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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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

fore, testing for function of the superior colliculus when its cortical inputs are missing may not reveal its normal abilities.

We have avoided this complication by testing the functional capability of the midbrain roof without removing the visual cortex. Instead we have used the split-brain preparation to determine if, in the absence of the forebrain commissures, information about direction of movement can transfer between the two halves of the brain. If transfer of discriminations based on movement is found, and if it can be prevented by additional section of the midbrain commissures, then we would suggest a prominent role for the midbrain roof in detection of movement. The basic assumption involved in this interpretation is straightforward: if a function, such as movement discrimination, is performed by particular bilateral neural structures, then it should be accessible to either side of the brain via the commissures interconnecting the structures in question. Conversely, sectioning the interconnecting commissures should prevent transfer of function between the structures. The existing data seem to support this assumption. It is necessary and sufficient to cut only the fibers interconnecting the occipital and inferotemporal visual areas of the cortex (that is, the splenium of the corpus callosum and the anterior commissure) to prevent interhemispheric transfer of visual pattern discriminations (*15*). At midbrain levels, intensity discriminations, which can be performed by destriate animals, have been reported to transfer via midbrain interconnections (*16*). In these experiments the optic chiasm is also sectioned in the midline in order to restrict the visual input from one eye to the half-brain on the same side. This allows the experimeter to train or test either half-brain simply by controlling which eye the animal uses.

Table 2. Comparison of learning ability by each hemisphere of four split-brain monkeys. R.E., right eye; L.E., left eve.

Subject	Trials to criterion		R.E.
	R.E.	L.E.	R.E. + L.E.
MLL	680	1030	0.40
	1850	1440	.56
	2730	560	.83
	2000	630	.76
SCN	1530	2150	.42
	1820	1370	.57
	4040	380	.91
	100	50	.67
FRD	2740	1500	.65
	2730	1160	.70
	1950	1400	.58
	1190	1350	.47
HPJ	3600	490	.88
	2460	70	.97
	4500	760	.86
	3420	660	.84

Four split-brain monkeys (*Macaca mulatta*) and four control monkeys, with only their optic chiasm sectioned, were trained with one eye on the problems described below to a criterion of 90 percent correct over 40 trials and overtrained until performance was maintained at 90 percent for 120 trials (*17*). Then the second eye was tested for transfer and was overtrained to the same degree. Two measures of transfer were calculated: the level of performance on the first 40 transfer trials (initial percent of transfer) and the overall advantage in learning with the untrained eye (percent of savings). The savings score, calculated from the trials taken by each eye to reach criterion, is defined as

$$\text{Percent of savings} = \frac{\text{1st eye (trials)} - \text{2nd eye (trials)}}{\text{1st eye (trials)} + \text{2nd eye (trials)}} \times 100$$

The apparatus used for testing the animals is the same as the one developed by Sperry and his associates (*18*). The monkey voluntarily positioned itself in a compartment that allowed control over which eye and hand the monkey was able to use. A panel placed before the monkey at eye level and within its reach contained two 4-cm translucent panels, one above the other, on which the stimuli were back-projected. A push on either panel activated an automated programming apparatus that started a 10-second intertrial interval, rewarded correct responses with a banana-flavored pellet, and tallied the data. A repeating 20-trial Gellerman sequence determined whether the top panel was correct or incorrect. On a given trial only the top panel was actually illuminated, either by the correct or incorrect stimulus. Thus the stimuli was presented successively as in a go, no-go task, but since a response was required on every trial, as in a conventional two-choice discrimination, the usual biases caused by responding to the negative stimulus were avoided. The animals were first taught a practice problem with conventional simultaneous presentation of both stimuli, and then the lower stimulus was turned off. All monkeys quickly generalized to this modified two-choice discrimination.

The stimuli consisted of a field of randomly distributed irregular spots flowing continuously across the top panel at about 10 degrees per second. They were produced by back-projecting a small portion of a large spotted disk that rotated in the film plane of a stereoprojector. The segment of the disk that was projected was so small that the curvature of the path of the dots was not noticeable; the two stimuli were identical in all respects except the direction of their movement. A Dove prism, placed before each projection lens, was used to control the direction of movement of the image projected by that lens. During an experimental session the stimuli were changed by switching the illumination from one half of the projector to the other. Four pairs of the moving stimuli were taught to each monkey: → versus ←, ↑ versus ↓, ← versus ↑, ↓ versus →. Half the animals learned the four problems in this order, and half learned the second two sets before the first two. Each learned the first and third problems with their right eye first and the second and fourth problems with their left eye first. The arm used was different on different problems, so that all possible combinations of eyes and hands were trained. Transfer tests were run on half the monkeys with the same hand and on the other half with the untrained hand. No differences in results were associated with either the hand or the specific stimuli used.

