cortex; field potential

The mammalian superior colliculus is a homologue of the optic tectum of lower vertebrates. Although the function of the optic tectum has been established as the main visual center, that of the superior colliculus is not fully understood. Recently evidence has accumulated that the superior colliculus of mammals is not a vestigial structure but plays an important role in visually-guided behavior

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The superior colliculus of the cat has a laminar structure, which consists of seven layers (Huber and Crosby, 1943); four prominent fiber layers and three cellular layers which are sandwiched between them. Among them the superficial three layers, i.e., the stratum zonale, stratum griseum superficiale and stratum opticum, are believed to receive visual inputs from retino-tectal fibers and also from cortico-tectal fibers originating from the visual cortex and its adjacent cortical areas (Barris et al. 1935, Beresford 1961, Altman 1962, Lund 1964, Meikle and Sprague 1964, Otani 1964, Garey 1965, Lund 1966, Garey et al. 1968). The deeper layers are associated with other sensory modalities such as somatosensory and acoustic and receive projection from cortical areas other than the visual cortex (Sprague 1963, Garey et al. 1968).

An increasing number of reports have been published concerning the function of the cortico-tectal input (Jassik-Gerschenfeld and Ascher 1963, Jassick-Gerschenfeld et al. 1966, Meuldres and Colle 1966, Sprague 1966, Wickelgren and Sterling 1969a, 1969b, McIlwain and Fields 1970, Hoffman and Straschill 1971). Jassik-Gerschenfeld et al. (1966) and Meuldres and Colle (1966) demonstrated that the magnitude of collicular field potentials evoked by light or stimulation of the optic nerve was diminished with ablation or temporary inactivation of the visual cortex, and maintained that this finding should be interpreted as being due to loss of cortical facilitatory influences. On the other hand, another group of authors claimed that visual cortical inactivation did not affect collicular field potentials (Altman and Malis 1962, Marchiafava and Pepeu 1966, Marchiafava et al. 1968). Although Marchiafava et al. (1968) observed the reduction of collicular field potential during cooling of the cerebral cortex, they interpreted this finding as being due to inhibitory effect of irritative discharges in the cortico-tectal pathway caused by cooling.

The present experiments were undertaken to shed more light upon the interaction between cortico-tectal and retino-tectal inputs. This paper is concerned with analyses of evoked collicular field potentials and the subsequent paper will deal with the same issue in terms of unitary discharges of collicular neurons.

**Methods**

Fifty-three adult cats were used in these experiments. They were anesthetized with ether for initial surgical operation and subsequently maintained with chloralose (70 mg/kg body weight) administered intravenously throughout the experiment. The head was firmly fixed on a stereotaxic head holder. During an experiment the animal was paralysed with gallamine triethiodide administered through a cannula inserted into the superficial vein of right forearm and maintained on artificial respiration.

The skull was opened by means of a dental burr at three sites. A small hole was made at 12.5 mm anterior to the interaural line, through which bipolar stimulating electrodes were inserted vertically into the optic tract. The second hole was situated 2 mm lateral to the sagittal suture at the interaural line, through which a recording electrode could reach the superior colliculus. The third opening was large enough to expose the visual cortex and its adjacent cortical areas. Unfavorable movements of the brain due to
pulsion and respiration were minimized by various manoeuvres, such as applying a plastic presser foot on the brain, pneumothorax, cisternal drainage and a skin pool filled with paraffin and/or 5% gelatin gel. Usually the last two means proved to be effective.

Complete mydriasis was attained by local application of a drop of cycloplegic mydriatic (Midrin-P). The corneas were protected with plastic contact lenses of appropriate power which was determined by means of a refractometer.

Stimulating electrodes were made from acupuncture needles insulated with Formvar enamel, their tips being bared for about 0.5 mm. One or several pairs of them were mounted with a 1.5 mm tip seperation on small plastic blocks and placed with stereoaxically or under visual control in aimed sites. Electric pulses were delivered through an isolation unit from an electronic pulse generator.

