21. A. N. Popper, in preparation. I have data for several other non-ostariophysans, including cichlids, holocentrids, and myctophids.
22. This work was done while I was in residence at the Kresge Hearing Research Institute and the Division of Biological Sciences, University of Michigan, Ann Arbor. I thank J. E. Hawkins, Jr., for providing me with facilities at the University of Michigan and for valued discussions during the course of my work. R. Preston aided in all phases of this work. I thank J. Corwin for suggesting use of the ultrasonic cleaner; the staff of the University of Michigan scanning electron microscopy–electron microprobe analysis laboratory for assistance; and the U.S. Fish and Wildlife Service, Great Lakes Fishery Laboratory, for supplying the fish. R. R. Fay, J. E. Hawkins, Jr., R. Preston, and W. C. Stebbins read the manuscript. Supported by NINCDS grants NS-09374 to A.N.P. and NS-05065 and NS-05679 to J. E. Hawkins, Jr., by program project grant NS-05785 to M. Lawrence, and by a biomedical science support grant from the University of Hawaii to A.N.P.

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Cross-Modal Matching and the Primate Frontal Cortex

Abstract. *Rhesus monkeys with selective lesions of the prefrontal system were tested on a tactile-visual cross-modal matching task. Monkeys with lesions in the banks and depths of the arcuate sulcus were impaired, while normal controls and monkeys with lesions in the banks and depths of the sulcus principalis and in the anterodorsal part of the head of the caudate nucleus were not.*

In a recent review of transfer of information between sensory modalities Ettlinger concluded that there is no unequivocal evidence of cross-modal matching abilities in the monkey, although such abilities are demonstrated by the chimpanzee and man (*1*). However, if the stimuli used in the cross-modal experiment are edible and inedible shapes (thus more easily discriminable and relevant to the animal), the rhesus monkey is capable of cross-modal matching (*2*). As revealed by neuroanatomical studies, several cortical areas in the monkey brain are foci where information from various modalities converges (*3*). These are the vicinity of the arcuate sulcus, the inferior parietal lobule, and the depths of the superior temporal sulcus. Damage to such areas might be expected to impair performance on a cross-modal task. We now report the effects of discrete prefrontal lesions on tactile-visual cross-modal matching by the monkey.

The subjects were 14 rhesus monkeys (*Macaca mulata*). Four of these sustained ablations confined to the banks and depths of the arcuate sulcus, four had both the banks and the depths of the sulcus principalis ablated, four had electrolytic lesions aimed at the anterodorsal part of the head of the caudate nucleus [which receives projections from the sulcus principalis (*4*) and is functionally related to this area (*5*)], and two served as normal controls. All the lesions were bilateral and were made at least 16 months before the monkeys were tested. As the animals are being used in further experiments, we have not yet made histological examinations. Prior to this experiment, the ability of the animals on delayed response and delayed alternation tasks was measured; as expected (*6, 7*), the animals with lesions within the sulcus principalis and in the head of the caudate nucleus were impaired on both of these tasks, but those with arcuate lesions were not.

The monkeys were tested in a Wisconsin General Test Apparatus (WGTA). The discrimination stimuli were palatable or unpalatable "cookies" of 16 shapes made from Dixons powdered diet for monkeys (41-B) according to procedures described earlier (*8*). Before the actual testing was begun, the monkeys were trained to accept the cookies in the darkened WGTA.

For a particular day's testing cookies of two shapes, one palatable (positive) and one unpalatable (negative), were used. The pair was chosen so that the shapes were clearly discriminable. Examples are a star paired with a sphere or a disk with a cross. Each day, ten palatable and ten unpalatable cookies were mixed together on a tray (17 by 18 cm) and presented to the monkey. In the darkened WGTA, the monkey was allowed to feel and eat the selected shapes. After the animal had eaten at least eight palatable positive shapes, the experimenter lowered the opaque screen and covered the tray beneath the transport cage with a cardboard sheet to prevent the animal from subsequently noticing the discarded negative shapes (the floor of the transport cage was constructed in such a way that discarded shapes dropped out of reach of the animal). The light of the WGTA was then turned on, and one new pair of shapes, which the animal had investigated and tasted in the dark, were placed on the tray 8 cm apart. The animal was allowed to look at the shapes as the experimenter manipulated them and placed them on the tray. The tray was pushed forward after 20 seconds, and the animal was allowed to choose one of the shapes. This procedure was repeated daily for 20 days. Eight pairs of stimuli were used during the first 8 days and then the shapes were recombined in various ways to form the pairs for the following 12 days' testing.

Table 1. Performance of monkeys on cross-modal and visual discrimination tasks.

