ment 2), and thus did not show that young infants attend solely or even mainly to real size rather than to distance or retinal size. The possibility remains, however, that an appreciation of perceptual constancies cannot be demonstrated by habituation methods with the use of an unlearned response which entails no external reinforcement. If operant training methods as used by Bower (*2*) permit size discrimination at distances well beyond the preferred range, they must also alter the relative salience of stimulus properties.

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19 June 1972

## Visual Input to the Pontine Nuclei

Abstract. *Visual input to the pons was studied by anatomical and physiological methods. Cortical area 18 sends a dense projection to the rostral pons. Pontine cells respond best to targets moving in a preferred direction over a large receptive field, which usually includes the center of gaze. The results suggest a role for pontocerebellar pathways in visual control of movement.*

The pons is one of the major targets for fibers that leave the cerebral cortex. Cells in the pontine nuclei, in turn, send their axons to the cerebellum. These anatomical facts are well established, but the function of the corticopontocerebellar pathway is not at all clear. We hoped that we could throw light on cerebellar mechanisms by studying connections to the pons of the cat's visual cortex, for which the response properties of neurons are well described (*1*). We first did an anatomical study to find the terminations of corticopontine fibers, and then recorded the type of information that is relayed to the cerebellum via the pontine nuclei (*2*).

We hoped our experiments would help us to understand another problem. In the cat the lateral geniculate nucleus sends parallel representations of the visual field to areas 17 and 18 (*3*). Since areas 17 and 18 receive independent visual maps, they may have different functions. Differences in the pattern of efferent projections from these two cortical areas might give a clue to what these functions might be.

We made lesions either by subpial suction or by stripping pia from the surface of the visual cortex in 11 cats. In one animal this was a large lesion which included almost all of areas 17, 18, and 19 on one side, in order to define the overall pattern of fiber projections from the visual cortex to the pons. Smaller lesions were placed in area 18 in six animals, and in area 17 in four others. The lesions were placed in the areas of the visual cortex that receive projections from the center of the visual fields. The animals were allowed to survive from 11 to 14 days. Eight brains were sectioned in a sagittal plane, three in a transverse plane. We stained the brains by a Nauta-Laidlaw method (*4*) to locate degenerating fibers, and determined the nature and extent of the cortical lesions with a Nissl stain.

We then recorded from pontine cells that responded to visual stimuli in 20 normal, unlesioned cats. Nembutal or Pentothal anesthesia was initially administered intraperitoneally, and the animal was maintained intravenously at a light anesthetic level throughout the experiment. There was no difference in results obtained with the two types of anesthetic. With the animal in a supine position we removed the larynx completely and drilled through the occipital bone between tympanic bullae, exposing the ventral surface of the pons. Tungsten microelectrodes with impedances between 1 and 5 megohms at 1000 hertz were then advanced into the pontine nuclei.

At the conclusion of each experiment the cats were perfused with saline followed by 10 percent formalin. The brain was removed, embedded, sectioned, and stained for reconstruction of electrode tracks. In some experiments the electrode was left in place during perfusion and fixation to make sure that we could find an important track.

In all the cats in which we destroyed a part of area 18 of the cortex we found a clear-cut focus of degenerating fibers among a group of cells of the pontine nuclei. Figure 1 illustrates the location of degenerating fiber terminals in the pons in two such cases. In all of these animals the lesion was largely confined to the cortex of area 18 on the dorsal surface of the lateral gyrus, sparing all of the posterolateral gyrus. In cat A the lesion was made by subpial suction, and the underlying white matter was slightly damaged. In cat B the lesion was made by stripping pia from the same area of the lateral gyrus, and there was only minimal invasion of white matter. In both cats degenerating preterminal fibers were found in the anterior portion of the pontine protuberance. Degenerating fibers began at about the midpoint of the pontine protuberance, extended anteriorly for about 2 mm, and were found laterally between 1 and 3 mm. Degeneration was found in the same general area of the pons in all animals in which lesions were made in area 18.

The projection from the visual cortex appeared to be entirely ipsilateral; we found degenerating fibers near pontine cells only on the same side of the brain. We have not yet studied the topographic organization of the corticopontine projection. All of our lesions were rather large for this purpose. We saw few, if any, degenerating fibers in the pons when the lesion was confined to area 17, but our lesions were restricted to the region of area 17 that receives an input from the center of the visual field.

In the physiological experiments we found a total of 42 pontine cells that were responsive to visual stimuli. These cells were in the same small rostral pontine region in which we had found degenerating fibers after lesions in area 18. Some of these cells could be activated about 25 msec after a bright flash, although moving targets were more effective. When we lowered the intensity of the flash there was an orderly increase in response latency.

