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12. The brain dissection was the following: the caudal end was separated from the spinal cord by a cut at the base of the occiput; the cranial end was separated from the telencephalon by a coronal cut at the level of the optic chiasm; the remainder of the telencephalon (mostly cortex) was peeled forward over the diencephalon and separated from the diencephalon by cutting along the stria terminals bilaterally; the cerebellum was then removed. The brainstem-diencephalon includes the hypothalamus as well as medulla and pons. The data from the telencephalon are not included in this report because the caudate nucleus, which is dopaminergic, accumulates ^{3}H-NE. The telencephalic data were obtained, however, in order to examine the distribution of the injected isotope. Reduced specific activity of NE in the brainstem-diencephalon cannot be explained on the basis of differential diffusion of the isotope or an increase in accumulation of the isotope by the telencephalon, since there was no difference in these measurements between the experimental group and the control groups.
13. The neurochemical assay is the following: the brain tissue is homogenized in 82 percent (by volume) ethanol, adjusted to *p*H 6.8, and centrifuged. An equal volume of water containing ethylenediaminetetraacetate (EDTA) (0.2 percent) and $Na_2S_2O_5$ (0.2 percent) is added to the supernatant which is then passed through an Amberlite CG 50 column buffered to *p*H 6.1. Catechols are eluted with 5 ml of 0.2*N* acetic acid. To the eluate is added 5 ml of water containing $Na_2S_2O_5$ (0.2 percent) and EDTA (4 percent). The mixture is adjusted to *p*H 8.4 with 2*N* tris buffer and passed through an alumina column buffered to *p*H 8.4 with 0.2*N* sodium acetate. The column is washed with 5 ml of 0.2*N* sodium acetate and then with 5 ml of H_2O. ^{3}H-NE and NE are eluted by passing through 5 ml of 0.2*N* HCl. A portion of the eluate is added to Bray's solution [*Anal. Biochem.* **1**, 279 (1960)] and ^{3}H-NE is counted with a Packard Tri-Carb liquid scintillation spectrometer. Another portion of the eluate is oxidized and measured fluorimetrically.
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Variations of the Visual Responses of the Superior Colliculus in Relation to Body Roll

Abstract. *A large percentage of the directional units of the superior colliculus of the curarized cat modify their response to a particular moving visual stimulus as a function of the position of rotation of the animal about its longitudinal axis.*

The message from a receptor can be modified by influences stemming from other receptors. For example, modifications in the judgment of size, shape, or orientation of an object occur after exposure to other visual or vestibular stimulation (*1*). Moreover, electrophysiological recordings have shown that some cells of the visual cortex of the cat modify their responses in relation to body roll (*2*).

We studied the effect of body roll on the visual responses of cells in the superficial layers of the superior colliculus of the cat. This structure shows convergence of many sensory modalities and therefore seems a suitable place for interaction between vestibular and visual messages (*3*).

Cells in the superior colliculus superficial layers can be subdivided into two classes, directional cells and nondirectional cells, depending on whether or not they respond equally to the various directions of a moving visual stimulus (*4*). We will show that a large percentage of directional units alter their responses as a function of body roll.

Two or three days before the experiment, adult cats ($n = 10$) were anesthetized with sodium pentobarbital, and a craniotomy was made over the projections of both superior colliculi. A metallic chamber was positioned stereotaxically around the opening and was fixed to the bone with dental cement. On the day of the experiment the animal was briefly anesthetized with halothane, and tracheal and venous cannulas were inserted. The wounds were carefully infiltrated with a local anesthetic. After the removal of the dura, the anesthesia was interrupted, curare was injected, and artificial ventilation was used.

Pupils were dilated with atropine. The refraction of the eyes of the cat was determined by means of retinoscopy and was corrected with suitable contact lenses. The animal was fixed by clamping the metallic chamber cemented on his head on a table that could be rotated up to 70 degrees about the longitudinal axis of the animal. Also, the body of the animal was fixed to the table. The optic stimulator and a tangent screen were both attached to the tilting table. The optic stimulating system projected the image of a slide on the tangent screen by reflection on a

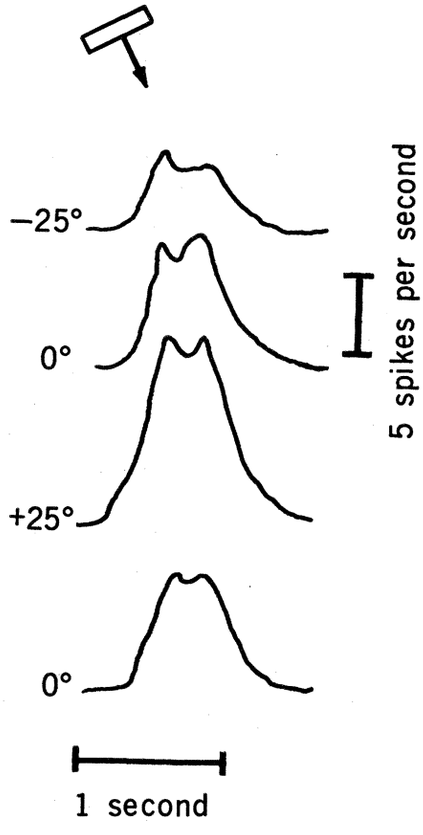

Fig. 1. Responses of an orientation sensitive unit of the left superior colliculus for three different positions of the tilting table. The stimulus was a luminous bar (15 degrees by 2 degrees; luminance, 10 cd/m^2 superimposed on a dimmer background) moving in the direction indicated by the arrow at a constant speed (18 degrees per second). This was the preferred direction of the cell when the table was horizontal and remained fixed with respect to the retina at the various positions of the table. Each record is the average of ten responses. The numbers on the left of each record indicate the degrees of roll (negative body roll means that the side where the electrode is placed is set downward). The bottom record is a control of the cell response for the 0-degree position of the table. The calibration (vertical line, spikes per second) on the right of the figure refers to a regular train of pulses. The average discharge of the cell did not change with the rotation of the table and was of the order of four to five impulses per second.

plane mirror, which could be rotated by a galvanometer driven by a function generator.

