Journal of Physiology (1991), **437**, *pp*. 449–460
With 5 figures
Printed in Great Britain

TONIC INTEROCULAR SUPPRESSION AND BINOCULAR SUMMATION IN HUMAN VISION

BY NOREEN DENNY*, THOMAS E. FRUMKES*†, MICHAEL C. BARRIS*
AND THOR EYSTEINSSON‡

*From the *Department of Psychology, Queens College of CUNY, Flushing, NY 11367, USA and the ‡Department of Physiology, University of Iceland, Reykjavik 101, Iceland*

(*Received 22 June 1990*)

SUMMARY

1. Spatial sensitivity of human foveal vision was examined using sinusoidally modulated gratings. Our primary concern was the influence of interocular light adaptation upon monocular visibility.

2. Interocular adapting influences depend upon spatial frequency and adapting luminance. Interocular adaptation has a negligible influence upon the sensitivity to 1 cycle/deg gratings. Any visible interocular adapting field improves the sensitivity to intermediate spatial frequencies (2–5 cycles/deg).

3. Brighter interocular backgrounds ($> 0{\cdot}1$ cd/m^2) improve sensitivity to higher spatial frequencies (10–20 cycles/deg).

4. The interocular adapting influences summarized in (2) and (3) above cannot be duplicated by monocular or binocular adaptation. Similarly, monocular or binocular adaptation have negligible influences upon binocular visibility.

5. The interocular adapting effect summarized in (3) above can be duplicated by pressure blinding the contralateral eye. We conclude that monocular spatial sensitivity is subject to a tonic interocular suppression (TIS) from the dark-adapted eye.

6. The spatial sensitivity resulting from binocular viewing is nearly identical to that observed by combining monocular viewing with interocular light adaptation. We suggest that the improvement in sensitivity resulting from two-eyed viewing may be attributable to the removal of TIS instead of to binocular physiological summation.

INTRODUCTION

Over the past century, a growing body of literature has been concerned with the means by which visual signals from the two eyes combine to produce a fused binocular percept (e.g. Fechner, 1860; Sherrington, 1904; von Helmholtz, 1909; Bartley, 1941; Pirenne, 1943; Hubel & Wiesel, 1962; Trick, Dawson & Compton,

---

† To whom all correspondence should be addressed.

1982; for review, see Blake & Fox, 1973*a*; Blake, Sloane & Fox, 1981). When research related to binocular rivalry and stereoscopic depth is set aside, most of the remaining literature references, which still number in the hundreds, are usually listed under the heading 'binocular summation' for the following reason. Under optimal conditions, binocular sensitivity can double (be 0·3 $\log_{10}$ units greater than) that obtained with one-eyed viewing. Since such binocular superiority cannot be accounted for merely by 'probability summation' as once proposed (Pirenne, 1943), it is assumed that monocular signals sum together physiologically to produce a larger binocular signal (for complete exposition, see Blake & Fox, 1973*a*). However, such apparent summation is not always obtained, particularly if the separate monocular stimuli differ in temporal and/or spatial detail (e.g. Fechner, 1860; Bartley, 1941; Trick *et al.* 1982). Therefore, a secondary, modifying role for various types of inhibition, particularly lateral inhibition, is sometimes also considered.

The four experiments reported here more strongly and directly contradict claims for 'binocular summation'. The first three experiments establish that monocular sensitivity to spatial gratings is tonicly suppressed by a photically unstimulated eye. Removal of this suppression with either light adaptation or pressure blinding markedly improves monocular visual sensitivity. The fourth experiment suggests that the improvement in sensitivity to spatial gratings resulting from binocular presentation is likely to reflect the removal of this tonic suppression rather than 'physiological summation'.

Preliminary versions of the present communication have been presented previously in abstract form (Denny, Frumkes & Barris, 1990; Eysteinsson, Denny & Frumkes, 1990). A more complete unpublished presentation of the data presented here will be found in the doctoral dissertation of the first author (N. Denny, unpublished manuscript).

METHODS

Optical stimulator and stimulus array

All stimuli were presented to the observer by means of a two-channel optical system: either channel could stimulate the left, right, or both eyes of the observer who was previously dark adapted for 25 min. The test stimulus consisted of horizontally oriented, sinusoidally modulated gratings. These were generated by a Vision Metrics grating generator and an XT-clone (Fountain) microprocessor, and displayed on a 12·5 cm Ikegami black–white monitor. The grating display was centred foveally, had a rectangular shape subtending a viewing angle with a 2·4 deg height by 3·2 deg width, and most commonly had a fixed average luminance of 10 cd/m^2. In many experiments we also used an adapting stimulus, a fluorescent photographic light box, which was usually presented to the contralateral eye. For some experiments, this had the same spatial dimensions as the test gratings. More usually and in all cases reported below, the adapting stimulus was a 15 deg height by 20·8 deg width rectangle, i.e. was much larger than the test grating. Use of the larger adapting field slightly reduced variability but did not otherwise influence results (Denny, 1991).

