stimulus duration; with small, brief flashes this curve would have started higher and would have a lower slope over most of its range. Although we have not yet tested for it, it is possible that the curve for the monkey also depends upon such parameters, but probably for very different reasons.

11. The constant K_r is equal to $(10{,}000)^{.70}$. The value of 10,000 is also the bleaching constant of Eq. 5. We are uncertain whether this agreement is fortuitous, or of theoretical significance.
12. There are scattered references to the concept of response compression [see, for example, R. M. Glantz, *Vision Res.* **8**, 1407 (1968); G. Werner and V. B. Mountcastle, *J. Neurophysiol.* **28**, 359 (1965); K. I. Naka and W. A. H. Rushton, *J. Physiol.* **185**, 587 (1966)]. Naka and Rushton discussed response compression but dismissed it as not fitting their data from fish S-potentials. Glantz used the concept implicitly to describe light adaptation in crayfish photoreceptors. Werner and Mountcastle used it to construct Weber functions for vertebrate mechanoreceptors, successfully mimicking human psychophysical results. The latter two studies both found a power law relationship between stimulus and response, and both used an equal response increment as the threshold criterion, just as we have done.
13. Consider the case where I_a equals 6 log trolands, which is sufficient to produce an essentially full bleach at steady state. In this case, if the light is delivered suddenly to the dark-adapted eye and left on, the late RP should rise quickly to its full value and then gradually settle down to half that value as bleaching progresses and the probability of quantum absorption becomes less. Although we observed this qualitatively, we could not measure it this way because the time course is too slow relative to the drift in the recording situation. One can, however, make the prediction that, if the steady-state adapting field at 6 log trolands is momentarily extinguished, a "negative response" should be produced that has just half of the response to a brief positive flash delivered to the previously dark-adapted eye. At the other extreme, where I_a is too weak to produce significant bleaching, such positive and negative responses should be of the same size. These predictions, and others applying to intermediate conditions of intensity, were experimentally tested and confirmed within experimental error.
14. See, for example (*9*) and H. B. Barlow, *Cold Spring Harbor Symp. Quant. Biol.* **30**, 539 (1965).
15. M. Alpern, W. A. H. Rushton, S. Torii, *J. Physiol.* **207**, 463 (1970).
16. R. W. Rodieck and R. W. Ford, *Vision Res.* **9**, 1 (1969).
17. Contrary to the assertion of Alpern *et al.* that electrophysiological signals from receptors and S-potentials are linear and fit by the expression V equals $I/I + K$, we find that I in the expression must be raised to an exponent less than 1.0. This is also the case with cat S-potentials [R. Steinberg, *Vision Res.* **9**, 1331 (1969)], and from some of Steinberg's more recent work (personal communication). The confusion arises from the close similarity of the curves V equals $I/I + K$ and V equals $I^n/I^n + K^n$ when plotted (as is the convention) on semilog coordinates.
18. We thank K. T. Brown and R. H. Steinberg for helpful discussions, and Mrs. P. Lacy for technical assistance. This work was done while R.M.B. was on leave from the University of Rochester (to which he has returned); he was supported by NIH special fellowship NB-00693-02. The work was supported also by NIH grants EY-00187 and EY-00468.

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Superior Colliculus: Single Unit Responses to Stimulation of Visual Cortex in the Cat

Abstract. *Electrical stimulation of area 18 of the cat visual cortex produces intense excitation of neurons in the superior colliculus. Excitation is followed by a period of decreased collicular responsiveness to light stimulation. These effects are seen in both directionally selective and nonselective units. The corticocollicular projection is retinotopically organized.*

Anatomical studies have repeatedly demonstrated substantial projections from the visual cortex to the superior colliculus in several species, including the cat (*1*). In recent years physiological and behavioral experiments have indicated that these connections mediate important functional relations between the cortical and tectal components of the visual system (*2–7*). Evidence from these studies has implicated both excitatory and inhibitory mechanisms in the corticocollicular influence. The experiments reported here show that electrical stimulation of the visual cortex produces excitation followed by functional inhibition of collicular neurons.