Subject	Cross-modal (percent correct)	Visual discrimination (percent correct)
Lesions within the arcuate sulcus		
1	50	85
2	50	100
3	60	100
4	60	70
Lesions within the principalis sulcus		
1	60*	75
2	65	85
3	75	95
4	80	80
Lesions in the caudate nucleus		
1	70	80
2	70	90
3	75	95
4	85	80
Normal controls		
1	70	75
2	75	75

*Because he demonstrated severe perseveratory deficits on previous tests, we suspect that this animal's lesion may have invaded the inferior convexity (*6*).

The normal monkeys were capable of cross-modal matching ($P = .01$, binomial two-tailed test) (Table 1) as were the monkeys with lesions of the sulcus principalis ($P < .01$) and the head of the caudate nucleus ($P < .01$). However, performance of the animals with arcuate lesions was no better than that predicted by chance ($P = .50$). The group of animals with arcuate lesions differed from the other groups [$2\hat{I} = 7.76$, d.f. = 1, $P < .01$, information statistic (*9*)], but the other groups did not differ significantly from each other ($2\hat{I} = 0.50$, d.f. = 2, $P < .80$).

The design of this transfer task cannot exclude the possibility that any observed impairment is due to loss of visual or tactile discrimination. Dorsolateral frontal lesions can, in some circumstances, produce impairment of visual, tactile, or auditory discrimination (*6*), characterized by difficulty in withholding responses to unrewarded stimuli in discrimination tasks. It is generally believed that this impairment is seen only when the dorsolateral lesion encroaches into response control areas on the inferior convexity of the frontal lobe (*6*); this area was not included in our lesions. As determined by earlier testing on an object discrimination reversal test, only one monkey had a perseveratory deficit.

However, it seemed important to exclude the possibility that the cross-modal transfer impairment in the animals with arcuate lesions was not associated with loss of either visual or tactile discrimination. Accordingly, in further testing, a video tape recorder (*10*) was used to monitor the behavior of the animals during the initial tactile discrimination experience. The performance of the animals with arcuate lesions was similar to that of the normal controls. Typically, the monkey, having examined a few of the adulterated shapes both by touch and mouth, was able to discriminate and to discard further negative shapes by touch alone. Such sampling would not be predicted in animals with impaired tactile discrimination.

We next investigated the possibility of disturbed visual functioning in the impaired animals. Each animal was tested for ten trials on two visual discrimination tasks with freshly prepared edible and inedible shapes. All groups performed well on these tasks ($P < .01$, binomial two-tailed test) (Table 2). An analysis of discrimination performance on trials 2 to 6 for the various groups revealed no difference ($2\hat{I} = 17.49$, d.f. = 15, $P < .30$, information statistic). Trials 2 to 6 were chosen for this analysis because the probability of the first trial is always .50, and trials 7 to 10 contained very few errors and thus could have masked any differences which might exist.

Very little is known about the functional significance of the arcuate sulcus. The arcuate sulcus is not the crucial focus for the deficits in delayed response and delayed alternation tasks (*7*), which have been the classical tasks sensitive to prefrontal damage in the monkey (*11*) and for which the crucial area has been shown to be the sulcus principalis (*12*).

Table 2. Total number of errors for each of the ten visual discrimination trials.

Groups	Errors after trials									
	1	2	3	4	5	6	7	8	9	10
Arcuate	2	1	2	1	0	1	1	0	1	0
Principalis	4	4	1	2	0	1	1	0	0	0
Caudate	1	1	3	1	0	0	2	2	1	1
Normal	1	3	0	2	2	0	1	0	1	0

Arcuate lesions on the other hand, impair performance on an auditory conditional position discrimination, in which an auditory signal from one spatial location demands one response from the animal, and a second auditory signal demands a different response (*7*).

There is anatomical (*3*) and physiological (*13*) evidence suggesting that the arcuate cortex may play an important role in multimodal tasks. The unilateral inattention to stimuli of all sensory modalities that results from unilateral lesions of the cortex in the arcuate sulcus supports this view (*14*). Poor performance on the auditory conditional position response (*7*), as well as the present cross-modal deficit, could be viewed as deficient ability either to integrate auditory, visual, and kinesthetic information or to use such multimodal information in the execution of an appropriate response. However, the cortex lying in the banks and depths of the arcuate sulcus may be a functionally heterogeneous area, as indicated by the different projections to various parts of this cortex (*15*). More precise localization of the source of the cross-modal deficit within the arcuate lesion would be interesting.

In addition to the arcuate sulcus, there are other multimodal convergence areas in the cortex, which may play roles in the integrative processes required for the cross-modal task. Further work must be done to specify the contribution of the anterior and posterior sensory convergence areas on this task.

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