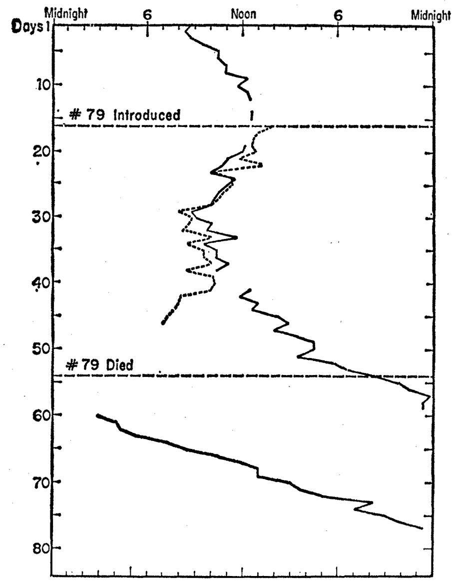

Fig. 2. Entrainment of one bird's activity rhythm by another bird. Lines have been drawn connecting each day's onset of activity (solid line, bird 70; dotted line, bird 79). Gaps indicate days on which the activity onsets were not clearly defined. Bird 70 occupied half of a double-breeding cage. On day 16 bird 79 was introduced into the other half. On day 46 the activity of bird 79 became diffuse and on day 54 it died.

but that the sparrow's clock can be influenced by way of auditory pathways (*8*). Biological clocks appear to be phylogenetically ancient adaptations, and environmental cycles of light and temperature must have impinged upon them continuously from their earliest beginnings (*10*). The mechanisms for entrainment to these cycles are thus likely to be a fundamental part of the organization of whatever oscillations underlie expressed circadian rhythms. On the other hand, auditory entrainment, no matter how unspecific the required sound may be, is predicated upon a high degree of organization of the central nervous system and must therefore represent a relatively recent evolutionary addition to the entrainment repertoire of these oscillations. A comparison of the pattern of entrainment to light cycles with the pattern of entrainment to auditory stimuli may thus provide insight into the phylogeny of biological clocks.

MICHAEL MENAKER
ARNOLD ESKIN
Department of Zoology, University of Texas, Austin

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7. The field recordings were transferred to a Cousino Audio Vendor which allowed continuous repetition of the tape loop. Variations in playing time for one revolution of the loop (2 seconds in some experiments, up to 20 minutes in others) did not affect the results. The tape recorder was controlled with a time switch, making it possible to present birds with a continuous signal of any duration automatically. Data was processed, and birds were housed in activity cages as previously reported [M. Menaker, in *Circadian Clocks*, J. Aschoff, Ed. (North-Holland, Amsterdam, 1965), p. 385]. The cages were placed in light-tight and relatively soundproof B. O. D. incubators at 23 ± 1°C in constant dim green light (approximately 0.1 lux) provided by electroluminescent panels. The birds were fed at approximately 14-day intervals at random times of day with no accompanying increase in light intensity. The sound stimulus was presented to each bird individually through a speaker mounted inside the incubator.
8. This is based on the reasonable assumption that the sound is not being sensed in some other undetermined way.
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Visual Adaptation: Increased Efficiency Resulting from Spectrally Distributed Mixtures of Stimuli

Abstract. *Visual adapting stimuli having different spectral distributions are used alone and then mixed together. It is found that the mixture is more effective, as an adapting field, than either component when used alone. This experiment, along with others, supports the following: although the most efficient stimulus for eliciting a visual sensation is "compact" in space, time, and wavelength, the most efficient adapting stimulus tends to be dispersed in each of these dimensions.*

The most efficient input for exciting a visual sensation can be characterized as being "compact" in space, time, and wavelength. For short, small flashes of fixed spectral distribution, the relation $L.A.t = C$ holds nearly exactly, meaning that luminance, area, and flash duration are interchangeable. This product is proportional to the energy content of the flash. As area or duration or both extend beyond the so-called "reciprocity" range, energy must be increased to maintain a constant visual effect. This generalization is based on very many experiments; there are none known to us indicating that an opposite result ever occurs when a *direct visual effect* (defined below) is under investigation. In other words, a long, large flash is never more efficient than a shorter, smaller one. Similarly, efficiency is either unchanged or reduced when flashes are broken up, spatially or temporally, into discrete components (*1*).