Action potentials of single neurons in the superior colliculus were recorded with tungsten microelectrodes in midpontine pretrigeminal cats prepared under ether anesthesia. The animals viewed a tangent screen at a distance of 1 m, and their eyes were corrected for this distance (*8*). After completion of surgery, the animals were paralyzed with Flaxedil and given artificial respiration. Expired CO_2 and femoral arterial pressure were continuously monitored, and body temperature was maintained at 37° to 38°C. The ipsilateral occipital cortex was covered with warm mineral oil and stimulated with a movable silver ball electrode, 0.5 mm in diameter. The other electrode pole was placed in surrounding muscle or grounded to the stereotaxic instrument. Bipolar stimulation of the visual cortex was used in some experiments. A Hewlett-Packard current probe monitored stimulus current. When a collicular unit was isolated, its receptive field was characterized by moving patterns on the tangent screen, which was diffusely illuminated at a constant photopic level. The unit's response to cortical stimulation was determined, and, finally, interactions between effects of light and cortical shock were investigated. Data were recorded on film and on magnetic tape for subsequent analysis. Recording sites were determined histologically from small electrolytic lesions placed in the electrode tracks.

Single electrical pulses to the visual cortex evoked a short latency discharge in superior collicular neurons (Fig. 1). As we gained skill in placing the cortical electrode (see below), this response was observed in all collicular units investigated. The typical response to a 0.5-msec current pulse to the ipsilateral visual cortex was a burst of spikes, often of very high frequency, which occurred during a negative evoked wave (Fig. 1). Latency to the first spike was variable at suprathreshold current intensities, which indicates orthodromic activation. Minimum latencies ranged from 1.2 to 9.0 msec with a mean of 3.17 ± 1.96 msec (standard deviation) in 26 units (*9*). The values are comparable to the 2.0- to 2.5-msec latencies of evoked potentials in the superior colliculus after cortical shock (*6*) and spontaneous strychnine spikes (*7*). Hayashi has described antidromic invasion of visual cortical units, after stimulation of the superior colliculus, with a mean latency of 2.8 ± 1.6 msec (standard deviation) in 60 cells (range of 0.9 to 9.0 msec) (*10*). The projecting fibers studied by Hayashi clearly provide a possible pathway for the excitatory effects that we have observed.

After the phase of synaptic excitation, the superior collicular neurons exhibited a period of depressed responsiveness which lasted for 50 to 100 msec, depending on cortical shock intensity. Figure 2 illustrates a control off response, which is markedly reduced when preceded by a cortical shock (lower two traces). In this case the cortical shock elicited a burst of spikes from the superior collicular neuron. It was commonly observed, however, that the cortical stimulus did not have to excite a unit in order to produce detectable inhibition. On the other hand, careful adjustment of cortical and visual stimulus parameters revealed the inhibitory phenomenon in the majority of units driven from the visual cortex.

All units studied in the superior colliculus were classified as directionally selective or directionally nonselec-

tive on the basis of their responses to moving stimuli (*8*, *11*). The effects of cortical stimulation were indistinguishable in the two groups. Both directionally selective and nonselective units showed strong driving and multiple discharges at high frequencies (Fig. 1). Latency distributions for the two groups were almost identical in our sample. Light responses in both classes could be inhibited effectively from the cortex.

The location of the stimulating electrode on the visual cortex was critical. Systematic exploration of accessible visual cortex revealed a small cortical area that at low stimulus intensities yielded unit driving and evoked potentials in the superior colliculus. Threshold currents for a standard response (unit driving or a 200-μv negative evoked wave) ranged from 0.2 to 0.8 ma. Moving the stimulating electrode in any direction away from this "best point" (*12*) by 2 to 4 mm markedly increased the threshold current requirement. Anodal pulses were employed more frequently than cathodal pulses in these experiments because previous work had indicated that such stimuli were more efficient in directly exciting cells in the deeper layers of the cortex (*13*). However, at the suprathreshold intensities used here, no marked differences were observed between effects of the two stimulus polarities.

