

us could not be distinguished in autoradiograms, although the adjacent caudal nucleus of the torus semicircularis is clearly visible (Fig. 3C). Thus, the laminar nucleus of the torus semicircularis is a mesencephalic auditory nucleus that contains cells that concentrate DHT and estradiol (3, 20).

To my knowledge this is the first report of steroid-concentrating cells in a functionally identified vertebrate auditory nucleus. Other stations of the auditory neural pathway in frogs may contain steroid-sensitive cells as well. With regard to the efferent pathway for vocal control in frogs, calling behavior is modulated by the anterior preoptic area, the ventral infundibulum, and the dorsal tegmental area of the medulla (21). As all these nuclei contain steroid-concentrating cells in *X. laevis* (3), we should consider the possibility that all stations of the neural pathway controlling calling are sensitive to hormones (4). Multiple sites of hormone action on neural pathways for reproductive behavior may ensure a high frequency of sexual behaviors during the breeding season and may synchronize the receptivity of females with the attraction behavior of males. Such evolutionary specializations are probably not confined to anurans but may be present in other vertebrates that breed seasonally, including birds and mammals.

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References and Notes

1. D. Kelley and D. Pfaff in *Biological Determinants of Sexual Behavior*, J. Hutchison, Ed. (Wiley-Interscience, New York, 1978), pp. 225-254; J. Morrell, D. Kelley, D. Pfaff in *Proceedings of the Second Brain-Endocrine Interaction Symposium*, K. Knigge, D. Scott, M. Kobayashi, S. Ishii, Eds. (Karger, Basel, 1975), pp. 230-256.
2. Examples of testosterone-concentrating motor neurons include the nucleus of cranial nerves IX and X in frogs (3), hypoglossal neurons in zebra finches (4), and motor neurons in the ventral horn in rats [M. Sar and W. E. Stumpf, *Science* **197**, 77 (1977)].
3. D. Kelley, J. Morrell, D. Pfaff, *J. Comp. Neurol.* **164**, 47 (1975); J. Morrell, D. Kelley, D. Pfaff, *ibid.*, p. 63.
4. As has also been described for CNS control of song in birds [A. Arnold, F. Nottebohm, D. Pfaff, *ibid.* **165**, 487 (1976)].
5. For example, dorsal horn cells in the spinal cord concentrate estradiol [D. A. Keefer and W. E. Stumpf, *Proc. Soc. Exp. Biol. Med.* **143**, 414 (1973)].
6. D. Kelley and D. Pfaff, *Horm. Behav.* **7**, 159 (1976); D. Kelley, unpublished observations.
7. Blood concentrations are given in nanograms per milliliter ($N = 2$) for each hormone condition. Intact male *X. laevis*: testosterone, 3.6/2.8; DHT, 1.4/3.5. Intact males injected with human chorionic gonadotropin: testosterone, 19.5/22.3; DHT 24.6/20.9. Castrated males injected with gonadotropin: testosterone, 0.7/0.9; DHT 4.9/1.0.
8. K. Ryan, *J. Biol. Chem.* **234**, 268 (1959); *Acta. Endocrinol.* **35**, 697 (1960).
9. New England Nuclear 200 Ci/mole. Each frog (mean weight, 44 g) was injected with 300 ng of DHT. This dose results in blood concentrations

