fect produced by the pathological consequences of the disease. It is possible that elevated spermidine in red blood cells of patients with cystic fibrosis is related to a conjugation defect that inhibits excretion, since the addition of exogenous spermidine to membranes alters their properties (*10*). A decreased spermidine excretion and consequent extracellular increase, therefore, could contribute to the membrane pathology associated with cystic fibrosis.

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References and Notes

1. D. H. Andersen, *Am. J. Dis. Child.* **56**, 344 (1976); P. A. diSant'Agnese and R. C. Talamo, *N. Engl. J. Med.* **277**, 1287, 1355, 1399 (1967).
2. P. A. diSant'Agnese, R. C. Darling, G. A. Perera, E. Shea, *Pediatrics* **12**, 549 (1953).
3. L. M. Taussig and L. I. Landau, in *Kelly's Practice of Pediatrics*, V. Kelly, Ed. (Harper & Row, Hagerstown, Md., 1976), vol. 4, p. 1; B. Bowman, L. Lockhart, M. McCombs, *Science* **164**, 325 (1969).
4. D. Lundgren, P. Farrell, P. diSant'Agnese, *Clin. Chim. Acta* **62**, 357 (1975).
5. L. F. Cohen, D. W. Lundgren, P. M. Farrell, *Blood* **48**, 469 (1976).
6. M. G. Rosenblum *et al.*, *Pediatr. Res.*, in press.
7. D. H. Russell, *Clin. Chem (Winston-Salem, N.C.)* **23**, 22 (1977).
8. M. G. Rosenblum and D. H. Russell, *Cancer Res.* **37**, 47 (1977).
9. M. G. Rosenblum *et al.*, *Proc. Am. Assoc. Cancer Res.* **17**, 15 (1976).
10. N. Seiler and K. Deckart, *Neurochem. Res.* **1**, 469 (1976).
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Is Binocular Vision Always Monocular?

Abstract. *Visual sensitivity of one eye was determined under binocular stimulus conditions yielding apparent fusion, stereopsis, monocular dominance, and monocular suppression. Marked losses in sensitivity accompanied monocular suppression but were not evident during stable single vision. The results are inconsistent with the hypothesis that suppression alone mediates binocular single vision.*

The singleness of binocular vision is so immediate and compelling that we are seldom aware of its dual monocular origins. Evidently inputs from the two eyes are unified by the brain, but the details of this inconspicuous process are incomplete. The most popular theory of binocular single vision assumes that the two monocular inputs are combined, or fused, in a cooperative fashion, such that each eye contributes more or less equally to the final binocular product (*1*). There is, however, an alternative theory that assumes that we actually see with only one eye at a time, owing to suppression of the partner eye's information (*2*, *3*). This so-called suppression theory, although somewhat counterintuitive, accounts for a variety of perceptual outcomes that are troublesome for fusion theory (*3*), and it is not incompatible with the occurrence of stereoscopic depth perception (*4*).

Because the two eyes ordinarily share a common view, phenomenal observation cannot tell us which process, fusion or suppression, operates to promote single vision (*5-7*). Suppression is evident, however, when the two eyes receive different views by dichoptic stimulation; instead of stable single vision, this situation produces alternating periods of dominance and suppression between the two eyes, an outcome known as binocular rivalry. Indeed, this phenomenon of binocular rivalry has served as a major impetus for suppression theories of binocular single vision. Work on binocular rivalry has shown that phenomenal suppression is accompanied by a general decrease in the visual sensitivity of the suppressed eye, relative to the eye's sensitivity during dominance (*8*). Now, if binocular vision always involves suppression, even under normal viewing conditions, losses in visual sensitivity should be a symptom of suppression when the two eyes receive identical stimulation. We have tested this possibility by measuring monocular detection thresholds under stimulus conditions yielding stereopsis, apparent fusion, monocular dominance, and monocular suppression.