When the recording microelectrode was withdrawn from the superior colliculus and thrust into the visual cortex at the previously determined "best point," the cortical neuronal receptive fields were always superimposed on the receptive fields of the superior collicular neurons just mapped on the tangent screen. This occurred from animal to animal, and also when widely separate locations in the superior colliculus were studied in the same animal. A detailed corticocollicular mapping was not performed, but the experiments clearly demonstrated that a shift in collicular recording site was accompanied by a shift of the cortical "best point" and that this "best point" was retinotopically in registration with the corresponding collicular location. These data corroborate the anatomical findings of Garey *et al.* (*1*), which indicated a retinotopic projection from both areas 17 and 18 to the superior colliculus of the cat.

For sites in the superior colliculus that represent peripheral visual regions, the cortical "best point" was always

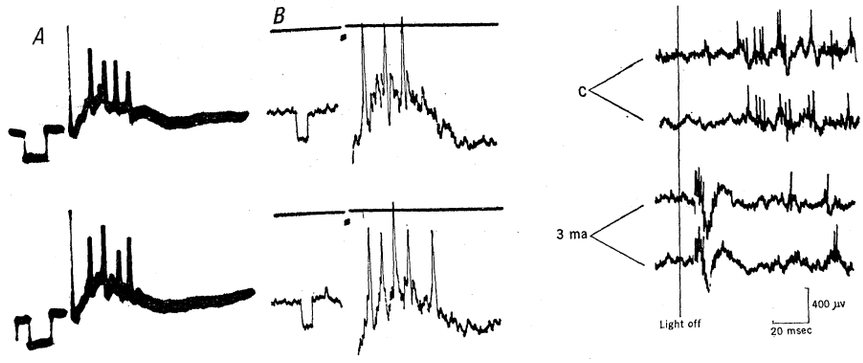

Fig. 1 (left). Superior collicular units driven from visual cortex. (A) A directionally selective unit in stratum griseum superficiale responding to bipolar cortical stimulation. Calibration: 2 msec, 500 μv. (B) A nondirectionally selective unit in stratum opticum responding to a 2-ma surface cathodal stimulation of visual cortex. Current pulse is in the upper trace; spikes are retouched. Calibration, 1 msec, 200 μv; negativity upward. Fig. 2 (right). Top two traces (*C*) show control off responses to small light spot in the receptive field of a nondirectionally selective neuron in stratum griseum superficiale. The lower two traces show the effect of a 3-ma anodal pulse to visual cortex introduced about 20 msec before the beginning of the off response. The off response reappeared full strength when the shock was omitted. Negativity upward.

on the dorsal convexity of the lateral gyrus, corresponding to area 18 in the map of Otsuka and Hassler (*14*). This location was confirmed by mapping receptive fields of cortical neurons on either side of the "best point." Medial placement of the microelectrode produced a shift of the receptive fields of the visual cortex toward the midline, whereas lateral placements yielded shifts toward the periphery. On the lateral gyrus, only area 18 has this retinotopic geometry (*15*). Attempts to elicit unit driving from the medial surface of the ipsilateral occipital pole (after aspirating the contralateral pole), from the dorsal posterolateral gyrus and from the dorsal surface of the suprasylvian gyrus were not successful, even when high current strengths were used.

When the recording site in the superior colliculus represented central vision, the cortical "best points" lay on the lateral gyrus near the junction of areas 17 and 18. Here, we were not able to exclude the possibility that area 17 was also stimulated by the current pulses. Indeed, our failure to identify effective points in areas 17 and 19 for peripheral visual field locations may reflect the inaccessibility of such points to our stimulating electrode. Hence, although projections from area 18 assuredly produce excitation of superior collicular neurons, similar effects from areas 17 and 19 were not excluded by our experiments. In this regard, Hayashi concluded that the highest density of units excited antidromically from the superior colliculus is found in areas 18 and 19; he was unable to locate such cells in area 17 (*10*). In addition, Jassik-Gerschenfeld *et al.* (*3*) found that strychnine enhanced evoked potentials in the superior colliculus more when applied to areas 18 and 19 than when applied to area 17 or suprasylvian gyrus.

