8. Thermal conductance includes heat losses by conduction, convection, radiation, and evaporation [B. K. McNab, *Physiol. Zool.* **53**, 145 (1980).
9. Although there is disagreement over how best to refer to this relation, the use of "Newtonian cooling" seems acceptable to most [W. A. Calder, *Comp. Biochem. Physiol.* **43A**, 13 (1974); C. R. Tracy, *Science* **181**, 185 (1973).
10. Metabolic rates (in milliliters of oxygen per gram of body mass per hour) at 10° and 20°C and body masses (in grams) were collected initially on nine species of dasyurid marsupials (*1*). More data were obtained from graphical representations or regression equations generated from tabular data (*17–26*). In all cases, metabolic rates were below thermoneutrality. Since there were no differences between the two data groups, they were combined (*11*).
11. Regression equations were calculated by the method of least squares after logarithmic transformations. Equations presented have slopes significantly different from zero (F test); the acceptable level of significance used throughout is $P < 0.05$. Differences between slopes and elevations were tested by analysis of covariance [G. W. Snedecor, *Statistical Methods* (Iowa State College, Ames, 1957), pp. 393–412]. Elevation of regression lines was compared only if the slopes were not significantly different; all differences in elevation between lines are presented at 450 g, which is the approximate mean body mass of the marsupial data.
12. B. K. McNab, *J. Comp. Physiol.* **125**, 115 (1978).
13. P. C. Withers, T. M. Casey, K. K. Casey, *Comp. Biochem. Physiol.* **64A**, 343 (1979). The equation for arctic mammals at 20°C includes some data within thermoneutrality; the y intercept and slope fall within the 95 percent confidence intervals of these variables for marsupials (Fig. 2). At 10°C the equation for arctic mammals has a slope that is steeper than the 95 percent confidence interval of the slope of the marsupial equation.
14. D. S. Hinds and R. E. MacMillen, in preparation. Allometric equations were obtained for heteromyid rodents at 5° and 15°C and were estimated at 10° and 20°C to compare with the marsupials; the prediction technique used is that described for 0°C by Hinds and MacMillen. To determine its accuracy we followed the same procedure at 5° and 15°C and compared these equations to those obtained when oxygen consumption was actually measured. The relation obtained from measured values had similar slopes to those obtained from predicted values; however, the latter equations are significantly elevated by 10 percent. Thus, the heteromyid equations (Fig. 2) have a greater elevation than if oxygen consumption had actually been measured.
15. For a generalized eutherian, the relation between oxygen consumption and mass below thermoneutrality can be derived from $H_m = h(T_b - T_a)$ where H_m is energy metabolism, h is thermal conductance, T_b is body temperature, and T_a is air temperature. At a T_a of 10°C, a T_b of 37°C, and h is related to body mass [C. F. Herreid and B. Kessel, *Comp. Biochem. Physiol.* **6A**, 57 (1962)] an estimate of this relation is: milliliters of oxygen per gram of body mass per hour = $27.81\ g^{-0.51}$ with g being body mass in grams.
16. Graphical representations of the marsupial data in the literature generally show the lines relating metabolism to air temperature intercepting zero metabolism at air temperatures equal to body temperatures; this is expected if the animal follows Newtonian cooling.
17. J. Arnold and J. Shield, *J. Zool. London* **160**, 391 (1970).
18. P. R. Morrison and B. K. McNab, *Comp. Biochem. Physiol.* **6A**, 57 (1962).
19. A. J. Hulbert and T. J. Dawson, *ibid.* **47A**, 583 (1974).
20. G. A. Bartholomew and J. W. Hudson, *Physiol. Zool.* **35**, 94 (1962).
21. T. J. Dawson and R. Degabriele, *J. Comp. Physiol.* **83**, 41 (1973).
22. A. Kinnear and J. W. Shield, *Comp. Biochem. Physiol.* **52A**, 235 (1975). Computed from body temperature and conductance assuming animals follow Newtonian cooling.
23. J. W. Hudson and T. J. Dawson, *Aust. J. Zool.* **23**, 453 (1975).
24. W. R. Dawson and A. F. Bennett, *Physiol. Zool.* **51**, 114 (1978).
25. T. J. Dawson, M. J. S. Denny, A. J. Hulbert, *Comp. Biochem. Physiol.* **31A**, 645 (1969).
26. T. J. Dawson, *ibid.* **46A**, 153 (1973). Average of summer and winter values.
27. We thank S. R. Morton for his valuable insight and comments and H. Bowler, F. D. Blume, L. DiMolfetto, and D. H. Ost for commenting on the manuscript. We appreciate editorial assistance of E. A. Halpern Hinds and constructive criticisms provided by the referees. This work was supported by NSF grants GB-5618 and DEB-7923808.