Observers with excellent acuity and stereopsis viewed displays generated electronically on two cathode-ray tube (CRT) displays and presented separately to the two eyes by a mirror stereoscope. Each display consisted of a rectangular field, 8° by 10° of visual angle, produced by placing a translucent mask over the CRT screen; the luminance of this surround field was 1.7 cd/m^2. In the center of each field was a circular aperture, 1° of visual angle in diameter, through which the CRT screen was exposed. Within each circular area could be displayed sinusoidal grating patterns, either vertical or horizontal, or a homogeneous area of the same average luminance as the grating, 5.1 cd/m^2. A briefly flashed spot of light 10 minutes in diameter could be superimposed optically in either the upper or lower portion of the circular target viewed by the left eye. Observers triggered the flash by depressing a button and indicated with a lever switch whether the flash appeared in the upper or lower position (*9*).

We began by determining for each observer the flash duration yielding approximately 90 percent correct performance when the left eye, which received the test flash, was dominant; durations ranged from 9.5 to 12 msec among observers. To promote dominance a 6 cycle/deg vertical grating was presented to the left eye while the right eye viewed a homogeneous field; grating contrast was 1 log unit above threshold, a value that ensured continuous visibility of the pattern (condition MD); these values

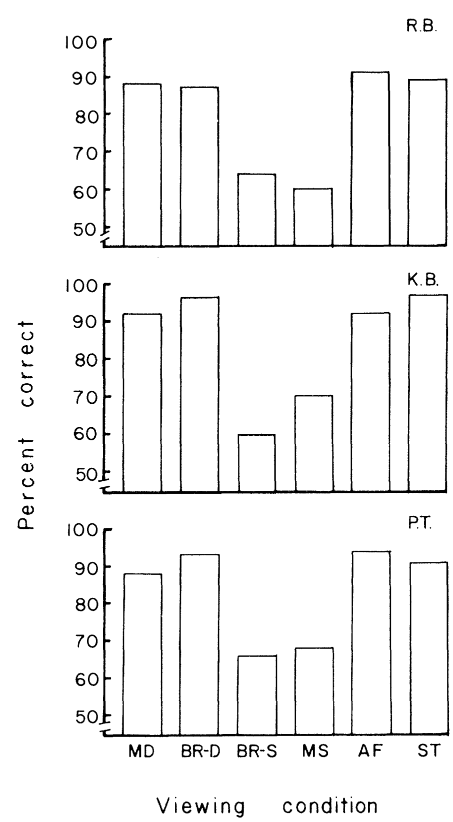

Fig. 1. Correct detection for each observer on a two-alternative forced-choice task. A small, brief test flash was presented in either the upper or lower portion of the display viewed by the left eye. The flash was delivered while the left eye was continuously dominant (*MD*), intermittently dominant (*BR-D*), intermittently suppressed (*BR-S*), continuously suppressed (*MS*), or while the left and right eye patterns were apparently fused (*AF*) and generated a stereoscopic sensation of depth (*ST*). Performance for conditions *BR-S* and *MS* differed significantly ($P < .01$) from all other conditions. Each value is based on at least 100 trials.

ranged from 20 to 30 percent among observers. Next, with that same test-flash duration, percentage correct detection was measured for the following stimulus conditions: (i) The left eye received a 6 cycle/deg vertical grating, and the right eye received a horizontal pattern of the same spatial frequency and contrast, an arrangement yielding binocular rivalry (BR). During one set of 100 trials, observers initiated test flashes only while the vertical grating to the left eye was dominant (BR-D), and during a second set of trials the flash was triggered when only the horizontal grating to the right eye was visible, the left eye being suppressed (BR-S). (ii) The left eye received an uncontoured field and the right eye received a 6 cycle/deg vertical grating that was continuously visible (MS). (iii) Both eyes received a 6 cycle/deg vertical grating, a combination yielding apparent fusion (AF). (iv) The left eye received a 6 cycle/deg vertical grating and the right eye received a vertical grating whose spatial frequency was 10 percent greater than that of the left-eye pattern (ST). Predictably (*10*), for all three observers this last condition yielded the stereoscopic sensation of a single grating rotated about its vertical axis, with its right side farthest from the observer.