Recent experiments by Kadoya *et al.* (*16*) revealed a class of neurons in and near stratum opticum of the squirrel monkey's superior colliculus that were excited after electrical stimulation of area 17. Although the corticocollicular projection is retinotopic, these units do not appear to have visual receptive fields. Also in their study, visually excited neurons in the superior colliculus were not driven from area 17. It is not known if this arrangement obtains in the cat, although our failure to drive collicular visual cells from area 17 suggests that it may. Since our experiments tended to select visually excited neurons for study, the cells described by Kadoya as receiving area 17 projections may well have been missed.

To summarize, the present experiments demonstrate a potent excitatory projection from visual cortex, particularly from area 18, to visually responsive cells in the superior colliculus. These projections are apparently as effective as the retinal inputs in exciting the superior collicular units and are similarly organized to preserve retinotopic information. These findings confirm and extend previous evoked po-

tential studies, which indicate an excitatory input to the superior colliculus from cat visual cortex (*3, 6, 7*). Tests of collicular excitability during cooling of visual cortex have suggested a descending inhibitory influence presumably activated by an "irritative" effect of the local hypothermia (*4*). Our experiments confirm the presence of cortically induced inhibition of superior collicular neurons, but the mechanism underlying this effect and its relationship to the sequelae of cortical cooling remain to be worked out (*17*).

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References and Notes

1. For a review of this literature with bibliography, see L. J. Garey, E. G. Jones, T. P. S. Powell, *J. Neurol. Neurosurg. Psychiat.* **31**, 135 (1968).
2. J. M. Sprague, *Science* **153**, 1544 (1966).
3. D. Jassik-Gerschenfeld and P. Ascher, *Experientia (Basel)* **19**, 655 (1963); D. Jassik-Gerschenfeld, P. Ascher, J. A. Guevara, *Arch. Ital. Biol.* **104**, 30 (1966).
4. P. L. Marchiafava, G. Rizzolatti, J. M. Sprague, *Arch. Ital. Biol.* **106**, 21 (1968); compare B. G. Wickelgren and P. Sterling, *J. Neurophysiol.* **32**, 16 (1968).
5. P. L. Marchiafava and G. Pepeu, *Experientia (Basel)* **22**, 51 (1966).
6. S. Shanzer and S. Dumont-Tyc, *J. Physiol. (Paris)* **53**, 473 (1961).
7. W. T. Niemer and J. Jimenez-Castellanos, *J. Comp. Neurol.* **93**, 101 (1950).
8. J. T. McIlwain and P. Buser, *Exp. Brain Res.* **5**, 314 (1968).
9. The point of initiation of smaller spikes was difficult to identify in some records because of background activity. To obtain a consistent and comparable measure for all cells, latency was taken from the beginning of the stimulus pulse to the peak of the first action potential. This procedure introduced into the measurements a constant bias of approximately 0.2 to 0.3 msec in the direction of longer latencies.
10. Y. Hayashi, *Vision Res.* **9**, 1367 (1969).
11. M. Straschill and A. Taghavy, *Exp. Brain Res.* **3**, 353 (1967).
12. S. Landgren, C. G. Phillips, R. Porter, *J. Physiol. (London)* **161**, 112 (1962).
13. J. E. C. Hern, S. Landgren, C. G. Phillips, R. Porter, *ibid.*, p. 73; C. G. Phillips and R. Porter, *ibid.* **162**, 532 (1962); O. D. Creutzfeldt, G. H. Fromm, H. Kapp, *Exp. Neurol.* **5**, 436 (1962); D. P. Purpura and J. G. McMurtry, *J. Neurophysiol.* **28**, 166 (1965); A. L. F. Gorman, *ibid.* **29**, 547 (1966).
14. R. Otsuka and R. Hassler, *Arch. Psychiat. Nerv.* **203**, 166 (1965).
15. D. H. Hubel and T. N. Wiesel, *J. Neurophysiol.* **28**, 299 (1965).
16. S. Kadova, L. C. Massopust, Jr., L. R. Wolin, *Physiologist* **13**, 238 (1970); personal communication.
17. In conducting the research described in this report, the investigators adhered to the "Guide for Laboratory Animal Facilities and Care," prepared by the Committee on Revision of the Guide for Laboratory Animal Facilities and Care of the Institute of Laboratory Animal Resources, National Academy of Sciences–National Research Council, Washington, D.C.