Both grating and adapting stimuli were placed at an optical distance of 1·83 m from the observer's eyes and, if necessary, the observers used their usual spectacle correction. Appropriately placed neutral density filters controlled the luminance of all stimuli. We used a large number of baffles to minimize the role of stray light in determining our findings. In addition, all stimuli were viewed with the relevant eye(s) through 2·5 mm diameter artificial pupils to rule out any role for consensual pupillary dilatation.

Observers

Three different observers were originally used. Two of these were the first two authors who obviously were fully informed of the purpose of all experiments. N.M. was a student volunteer who, at the time the illustrated data in Fig. 5 were collected, only knew that we were interested in 'binocular vision', but was naive regarding the purpose of experimentation. All observers, including five others subsequently used, were fully informed *a priori* of all procedures to be used as acknowledged by them in writing prior to participation in this study. Only the first two authors served as observers in the type of experiment illustrated in Fig. 3. All experimental protocols were approved by the Human Subjects Committee of Queens College CUNY.

Psychophysical methodology

The following procedure was used in collecting data such as those illustrated for observer N.D. in Figs 1, 2 and 4 with all three observers originally used. The observer was first binocularly dark adapted for 25 min, and subsequently adapted to the particular adapting field to be used. The spatially unmodulated cathode ray display was then continuously presented to the observer as a homogeneous field, in most experiments only to one eye. A sinusoidal grating of fixed spatial frequency but of the same average luminance (10 cd/m^2) was then presented on the cathode ray display for 0·5 s. By depressing the appropriate push-button, the observer would then increase or decrease the contrast of the grating in 3 dB steps for coarse adjustment, or 1 dB steps for fine adjustment. This procedure was repeated until the observer was satisfied that the grating contrast was at threshold. In order to minimize any adaptation effect to specific gratings, we recycled stimulus presentation at a very slow rate (once every 5 s), and the initial contrast value used was almost always subliminal. In collecting such 'method of adjustment' data, as much randomization as possible was used in sequencing the order of stimulus presentation. Each datum represents the mean of at least six individual threshold values obtained in at least three separate experimental sessions. The standard error for each datum was typically about half the size of the symbol used for plotting the functions represented by Figs 1, 2 and 4; the standard error never exceeded the size of a plotted symbol by more than 10%.

The psychophysical method of adjustment entails repetitive presentation of the same spatial frequency stimulus; therefore, its use may bias results. For this reason, we additionally collected the same types of data illustrated in Figs 1, 2 and 4 using a variety of different psychophysical methods. These included a two-alternative forced-choice staircase procedure supplied by Vision Metrics (their 'PGCONSEN' program) in which the spatial frequency presented on any trial was unknown to the observer. In a given session a 'threshold' represented the mean of six reversals. Such results (obtained about 3 months earlier than the data in Figs 1–4) are presented in Fig. 5 in which every plotted datum represents the mean of results obtained in three separate experimental sessions. As indicated below, results obtained with both psychophysical methods as well as the three observers most carefully studied were invariably in qualitative agreement indicating that these results are both robust and reliable.

The methodology used in collecting the data described by Fig. 3 (from observer N.D.) is presented within the text of the 'Results' section.

RESULTS

Figure 1 shows the sensitivity to monocularly presented gratings as a function of their frequency, which is plotted along the abscissa in cycles/deg. The functions plotted with filled circles are data obtained with no adapting field present. Confirming well-known findings (Kelly, 1977), sensitivity is greatest with an intermediate spatial frequency (5 cycles/deg) and falls off as frequency either increases or decreases. The other data points show data collected in the presence of an interocular adapting field. Any interocular adapting field has a negligible influence upon sensitivity for 1 cycle/deg gratings. For intermediate spatial frequencies (2–5 cycles/deg), interocular adapting fields of any luminance improve grating sensitivity. For still higher spatial frequencies (10–20 cycles/deg), sensitivity is uninfluenced by interocular adapting fields $\leqslant$ 0·1 cd/m^2 (■ and ◆), but is improved by brighter interocular adapting fields (○, □ and △). The spatial frequency dependence of interocular adaptation, which is only of parenthetical interest, may