The "direct visual effect" has most often been a threshold probability of seeing, but the generalization holds also for those relatively fewer experiments where suprathreshold brightness has instead been the response criterion.

Much less work has been done on the spectral aspect of this problem (*2*). The approach that we have used in previous work is as follows: (i) A threshold is determined for a flash of wavelength λ_1 and this is arbitrarily called 1 "S-unit" of radiance. (ii) Another threshold is determined for wavelength λ_2 and this also is called 1 S-unit of radiance. (iii) The two flashes are additively and simultaneously mixed together in some fixed ratio of their S-units. By proportionally varying the radiance of each, without altering the ratio, it is possible to determine a new threshold, and this is done for various ratios. In an eye containing only one type of receptor, like the human eye under scotopic conditions where only rods are functional, the number of S-units in the mixture, ΣS, must, within experimental error, always be unity at threshold for the mixture. Under photopic conditions, where at least three classes of cone receptors absorb light (each with a different action spectrum) it has been found experimentally that ΣS equals or exceeds, but is never less than, 1.0. This result implies that, when a direct visual effect is under investigation, the most efficient stimulus must be spectrally compact, as well as spatially and temporally so.

When ΣS exceeds 1.0, as it does in these cases, a failure of linear summation between the outputs of separate cone mechanisms is suggested as the cause of the reduction in visual efficiency. When ΣS is more than what is predicted on the assumption of probability summation of independent mechanisms, inhibition is implied. We found this to be a common result for spectral mixtures. It has also been observed in the temporal domain for double flashes separated by about 50 msec (*3*).

We summarize and generalize the results of these various experiments in this way: the more receptors that are stimulated and/or the longer the stimulation is allowed to occur, the less opportunity seems to exist for linear summation to take place within the receptors or among their outputs, and the less efficient the visual stimulus becomes.

Thus it is of interest to note here an opposite effect, which we have consistently obtained in many recent experimental sessions where the adaptive effect of spectrally distributing the stimuli was under evaluation (*4*). The results of one such experiment, based on a single human subject, will be reported here as an example. In this experiment, the number of S-units in the adapting field is kept constant while its spectral distribution is varied; threshold radiance of the test flash is the dependent variable.

The subject is dark adapted and the threshold luminance of a 1° (square), 10-msec, centrally fixated flash of light of 600 nm, repeating every second, is determined. This luminance is then increased by a factor of 30, and is left at this level for the first part of the experiment. Two adapting fields are used: one is red ($\lambda_r = 667$ nm) and the other is blue ($\lambda_b = 456$ nm). In turn, the luminances of these two adapting fields required to bring the test flash to an increment threshold with respect to each background are determined by the method of adjustment. Calling each of these values 1 S-unit as before, four other conditions are investigated wherein test thresholds are determined when the red adapting field makes up 20, 40, 60, and 80 percent of the total, while $S_r + S_b = 1.0$ under all conditions (*5*).

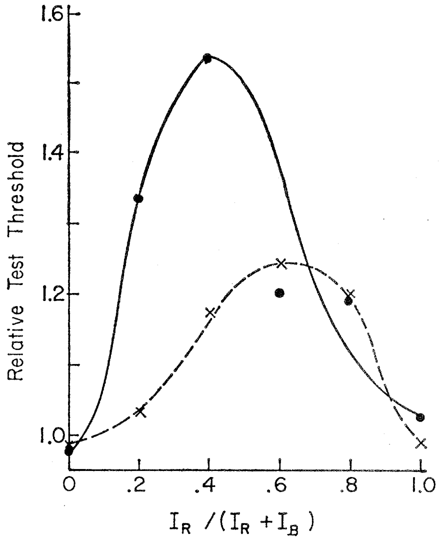

Fig. 1. Relative threshold of a 600 nm test flash seen against an adapting field consisting of a red-blue mixture of the ratio shown. Threshold for either adapting field used alone is taken as 1.0. Solid curve is for adapting fields which raise the absolute threshold of the test flash 30 times above absolute threshold; dotted curve is for fields producing a threefold elevation.