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Visual Discrimination of Movement: Midbrain or Forebrain?

Abstract. *Monkeys whose optic chiasm and forebrain commissures had been sectioned and control monkeys with only the optic chiasm cut were tested for interocular transfer of discriminations based on direction of movement. Only the control animals showed transfer to the untrained eye, which suggests that discrimination of movement, like pattern, is a function strongly dependent on the cortex.*

In the more specialized mammals the midbrain roof, particularly the superior colliculus and pretectal area, traditionally has been considered a somewhat vestigial center largely concerned with the reflex control of eye and head movements (*1*). During the past 10 years, however, several lines of research have pointed to a more complex role for the midbrain in visuomotor coordination and spatial localization (*2–5*). Recently a number of authors have suggested that the traditional concepts of superior collicular function be further revised to include an even more prominent role in visual perception, especially spatially structured vision (*6–8*).

In the experiment reported here, we have sought to determine if discriminations based on stimuli useful in spatial orientation might be performed at midbrain levels. Movement was chosen as the variable to be discriminated because of its prominent role in spatial perception and its notable success as a stimulus for eliciting responses from neurons in the superior colliculus (*8–10*). The results of the present experiment favor, however, a cortically dependent mechanism for discrimination of movement, similar to mechanisms involved in the discrimination of patterns.

Tests for localization of function usually employ either ablation of a structure, to determine if it is necessary for performance of the function, or ablation of other functionally associated structures, to examine the sufficiency of the isolated structure. In general, ablation of the superior colliculus has not affected discriminability of patterns or intensities, although one of these studies reported some impairment, largely temporary, of the discrimination of rate of movement (*3, 7, 11*). It seems reasonably clear, therefore, that the superior colliculus is not necessary for performing most visual discriminations. Whether it is normally used, or is capable of making such discriminations in the absence of visual cortex, is less clear. Ablation of cortex receiving projections from the lateral geniculate nucleus usually abolishes discrimination of patterns but not discrimination of light intensity (*5, 12*). In primates significant discriminability of patterns may survive removal of the striate cortex, which suggests an even greater role in perception for the colliculus (*13*). Movement has been discriminated by destriate monkeys in some of these experiments although not in others.

The interpretation of the surviving performance by animals with lesions in the visual cortex is complicated by the fact that the superior colliculus receives a large input from the cortex and hence its normal function may be significantly depressed or even altered by cortical removal. Behavioral evidence suggests that this may be true in cats (*4*). Furthermore, it appears that single cells in the superior colliculus, which are normally very sensitive to moving but not to stationary stimuli, lose their directional sensitivity and respond to stationary stimuli when the visual cortex in cats has been removed for approximately 2 weeks (*14*). There-

Table 1. Interocular transfer and savings on four movement discriminations.

Chiasm-sectioned subjects			Split-brain subjects		
Subject	Median initial transfer (%)	Median savings (%)	Subject	Median initial transfer (%)	Median savings (%)
ART	67	37	MLL	45	−16
SCR	66	46	SCN	49	−16
ABE	76	90	FRD	56	11
SRH	78	94	HPJ	46	2
Mean	72	67	Mean	49	−5