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The Ultraviolet Receptor of Bird Retinas

Abstract. *The eyes of 15 species of birds from 10 families have some cones maximally sensitive at 370 nanometers in the near-ultraviolet. Spectral sensitivity was measured by recording extracellularly in opened eyecups, and a maximum in the ultraviolet was revealed by selectively adapting the retina with yellow background lights. The 370-nanometer spectral sensitivity function is attributed to receptors because its spectral position does not vary with the strength of adaptation and because it is present when the receptor potentials are isolated from the contributions of higher order retinal neurons by exposing the retina to sodium aspartate. These measurements demonstrate the basis for the ultraviolet sensitivity of birds that has been seen in behavioral experiments, and they provide further evidence that many vertebrates share with insects vision in the near-ultraviolet.*

Although it is widely believed that birds have color vision, in only a few species have demanding behavioral criteria been met, primarily in the pigeon (*1, 2*). Daws (*3*) and hummingbirds (*4, 5*) have also received critical attention.

In the retinas of birds (and some reptiles) each cone cell has a colored oil droplet at the distal end of the inner segment, so placed as to filter the light reaching the visual pigment. These droplets contain carotenoids with absorbances that can be greater than 20 (*6*). Because carotenoids absorb in the blue and violet regions of the spectrum, the traditional presumption has been that the vision of birds must be most effective at the long wavelength end of the visible spectrum. The functions of the cone oil droplets have been the subject of much speculation (*7*).

In recent years evidence has accumulated for multiple cone pigments in the retinas of pigeons and chickens. These new data lay to rest the idea that the cone oil droplets work together with a single cone visual pigment to produce several kinds of receptors with different spectral sensitivities. In chicken and pigeon direct evidence exists, from both retinal physiology (*8, 9*) and digitonin extraction (*10*), not only for several cone pigments, but for one with peak of absorption at 415 nm. Moreover, hummingbirds discriminate wavelengths as well in the violet as elsewhere in the visible spectrum (*5*). Still other behavioral evidence suggests that the visible spectrum of pigeons (*11*), hummingbirds (*12*), ducks (*13*), and a variety of passerines (*14*) extends into the near-ultraviolet (UV), but the basis for vision at such short wavelengths has not been demonstrated in birds.

We now report electrophysiological evidence that the retinas of hummingbirds and several species of passerines have cones with peak sensitivity in the UV at 370 nm. Birds were netted in southern Connecticut and dark-adapted overnight. They were anesthetized, their eyes were enucleated, and the front half of the eye was removed under dim red light. The back half of the eye was mounted in a moist chamber, and the eye was stimulated with light from a 150-W, optically stabilized xenon arc and a grating monochromator (*15*). Transretinal voltage responses were recorded with flat chlorided silver rings (*16*). Intensity of the stimulus was controlled with a pair of counterrotating optical wedges made of graded films of Inconel on quartz substrates. Stimuli consisted either of 100-msec flashes or a 25-Hz flicker, to which the rods respond poorly (*16*). In the latter case, the amplifier was also tuned to 25 Hz and had a noise level of about 0.2 μV. The stimuli were either presented in the dark or, to unmask the UV receptor, superimposed on a yellow background light (Schott sharp-cut filter, wavelengths longer than 530 nm), which was obtained from a 100-W tungsten-halogen lamp and combined with the stimulus beam by means of a dielectric beam splitter. Spectral sensitivity was determined by measuring the quantum flux required for a criterion response of 5 μV (single flashes) or 1 μV (25-Hz stimulus).