Electrical activities in the superior colliculus were led off with a tungsten microelectrode prepared after the Hubel's method. Their electrical resistance was more or less 10 Megohm. On some occasions acupuncture needle electrodes were employed for recording instead of the tungsten electrode. Evoked potentials were amplified by means of a conventional R.C. amplifier with a cathode follower input stage.

Throughout the experiment some doses of antibiotics were injected intravenously every two hours. Synthetized corticosteroid hormone was also injected intramuscularly every five hours which proved to be effective against brain edema. The cat's body temperature was maintained at 38°C by an electric heating pad placed under the body.

In all experiments the position of the tip of recording electrodes was checked in such a way that an electrolytic lesion was made by applying direct current of 10 to 20 µA for 20 sec. Animals were sacrificed by cardiac perfusion with 1 litter of warm saline followed by the same amount of 10% formal-saline. The brain was removed and fixed in the same solution for more than one week. Histological sections of the superior colliculus were cut serially at 35 µ on a freezing microtome. They were usually examined without being stained under a light microscope for an electrolytic lesion. Such non-stained preparations were found to be much more useful for localization of an electrolytic lesion in the superior colliculus than stained preparations, for the former had not suffered a shrinkage due to dehydration process necessary for embedding and also provided a distinct view of the stratum opticum where bundles of myelinated nerve fibers run rostro-caudally.

Fig. 1. Depth recordings of field potentials in the superior colliculus evoked by electrical stimulation of ipsilateral optic tract. Field potential recorded monopolarly at each depth below collicular surface, indicated by numeral to the left, is represented at two different sweep speeds. Negativity of recording electrode is expressed by downward deflection in this and all subsequent records. Time calibrations indicate 10 msec. Electrolytic lesion made at depth of 0.9 mm is shown in schematic drawing of superior colliculus at A = 1.5 of stereotaxic coordinates. Crosshatched region represents optic layer of colliculus.
Amplitude of field potential was measured at the time of negative peak of surface response and plotted against depth at which each response was recorded. Filled and open circles stand for tract-evoked and cortically evoked responses respectively. Sample records of collicular responses to stimulation of optic tract (OT) and visual cortex (Cortex) are shown to left.

RESULTS

1. Laminar distribution of field potentials in the superior colliculus

When the recording electrode reached the superior colliculus vertically through the overlying cortex, a sequence of negative-positive potential wave was recorded at the surface of the superior colliculus in response to stimulation of the ipsilateral optic tract as already described by Bishop and O'Leary (1941) and Pickering and Freeman (1968) (see the right-hand column of Fig. 1). The peak latencies of the negative and positive wave were 8–10 msec and 30 msec, respectively.

In the present experiments we confined our observations largely to the early negative wave in association with the subsequent paper, in which unitary spike discharges in the collicular neurons were investigated.

As the electrode was advanced into the colliculus, the configuration of recorded potentials gradually changed. At a depth of 0.2 mm from the collicular surface, spiky potentials of high frequency were observed to be superimposed upon the
Fig. 3. Relation between collicular responses and stimulus intensity. Upper part of this figure shows collicular responses evoked by stimulation of visual cortex and lower part those evoked by stimulation of optic tract. In each case recording electrode was fixed at depth where maximal deep positivity was recorded. In graphs relative amplitude of responses is plotted against stimulus intensity (0.02 msec in duration).

negative wave over the range of 3 to 15 msec after stimulation. At 0.5 mm depth the negative peak had reversed in polarity to yield a positive wave with more or less prominent spiky potentials superimposed. With further advance of the electrode the positive counterpart of the surface negative peak increased in size to reach a maximum at a depth of about 0.9 mm. Beyond this depth the amplitude of the positive wave gradually decreased without changing polarity. In this experiment an electrolytic lesion was made at the depth where the deep positive wave was maximal in amplitude. Histological examination showed that the lesion was located in the stratum opticum (Fig. 1). Consequently the reversal site of the surface negative wave was considered to be in the middle of the stratum griseum superficiale.