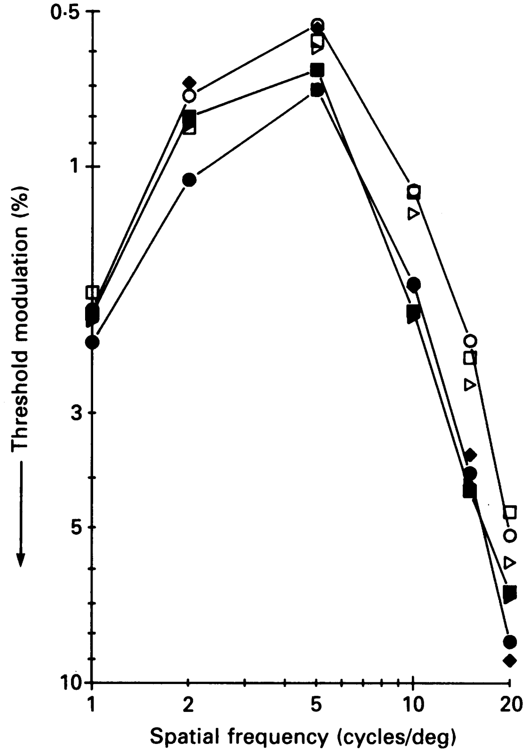

Fig. 1. Percentage threshold modulation (increasing downward along the ordinate) for a monocularly presented sine wave grating as a function of its spatial frequency (along abscissa in cycles/deg). With such a plot, an increase in spatial sensitivity is represented by an upward shift along the ordinate as is conventional in the spatial modulation literature. Thresholds were obtained when the contralateral eye was either dark adapted (●) or adapted to a large, homogeneous adpating field with the following luminance values (in cd/m^2): ◆, 0·001; ■, 0·01; ▲, 0·1; △, 1; ○, 10; □, 100. Results were obtained from observer N.D. using the psychophysical method of adjustment.

reflect differences between the spatially larger grained magnocellular branch of the cerebral visual pathway which is sensitive to dimmer levels of illumination *vs.* the more fine-grained parvocellular branch which is relatively insensitive to dim illumination (Purpura, Kaplan & Shapley, 1988). Although not illustrated, we also obtained data similar to Fig. 1 using test gratings with an average luminance of 0·1 and 1·0 cd/m^2 (N. Denny, unpublished thesis). The extent of interocular adaptation effects did not depend upon test grating luminance.

To show that the results in Fig. 1 reflect a unique interocular influence, we again presented the test stimulus to one eye and presented a 10 cd/m^2 adapting stimulus to either the same, the contralateral, or to both eyes. Figure 2 again shows that interocular adaptation increases sensitivity to the test grating, but that direct adaptation of the test eye slightly decreases sensitivity. This latter result should not be surprising. Since the adapting field and test grating have the same average luminance but only the test stimulus is spatially modulated, presentation of both together in one eye doubles the luminance and, more importantly, halves the physical contrast of the summed retinal image. A binocularly presented adapting field is also relatively ineffective. As described below, we also showed that neither binocular nor monocular adapting fields improved sensitivity to binocularly presented gratings.

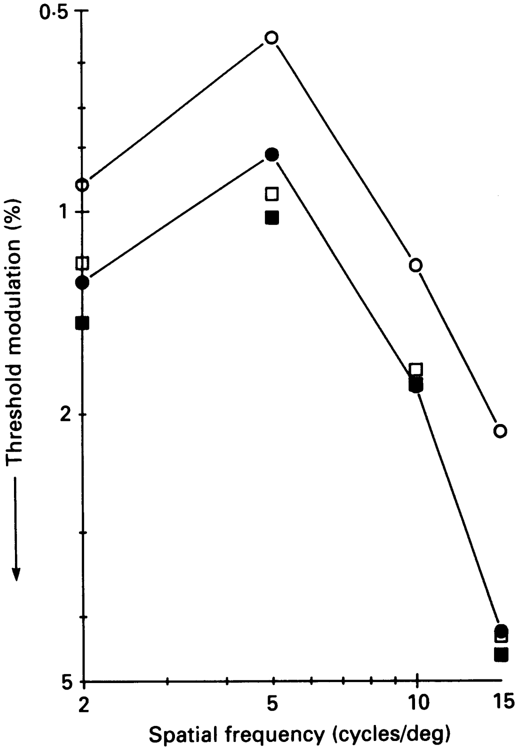

Fig. 2. Percentage threshold modulation for a monocularly presented sine wave grating as a function of its spatial frequency. Thresholds were obtained when no adapting field was present (●), or when a large homogeneous adapting field was presented to the test eye (■), the contralateral eye (○), or both eyes (□). Results were obtained from observer N.D. using the psychophysical method of adjustment.