Figure 1A shows some results from the eye of a gray catbird (*Dumetella carolinensis*). Spectral sensitivity of the dark-adapted eye to single flashes peaked near 510 nm, and the response was dominated by rods. When the eye was stimulated with 25-Hz flicker, the spectral sensitivity peaked at about 580 nm and seemed to be due entirely to cones.

When the test lights were superim-

Table 1. List of families or subfamilies and species of birds in which there is electrophysiological evidence for retinal cones that are maximally sensitive at 370 nm.

Family or subfamily	Common name	Species
Columbidae	Rock dove (pigeon)	*Columba livia*
Trochilidae	Ruby-throated hummingbird	*Archilochus colubris*
Corvidae	Blue jay	*Cyanocitta cristata*
Hirundinidae	Barn swallow	*Hirundo rustica*
Paridae	Black-capped chickadee	*Parus atricapillus*
Mimidae	Gray catbird	*Dumetella carolinensis*
	Brown thrasher	*Toxostoma rufum*
Turdinae	Wood thrush	*Hylocichla mustelina*
	American robin	*Turdus migratorius*
Passerinae	House sparrow	*Passer domesticus*
Carduelinae	House finch	*Carpodacus mexicanus*
Cardinalinae	Northern cardinal	*Cardinalis cardinalis*
Icterinae	Red-winged blackbird	*Agelaius phoeniceus*
Emberizinae	Song sparrow	*Melospiza melodia*
	White-throated sparrow	*Zonotrichia albicollis*

posed on a steady yellow background field, the cones with peak sensitivity in the region of 580 nm suffered selective adaptation, and receptors responding maximally at shorter wavelengths were revealed. The cone that was sensitive at shortest wavelengths was maximally sensitive at 370 nm. Although its presence was evident with the 25-Hz flicker (not shown), more effective isolation was obtained when it was measured with single test flashes superimposed on the yellow adapting field, and the separation was more complete the brighter the adapting light (Fig. 1A).

If the peak at 370 nm is due to a cone whose sensitivity maximum is located in the near-UV, it should be possible to depress selectively the sensitivity of the retina in this spectral region by using a UV-adapting field. If, on the other hand, the retina contained a single spectral class of cones with a secondary absorption band at 370 nm, both the visible and UV-sensitivity maxima would adapt together, regardless of the spectral composition of the adapting field. This prediction is valid whether or not the spectral sensitivity function is modified by the presence of an inert screening pigment—for example, an oil droplet. Figure 2A shows the results of UV adaptation of the retina of the black-capped chickadee (*Parus atricapillus*). That the depression of sensitivity was greatest in the spectral region occupied by the adapting light (compare Figs. 1 and 2A) is consistent with the presence of more than one spectral class of cone, one of which absorbs maximally at 370 nm. That adaptation to UV light causes a depression of sensitivity in the visible as well as the UV was also expected because all visual pigments have some sensitivity to near-UV light.