- equivalent to those of intact males injected with gonadotropin (7).
10. The criterion for a labeled cell was that the number of silver grains over the stained cell body equal or exceed five times the number of grains over adjacent, cell-sized areas of neuropil (background).
 11. D. Kelley, *Am. Zool.* **18**, 477 (1978).
 12. D. Kelley, I. Lieberburg, B. McEwen, D. Pfaff, *Brain Res.* **140**, 287 (1978).
 13. J. LaVail and M. LaVail, *J. Comp. Neurol.* **157**, 303 (1974).
 14. W. Ridewood, *Linn. Soc. J. Zool.* **26**, 53 (1897); A. Rabb, *Copeia* **1960-IV**, 369 (1960); D. Yager, personal communication.
 15. M.-M. Mesulam, *J. Histochem. Cytochem.* **26**, 106 (1978); J. Adams, *Neurosci.* **2**, 141 (1977).
 16. The percentage of HRP-labeled cells in N IX-X was determined by counting labeled and unlabeled cells on every other 50 μ m neutral red counterstained section through the nucleus. Depending on injection size and survival time, the percentage of ipsilateral labeled cells ranged from 48 percent (small injection, 1 day survival, only ipsilateral cells labeled) to 97 percent (large injection, 2 days survival, many contralateral cells labeled). Autoradiograms (thickness, 10 μ m) were analyzed at 50 μ m intervals. Using the background criterion for labeled cells (10), between 57 and 63 percent of N IX-X cells were categorized as androgen concentrating.
 17. H. Potter, *J. Neurophysiol.* **28**, 1155 (1965).

18. L. Sokoloff, *J. Neurochem.* **29**, 13 (1977). Studies of 14 C-labeled 2DG in the rat demonstrated that occlusion of the external auditory meatus on one side decreased 2DG uptake in the contralateral inferior colliculus by 75 percent. The inferior colliculus is generally believed to represent the mammalian homolog of the torus semicircularis (17).
19. T. Sejnowski, D. Kelley, J. Paton, M. Yodlowski, *Abstr. Soc. Neurosci.* **5**, 30 (1979); D. Kelley, J. Paton, T. Sejnowski, M. Yodlowski, in preparation. The maximum sound intensity of the taped vocalizations was 300 dyne/cm².
20. We do not yet know whether there are separate receptors for DHT and estradiol in the laminar nucleus of the torus semicircularis. Recent experiments in rats have shown that estradiol has a strong affinity for the DHT receptor, but that DHT binds very weakly to the estradiol receptor [G. Chamness, T. King, P. Sheridan, *Brain Res.* **161**, 267 (1979)].
21. R. Schmidt, *Am. Zool.* **13**, 1169 (1973); *J. Comp. Physiol.* **92**, 229 (1974).
22. I thank B. Goun and C. Szmauz for expert technical assistance; J. Paton for preparing some of the 2DG autoradiograms; H. Feder for providing the radioimmunoassay data; B. Campbell, D. Griffin, C. Gross, and B. Hoebe for lending equipment. Supported by grant HD12126 from the National Institutes of Health.

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Spatial Adaptation of Short-Wavelength Pathways in Humans

Abstract. Color-selective spatial adaptation of the short-wavelength, or blue-sensitive, pathway was demonstrated. The adaptation was orientation selective and strongly monocular. Adaptation was assessed by measuring visibility thresholds for monochromatic gratings in subjects adapted to high-contrast violet gratings designed to stimulate only blue-sensitive cones. The results showed spatially selective, adaptable channels within the short-wavelength pathway.

Spatial adaptation has revealed form-selective mechanisms in human vision. Prolonged viewing of a grating of stripes will selectively elevate the contrast threshold of a test grating of similar orientation (1) and spatial frequency (2, 3). We present results to show that an adapting pattern that selectively stimulates the short-wavelength (blue) cones strongly elevates the threshold only for a grating test pattern that also selectively stimulates the same cones.

Previous failures (4) to find color-se-

lective spatial adaptation may be accounted for by lack of isolation of the different cone mechanisms. We used Stiles's (5, 6) two-color methods to separately stimulate different spectral classes of cones. We have investigated the short-wavelength pathways because the blue-sensitive cones can be readily isolated and because initial observations showed that fine spatial patterns seen only with the blue-sensitive cones rapidly fade from view and thus might produce strong spatial adaptation (7).