The interocular adapting influence described in Figs 1 and 2 could either reflect a facilitatory influence stemming from the light-adapted eye, or a suppressive influence from the dark-adapted eye. In order to choose between these possibilities, we performed the following sequence of manipulations in one experimental session. We first compared the sensitivity of the test eye to a 10 cycle/deg grating under conditions in which the contralateral eye was adapted to a 10 cd/m^2 background or was dark adapted. These threshold values, with 95% confidence intervals (±2 standard errors), are shown in Fig. 3. We then repetitively presented a grating with 1% modulation to the test eye when the 'adapting eye' was in the dark. As indicated, this grating could not be seen under these conditions. We then pressure blinded the 'adapting eye' for about 30 s. Such pressure blindness acts by removing the blood supply to the retinal ganglion cells, hence eliminating their signal to the brain (for evidence in humans, see Blake & Fox, 1973*b*; Makous, Teller & Boothe, 1976). Over a 30 s period while the 'adapting eye' was pressure blinded, the grating gradually became clearly visible; within a few seconds after removing pressure blinding, the grating again became invisible. This strongly suggests that with monocular viewing, a dark-adapted eye tonically suppresses vision in the contralateral eye.

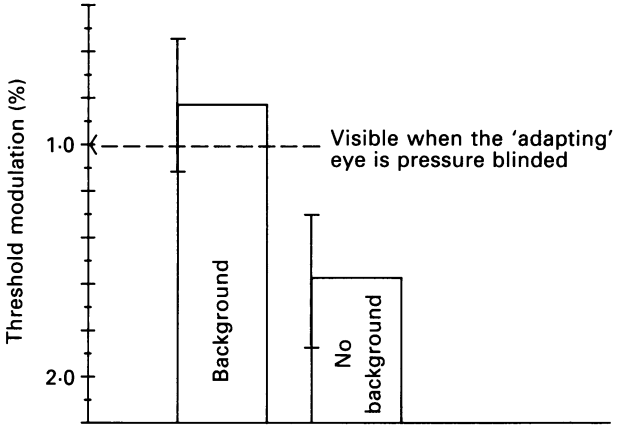

Fig. 3. Percentage threshold modulation for a monocularly presented sine wave grating of 10 cycles/deg obtained when no background field was present, or in the presence of a contralaterally presented adapting field. The error bars indicate 95% confidence intervals for each threshold value. These data show that without contralateral light adaptation, a test grating modulated 1% is invisible. But as described in the text, a 1% modulated test grating becomes visible when the contralateral eye is pressure blinded. Results were obtained from observer N.D.

In our last experiment we compared the change in sensitivity resulting from contralateral light adaptation with the change resulting from binocular presentation. The filled circles and triangles in Fig. 4 show, respectively, monocular and binocular grating sensitivity when no adapting field was presented; the open circles show monocular sensitivity in the presence of an interocular adapting field. Interocular adaptation and binocular presentation similarly improve grating sensitivity; the slightly greater sensitivity of binocular viewing in comparison with that observed with interocular adaptation most likely reflects probability summation. A very similar relationship between the improvement in sensitivity produced by interocular adaptation and binocular viewing situations was also found in the two other observers carefully examined (N. Denny, unpublished thesis). For observer N.D., the remaining data points in Fig. 4 show that the addition of a monocular or binocular adapting field slightly decreases sensitivity to binocularly presented gratings.

Figure 5 shows data similar to Fig. 4 but obtained with a two-alternative, forced-choice staircase psychophysical procedure. These results were obtained from three different observers including that used for collecting the data in Figs 1–4 (N.D. in *A*) and a naive observer (N.M. in *B*). All three co-ordinates compare sensitivity to gratings when viewed monocularly with the other eye dark adapted (●), when viewed monocularly with the other eye adapted to a 10 cd/m^2 background field (▲), or when viewed binocularly with no adapting field present (○). For all three observers, interocular adaptation and binocular presentation produce a similar increase in grating sensitivity. These data establish that our results are reliable in different observers and do not depend upon the specific psychophysical methodology employed.