The results are presented in Fig. 1. Keep in mind that the test-flash luminance and duration, which yielded around 90 percent correct with the left eye dominant (condition MD), were invariant. For the binocular rivalry conditions, detection was very accurate when the left eye was dominant (BR-D) but impaired when the left eye was suppressed (BR-S). This pattern of results confirms that suppression involves a loss in visual sensitivity, the symptom of suppression demonstrated previously (*8*). A comparable decrement was seen when only the right eye received contour information (MS), with the left eye viewing an uncontoured field (*11*). Evidently, as predicted by suppression theory, monocular suppression can occur even in the absence of conflicting pattern information from the two eyes. Contrary to the prediction from suppression theory, however, performance remained accurate when the two eyes received congruous pattern information (AF and ST). On the basis of suppression theory we would expect at least some decrement in performance for these two conditions, although probably not by an amount equivalent to conditions BR-S and MS (*12*). The absence of any such a decrement must indicate that both eyes participate fully during fusion and stereopsis.

In a second experiment, we examined

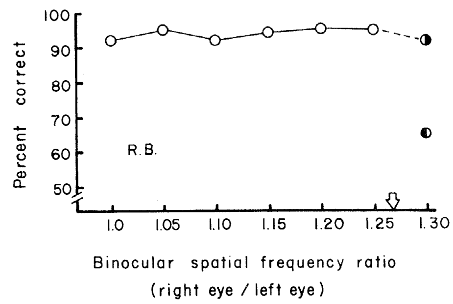

Fig. 2. Correct detection plotted as the function of the difference in spatial frequency between dichoptically viewed vertical gratings; this difference is expressed as a ratio of the two values. The arrow along the abscissa denotes for observer RB the spatial frequency difference beyond which the percept of a single grating rotated in depth gave way to binocular rivalry. This value was determined by gradually increasing the spatial frequency to the right eye until the observer reported the loss of fusion. Open circles give results when a stable, single grating was perceived; half-filled symbols show performance when the pattern to the left eye was dominant (◑) and suppressed (◐). Each point is based on 100 trials.

whether introducing graded dissimilarities between the gratings viewed by the two eyes would produce evidence for a graded degree of suppression in the form of a steady decrease in visual sensitivity. The left eye always received a 6 cycle/deg vertical grating; the spatial frequency of the vertical grating presented to the right eye was varied over the range 6 to 7.8 cycle/deg. For each dichoptic combination of spatial frequencies, the percentage of correct detections was measured with the forced-choice procedures used in experiment 1. The results provide no evidence for a graded loss in sensitivity (Fig. 2). Phenomenally, the binocular combination of these discrepant gratings yielded the global percept of a single grating rotated in depth, with the degree of rotation increasing with spatial frequency to the right eye. For the observer tested, the impression of depth and fusion abruptly disappeared when the spatial frequency of the two gratings differed by more than 25 percent. Beyond this point, the gratings engaged in binocular rivalry, and performance by the left eye depended on whether the observer initiated trials with the left eye dominant or suppressed. These findings indicate that monocular suppression is triggered only when stimulus differences between the two eyes exceed some critical limit for stable single vision.