All the pontine visual cells which we tested responded to an input from

either eye, and all had receptive fields centered in the contralateral visual fields. All the cells responded best to appropriately oriented bars and edges moving in a preferred direction in the contralateral hemifield. The size of the receptive fields was quite large, of the order of 20° to 30°. However, the receptive field borders were hard to establish precisely, since activity did not stop sharply but was simply weaker at the edges of the receptive field. Figure 2 shows representative tracings of the firing patterns of two different pontine cells in response to a moving target. Cell A shows absolute directional selectivity; cell B shows a greater response in one direction, but the cell fired weakly when the target crossed its receptive field in the reverse direction. In at least one of the cells that we studied there was a definite hypercomplex receptive field. The cell fired when a small bar was moved across its receptive field, but failed to fire when the width of the bar was increased. Despite the preferential response to appropriately oriented moving lines and edges, many of the receptive fields could be analyzed with small moving spots as well. Our sample of units is not yet big enough to give meaningful percentages of cells with different receptive field properties. In every case in which we recorded an isolated visual unit in the pons we tested to see if that cell could be activated by stimulation of other sense modalities. In no case did we find a visual cell that responded to clicks or tactile stimuli applied to the fur or skin. Pontine visual cells seem to be exclusively visual in their function.

We have described a group of exclusively visual cells in a small area in the pons which serve to relay information from the cerebral cortex to the cerebellum. Garey *et al.* (*5*) and Brodal (*6*) described a connection from area 17 to the pontine nuclei of cats. Brodal noted, however, that the region of area 17 that projects most densely to the pons is the region that receives its input from peripheral visual fields. He found only scanty degeneration from the region of area 17 that receives its input from the center of the visual fields. Since the receptive fields of most of the cells we studied included the center of gaze it is likely that their major input was from area 18.

There are other visual inputs to the pons. Altman and Carpenter (*7*) found a connection from the superior colliculus to the pontine nuclei. The receptive fields of the pontine cells from which we recorded resemble those of cells in the superior colliculus (*8*), so pontine visual responses may be affected by collicular as well as cortical input.

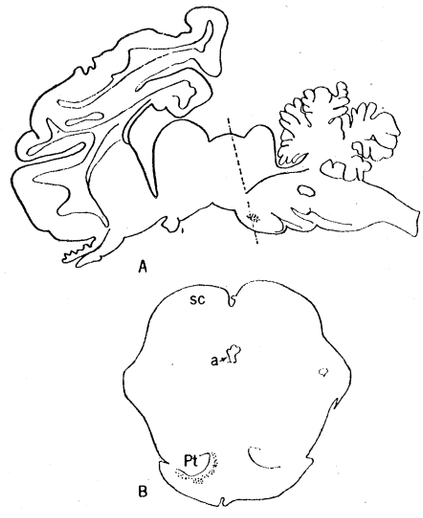


Fig. 1. Sections of Nauta-stained cat brain after lesions in area 18. The locus of degenerating corticopontine fibers is dotted. (A) Parasagittal section; (B) transverse section. The plane of the section in B is indicated by a dotted line in A. The symbols are *sc*, superior colliculus; *a*, cerebral aqueduct; *Pt*, pyramidal trace. Degeneration has been charted only for the pontine nuclei.

Since cells in the pontine visual area respond preferentially to lines or edges of a preferred orientation moving in a preferred direction, we suggest that the visual cells of the pons relay information about the direction and velocity of moving objects to the cerebellum. The cerebellum also receives input from proprioceptors, which give information about limb and trunk movement. The cerebellum may interpret information about the movement of visual targets in the light of this proprioceptive feedback. Such a comparison could be used to control movements in response to moving targets or to interpret moving targets in relation to movement of the limbs and trunk. If these speculations are correct we might expect anatomical overlap and physiological interactions between visual and proprioceptive inputs in the cerebellar cortex.

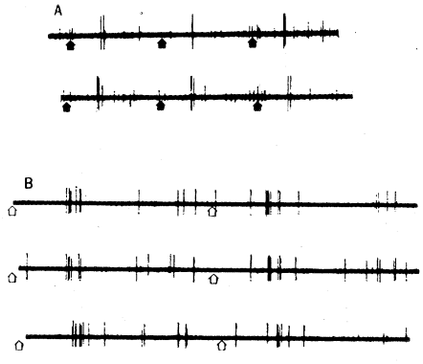


Fig. 2. Unit recordings from cells in the pontine nuclei. (A) Response of a pontine cell to a horizontal bar moving vertically upward across its receptive field. The cell fired only when the target moved in one direction. The target started upward movement at the arrow and then returned. (B) Response of a pontine cell to a vertically oriented bar moving horizontally. The cell fired briskly when the target crossed the receptive field in one direction, and weakly when the target crossed the receptive field in the opposite direction. The target started lateral movement at the arrow and then returned.

The results also add more information toward understanding the functions of areas 17 and 18 of the cat cerebral cortex. Each of these areas receives a dense input from the lateral geniculate nucleus (*3*). The pattern of projection from area 18 to the pons is further evidence that area 18 may be functionally separate from area 17. Cells in area 18 (*1*) and in the pons are especially responsive to target movement. We propose that in the cat area 18 is a cortical region specialized for the detection of moving targets. The projections from area 18 to the pontine nuclei may serve as one anatomical route for visual control of movement.

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13 April 1972; revised 2 August 1972