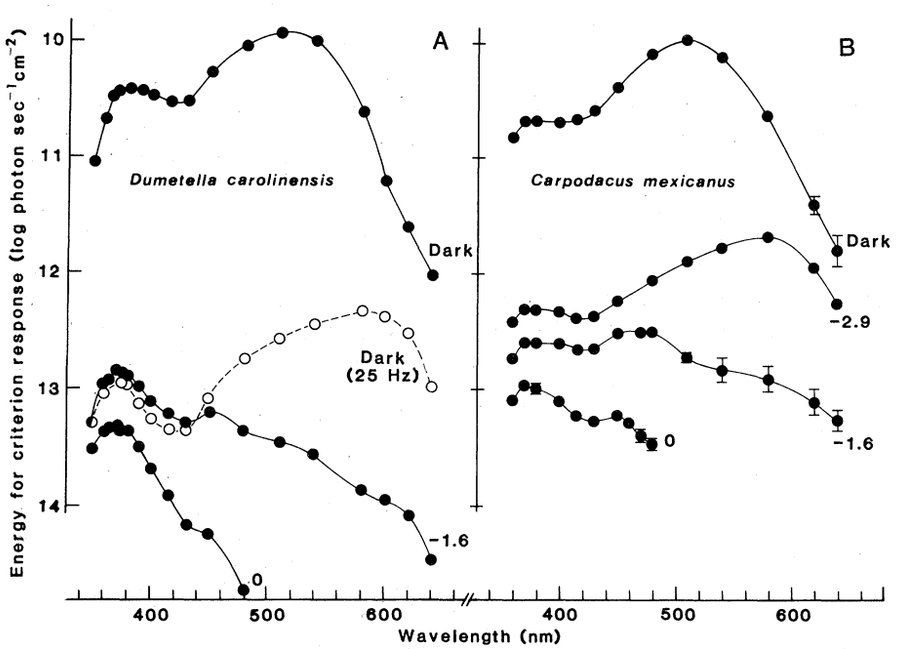

Fig. 1. (A) Spectral sensitivity of a gray catbird (*Dumetella carolinensis*) retina, measured in response to single flashes (filled circles and solid curves; 5-μV criterion response) or a light flickering at 25 Hz (open circles, dashed curve; 1-μV criterion response). The log level (relative units) of the yellow background adapting field is specified at the right end of each curve; log I = 0 corresponds to a quantum flux of approximately 6.5×10^{15} photon sec^{-1} cm^{-2} in the wavelength band between 530 and 640 nm. "Dark" signifies the absence of the second adapting light. Long-wavelength adaptation shows the presence of a cone with peak sensitivity at about 370 nm in the near-UV. (B) Spectral sensitivity of the house finch (*Carpodacus mexicanus*) to single flashes in the dark-adapted state (upper curve) and with three levels of background adaptation to yellow light. Values are given as means ± standard error of the mean for six eyes. Long wavelength–sensitive cones dominate the response at the lowest background intensity (log I = 2.9), and although the UV receptor is evident at log I = 0, it does not isolate as cleanly as in the eyecup of the gray catbird (A).

In principle, a sensitivity maximum in the UV could be caused by secondary excitation of visual pigment due to fluorescence or by energy transfer from a UV-absorbing antenna pigment as in the photoreceptor membranes of flies (*17*). In either case, adapting the receptor containing the visual pigment with long-wavelength light should depress sensitivity to UV by an equivalent amount. In the limiting case, bleaching the visual pigment should render the receptor insensitive to UV light. But just the opposite was observed. Increasing the intensity of a yellow adapting field had relatively little effect on the 370-nm peak (Fig. 1A) while greatly depressing the sensitivity at long wavelengths. Even with a quantum efficiency of fluorescence or of energy transfer of 1, a very special and improbable set of ad hoc assumptions would have to be made to account for a sensitivity at 370 nm more than 1 log unit greater than at all wavelengths longer than 460 nm (lowest curve in Fig. 1A). The effects of long-wavelength adaptation are therefore not easily reconciled with either of these alternative explanations for the 370-nm peak of sensitivity.

The selective depression of sensitivity in the UV by a UV-adapting light (Fig. 2A) is likewise inconsistent with the hypothesis of either a photostable source of fluorescence or a photostable antenna pigment. With either fluorescence or radiationless energy transfer, selective adaptation would be expected only if the accessory pigment were photoinactivated at quantum fluxes that spared the

visual pigment. As all visual pigments are somewhat sensitive in the near-UV, this would require an accessory pigment of comparably high photosensitivity. No such accessory pigment is currently known. On the other hand, both the depression of sensitivity in the UV and its subsequent recovery in the dark (Fig. 2A) are consistent with the adaptation of a cone maximally sensitive at 370 nm.

