posed to a light cycle after many days of arrhythmicity in DD. The activity rhythm is evident from day 1 of the light cycle, whereas it is at least 4 days until a clear body temperature rhythm can be discerned.

There are two effects of pinealectomy on the body temperature regulation of *P. domesticus*. The circadian rhythm is abolished, and the amplitude of the temperature fluctuations is reduced. These two effects may be but are not necessarily related. One could imagine that it would be possible to produce arrhythmicity without affecting amplitude or conversely to affect amplitude without abolishing rhythmicity. Thus it may be that independent of its role in the circadian system, the pineal is involved in the fine tuning of the hypothalamic thermostat (*8*).

The pineal organ and its metabolites have both been linked to circadian rhythmicity and to the control of body temperature. In two independent studies (*9*), pinealectomized rats shifted the phase of their activity rhythms more rapidly than did normals in response to a change in the phase of the light cycle. Daily rhythms in pineal level of serotonin, melatonin, and norepinepherine have been described, as have rhythms in the activity of two enzymes (hydroxindole-*O*-methyl transferase and *N*-acetyltransferase) involved in the conversion of serotonin to melatonin (*10, 11*). Melatonin injected subcutaneously in mice lowers the body temperature by 2° to 3°C (*12*). Pinealectomy lowers cloacal temperature in lizards (*13*)—an effect that may be due either to a change in thermoregulatory behavior or to direct interference with physiological mechanisms of temperature control.

In most previous studies the circadian system has been treated as a "black box"; the organism has been subjected to environmental "input" (usually light or temperature signals), and the resulting changes in its rhythmic behavior have been measured and analyzed as "output." Our own results and those of others indicate that further analysis of pineal function may provide a lever with which to pry the lid off the "black box" of circadian organization.

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Color- and Edge-Sensitive Channels in the Human Visual System: Tuning for Orientation

Abstract. *After subjects scanned red stripes tilted clockwise off vertical and green stripes tilted equally but counterclockwise, vertical test stripes appeared tilted counterclockwise when red but clockwise when green. As the angle between scanned and test stripes was increased from 0° to 75°, the magnitude of the tilt aftereffect rapidly increased to a peak between 10° and 15° and then dropped close to zero at about 40°, a result consistent with narrowly tuned edge-sensitive channels.*

The existence of channels in the human visual system which are both selectively sensitive to color and tuned to a limited range of edge orientations was suggested by early observations and has been further supported by recent psychophysical experiments (*1*). In 1965 McCollough (*2*) reported that following a period of alternately scanning an orange-black vertical grating and a blue-black horizontal grating, a vertical black-white test grating appeared faintly blue-green, while its horizontal counterpart appeared faintly orange. When ordinary chromatic afterimages are excluded as an explanation (*3*), McCollough's demonstration implies desensitization of color and edge-orientation specific channels, although the breadth of tuning for orientation remains unspecified (*4*). We have found confirming evidence for such channels by showing that the perceived orientation of test bars can be made dependent upon color. Furthermore, our measurements reveal that these channels are narrowly tuned for edge orientation.

Consider the tilt aftereffect illustrated in Fig. 1A. If an observer scans the adapting pattern for 1 minute by continuous refixations on the dots shown along the horizontal division, then the test field, fixated at its center, takes on the appearance indicated (*5*). Its bars appear slightly tilted in the direction away from the bars of the adapting pattern. This aftereffect may be explained by assuming the existence of many channels selectively sensitive to different but overlapping ranges of edge orientation. Each channel is excited maximally by an edge of one particular orientation and is progressively less excited as the edge increasingly deviates from that orientation. An edge of a given orientation will then excite a set of such channels, at levels varying from a peak in the channel most sensitive to the orientation of the edge itself, to lower levels in channels whose optimal excitation would be produced by edges that deviate from the orientation of the test bar. Prolonged exposure to the bars of an adapting pattern at one particular orientation reduces the sensitivity of excited channels. Assume that the perceived orientation of the test bars corresponds to the central tendency of the distribution of excitation which they produce. If this central tendency is shifted after adapting to a tilted grating, then the bars of the test field should appear tilted away from those of the adapting pattern (*6*).