Results are shown in Fig. 1 as the filled circles. At peak, the mixture produces a 50 percent rise in threshold of the test flash. That is, 50 percent more light is required in the test flash for threshold when it is seen against the 40-60 mixture than against either component of that mixture used alone. The open circles in Fig. 1 are for a test flash set only three times above its absolute threshold. Here the effect, though smaller, is still clearly evident.

This result implies that to keep the increment threshold at its original level, only about two-thirds as much light in the adaptive mixture would be needed as compared to the requirement for each adapting field when used alone (*6*). As applied to the components of the adapting field, such an enhancement effect may be called "super-summation"; we have found super-summation by direct experiment for many combinations of test and adapting wavelengths (*4*). In other experiments of this type we have sometimes found complete summation, but more often super-summation ($\Sigma S < 1$) has been found, as is implied in the example here. An S-unit sum of slightly more than unity has been found sporadically, but has not been established beyond the bounds of experimental error.

Photopic adaptation therefore may sometimes be mediated by only one mechanism, or possibly by a linear summation of output among two or more of them. More often, however, the interaction is nonlinear and of a sort to favor the effectiveness of the spectrally distributed, rather than the spectrally compact, adapting stimulus.

After obtaining this result, we were reminded of an experiment by Kaplan and Ripps (*7*). These investigators studied the effect of eight symmetrically arranged inducing fields upon the threshold of a single, larger test flash. Under some conditions, they found that ". . . adding a second inducer opposite the first was as effective as a tenfold increase in the luminance of one inducer, while adding a second inducer next to the first had [relatively] little effect. . . ." To put their result in our terms, they also found the compact adapting stimulus to be less efficient than the distributed one. It then occurred to us that in a number of studies, starting with Wald and Clark in 1937 (*8*), it has been noted that a long, dim adapting stimulus is more efficient (delays recovery longer) than a short, bright one of the same total flux. Thus we may generalize, in the realm of visual *adaptation*, that the following is often the case: the more receptors that are stimulated, and/or the longer the stimulation is allowed to occur, the more opportunity seems to exist for summation of adaptive effect mediated by separate receptors, and the more efficient the adapting stimulus becomes.

This generalization is clearly the exact opposite of what has been found for direct visual effects. The limits of such a generalization remain to be tested. Possibly the effect may be explained partly in terms of the reduction of mutual inhibition among mechanisms as the stimulus energy is more and more spread out in space or time, or both. But why this does not also affect direct vision is not at all clear. What is clear is that the visual system processes input very differently for purposes of vision than for adaptation.

ROBERT M. BOYNTON
Center for Visual Science,
University of Rochester,
Rochester, New York 14627
S. R. DAS*
National Physical Laboratory,
New Delhi, India

References and Notes

1. The studies that have been done which support these statements are far too numerous to be cited individually. Where reciprocity holds, the L.A = C relation is known as "Ricco's law" and the L.t = C relation as "Bloch's law," in honor of those who first demonstrated them.
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4. These studies are reported in more detail else-

where (R. M. Boynton, S. R. Das, J. Gardiner, *ibid.*, in press).

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* Work done while at the Center for Visual Science, University of Rochester, Rochester, N.Y.

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Pupil Diameter and Load on Memory

Abstract. *During a short-term memory task, pupil diameter is a measure of the amount of material which is under active processing at any time. The pupil dilates as the material is presented and constricts during report. The rate of change of these functions is related to task difficulty.*

In a recent series of articles, Hess and Polt have called attention to the fact that changes of pupil diameter can serve as a sensitive and useful indicator of mental state. The pupil dilates with pleasure and constricts with displeasure (*1, 2*). The pupil also dilates during mental activity, for example, when solving arithmetic problems (*2, 3*). Hess noted (*2*, p. 53) that the major constriction of the pupil occurs only after the subject reports his answer to a problem, even if this report is requested some time after the problem has been solved. This observation suggests that the pupil may serve as an indicator of the amount of load on memory, or, more precisely, of the amount of effort involved in storing information for report. Pilot experiments in our laboratory strongly confirmed this suggestion: in a short-term memory task, the pupil dilates while the subject listens to information, and constricts as he reports. The present study is concerned with this effect.