The interpretation that the 370-nm peak represents the presence of a UV-sensitive cone and is not the result of higher-order neural interactions is based on two arguments. First, the spectral position of the wavelength maximum remains the same with different intensities of the adapting background. By itself, this argument is not totally persuasive, because it assumes that the proposed opponent mechanisms are not invariant over a broad range of intensities. We have therefore sought the UV peak in the presence of 50 m*M* sodium aspartate (Fig. 2B), which blocks transmission between receptors and retinal interneurons and simplifies the waveform of the electrical response (*18*).

Not all the birds that we have examined show an UV receptor with the prominence of Fig. 1A. For example, in the house finch (*Carpodacus mexicanus*), UV-sensitive cones made a relatively smaller contribution to the electroretinogram. In the dark-adapted eye, the difference in sensitivity between 510 and 370 nm was 0.7 log units, whereas in the catbird it was 0.5 log units. More important, the 370-nm peak is more difficult to isolate by selective adaptation (Fig. 1B).

The relationship between the 370-nm receptor and the oil droplets of bird retinas is not clear, but the following observation is suggestive. A small fraction of the oil droplets contain no carotenoid and do not absorb at wavelengths down to (at least) 325 nm. Although it is possible for near-UV light to penetrate certain of the other oil droplets (*6*), cones with transparent droplets would seem to be the most likely candidates to be UV receptors. In indirect support of this hypothesis, we found that transparent droplets account for less than 5 percent of the total in the house finch retina but are typically 10 to 15 percent of the droplets in hummingbirds and in other passerines that we have examined (*6*). The cornea and lens of birds are transparent to 340 nm (*9*) or 310 nm (*19*).

Table 1 lists the birds that we have studied to date; in all of them we found evidence for UV receptors. Although the sample of species in this preliminary report is small, 10 families are represented, and all of the 15 species have receptors peaking at 370 nm. None of these birds has a prominent receptor at 415 nm, as do chicken and pigeon (*8, 9, 16*). Chickens lack the 370-nm receptor; pigeons have it (Table 1). Although we infer from these data that UV receptors are likely to be widespread among birds, there is a suggestion that their relative numbers may not represent a very conservative evolutionary feature (compare A and B in Fig. 1).

Since the discovery that the visible spectrum for many insects extends into the near-UV (*20, 21*), much effort has been invested in looking for natural UV signals in the nectar guides of flowers (*22–24*) and the patterns of reflectance of butterfly wings (*23–25*). The idea has developed that insects have a sensory subchannel available in the near-UV that they do not share with vertebrates in general and vertebrate predators in particular (*24*). The finding that birds have cones maximally sensitive in the near-UV forces a reexamination of this idea. For example, the wax bloom on many berries reflects near-UV, and for birds, this may enhance the contrast of small fruits seen against green, UV-absorbing leaves (*26*). Birds (*3, 8–10*), like some fish (*27*), may well have four cone pigments and a tetrachromatic color vision. Honeybees see near-UV light as a distinct color (*21*), but analogous behavioral experiments have yet to be done on birds. In any event, sensitivity to near-UV light by a variety of vertebrates is more common than our own visual experience has led us to expect (*12, 26*).