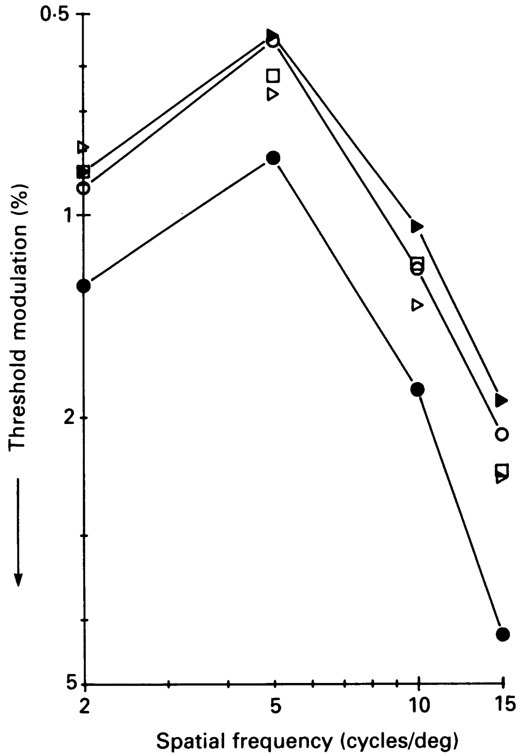

Fig. 4. Percentage threshold modulation for sine wave gratings as a function of spatial frequency. The different shaped symbols indicate whether the grating was presented monocularly or binocularly, and whether or not an adapting field was absent or presented monocularly or binocularly. ●, monocular grating, no adapting field; ○, monocular grating, interocular adapting field; ▲, binocular grating, no adapting field; □, binocular grating, monocular adapting field; △, binocular grating, binocular adapting field.

Parenthetically, we should note that previous psychophysical studies of grating visibility (e.g. Campbell & Green, 1965; Blakemore & Hague, 1972; Blake & Levinson, 1977) show the ratio of binocular to monocular sensitivity to be approximately 1·4, while the data of Figs 4 and 5 indicate a higher ratio; for the 15 cycle/deg data shown in Fig. 4 and the 15 cycle/deg data for observer T.E.F. shown in Fig. 5, this ratio exceeds 2·0. We attribute the greater binocular effect in our study