The action potentials of the cells of the superficial layers of the superior colliculus were recorded by means of tungsten microelectrodes. Once the action potential of a single cell was well isolated, it was fed into a Schmitt trigger which gave, for each impulse, a square wave of fixed amplitude and width (500 per microsecond). These pulses were then fed into a low-pass filter with a time constant of 300 msec and computer averaged (CAT 400B, Mnemotron Corp.).

In cats with fissurated pupils, photographs were taken of the pupils and of a reference system mounted in front of the eyes and fixed to the table. These photographs were taken for various positions of the tilting table by a camera that was rigidly fixed to the table. No appreciable rotation of the pupils was observed in the photographs. The possibility that a rotation of the eyes might be responsible for the variations of the cell response seems to be ruled out also by the fact that units sensitive and insensitive to roll were recorded in the same track of the microelectrode.

The procedure of the experiment was as follows. As soon as a collicular unit was well isolated a luminous bar was moved in its preferred direction, and an average response to several passages of the visual stimulus was taken. The table was then gently rotated by a given amount. Since the optic stimulus and the screen were fixed to the table, the image of the luminous bar and its direction and orientation remained unaltered on the retina. To avoid possible transient effects, we took a new record 2 to 3 minutes after the table was rotated. Then the table was moved to another position.

Out of 74 cells fully analyzed, 42 were directional and 32 nondirectional units. Our results will mainly be concerned with the directional units, since in this class the percentage of units sensitive to the body roll of the animal is clearly greater with respect to the class of nondirectional units. In fact, among directional units, 24 (~ 57 percent) showed clear variations in the responses to the visual stimulus when the body of the animal was rotated, 4 (~ 9 percent) units showed to a qualitative analysis small or doubtful variations,

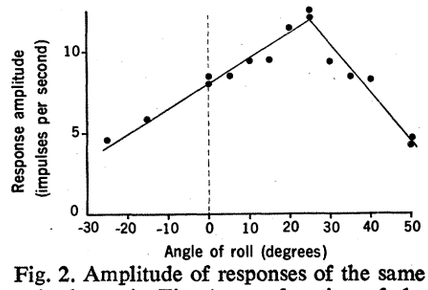

Fig. 2. Amplitude of responses of the same unit shown in Fig. 1 as a function of the body roll of the animal. In this case, when the response shows a double peak, the amplitude was evaluated by taking the average height of the two peaks with respect to the base line.

whereas 14 (~ 33 percent) did not show any effect. An example of the variations in the responses of the directional units, with the rotation of the body of the animal, is reported in Fig. 1. The 0-degree position corresponds to the experimental condition in which the table, where the cat is positioned, is horizontal. The minus sign (−25 degrees) and the plus sign (+25 degrees), correspond to body rolls side down or side up, respectively (side alludes to where the recording electrode is placed). The cell response to a luminous bar moving downward decreases when the body is rolled side down, whereas it clearly increases when it is rolled side up. In all directional units investigated a clear relation between the amount of body roll and the amplitude of the responses was found. Usually the units showed their greatest response for a given position of the body, which could be at 0 degree or at a certain degree of roll. Other positions of the animal caused a decrease in the response amplitude that was, at first approximation, related linearly to the amount of rotation. For example, one of the cells showed a maximum response for a roll side up of 25 degrees (Fig. 2). No persistent change of the average discharge was observed after the rotation of the table. In the present series of experiments it was not tested whether or not the preferred stimulus direction for a given cell changed with roll.

Among the 32 nondirectional units, only 9 (~ 28 percent) showed variations of their responses correlated with the roll of the body of the animal, whereas 23 units gave uncertain variations in the response or no variation at all. The variations in the responses showed by the nondirectional units present no clear relation with the amount of body roll.

Our results show that the effect of rotation of the animal about the longitudinal axis of its body is encoded in the visual message of a large percentage of collicular directional units with a high degree of precision. Indeed, at first approximation there is a linear relation between the amount of rotation and the amplitude of the response to the moving luminous bar. The experimental conditions were such that the visual stimulus did not change on the retina with the rotation of the animal; the collicular directional units, however, were able to signal that the same retinal message was coming from various orientations of the body.

If we look at vertical lines with the head in the upright position, the lines appear vertical. If however we tilt our body or our head together with the lines and to the same degree in such a way that the same retinal receptors are stimulated by the images of the lines, the lines appear oblique. Some information on the roll of the body of the subject must have modified the retinal message in such a way that at a perceptual level its interpretation is different, oblique instead of vertical lines. The present electrophysiological findings, which show that directional units of the superior colliculus change their visual message as a function of the position of rotation of the body of the animal, could account for the perceptual phenomenon described above.

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