The observer monocularly fixated in Maxwellian view an intense, uniform yellow-green field 4° in diameter and of 560 nm (13-nm bandwidth) and 200,000 trolands or 11.40 log quanta deg⁻² sec⁻¹ (8, 9). Red (632.8 nm) or violet (441.6 nm) sinusoidal gratings were superimposed over the entire adapting field. The red and violet patterns selectively stimu-

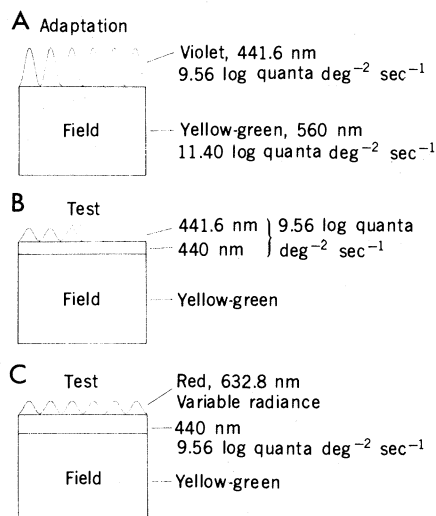


Fig. 1. Spatial radiance profiles of the sinusoidal violet adapting grating (A) and the violet (B) and red (C) test gratings. Gratings were superimposed on an intense, uniform yellow-green (560-nm) field. The mean spatial radiance of the violet light was kept constant. The contrast of the violet test grating (B) was varied by changing the ratio of the radiance of violet grating and violet (440-nm) dilution field while keeping their sum constant. The radiance of the red test grating (C) was varied.

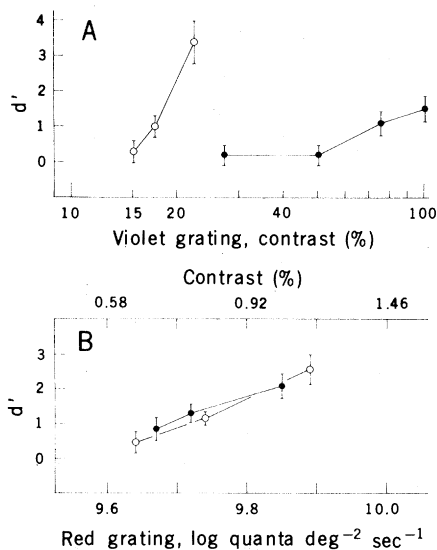


Fig. 2. Effects of adapting to an 8 cycle/deg vertical violet grating of zero contrast (○, uniform field) or unity contrast (●, Fig. 1A). The plots show detectability, $d' \pm 1.0$ standard error, of 8 cycle/deg vertical test gratings that were violet (A) or red (B). In (B), the bottom abscissa expresses radiance of the red grating, and the top abscissa expresses calculated contrast for the long-wavelength Π_5 mechanism (21).

late the long-wavelength Π_5 and short-wavelength Π_3 mechanisms, respectively (6, 10), or the long- and short-wavelength cones. The gratings were generated as interference patterns directly on the retina with laser beams in polarization interferometers (9). Such interference gratings are not affected by the eye's focus (11), and thus the chromatic aberration of the eye does not affect the visibility of the patterns. The adaptation and test patterns are depicted in Fig. 1.

A 5-second presentation of the violet adapting grating continuously alternated with a 1.4-second presentation of the test pattern, which was violet or red. Stimuli were alternated with shutters. The adapting pattern was a violet grating of $9.56 \log \text{ quanta deg}^{-2} \text{ sec}^{-1}$, of either unity contrast or zero contrast (uniform adapting field). When the adapting pattern was removed and the test pattern substituted, the radiance of the violet light was held constant in order to keep the short-wavelength Π_3 mechanism in a constant state of light adaptation, for the mechanism is much more sensitive to the violet light than to yellow-green light (6, 12). This was accomplished by presenting a uniform field of violet light (440 nm, with a bandwidth of 15 nm) along with the test patterns. The uniform violet field served in part to dilute the contrast of the violet test grating (Fig. 1B). The contrast of the violet test pattern (consisting of a violet grating at unity contrast and a vio-

let dilution field) was varied by varying the ratio of the radiances of grating and dilution field while keeping the sum of their radiances equivalent to that of the violet adapting grating. The red test pattern (Fig. 1C) was presented as an incremental flash for the entire test period, and the radiance of this unity contrast grating was varied to change its visibility (13). The threshold-level red flash has little effect on the light adaptation of the long-wavelength Π_5 mechanism since the mechanism is strongly stimulated by the intense yellow-green adapting field (12). The red flash also has negligible effect on the short-wavelength Π_3 mechanism (12).