Our results demonstrate that the contribution to single vision and stereopsis by one eye is not always achieved at the complete expense of the partner eye's input. On the contrary, when congruous images strike corresponding retinal areas, binocular vision is indeed binocular. Hence we must reject the more conventional formulations of suppression theory, which posit that single vision consists exclusively of a mosaic of monocular components (*2, 3*). This is not to say, however, that suppression plays no role in single vision, for almost certainly it must within certain localized regions of the binocular visual field. The geometry of binocular visual space dictates the existence of potential ambiguities concerning the visual direction of objects situated in front of or behind the plane of binocular fixation (*13*). Because they strike noncorresponding retinal areas, the images from these objects should give rise to diplopia and confusion (*3*), yet during ordinary binocular vision neither of those outcomes is experienced. It follows from geometry that these potential ambiguities must involve dissimilar stimulation of corresponding retinal areas. Our results and others (*8*) demonstrate that these are the stimulus conditions that lead to binocular suppression. Evidently, for those local regions of visual space where potential ambiguity exists between the two eyes, binocular vision is monocular. Our results indicate that theories of binocular vision should incorporate the phenomena of both fusion and suppression.

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References and Notes

1. E. G. Boring, *Physical Dimensions of Consciousness* (Century, New York, 1933); J. R. Charnwood, *Essay on Binocular Vision* (Halton, London, 1952); P. Dodwell and G. Engel, *Nature (London)* **198**, 39 (1963); P. O. Bishop, in *Handbook of Sensory Physiology*, R. Jung, Ed. (Springer-Verlag, New York, 1973), vol. 7, part 3.
2. F. Verhoeff, *Arch. Ophthalmol.* **13**, 151 (1935); H. Asher, *Br. J. Ophthalmol.* **37**, 37 (1953); J. Hochberg, *Science* **145**, 1334 (1964); W. J. M. Levelt, *Percept. Psychophys.* **1**, 39 (1966).
3. L. Kaufman, *Sight and Mind* (Oxford, New York, 1974).
4. L. Kaufman and C. Pitblado, *Percept. Psychophys.* **6**, 10 (1969): B. Julesz and J. Miller, *Perception* **4**, 125 (19 L. Kaufman, *Am. J. Psychol.* **77**, 393 (1964); J. Mayhew and J. Frisby, *Nature (London)* **264**, 53 (1976).
5. Efforts to distinguish fusion from suppression in binocular vision have relied chiefly on the phenomenon of displacement, or allelotropia [H. Werner, *Psychol. Monogr.* **49**, 1 (1937); P. Dodwell, *Visual Pattern Recognition* (Holt, Rinehart & Winston, New York, 1970); Kertesz and Jones (*6*); Ono *et al.* (*7*)]. It is reasoned that fusion has occurred if the visual direction of disparate half-images viewed stereoscopically assumes a value intermediate to that of either half-image. Suppression, on the other hand, should yield a visual direction equivalent to that of one of the two half-images. There have been several demonstrations apparently supporting the fusion outcome, in that displacement was reported, but for several reasons critics have argued that those demonstrations are inconclusive. According to one argument, small vergence errors dur-