Essentially identical potential waves were elicited in the superior colliculus by stimulation of the ipsilateral visual cortex and its adjacent areas. Cortically
evoked collicular responses showed similar changes in configuration with penetration of the recording electrode into the colliculus as well. Fig. 2 illustrates the whole series of depth recordings of potential waves evoked by stimulation of the optic tract and visual cortex in another cat. In this figure is also shown the depth distribution of the amplitude of potentials measured at the peak time of the surface negative wave where open circles stand for potentials evoked by stimulation of the cortex and filled ones for those by tract stimulation.

2. Intensity-response relationship of collicular evoked potentials

To clarify the relation between stimulus strength and the size of collicular evoked responses, the recording electrode was fixed in the site where the deep positive potential wave was maximal in amplitude. As shown in Fig. 3, both tract and cortically evoked collicular responses increased with an increase in stimulus intensity. In addition, sample records illustrated to the left show that spiky potentials superimposed upon the positive waves became more pronounced with increasing stimulus intensity.

3. Effects of barbiturate on collicular evoked potentials

There is good reason to believe that the spiky potentials superimposed upon the slow positive potential wave are derived from repetitive discharges of internuncial neurons in the superior colliculus.

In early experiments, animals were anesthetized with an initial dose of 35 mg/kg body weight of sodium pentobarbital injected intraperitoneally and during experiments additional 10 mg of the drug were intermittently administered intravenously to maintain a good anesthetic level. With thus anesthetized animals we could not obtain large collicular responses as illustrated in the present paper where chloralose was substituted for sodium pentobarbital. Based on this experience, effects of sodium pentobarbital on collicular evoked responses were tested. Results are shown in Fig. 4. After control collicular evoked potentials were recorded in response to stimulation of the optic tract, 30 mg of sodium pentobarbital were administered intravenously. An effect appeared as early as half a minute after injection. The spiky potentials were attenuated and at last completely disappeared by four minutes after drug application. The slow potential wave, however, was not affected to a noticeable degree. Sixteen minutes after drug application the spiky potentials began to recover. At this moment additional 30 mg of the anesthetics were given. This treatment depressed not only the spiky potentials but also the slow potential wave. A photographic record taken seven minutes after the second application of the drug is shown at the right-hand corner in Fig. 4.

4. Contribution of the cortex to collicular responses evoked by optic tract stimulation

In view of the present results showing that collicular evoked potentials obtained on stimulation of either the optic tract or visual cortical areas are very
Fig. 4. Effects of pentobarbital sodium on collicular responses to stimulation of optic tract. Graph shows amplitude of deep positivity (expressed by percentage of control response) after intravenous injection of pentobarbital sodium. Drug was given twice at time interval of 16 min. Amplitude of collicular response after first injection is plotted with open circle, and that after second injection is with filled circle. In lower part of this figure are shown photographic records of collicular responses taken at times (min) elapsed after first injection (indicated by numerals).

Similar to each other not only in wave shape but also in depth distribution of potentials, we naturally inferred that the cortical activity might contribute more or less to the generation of collicular responses by optic tract stimulation. In order to test this inference, effects of the elimination of cortical activities on the tract-evoked responses were studied. Cortical activities were eliminated by either of the following three procedures.

1) Spreading cortical depression induced by topical application of a small piece of filter paper soaked in 5% KCl solution.
2) Maintained cooling of the cortex by application of dry ice.
3) Ablation of the cortical areas by suction.

Fig. 5 shows the results obtained by the first procedure. A piece of KCl-soaked filter paper (1.5×1.5 mm) was applied on the lateral gyrus about 2 mm
Fig. 5. Tract-evoked collicular responses during cortical spreading depression.