A signal detection method (14) was used to measure the effects of spatial adaptation. For each run, a single adapting pattern and a single test pattern of given contrast or radiance were used. The observer adapted for 3 minutes to the stimulus sequence before data were collected. "Signal" and "blank" test trials were then presented in a random order. The contrast of the laser test grating was electronically turned on and off with a twisted-nematic liquid crystal (9) that did not change the mean spatial radiance of the test patterns or polarization of the laser beams entering the eye. Thus, the observer was required to distinguish whether or not the test field contained grating stripes. Results are given for observer C.F.S., and confirmatory results are mentioned for a second observer.

A vertical violet adapting grating of 8 cycle/deg strongly reduced the detectability of a similar violet test grating, but had virtually no effect on the detectability of a red test grating (Fig. 2). Similar results were obtained with a second observer, J.C.M., with gratings of 6 cycle/deg (15). The adaptation was thus confined to the short-wavelength pathway. This adaptation was orientation selective: An 8 cycle/deg horizontal violet adapting grating had little adaptive effect on the visibility of an 8 cycle/deg vertical violet test grating (Fig. 3). Similar results were obtained with observer J.C.M. with gratings of 2 cycle/deg in an 8° field (16). This result shows that the adaptation was spatially selective and not simply due to a general decrease in the sensitivity of the short-wavelength cones or Π_3 pathway.

This orientation-selective adaptation was also largely monocular. Both eyes were presented with the yellow-green and violet field, through the use of a dichoptic interferometer. The right eye alone was exposed to the vertical violet

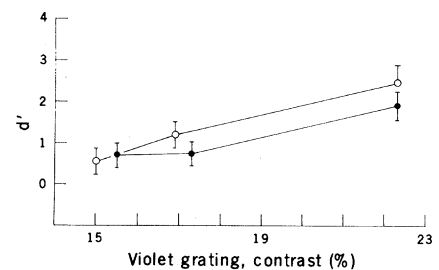


Fig. 3. Similar to Fig. 2A, but the violet adapting grating was horizontal and the violet test grating was vertical, as before. Violet adapting grating was zero contrast (○) or unity contrast (●). The abscissa has been greatly expanded relative to that in Fig. 2A.

adapting grating, and the left eye was used to detect the vertical violet test grating. Results for observer C.F.S., obtained with 8 cycle/deg gratings, showed that the adaptation did not transfer interocularly. The adapting grating was presented continuously and was viewed long enough that it faded from view before data were collected (17). The strong monocularity is surprising, for other studies on spatial adaptation have shown strong interocular transfer (3, 18).

The results show that spatial adaptation can be confined to the short-wavelength pathway. This adaptation is orientation selective and virtually monocular. Signals from the short-wavelength cones have been shown to travel in pathways that are strongly stimulated in an opponent manner by signals from the middle- and long-wavelength cones (19). That the visibility of a red test grating is virtually unaffected by a violet adapting grating indicates that signals from the long-wavelength cones also travel in other pathways—a hypothesis supported by electrophysiological studies of single cells in monkeys (20).

Our experiments demonstrate that spatial and color-selective channels can be revealed with the technique of spatial adaptation. We hope that this tool can be used to reveal the spatial properties of various color-selective mechanisms.

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References and Notes

1. A. S. Gilinsky, *J. Opt. Soc. Am.* **58**, 13 (1968).
2. A. Pantle and R. Sekuler, *Science* **162**, 1146 (1968).
3. C. Blakemore and F. W. Campbell, *J. Physiol. (London)* **203**, 237 (1969).
4. C. F. Stromeyer III [in *Handbook of Sensory Physiology*, vol. 8, *Perception*, R. Held, H. W. Leibowitz, H.-L. Teuber, Eds. (Springer-Ver-