ing binocular fixation can introduce shifts in visual direction that mimic the outcome expected with fusion [K. Ogle, *Researches in Binocular Vision* (Saunders, Philadelphia, 1950); Kaufman (*3*)]. This possibility can be minimized by using briefly flashed stimuli [Ono *et al.* (*7*)] or by measuring eye movements [Kertesz and Jones (*6*)]. A second, more general criticism of displacement phenomena concerns the potential ambiguities in criteria for reporting shifts in visual direction and in the sensitivity of the psychophysical procedures typically used [L. Kaufman and A. Arditi, *Vision Res.* **16**, 535 (1976)]. In general, these criticisms underscore the difficulty of distinguishing fusion from suppression on the basis of phenomenal report alone. To avoid these difficulties, others [R. Fox and R. Check, *Percept. Psychophys.* **1**, 331 (1966); R. Fox and C. McIntyre, *Psychon. Sci.* **8**, 143 (1967); W. Makous and R. K. Sanders, in *Visual Psychophysics: Its Physiological Basis*, J. Armington, J. Krauskopf, B. Wooten, Eds. (Erlbaum, Hillsdale, N.J., in press)] have used indirect techniques somewhat similar to ours, but the results have not been consistent.
6. A. Kertesz and R. W. Jones, *Vision Res.* **10**, 891 (1970).
7. H. Ono, R. Angus, P. Gregor, *Percept. Psychophys.* **21**, 513 (1977).
8. R. Fox and R. Check, *J. Exp. Psychol.* **78**, 388 (1968); R. Wales and R. Fox, *Percept. Psychophys.* **8**, 90 (1972); R. Blake and R. Fox, *Vision Res.* **14**, 687 (1974); R. Blake and S. Lema, *Vision Res.*, in press.
9. The test flash was generated by the driver and timing unit of a tachistoscope (Scientific Prototype model GB). The lamp was a cold-cathode fluorescent tube with a rise time to maximum intensity of approximately 1 msec. The position of the test flash within the left-eye display was controlled by a shutter. The center of the 10-minute circular test flash fell 15 minutes of arc from either the upper or lower edge of the left-eye target, depending on whether the flash was in the top or bottom position. Test flash luminance was 5.1 cd/m², and the circular spot was in cosine phase with respect to the sinusoidal striations of the grating, such that it covered one complete cycle of the grating. The observer viewed the entire display through natural pupils with the head firmly positioned on a dental impression board. A variable prism placed before one eye was used, if necessary, to achieve binocular alignment of the two CRT displays; the 1° circular aperture, which delimited the grating pattern, and the outer boundaries of the 8° by 10° CRT screen provided strong fusional stimuli for the maintenance of stable binocular alignment. Observers were instructed always to fixate the center of the circular aperture. The CRT screens provided the only illumination within the darkened test booth, and observers adapted to this prevailing level for at least 5 minutes before trials were begun. The position of the test flash was varied randomly from trial to trial under the control of a computer (PDP-8I), which also read and stored the observer's response on each trial. The results have been replicated upon repeated testing.
10. C. Blakemore, *Vision Res.* **10**, 1181 (1970); A. Fiorentini and L. Maffei, *ibid.* **11**, 1299 (1971); H. Wilson, *ibid.* **16**, 983 (1976).
11. We have also measured detection for the condition in which both eyes received uncontoured fields and the test probe went to the left eye. Performance was equivalent (about 90 percent) to that measured for conditions MD and BR-D, which indicates that the significant reduction in performance for condition MS, in which the left eye received an uncontoured field, arises from the contralateral pattern and not from fixation disparity, uncertainty about test flash location, or the absence of contour in the left eye.
12. For conditions BR-S and MS, the observer triggered test flash presentations while the grating viewed by the right eye was dominant. Although for conditions AF and ST, it would be impossible for observers to adopt this same strategy, on the basis of statistical considerations we would expect some decrement in performance even if suppression of the left eye were intermittent, as in the case of binocular rivalry. For each observer, when orthogonally oriented gratings were presented to the two eyes, the temporal pattern of binocular rivalry yielded approximately 50 percent predominance (percentage of time visible) for each eye, with average dominance durations on the order of 2 to 3 seconds. If we assume a comparable pattern of predominance during conditions AF and ST, detection performance for these conditions should be between 70 to 75 percent if suppression occurred intermittently. Performance was more accurate than this. It seems unlikely that a complete cycle of dominance and suppression could occur within the duration of the test flash, which ranged from 9.5 to 12 msec among observers. Moreover, we are confident these results are not due to eye dominance, since KB and PT are right-eye dominant while RB is left-eye dominant, as determined by conventional sighting tests [C. Porac and S. Coren, *Psychol. Bull.* **83**, 880 (1976)].
13. This locus of binocular fixation is on a plane known as the horopter and, according to the most accepted definition, is composed of those positions in visual space which appear to lie in the same direction in the visual field of both eyes [T. Shipley and S. Rawlings, *Vision Res.* **10**, 1225 (1970)].
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Insecticidal Benzoylphenyl Ureas: Structure-Activity Relationships as Chitin Synthesis Inhibitors