A piece of filter paper soaked in 5% KCl was applied on to a cortical area as shown by black square in inset and potential changes of visual cortex associated with spreading depression were recorded at a site indicated by black circle. Upper graph shows amplitudes expressed by percentage of control response of collicular response (open circle) and visual cortical response (filled circle) evoked by stimulation of ipsilateral optic tract as a function of time elapsed after application of KCl. Lower graph represents cortical slow potential changes associated with spreading depression. Negativity is up in this case.

It is seen that the collicular evoked responses remained almost unaltered while the large negative potential wave accompanying cortical depression was recorded, although the spiky potentials superimposed upon the collicular responses were suppressed to some degree as shown in sample records.

On the other hand, when maintained cooling of cortical areas including suprasylvian, lateral and postlateral gyri was performed, the tract-evoked collicular responses were noticeably depressed with a gradual recovery to the original level after withdrawal of the cooling agent (Fig. 6). Fig. 7 shows changes in collicular and cortical responses to tract stimulation before, during and after application of dry ice in the same experiment as in Fig. 6. Cortical responses, which were recorded at the postlateral gyrus, were highly suppressed during five minute cooling, leaving only an initial positive spike which is now generally known to be due to an afferent volley. Along with such changes in cortical
Fig. 6. Depression of tract-evoked collicular response by means of cooling of visual and adjacent areas of cortex.

Dry ice was applied for four and a half minutes on to dotted areas as shown in inset. Amplitude of collicular responses is plotted as percentage of control response against time elapsed after onset of cooling of cortex. Period of cooling was indicated by thick horizontal bar. Two sample records of collicular responses are shown: one is control response (Cont), the other (5) taken 5 min after onset of cooling.

responses collicular responses were also depressed during cooling, but recovered gradually to the initial level after its withdrawal. In this experiment the spiky potentials were depressed as well.

When the cooling was restricted to only the primary visual area, no detectable depression of the tract-evoked collicular response was observed. These findings reveal that cortical areas adjacent to the primary visual area were responsible to some extent for tract-evoked collicular responses.

Ablation of cortical areas in an acute experiment always caused a great depression of the collicular responses. But since such depressive effects were irreversible and also there is good reason to believe that such surgical manoeuvre caused a disturbance of blood circulation and changes in milieu interior of the brain, the results thus obtained will not be considered further.

5. Effective sites in the cortex for collicular responses

In the present series of experiments we noticed that stimulation of the posterior suprasylvian gyrus gave rise to larger collicular responses whereas stimulation of the postlateral gyrus produced very small responses. Sample records are shown in Fig. 8.

It is known that the visual and adjacent cortical areas send corticofugal fibers to the superior colliculus (Beresford 1961, Sprague 1963, Meikle and Sprague 1964, Otani 1964). In particular, Garey (1965) has shown that topographical interrelationships exist between the visual cortex and the superior colliculus in the cat. On
the basis of these histological investigations, an attempt was made to demonstrate such cortico-tectal interrelationships.

For this purpose a pair of silver ball electrodes with a tip separation of 1.0 mm were used for stimulating the surface of the cortex. They were shifted systematically at 1.0 mm steps along the parasagittal line and in the medio-lateral direction so that stimulated points on the cortex formed a grid. Collicular responses were recorded at three separate points along a parasagittal line 2 mm lateral to the sagittal plane. At each point the tip of the recording electrode was positioned so as to record the deep positive potential of maximal amplitude on stimulation of the optic tract. Positions of the tip were checked by the electrolytic lesion technique. The results are shown in Fig. 9, where a filled circle is allotted to each stimulated point of which the diameter is proportional to the size of the positive wave evoked from that cortical point. It is seen that when the recording electrode was positioned at A=2.0 in the Horsley-Clark coordinates, stimulation...
Fig. 8. Typical collicular responses evoked by stimulation of ipsilateral optic tract and of five different sites of cortex. Responses are displayed at two different sweep speeds. Numeral besides each pair of traces corresponds to that indicated on cortex which shows position of stimulating electrodes on cortex. OT stands for optic tract stimulation. Recording electrode was positioned at depth giving maximal response. Time scales of 1 msec and 10 msec are for upper and lower traces in each pair respectively.