- lag, Berlin, 1978)] has reviewed studies on color-selective spatial adaptation.
5. W. S. Stiles, *Proc. R. Soc. London Ser. B* **127**, 64 (1939).
 6. ———, *Coloq. Probl. Opt. Vision (Madrid)* **1**, 65 (1953) [reprinted in W. S. Stiles, *Mechanisms of Colour Vision* (Academic Press, New York, 1978)].
 7. Gratings of 8 cycle/deg were used, for these appeared to produce particularly strong adaptation. Such gratings approach the acuity limit of the short-wavelength pathway, which has poor spatial resolution [W. S. Stiles, *Doc. Ophthalmol.* **3**, 138 (1949)]. Studies reviewed by Brindley suggest that this pathway might more readily adapt to fine than to coarse spatial configurations [G. S. Brindley, *Physiology of the Retina and Visual Pathway* (Arnold, London, 1970), pp. 241–244].
 8. C. F. Stromeyer III *et al.*, *Sens. Processes* **2**, 248 (1978).
 9. C. F. Stromeyer III, R. E. Kronauer, J. C. Madsen, "Responses of short-wavelength cone pathways to different spatial frequencies," in preparation.
 10. See, for example, R. M. Boynton, M. Ikeda, W. S. Stiles, *Vision Res.* **4**, 87 (1964). The violet adapting grating stimulated only Π_3 , for our field sensitivity (5, 6) measurements showed that the pattern was approximately 1 log unit below the threshold of the next most sensitive mechanism, the middle-wavelength Π_4 mechanism.
 11. F. W. Campbell and D. G. Green, *J. Physiol. (London)* **181**, 576 (1965).
 12. G. Wyszecki and W. S. Stiles, *Color Science: Concepts and Methods, Quantitative Data and Formulas* (Wiley, New York, 1967), p. 579.
 13. Both observers reported that when the red test pattern was presented in this flashed mode, the pattern appeared neither as a flash nor as a change of hue. The predominant appearance of the red grating at threshold was a pattern of just-visible vertical stripes. Additional experiments in which the mean spatial radiance of the red stimuli was constant gave results similar to those reported here; that is, the presence of the violet adapting grating did not affect the visibility of the red test grating.
 14. D. M. Green and J. A. Swets, *Signal Detection Theory and Psychophysics* (Wiley, New York, 1966). We used a rating method, and d' was calculated from a maximal likelihood estimation (C. F. Stromeyer III, S. Klein, C. E. Sternheim, *Vision Res.* **17**, 603, 1977).
 15. Results similar to those in Fig. 2 were also obtained with two observers using a field 8° in diameter with the central 1.5° occluded. The observer fixated the center of the field. The central region was occluded so that the observer could not detect the red grating with the blue-blind central area of the fovea [G. Wald, *J. Opt. Soc. Am.* **57**, 1289 (1967)], which is presumably not strongly adapted by the violet adaptation grating.
 16. For this experiment the mean spatial radiance of the violet light was 8.62 log quanta deg⁻² sec⁻¹.
 17. Interocular transfer of less than 10 percent was obtained with another observer. Adapting and test gratings were 4 cycle/deg and were presented in alternation.
 18. C. Ware and D. E. Mitchell, *Vision Res.* **14**, 731 (1974).
 19. E. J. Augenstein and E. N. Pugh, Jr., *J. Physiol. (London)* **272**, 247 (1977); J. D. Mollon and P. G. Polden, *Philos. Trans. R. Soc. London Ser. B* **278**, 207 (1977); E. N. Pugh, Jr., and J. D. Mollon, *Vision Res.* **19**, 293 (1978); C. F. Stromeyer III, R. E. Kronauer, J. C. Madsen, *Science* **202**, 217 (1978); *Vision Res.* **19**, 1025 (1979).
 20. R. L. DeValois in *Handbook of Sensory Physiology*, vol. 7, part 3, *Central Processing of Visual Information A: Integrative Functions and Comparative Data*, R. Jung, Ed. (Springer-Verlag, Berlin, 1973).
 21. The yellow-green field was neglected in determining the contrast of violet test gratings, for the Π_3 mechanism is ~ 20 times more sensitive to the violet than to yellow-green light (12). The contrast of the red gratings was calculated by weighting the light with the mean spectral field sensitivity function of Π_3 based on Stiles's four observers (12). Bleaching of photopigments in "red" receptors, caused by our intense lights partially changes spectral sensitivity of these receptors [G. S. Brindley, *J. Physiol. (London)* **122**, 332 (1953)]. Thus, the calculated contrast of the red gratings for Π_3 is only an approximate estimation, and this is why we also specify the radiance of the red gratings.
 22. Supported by NIH grant 5-R01-EY-01808.