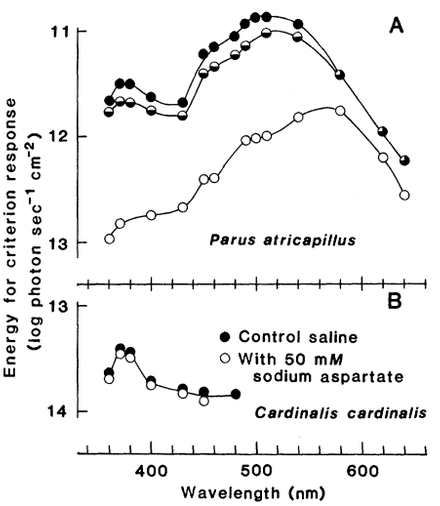

Fig. 2 (A) Spectral sensitivity of a chickadee (*Parus atricapillus*) retina, measured in response to single flashes. Because of the smaller size of the eye, the apparent threshold of the dark-adapted retina (filled circles) was somewhat higher than in either species illustrated in Fig. 1. Because the test lights were brighter, conditions were not strictly scotopic, and a contribution from the UV-sensitive cones is evident as a more distinct secondary peak at 370 nm. This UV peak was abolished (open circles) by a background adapting field of near-UV light (Corning filter 7-54 on a 100-W quartz-iodine lamp). After a subsequent hour in the dark, the original spectral sensitivity recovered (half-filled circles). The sensitivity peak at 370 nm therefore adapts to both light and dark, as is expected of a receptor. (B) Spectral sensitivity at short wavelengths of the right eye of a northern cardinal (*Cardinalis cardinalis*) (filled circles, control) and the left eye (open circles, after exposure to 50 m*M* sodium aspartate) measured in the presence of a bright yellow adapting light ($\lambda > 530$ nm). The occurrence of the UV peak in the presence of aspartate indicates that it is due to a cone that is maximally sensitive at 370 nm and is not likely the result of higher order neural interactions between cones of different spectral sensitivities.

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References and Notes

1. W. F. Hamilton and T. B. Coleman, *J. Comp. Psychol.* **15**, 183 (1933).
2. A. M. Granda and J. H. Maxwell, Eds., *Neural Mechanisms of Behavior in the Pigeon* (Plenum, New York, 1979).
3. R. H. A. Wessels, thesis, Rijksuniversiteit, Utrecht (1974).
4. T. H. Goldsmith and K. M. Goldsmith, *J. Comp. Physiol.* **130**, 209 (1979).
5. T. H. Goldsmith, J. S. Collins, D. L. Perlman, *ibid.* **143**, 103 (1981).
6. T. H. Goldsmith, J. S. Collins, S. Licht, *Vision Res.*, in press.
7. W. R. A. Muntz, in *Handbook of Sensory Physiology*, vol. 7, part 1, *Photochemistry of Vision*, H. J. A. Dartnall, Ed. (Springer, Berlin, 1972), p. 529; M. L. Wolbarsht, *Fed. Proc. Fed. Am. Soc. Exp. Biol.* **35**, 44 (1976); W. H. Miller, in *Handbook of Sensory Physiology*, vol. 7, part 6A, *Vision in Invertebrates*, H. Autrum, Ed. (Springer, Berlin, 1979), p. 69.
8. D. V. Norren, *Vision Res.* **15**, 1164 (1975); V. Graf, in (*2*), p. 129.
9. V. I. Govardovskii and L. V. Zueva, *Vision Res.* **17**, 537 (1977).
10. L. Y. Fager and R. S. Fager, *ibid.* **21**, 581 (1981).
11. A. A. Wright, *J. Exp. Anal. Behav.* **17**, 325 (1972); J. D. Delius and J. Emmerton, in (*2*), p. 51; M. L. Kreithen and T. H. Eisner, *Nature (London)* **272**, 347 (1978).
12. H.-H. Huth and D. Burkhardt, *Naturwissenschaften* **59**, 650 (1972); T. H. Goldsmith, *Science* **207**, 786 (1980).
13. J. Parrish, R. Benjamin, R. Smith, *Auk* **98**, 627 (1981).
14. J. Parrish, R. Smith, R. Benjamin, J. Ptacek, *Trans. Kansas Acad. Sci.* **84**, 147 (1981); J. W. Parrish, J. A. Ptacek, K. L. Will, *Auk*, in press.
15. Ealing (Natick, Mass.), "Stabilarc 250"; Bausch and Lomb (Rochester, N.Y.), 250-mm focal length, slits set for a 10-nm half bandpass.
16. This technique for studying spectral sensitivity of bird retinas was introduced by V. Graf and D. V. Norren [*Vision Res.* **14**, 1203 (1974)]. Elsewhere [D.-M. Chen and T. H. Goldsmith, *J. Exp. Zool.* **229**, 265 (1984)], we have shown that in chicken eyecups the use of the 25-Hz stimulus selects for cones, particularly cones with maximum sensitivity at the long wavelength end of the spectrum, and that the adapting fields used in the present experiments produce a photopic state in the avian retina.
17. K. Kirschfeld, N. Franceschini, B. Minke, *Nature (London)* **269**, 386 (1977); B. Minke and K. Kirschfeld, *J. Gen. Physiol.* **73**, 517 (1979).
18. J. E. Dowling and H. Ripps, *J. Gen. Physiol.* **60**, 698 (1972).
19. J. Emmerton, J. Schwemer, J. Muta, P. Schlect, *Invest. Ophthalmol. Vis. Sci.* **19**, 1382 (1980).