of the lateral side of the posterior suprasylvian gyrus gave rise to the biggest response, and at A=1.0 and at P=0.5 stimulation of the medial side of the posterior suprasylvian and of the junctional part between the lateral and post-lateral gyri produced the biggest responses, respectively.

It is to be noted that these effective sites were not located in the primary visual cortex, but rather in cortical areas surrounding the visual cortex. From these findings we can say that the rostral portion of effective cortical areas is associated with the caudal part of the superior colliculus and the caudal portion of the cortical areas with the rostral part of the superior colliculus.

6. Interaction between retino-tectal and cortico-tectal inflows

At present there is no doubt that both retino-tectal and cortico-tectal fibers enter the stratum opticum via the lateral brachium of the superior colliculus and terminate mainly in the stratum griseum superficiale. Consequently, it is natural that a question should be raised: What sort of interaction between these two afferents should occur in the superior colliculus?

In the present experiments the recovery cycle of afferents was studied by measuring the amplitude of the collicular responses evoked by test shocks given to either of the two afferents following a conditioning shock delivered to the other afferent.

Fig. 10 shows one of recovery curves in which a conditioning shock was applied to the posterior suprasylvian gyrus and test shocks were delivered to the optic
Fig. 9. Topographical representation of effective sites in cortex to produce collicular responses.

Position of collicular electrode in antero-posterior dimension is shown by coronal section of superior colliculus in lower part of figure and effective cortical sites corresponding to a given position of collicular electrode are represented by black circles in schematic drawing of cortex presented just above. Diameter of a circle is proportional to amplitude of collicular response. \( A=1.0 \) at stereotaxic coordinates is indicated on cortex by broken line.

tract. Numerals attached to sample records indicate intershock intervals. The amplitude of the tract-evoked response at each intershock interval is expressed as a percentage of that of the control response. It is seen that there is an initial facilitatory phase from about 50 msec to 200 msec after the conditioning cortical shock followed by a depressive phase up to over 500 msec. Occasionally a second weak facilitatory phase was superimposed upon this depressive phase at about 350 msec after the conditioning shock.

Similar but weak effects were also observed when a conditioning shock was applied to the optic tract and test shocks were to the cortex.

**DISCUSSION**

According to histological studies on the mammalian superior colliculus the superficial layers, i.e., the stratum griseum superficiale and stratum opticum receive projections from the optic fibers and the visual cortical areas (Barris et al. 1935, Altman 1962, Sprague 1963, Meikle and Sprague 1964, Garey 1965, Laties and Sprague 1966, Lund 1966, Garey et al. 1968).

This was confirmed by the present analyses of field potentials which showed that stimulation of the ipsilateral optic tract and the visual cortical areas
Fig. 10. Effects of preceding cortical stimulation upon tract-evoked collicular responses. Amplitude of tract-evoked collicular responses is plotted against time intervals between tract and preceding cortical shocks. Amplitude is expressed by percentage of control response. Top records show cortically evoked collicular response followed by tract-evoked collicular response at time intervals indicated by numerals.

produced similar field potentials in the superior colliculus having a negative-positive wave at the surface which reversed to a mirror image of a positive-negative wave at layers deeper than the optic layer.

On the other hand, these electrophysiological findings suggested that the same neural elements or populations should be responsible for the generation of field potentials in either case of stimulation and that some interaction between cortico-tectal and retino-tectal inputs should occur.