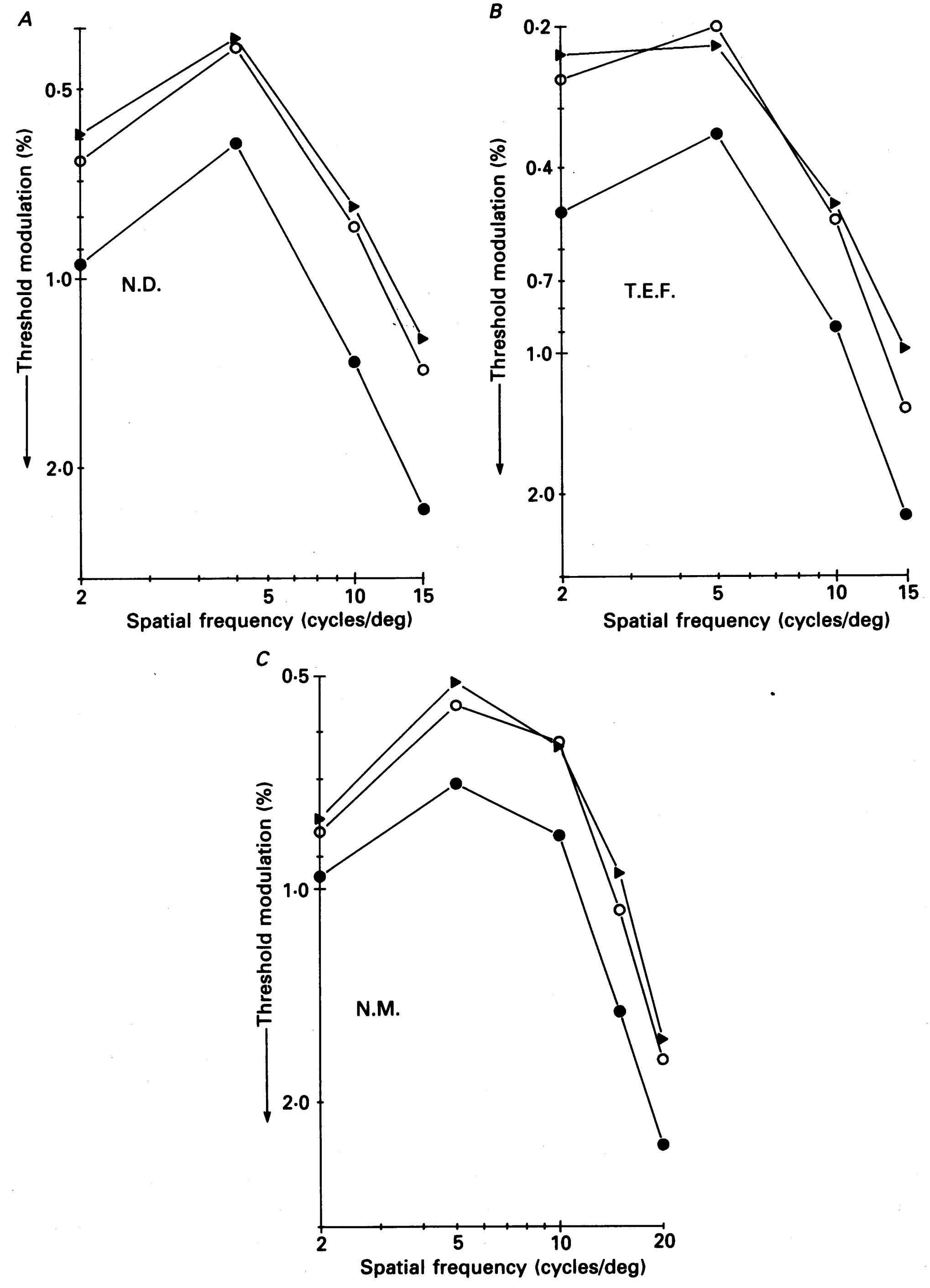

Fig. 5. Percentage threshold modulation for sine wave gratings as a function of spatial frequency. Results were obtained from three different observers as indicated by the initials including that used for Figs 1–4 (N.D., *A*) and a naive observer (N.M., *C*). Unlike the results in Figs 1, 2 and 4, these data were collected with a two-alternative forced-choice procedure which is less subject to bias than the method of adjustment. For all three observers and in comparison with results obtained with monocular stimulus presentation (●), interocular adaptation (○) and binocular presentation (▲) produce similar improvement in sensitivity.

to more rigorous elimination of stray light and to a more completely dark-adapted condition of our observers. Although inconsistent with some theories, we emphasize the lack of any established *empiricial* limit to the improvement in sensitivity resulting from binocular presentation. With parafoveal stimulus presentation, N. Denny (unpublished thesis) found ratios of binocular to monocular sensitivity approaching 4·0 using grating visibility procedures essentially identical to those reported here. With foveally centred gratings and evoked potential procedures, Tyler, Apkarian & Nakayama (1978) observed even larger binocular to monocular sensitivity ratios.

DISCUSSION

Tonic interocular suppression

We have shown that tonic interocular suppression (TIS) plays a critical role in binocular vision. This finding is not entirely new. Using detection thresholds rather than grating visibility, several prior psychophysical studies showed a similar influence of contralateral light and dark adaptation upon vision (Lansford & Baker, 1969; Auerbach & Peachey, 1984; Reeves, Peachey & Auerbach, 1986); Makous *et al.* (1976) used pressure blindness to show this effect involves TIS. Unlike the present grating visibility findings, these interocular influences upon detection threshold cannot be demonstrated with foveal stimulus presentation. Using foveally centred stimuli, the pattern cortical potential evoked by one eye has also been shown to be enhanced by light adapting the contralateral eye (Schmeisser & Dawson, 1982; Eysteinsson *et al.* 1990). Although not precluding other possibilities, these evoked-potential data are certainly consistent with a TIS mechanism.

A consideration of a wider body of literature suggests the present demonstration of TIS with grating visibility to be merely one demonstration of a much more general type of mechanism. TIS has been postulated to account for some of the effects of monocular deprivation upon the development of visual cortex in kittens (Kratz & Spear, 1976; Smith, Spear & Kratz, 1978; van Sluyters, 1978). Nor are contralateral suppressive mechanisms restricted to cerebral vision. For example, a much older body of literature established a role for a tonic, contralateral, suppressive influence in the development and function of motor systems in both vertebrates and invertebrates (for review, see Taub & Berman, 1968; Govind, 1989). Interaural masking effects, which are in many ways analogous to the present TIS findings and described under the rubric ‘masking level difference’, have long been studied in audition (for review, see Jeffress, 1972). Finally, prior work from our own laboratory shows tonic inhibition to play a large role in the normal functioning of the distal (Frumkes & Eysteinsson, 1988) and proximal retina (Frumkes, Miller, Slaughter & Dacheux, 1981), and Singer (1977) specifically proposed a role for a TIS mechanism in the cerebral visual system of cat.