20. J. Lubbock, *Ants, Bees and Wasps* (Appleton, New York, 1892); A. Kuhn, *Z. Vgl. Physiol.* **5**, 762 (1927); R. Menzel, in *The Compound Eye and Vision of Insects*, G. A. Horridge, Ed. (Clarendon, Oxford, 1975), p. 121.
21. K. Daumer, *Z. Vgl. Physiol.* **38**, 413 (1956).
22. K. Daumer, *ibid.* **41**, 49 (1958); F. E. Lutz, *Ann. N.Y. Acad. Sci.* **29**, 181 (1924).
23. G. A. Mazokhin-Porshnyakov, *Insect Vision* (Plenum, New York, 1969).
24. T. Eisner *et al.*, *Science* **166**, 1172 (1969).
25. Y. Obara, *Z. Vgl. Physiol.* **69**, 99 (1970).
26. D. Burkhard, *Naturwissenschaften* **69**, 153 (1982).
27. F. I. Hárosi and Y. Hashimoto, *Science* **222**, 1021 (1983); J. A. Avery, J. K. Bowmaker, M. B. A. Djamgoz, J. E. G. Downing, *J. Physiol. (London)* **334**, 23P (1983).
28. Supported by grants EY00222 and EY03266 from the National Eye Institute. T.H.G. holds appropriate federal and state collecting permits for experimental work with migratory birds.

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G_{M1} Ganglioside Treatment Facilitates Behavioral Recovery from Bilateral Brain Damage

Abstract. *Adult rats with bilateral lesions of the caudate nucleus were treated with G_{M1} ganglioside. Although animals injected with a control solution were severely impaired in their ability to learn a complex spatial task, those treated with ganglioside were able to learn spatial reversals.*

Until recently the central nervous system was believed to lack the capacity for repair, and damage to the brain was believed to result in permanent loss of critical mental and motor functions. As a result of this pessimistic view, virtually no effort had been made to develop effective treatments to restore function lost as a result of traumatic brain injuries. However, this view is now gradually changing (*1*).

Within the last few years, a number of neurotrophic factors known to play an important role in the stimulation and guidance of regrowing axons after damage in the peripheral and the central nervous system have been isolated from mammalian brain tissue (*2*).

Gangliosides, glycolipid molecules located in the outer leaflet of neuronal membranes (*3*), are among these neurotrophic factors now being examined for their potential capacity to restore function of damaged neuronal tissue. When applied to neuronal cell cultures gangliosides stimulate neurite outgrowth (*4*), and when injected systemically into animals with peripheral nerve damage (*5*) they promote sprouting into the denervated target area. Nevertheless, the question of whether gangliosides facilitate central sprouting after brain injury (*6, 7*) or enhance recovery from resulting behavioral deficits is just beginning to be addressed (*7, 8*).

We now report that ganglioside injected after bilateral injury to the caudate nucleus significantly reduces behavioral deficits in spatial learning ability.