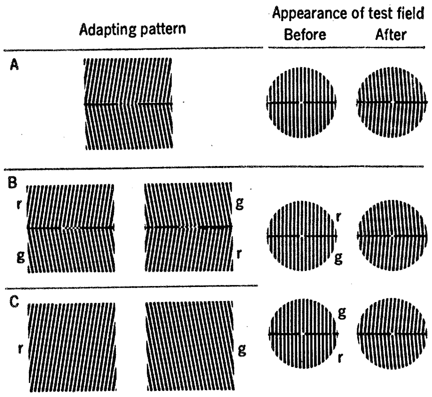

Fig. 1. (A) Achromatic tilt aftereffect showing appearance of test field before and after exposure to adapting pattern. (B and C) Color-dependent tilt aftereffects showing appearance (exaggerated) of straight line target before and after exposure to adapting patterns; *r*, red; *g*, green.

Existing data suggest that the aftereffects of Fig. 1A depend primarily upon the luminance gradient defining the bars (*7*). The entire visible spectrum contributes to channels that are tuned to the orientation of edges defined by luminance gradients. We intended to show dependence of perceived edge orientation on channels having selective spectral sensitivity. We reasoned that equally luminous but differently colored adapting fields with equal but opposite tilts off vertical would eliminate that portion of the aftereffect produced by edges defined by luminance gradients alone (*8*). However, color-specific edge channels should be desensitized by the different colors of the adapting gratings so as to produce tilts of opposite direction on test fields of the corresponding colors. For this purpose, we used the adapting pattern and test fields shown schematically in Fig. 1B. The two adapting gratings differed only slightly in luminance (see below) and had equal but opposite tilts with respect to the vertical orientation of the test field bars. Since they were exposed for equal durations, little or no net tilt of the test bars should appear as an aftereffect resulting from adaptation to the luminance-defined edges. Moreover, the test procedure measured only differential tilt between colored test half-fields.

Both exposure and test fields were produced by slides rear-projected on a translucent screen in an otherwise dark room, with a tungsten light source. The screen was viewed binocularly at a distance of 3 m. The grating patterns consisted of black bars subtending a visual angle of 5 minutes and spaced apart by one bar width. Spectral bands (green and red-hued) were produced by Wratten gel filters, No. 55 (dominant wavelength in illuminant A, 524.1 nm) and No. 26 (dominant wavelength in illuminant A, 620.6 nm), mounted on the slides. Luminance of the green was 478 ml, and that of the red, 258 ml, a difference of less than 0.3 log unit.

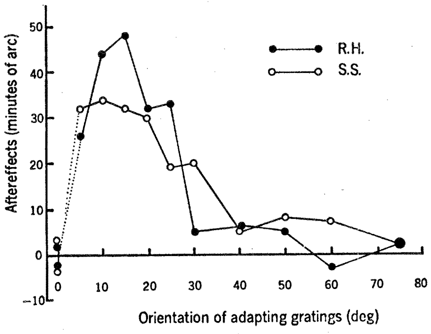

Fig. 2. Magnitude of aftereffect as a function of tilt of the adapting patterns.

The two adapting patterns were squares with sides measuring 5° in visual angle (Fig. 1B). The bars of the gratings deviated from vertical by 10°, forming an obtuse angle of 160°. The upper half of one pattern was red, and the lower, green; the colors were reversed on the other pattern. The angle formed by the bars of one pointed left, and the other, right. Thus, all green-illuminated bars were tilted one way, and all red, the other. These orientations were reversed for half the subjects. During exposure, observers were instructed to scan, by continued refixations on the dots along the middle third of the horizontal line bisecting the pattern. The adapting patterns were alternated at 5-second intervals, for a total of 10 minutes.

Circular test fields divided by a horizontal bar into upper and lower halves and subtending 4° of visual angle were used to measure the expected aftereffect (Fig. 1, B and C). Either the upper or lower half was red and the other half was green. Both upper and lower grating sections were equally, but oppositely, tilted off the vertical so that the test fields formed a series of large obtuse angles ranging from left-pointing through straight to right-pointing. Their deviations from 180° were convex left 1.5°, left 1°, left 40′, left 20′, zero; convex right 20′, right 40′, right 1°, and right 1.5°, and the nine patterns were presented in order, from largest left-pointing through straight to largest right-pointing, and back, ten times, for a total of 170 observations. Half of these presentations were made with the upper half of the field red and the lower half green, and half with the color reversed, thereby equating chromatic adaptation to the illuminants over the course of testing.