Subjects in this experiment were five female college students who reported adequate uncorrected vision in both eyes. The session began with practice on all experimental tasks (one additional subject was rejected at this point because of frequent failures in immediate recall of strings of seven digits).

The main experiment consisted of four blocks of seven trials: in each block the subject heard (i) strings of digits (three to seven digits per string) presented for immediate recall; (ii) a string of four high-frequency monosyllabic nouns presented for immediate recall; (iii) a string of four digits presented for transformation (the subject was to add one to each digit). The subject was informed of the task just before each trial began. Five pictures of the subject's eye were then taken at a rate of one per second. On the sixth click of the camera, the experimenter began the presentation of the string, calling out digits or words in time with the camera. The subject was instructed to wait for two clicks after the experimenter finished speaking before she began responding, again in time with the camera. Four additional pictures were taken after the completion of the subject's report. A synchronous record of the speech of both experimenter and subject and of the timing of the pictures was made on a Bausch and Lomb VOM-5 recorder. Errors of recall and errors of timing were both rare, and such trials were immediately replaced.

Photographs of the eye were taken through a half-mirror on Kodak Tri-X film with a Grass C4D camera (1/25 second; $f = 8$). During this part of the experiment, the subject looked through the mirror at a white card (luminance 220 lu/m^2), 6 inches (15 cm) from her eyes, which filled her field of view. A faint gray circle ¾ inch in diameter was drawn on the card for fixation. Additional illumination of the eye was provided by a fluorescent tube which could be seen in peripheral vision. Total illumination at the eye was 1980 lu/m^2. All photographs were taken of the right eye, with the left eye occluded.

The development of the pupillary response during the presentation and recall of strings of digits is shown in Fig. 1 (left), where each point is an average of 20 measurements (four each for five subjects). Although there are marked differences among subjects in the magnitude of the pupillary response, the general features of the response are quite consistent. Large spontaneous variations of pupil size are notable by their absence in this situation where subjects' thought processes are effectively controlled by the task. Two distinct phases are apparent in the pupillary response to this immediate memory task: a loading phase during which the pupil dilates with every digit heard, and an unloading phase during which the pupil constricts with every digit reported. The peak pupillary diameters obtained (typically in the latter part of the pause) are directly related to the number of digits in the string. This ordering of peaks was found with no inversions in the responses of four of the five subjects, and with a single inversion for the remaining subject ($p < 10^{-4}$ by chi-square test). An anticipation effect was also noted: when subjects are warned that a difficult trial is coming, their pupils tend to dilate slightly. This effect of length of string on pupil size during the early control pictures is significant by trend analysis ($F = 6.62$ 1/16 df, $p < .05$), but it is restricted in magnitude (as Fig. 1, left, indicates) and does not account for the main results.

Two additional tasks, recall of words and transformation of digits, were included in the experimental design to permit an investigation of the effect of task difficulty on the pupillary response. The two tasks are clearly more difficult than the recall of digits; for our subjects the mean span for recall of digits was 7.8, while the mean span was 5.7 for words and 4.5 for the transformation task. In Fig. 1 (right), the pupillary response during the presentation and recall of four digits is compared with the response for the recall of four words and for the transformation of four digits. The expectation that pupillary dilation will be related to task difficulty is strongly confirmed; the loading function is substantially steeper in the more difficult tasks than in the recall of digit series of all lengths ($t = 3.85$, 24 df, $p < .001$).

The comparison of the results for digit transformation with those for digit recall is of particular interest; the physical conditions of stimulation are precisely identical but the loading response is more pronounced when the subject is storing digits for transformation than when she is storing digits for recall. While physical conditions are identical, the process of storing information is probably different in the two tasks; for example, grouping is advantageous for recall, but obviously detrimental to transformation. Incidental evidence suggests that the difference in slope is not due to subjects' performing the transformation operation during the listening phase. Subjects characteristically report that they are con-