Prior to surgery, male albino rats (Sprague-Dawley, 320 to 420 g, 90 to 95 days old) were handled daily for 1 week and then tested for 2 days on a two-choice footshock discrimination-learning maze (*9*). In the preoperative phase, the rats were given ten daily trials in which they could escape from or avoid footshock by running into one of two safe goal areas (*10*). On the first day of training we evaluated the animal's choice preference. The side to which the animal escaped or avoided the footshock more than 50 percent of the time was considered its preferred side. On the next day, the rats were trained to run straight to their nonpreferred side. Those rats that did not run eight out of ten trials were eliminated from the study. Although this training procedure was too short for the rats to acquire spatial reversal habits, it did permit us to eliminate animals that refused to run at all in the test situation. Approximately 20 percent of the animals were thus eliminated from the study.

The remaining animals were randomly assigned to one of three surgical groups: the control group (group C) (n = 8) underwent sham surgery, and the lesion group (group L) (n = 8) were given radio-frequency–induced bilateral lesions of the caudate nucleus (*9*). Both groups received daily intraperitoneal injections of Ringer solution for 14 days. The lesion-ganglioside group (group LG) (n = 7) received, in addition to the same bilateral caudate lesions, daily intraperitoneal injections of G_{M1} ganglioside for 14 days (*11*).

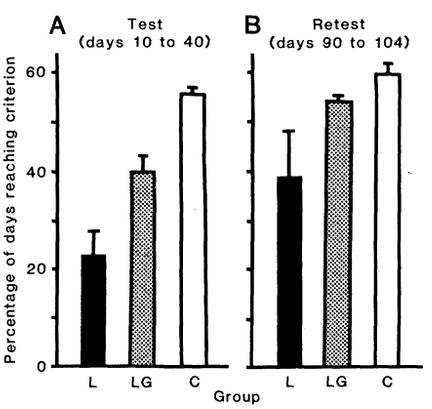

Fig. 1. Mean percentage of days (with standard errors) on which animals reached criterion (nine out of ten responses correct). The groups are L, bilateral caudate nucleus lesion with control injections; LG, bilateral caudate nucleus lesion with injections of G_{M1} ganglioside; C, no lesion with control injections.

According to our previous procedures (*9*), postoperative behavioral testing began after a 9-day recovery period and continued to the nonpreferred side until the rats met a criterion of avoiding or escaping shock correctly on every trial for two consecutive days. Thereafter, the animals were trained to the opposite side of the goal area with the same criterion. In this manner, animals underwent a continuous series of spatial habit reversals for 30 days of testing (with a total of 300 trials). Starting on postoperative day 90, all animals were retested on the same task for 14 days (140 trials).

Each trial was scored for the animals' response to shock (escape or avoidance) and perseverative errors (response to the wrong side after reversal of the correct side). The behavioral data were analyzed separately for the first 30-day testing session and for the 14-day retest period.

For the first testing period, a one-way analysis of variance revealed differences among the three groups for the following measures: (i) number of failures to reach the goal area per reversal [$F(2, 20) = 8.05$, $P < 0.01$], (ii) number of days to reach a criterion after the first reversal [$F(2, 20) = 16.0$, $P < 0.01$], and (iii) the percentage of days on which a criterion of nine correct responses out of ten trials (9/10) was attained [$F(2, 20) = 19.7$, $P < 0.01$].

Subsequent a priori comparisons with Dunnett's test (based on one-tailed probabilities) revealed that animals with lesions but no treatment (group L) were significantly impaired on the behavioral task when compared with animals without brain damage (group C). In contrast, brain-damaged animals treated with G_{M1} showed little impairment, differing significantly in only the percentage of days on which criterion was reached from controls (*12*) (Fig. 1A).

When compared with their untreated, brain-damaged counterparts (group L), animals given G_{M1} ganglioside reached the goal area significantly more often per reversal ($t = 2.86$, $P < 0.01$), took fewer days to reach criterion after the first reversal ($t = 4.46$, $P < 0.01$), and reached criterion (9/10) more often ($t = 3.09$, $P < 0.01$) (Table 1). With respect to the ganglioside-induced im-