The observer was instructed to fixate on the point marked at the center of the horizontal black bar, and report whether the angle formed by the bars of the grating "pointed" to the left or the right. A response required 2 seconds or less of exposure to the test stimulus. The same testing procedure was used before and after the adaptation period. Ten observers were drawn from the undergraduate population at Massachusetts Institute of Technology. They were screened for red-green color weakness with Ishihara plants, and for ability to judge the small tilts required by the testing procedure.

The angle of the test field which is judged left-pointing 50 percent of the time (and right-pointing 50 percent of the time) represents perceived straightness and was determined from psychometric plots of the observer's responses. Before adaptation, the mean angle for the ten observers deviated by only 3′ from geometric straightness. After adaptation, all observers shifted their judgments of perceived straightness in the predicted directions for both sets of the test fields. In other words, after adaptation the test bars were tilted away from the adapting bars so that observers judged as straight an angle pointing in the direction of the adapting pattern (Fig. 1, B and C). The average shift of the angle representing perceived straightness summing the aftereffects on both halves of the field was 30.7′ of arc, with a range from 10′ to 64′. The orientations of the bars of the adapting patterns, either red tilted left and green tilted right, or vice versa, made no significant difference. After 24 hours an aftereffect was again measured, although it was not statistically significant.

Having demonstrated this aftereffect, we proceeded to determine its magnitude as a function of the angle between adapting and test bars. This function should indirectly reveal the breadth of tuning for edge orientation.

The experiments were carried out with the same procedures as before, except that the adapting patterns were simplified to those shown in Fig. 1C. Their tilts (off vertical) were 0, 5°, 10°, 15°, 20°, 25°, 30°, 40°, 50°, 60°, and 75°. Scanning was restricted to the central region of the pattern. Two observers (the authors) were run, once at each tilt with color pairs assigned randomly to direction of tilt. The results are shown in Fig. 2. The magnitude of the aftereffect peaks at an adapting tilt between 10° and 15° and approaches zero at a tilt of 40° (*9*). The shape of these curves is consonant with data on tilt aftereffects generated under comparable conditions with colorless adapting patterns (*10, 11*). It is also consistent with estimates of the breadth of tuning for orientation in the human visual system based upon masking experiments (*11, 12*).

Are the channels demonstrated by our results the same as those responsible for the McCollough effect? We suspect so, but the definitive answer must come from parallels established by further investigation of both phenomena.

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Carbon and Atmospheric Oxygen

Van Valen (*1*) maintains that the initial accumulation of free oxygen in our atmosphere cannot be satisfactorily explained by photosynthesis, apparently on the grounds that (i) the net photosynthetic production of oxygen today (rate of release by photosynthesis minus rate of consumption by oxidation of the biosphere and its fossils) is just sufficient to hold in check the oxygen sinks recognized by Holland (*2*) and others in volcanic gases, ferrous iron, and the like; and (ii) these sinks were more demanding in the past than now, whereas photosynthesis was presumably less productive. I will accept these two assumptions and attempt to show that Van Valen's conclusion does not necessarily follow from them.

As Van Valen points out, a large amount of organic carbon is stored in the sedimentary rocks and may be taken as corresponding to the aggregate net photosynthetic production of oxygen throughout geologic time. According to recent estimates the total mass of the sediments is 2×10^{24} grams or more (*3*) and their average carbon content is 0.4 percent (*4*), making 8×10^{21} grams of carbon which corresponds, at a molar carbon-oxygen ratio of unity, to 2×10^{22} grams of oxygen (*5*). This agrees quite well with Holland's estimate (*2*) of the aggregate capacity of inorganic oxygen sinks throughout geologic time (1.8×10^{22} grams) and leaves a little bit (0.2×10^{22} grams) over for the atmosphere (which in fact contains only 0.1×10^{22} grams).

One possible view of atmospheric history is the following—for a considerable time after photosynthesis began carbon accumulated while the partial pressure of oxygen was held close to zero by the backlog of reducing agents derived from volcanic activity of the primitive earth. The eventual neutralization of these sinks required a net production of oxygen that exceeded the rate of continuing emanation of inorganic reducing agents; but as at that time the atmospheric oxygen concentration was too low to oxidize the biosphere appreciably and consequently the net production of oxygen was nearly equal to the rate of release by photosynthesis, it need not have been difficult to meet this requirement (*6*). Once the