In our experiments it was shown that the preceding activation of the cortico-tectal input exerted an initially facilitatory effect between 50 msec and 200 msec after cortical stimulation followed by a depressive effect on the field potential evoked by stimulation of the ipsilateral optic tract. These effects were diminished or even eliminated when chloralose anesthesia was deepened or pentobarbital sodium was used for anesthesia. Under such conditions, collicular field potentials superimposed upon the slow potential wave were reduced. These findings would allow us to think that the cortical effects were due to the activation of interneurons in the colliculus.

In recent years retinotopic interrelationships of the visual cortex and the superior colliculus have been anatomically demonstrated not only in the cat (Garey 1965, Garey et al. 1968), but also in the rabbit (Giolli and Guthrie 1967). According to Garey (1965), and Garey et al. (1968), the anterior part of the cat’s visual cortex is related to the postero-lateral half of the colliculus and the posterior
cortex to the antero-medial half. Taking as an index the amplitude of field potentials evoked by stimulation of various sites in the visual cortex and adjacent cortical areas, we studied such interrelationships. In these experiments, we found that stimulation of the non-visual cortex adjacent to the visual cortex gave rise to a bigger field potential than that of the visual cortex did in a given point within the superior colliculus. In some preparations, no detectable response was obtained by stimulation of the visual cortex, although stimulation of the posterior suprasylvian gyrus produced a big response. At the present time it would be difficult to explain properly such relative ineffectiveness of the visual cortex to produce a field potential in the superior colliculus. But the results reported by Hayashi (1969) would be helpful in this respect in that visual cortical cells activated antidromically by stimulation of the superior colliculus (VCSC cells in Hayashi’s nomenclature) were located in areas 18 and 19, but not in area 17.

Taking into account Garey et al.’s report (1968) that the posterior and middle suprasylvian gyr project upon the same superficial layers of the superior colliculus as does the cortex of areas 17 and 18, our results, as seen in Fig. 9, would rather represent the topographical interrelationships between extrastriate cortical areas and the superior colliculus. At any rate the finding that the junctional area between the lateral and postlateral gyri is related to the posterior part of the superior colliculus and the upper part of the posterior suprasylvian gyrus to the anterior part of the colliculus is compatible with histological findings.

Another point to be discussed here is how much cortico-tectal inflows contribute to the collicular field potential evoked by stimulation of the optic tract. For this purpose we introduced a temporary inactivation of the cerebral cortex by inducing a spreading depression by means of local application of 5% KCl, while recording collicular field potentials evoked by stimulation of the optic tract. As seen in Fig. 5, the cortical activity was suppressed during spreading depression, but practically no changes in collicular field potentials were observed. In view of the widely accepted knowledge that neurons existing only in the superficial layers of the cerebral cortex are involved in spreading depression (Phillis and Ochs 1971) and that corticofugal axons originate primarily from neurons in layers V and VI (Kruger and Malis 1964), this observation would be readily explainable. Incidentally Weis and Fifkova (1961) reported that spreading depression produced in the rat cerebral cortex did not affect neuronal activities in the superior colliculus.

In contrast to this, reversible cerebral inactivation by local cooling resulted in a decrease in the magnitude of the collicular field potentials by about 30% with a gradual recovery after withdrawal of the cooling agent. This result indicates that the cortico-tectal inflows are normally involved for the activation of collicular neurons by stimulation of the optic fibers, and is in accord with the conclusion reached by Jassik-Gerschenfeld et al. (1966) and Meulders and Colle (1966). From their analyses concerning the effects of the ablation of the visual cortex on response characteristics of unitary discharges of superior collicular neurons, Wickelgren and Sterling (1969a) demonstrated that important features of collicular receptive fields
are contingent on cortical input to the colliculus for their elaboration. They also showed that cooling the visual cortex and adjacent cortical areas caused a precipitous drop in the excitability of collicular units. These findings are also consistent with our results. To understand interaction between the cortico-tectal and retino-tectal inputs in further detail, a study will be needed at the level of a single neuron.

References