Collectively, the foregoing suggests TIS to be a mechanism which plays an important and ubiquitous role in binocular vision for which, however, the underlying neural substrate is unknown. The best understood tonic suppressive mechanisms in vision are in the proximal retina; these involve the neurotransmitters GABA and glycine and classical inhibitory chloride mechanisms (Frumkes *et al.* 1981; Belgum, Dvorak, McReynolds & Miyachi, 1987). Such mechanisms can easily alter the sensitivity of the visual system by several $\log_{10}$ units. On the other hand, the present data show a much more limited TIS effect, i.e. about 0·3 $\log_{10}$ units for the conditions represented by Figs 1–4. It is of interest that analogous findings in the auditory literature are usually explained in terms of an alteration in signal-to-noise ratio at a site for binaural convergence within the brain (see Jeffress, 1972). We are currently studying the possibility that TIS acts by altering signal-to-noise relationships.

Relationship of interocular suppression to claims for 'binocular summation'

The present results also show that optimal spatial sensitivity can be achieved with either one- or two-eyed viewing. Two types of interocular influences must be removed to achieve this optimal sensitivity: (1) TIS from a dark-adapted eye must be removed by light adaptation; (2) the contralateral eye cannot be stimulated with spatial patterns producing non-corresponding retinal images resulting in binocular rivalry. Both types of interocular influences are removed by presenting the identical stimulus binocularly, or by monocularly light adapting one eye. These results suggest that a removal of TIS is at least as likely an explanation as 'binocular summation' for the superiority of binocular sensitivity.

Certainly, the present study does not totally disprove the existence of 'binocular summation'. It is possible that the near-identical improvement in sensitivity resulting from binocular presentation and interocular adaptation (Fig. 4) is coincidental. Moreover, the present study was not concerned with colour, brightness and temporal summation data (reviewed by Blake & Fox, 1973*a*; Blake *et al.* 1981) often cited as evidence for 'binocular summation'. Along these lines, older psychophysical literature shows that interocular light adaptation apparently *decreases* sensitivity to flicker (Perrin, 1954); as first reported by Fechner (1860), stimulating the two eyes with different luminance stimuli often results in an apparent brightness level in between that observed monocularly by the 'bright-exposed' and 'dim-exposed' eye alone. Informal subjective results from our laboratory show these flicker and brightness findings depend upon specific stimulus conditions. We are beginning to examine these other visual attributes using the rigorous controls we employed for studying spatial vision.

Our findings decisively indicate the fallacy in accepting binocular improvement in sensitivity as definitive evidence for binocular summation. The relative importance for TIS *versus* summation more generally can only be established clearly by a whole new body of research.

This research was supported in part by NIH grant EY05984 awarded to T. E. Frumkes, and by a Biomedical Grant awarded to Queens College. The authors thank Ms Nan Min for serving as an observer and gratefully acknowledge criticisms of an earlier version of this manuscript by R. Blake, G. Lange, W. Makous and N. Peachey.

REFERENCES

Auerbach, E. & Peachey, N. S. (1984). Interocular transfer and dark adaptation to long-wave test lights. *Vision Research* **24**, 1043–1048.

Bartley, S. H. (1941). *Vision*. von Nostrand, New York.

Belgum, J. H., Dvorak, D. R., McReynolds, J. S. & Miyachi, E. (1987). Push–pull effect of surround illumination on excitatory and inhibitory inputs to mudpuppy retinal ganglion cells. *Journal of Physiology* **388**, 233–243.

Blake, R. & Fox, R. (1973*a*). The psychophysical inquiry into binocular summation. *Perception and Psychophysics* **14**, 161–185.

BLAKE, R. & FOX, R. (1973*b*). Visual evoked cortical potentials during pressure blinding. *Vision Research* **13**, 501–503.

BLAKE, R. & LEVINSON, E. (1977). Spatial properties of binocular neurones in the human visual system. *Experimental Brain Research* **27**, 221–232.

BLAKE, R., SLOANE, M. & FOX, R. (1981). Further developments in binocular summation. *Perception and Psychophysics* **30**, 266–276.

BLAKEMORE, C. & HAGUE, B. (1972). Evidence for disparity detecting neurones in the human visual system. *Journal of Physiology* **225**, 437–455.

CAMPBELL, F. W. & GREEN, D. G. (1965). Monocular versus binocular visual acuity. *Nature* **208**, 191–192.