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Affective Discrimination of Stimuli That Cannot Be Recognized

Abstract. *Animal and human subjects readily develop strong preferences for objects that have become familiar through repeated exposures. Experimental evidence is presented that these preferences can develop even when the exposures are so degraded that recognition is precluded.*

A substantial body of evidence demonstrates that the mere repeated exposure of a stimulus object increases its attractiveness (1). Both human (2) and animal subjects (3) exhibit the exposure effect with a variety of stimuli, exposure methods, and outcome measures of stimulus attractiveness.

In addition to its effects on preferences, exposure experience also allows the individual to learn a great deal about the stimulus object, so that the ability to recognize, discriminate, and categorize the object generally improves. Traditionally, theorists have assumed that this cognitive mastery resulting from experience with the stimulus mediated the growth of positive affect [for example, Harrison's response competition theory (4) and Berlyne's theory of optimal arousal (5)]. Thus, as the individual comes to "know" the stimulus better,

his affective reaction to it is likely to become increasingly positive. For example, much of the literature on esthetic reactions to music suggests that experience leading to the recognition of familiar patterns and the ability to anticipate development is pleasurable and makes the composition attractive (6).

Recent research, however, suggests that overt affective responses may be unrelated to prior cognitive outcomes which result from stimulus exposure. For example, Moreland and Zajonc (7) have shown by a correlational analysis that repeated exposure increases preference for stimuli even when recognition is held constant, and Wilson (8) has demonstrated by experimental methods that auditory stimuli gain in attractiveness by virtue of repeated exposure, even when their registration and subsequent recognition had been considerably impaired in

the course of a dichotic listening task.

In the present experiment, a more stringent test was used to determine whether the exposure effect could be obtained when recognition was drastically reduced. Through preliminary studies, the conditions of stimulus exposure were systematically impoverished until recognition performance was brought down just to a chance level. A new group of subjects was then exposed to stimuli under these impoverished conditions, and judgments of attractiveness and measures of recognition memory for these stimuli and for stimuli not previously exposed were obtained. The results revealed clear preferences for exposed stimuli, even though subjects in a recognition memory test could not discriminate them from novel stimuli.

The experiment consisted of an exposure phase and of a test series. The stimuli were 20 irregular octagons constructed by a random process. Octagons of this type were used previously in exposure research, and subjects found no difficulty in making clear cognitive and affective discriminations among them (9). The 20 stimuli were divided into two sets of ten, sets A and B. In the exposure phase, half of the subjects saw set A and half set B. All subjects saw sets A and B in the test series. During the exposure phase, subjects fixated the center of a 23 by 17 cm rear projection screen mounted at the end of a viewing tunnel 91 cm long. Five exposures of each stimulus from the set of ten stimuli were shown in a random sequence. The octagons were solid black on white background; because of their high contrast, chance recognition could be obtained only after exposures were reduced to a 1-msec duration and illumination was lowered by a neutral density (ND8X) and a red gelatin filter. The instructions to subjects at the beginning of the exposure phase were that the experiment consisted of two parts and that during the first part slides would be shown on the screen at durations so brief that one could not really see what was being presented. Nevertheless, the subject was instructed to pay close attention to the flashes, even if nothing could be distinguished, and to acknowledge verbally the occurrence of each flash.

The second part of the experiment required subjects to make paired comparisons between slides from set A and set B. Now the slides were presented under adequate viewing conditions (exposure time was extended to 1 second). For each of the ten pairs, all containing one octagon previously exposed and one new, the subjects had to indicate (i) the