Abstract. *The 1-benzoyl-3-phenylurea insecticide diflubenzuron is a potent inhibitor for the conversion of* [14]*C-labeled glucose to* [14]*C-labeled chitin in isolated abdomens of newly emerged adult milkweed bugs* (Oncopeltus fasciatus *Dallas*)*. The inhibitory activity of 24 diflubenzuron analogs in this in vitro chitin-synthesizing system is in good agreement with their toxicity to fifth instar nymphs of this species. These insecticides act quickly and directly within the integument to ultimately block the terminal polymerization step in chitin formation.*

Chitin is the most abundant organic skeletal component of insects, other invertebrates, and many fungi, but it is absent in vertebrates and higher plants (*1*). Insecticides that disrupt chitin deposition therefore have selectivity advantages over earlier types that alter nerve action or bioenergetic reactions that are similar in insects and mammals. Diflubenzuron [2,6-F_2-C_6H_3-C(O)NHC(O)-NH-C_6H_4-Cl-4] and several other benzoylphenyl ureas effectively control major insect pests by interfering with the molting process or by acting as ovicides and chemosterilants (*2*).The larvicidal activity is attributable to disruption of chitin deposition (*2*). This benzoylphenyl urea action may be indirect by altering ecdysone or juvenile hormone levels (*3*) or direct by inhibiting a critical step in chitin formation (*4*). An insect system for in vitro chitin biosynthesis is required to differentiate between these hypotheses. We find, using abdomens of newly emerged adult milkweed bugs (*Oncopeltus fasciatus* Dallas) as reaction vessels, that benzoylphenyl ureas act directly within the integument to block the terminal polymerization step in chitin formation (*5*).

An ideal insect system for studies on inhibitors of chitin biosynthesis should meet the following specifications: rapid and consistent in vitro formation of [14]C-labeled chitin in reasonable yields from convenient [14]C precursors such as glucose, glucosamine, and *N*-acetylglucosamine; sensitivity to polyoxin D, a chitin synthetase inhibitor (*6*), and to diflubenzuron and its insecticidal analogs; and no involvement of exogenous hormones during the period of insecticide action. Cultures of cockroach leg regenerates meet some of these requirements, but this system requires activation by exogenous β-ecdysone and an assay period of 2 weeks (*7*). In developing our system, we used milkweed bugs for several reasons. They are easy to rear and handle, and the fifth instar nymphs are highly sensitive to topically applied diflubenzuron and its analogs (*8*). Insecticidal levels of diflubenzuron do not alter the in vivo metabolic conversion of α-ecdysone to β-ecdysone or the subsequent metabolism of β-ecdysone in fifth instar milkweed bug nymphs (*5*) or the endogenous β-ecdysone titers in pharate pupae of *Stomoxys calcitrans* whose larvae had been exposed to the insecticide (*9*). Although these findings tend to rule out hormone mediation in the action of diflubenzuron, we chose to further minimize the possibility of hormone effects by using young adults since their endogenous ecdysone levels are low (*10*); in immature insects the β-ecdysone titers reach maximum levels shortly before molting (*10*) and strongly influence chitin biosynthesis (*11*).

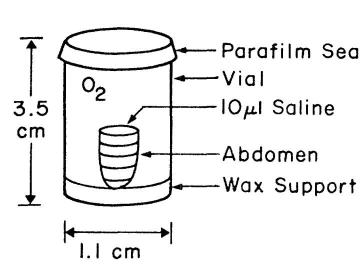

Fig. 1. Diagram of the isolated adult milkweed bug abdomen used as reaction vessel for chitin biosynthesis.

Milkweed bug adults were used 12 hours after emergence because at this time their activity for converting [[14]C]glucose to [[14]C]chitin is higher than it is either earlier or later. The abdomen

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