DENNY, N., FRUMKES, T. E. & BARRIS, M. C. (1990). Tonic inhibition from a dark-adapted eye upon spatial vision mediated by the contralateral eye. *Investigative Ophthalmology and Visual Science* suppl. **31**, 304.

EYSTEINSSON, T., DENNY, N. & FRUMKES, T. E. (1990). Tonic suppressive influence from the dark adapted eye. *Society for Neuroscience Abstracts* **16**, 104.

FECHNER, G. T. (1860). *Elemente der Psychophysik*. Breitkopf and Haertel, Leipzig.

FRUMKES, T. E. & EYSTEINSSON, T. (1988). The cellular basis for suppressive rod–cone interaction. *Visual Neuroscience* **1**, 263–273.

FRUMKES, T. E., MILLER, R. F., SLAUGHTER, M. M. & DACHEUX, R. F. (1981). Physiological and pharmacological basis of GABA and glycine action on neurons of mudpuppy retina. III. Amacrine-mediated inhibitory influences on ganglion cell receptive-field organization; a model. *Journal of Neurophysiology* **45**, 783–804.

GOVIND, C. K. (1989). Asymmetry in lobster claws. *American Scientist* **77**, 468–474.

HUBEL, D. H. & WIESEL, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology* **160**, 106–154.

JEFFRESS, L. A. (1972). Binaural signal detection: equalization and cancellation theory. In *Foundations of Modern Auditory Theory*, vol. II, ed. TOBIAS, J. V., pp. 349–367. Academic Press, New York.

KELLY, D. H. (1977). Visual contrast sensitivity. *Optica Acta* **24**, 107–129.

KRATZ, K. E. & SPEAR, P. D. (1976). Effects of visual deprivation and alterations in binocular competition on responses of striate cortex neurons in the cat. *Journal of Comparative Neurology* **170**, 141–151.

LANSFORD, T. G. & BAKER, H. D. (1969). Dark adaptation: an interocular light-adaptation effect. *Science* **164**, 1307–1309.

MAKOUS, W., TELLER, D. & BOOTHE, R. (1976). Binocular interaction in the dark. *Vision Research* **16**, 473–476.

PERRIN, E. H. (1954). A study in binocular flicker. *Journal of the Optical Society of America* **44**, 60–69.

PIRENNE, M. H. (1943). Binocular and uniocular thresholds in vision. *Nature* **152**, 698–699.

PURPURA, K., KAPLAN, E. & SHAPLEY, R. M. (1988). Background light and the contrast gain of primat P and M retinal ganglion cells. *Proceedings of the National Academy of Sciences of the USA* **85**, 4534–4537.

REEVES, A., PEACHEY, N. S. & AUERBACH, E. (1986). Interocular sensitization to a rod-detected test. *Vision Research* **26**, 1119–1127.

SCHMEISSER, E. T. & DAWSON, W. W. (1982). Dichoptic interaction of harmonically related spatial and temporal frequencies. *Documenta Ophthalmologica* **53**, 37–50.

SHERRINGTON, C. S. (1904). On binocular flicker and the correlation of activity of "corresponding retinal points". *British Journal of Psychology* **1**, 26–60.

SINGER, W. (1977). Effects of monocular deprivation on excitatory and inhibitory pathways in cat striate cortex. *Experimental Brain Research* **134**, 568–572.

SMITH, D. C., SPEAR, D. & KRATZ, K. B. (1978). Role of visual experience in postcritical period reversal of effects of monocular deprivation in cat striate cortex. *Journal of Comparative Neurology* **178**, 313–328.

TAUB, E. & BERMAN, A. J. (1968). Movement and learning in the absence of sensory feedback. In *The Neuropsychology of Spatially Oriented Behavior*, ed. FREEMAN, S. J., pp. 305–333. Dorsey Press, Homewood, IL, USA.

TRICK, G. L., DAWSON, W. W. & COMPTON, J. R. (1982). Interocular luminance differences and the binocular pattern-reversal visual-evoked response. *Investigative Ophthalmology and Visual Science* **22**, 394–401.

TYLER, C. W., APKARIAN, P. & NAKAYAMA, K. (1978). Multiple spatial-frequency tuning of electrical responses from human visual cortex. *Experimental Brain Research* **33**, 535–550.

VAN SLUYTERS, R. C. (1978). Reversal of the physiological effects of brief periods of monocular deprivation in the kitten. *Journal of Physiology* **284**, 1–17.

VON HELMHOLTZ, H. (1909). *Handbuch der Physiologischen Optik*, 3rd edn. Leopold Voss, Hamburg.