The principal results are summarized in Table 1. Both the initial level of performance (chance is 50 percent) and the savings on trials to criterion with the second eye (0 percent means no savings) were well above chance for the chiasm-sectioned subjects. By contrast, the split-brain subjects showed no advantage when the second eye was tested; the average initial performance was about chance (49 percent), and the average savings was insignificant (− 5 percent). Therefore there is no indication from the transfer tests that the midbrain was used for the discrimination of direction of movement. The positive transfer found in the chiasm-sectioned controls suggests, on the other hand, that the movement discrimination utilized cortical mechanisms, since the commissural connections between these areas allowed interocular transfer of the discrimination.

An easier problem, the discrimination of stationary from moving dots, was then tested on the four split-brain monkeys in the same apparatus. Half the animals had the stationary stimulus positive and half had the moving stimulus positive. All monkeys used the hand contralateral to the eye that was unoccluded. Again no significant transfer was seen (mean initial transfer, 52 percent; mean savings, 22 percent).

It should be noted that use of large fields of moving dots, which would look more like the visual flow patterns discussed by Gibson, rather than the small fields used here might reveal a contribution of midbrain mechanisms to discrimination (*9*). Alternatively, tests not involving learning at all might be more likely to show a midbrain contribution to spatial perception. However, under the present conditions it would seem that forebrain mechanisms are the likely candidates for discriminating movement.

A rather striking variability in the savings scores for the four discriminations involving direction of movement was noticed for each split-brain monkey. Although the mean savings score was nearly zero, there were several cases of large positive and negative scores. This variability could be attributed to a strong tendency for the left hemisphere to learn the discriminations more quickly than the right, regardless of whether it was the first or second hemisphere to be taught the problem. Table 2, which contains the raw data on which part of Table 1 is based, presents the trials to criterion for each hemisphere and the ratio of right hemisphere trials to total trials for the two hemispheres. The data for each monkey are arranged in the same order that was given above for the presentation of stimuli; therefore, the right eye was trained first on the first and third discriminations, and the left eye first on the others. Of the 16 discriminations, 13 were learned more quickly by the left hemisphere, as indicated in the third column by ratios greater than 0.50. A t test on the median ratios shows this to be significant at $P < .05$ [$t(3) = 3.2$]. No such "cerebral dominance" effect was seen on two pattern discriminations previously trained in the same apparatus to each of these split-brain monkeys. This control, plus the fact that it was the left hemisphere that was retracted during surgery, makes it unlikely that the asymmetry found in learning these spatial discriminations was artificially induced. It seems probable that the dominance relates to the orientational aspects of the stimulus rather than to the movement, since no cerebral dominance was seen on the discrimination of moving from stationary dots.

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Energy and Epilepsy

The report by Sanders *et al.* (*1*) relating decreased concentrations of adenosine triphosphate (ATP) in rat brains coincident with the onset of seizures deserves critical debate. Their conclusion that the common denominator and possible etiological factor of various convulsants (for example, hypoxia, hydroxylamine, Metrazol, and methionine sulphoximine) is a fall in the amount of ATP in the brain contrasts with previous results. It has been found that, when mice are given insulin, Metrazol, or methionine sulphoximine, seizures occur without a significant drop in ATP (*2*). Conversely, with secobarbitone anesthesia and electroshock, significant decreases in ATP occur without behavioral signs of a seizure. Similar dissociation in metabolism and seizures has been found in monkeys, dogs, and mice after treatment with Metrazol or electroshock (*3*). Cortical discharge and increased cerebral blood flow occur during a convulsion in the absence of demonstrable metabolic changes in blood or brain energy substrates when animals are paralyzed and well ventilated.

Part of the discrepancy in the findings of Sanders *et al.* may be due to methodology. They attribute the low control ATP value in part to a delay in the freezing of the rat brain. Other investigators have circumvented this by using only the outer cortex of the smaller mouse brain (*2*). A delay in freezing would prolong anoxic catabolism and would bias tissue samples toward low ATP; this trend would be accentuated by any condition that either limited energy supply, such as hypoxia, or increased energy consumption, such as Metrazol.

Both the report by Sanders *et al.* and the hypothesis by Hillman (*4*) focus attention on the possibility that a failure to supply ATP to the sodium pump may cause an electrolyte imbalance that initiates a convulsive discharge. This idea warrants careful documentation, but unfortunately at present the