

RESEARCH NOTE

ROD-CONE INTERACTION IN MONOCULAR BUT NOT BINOCULAR PATHWAYS

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(Received 1 May 1985; in revised form 24 July 1986)

Abstract—Photopic background stimulation elevates scotopic increment thresholds (rod-cone interaction) at moderate background levels when both test and concentric disk-background stimuli enter the same eye (monocular condition) but not when they enter different eyes (dichoptic condition). Only when background levels are made extremely high is there any measurable dichoptic interaction, and this interaction does not resemble that observed monocularly. Rod-cone interaction, as usually studied, is a property of monocular pathways in human vision.

Rod-cone interaction Binocular vision Monocular vision Dichoptic stimulation Increment thresholds Humans

Many studies have examined the spatial and temporal properties of rod-cone interaction, the change of scotopic incremental thresholds caused by photopic background stimulation (Buck *et al.*, 1979, 1984; Buck and Makous, 1981; Frumkes and Temme, 1977; Latch and Lennie, 1977; Lennie and MacLeod, 1973). Although the interacting signals originate in different receptors, the effect of cone signals on rod signals need not occur at the receptor, or even the retinal, level. These interactions have been studied extensively by means of monocularly presented stimuli (test and background stimuli to the same eye) but not by means of dichoptically presented stimuli (test and background stimuli to different eyes). At issue is whether rod-cone interactions are properties of monocular or binocular visual pathways.

Scotopic increment thresholds were measured with a 490-nm, 5' diameter, 20-msec duration test flash which was presented every 3 sec at 7° in the perifoveal retina. Scotopic detection of the test stimulus in all experimental conditions was assured because the experimental thresholds were safely below cone plateau thresholds measured during dark adaptation (see Buck and Makous, 1981, for further details). Photopic background stimulation was modulated over time by exchanging concentric 490 and 630-nm background fields every 1.5 sec. The relative illuminances of these alternating backgrounds

were chosen to be scotopically equal, thereby providing constant scotopic excitation over time. The 630-nm background, however, provided about 2.5 log units greater photopic stimulation than the 490-nm background. Scotopic matches were determined from absolute thresholds for detecting 1° diameter, 500-msec duration background presentations in the manner described in Buck *et al.* (1979, 1984). Absolute background illuminances were selected to be as high as possible for measurement of scotopic thresholds and were 0 (EP) or -0.3 (LS) log scot td in the monocular conditions and up to 2 log scot td in the dichoptic condition.

All observations were made by means of the binocular Maxwellian-view apparatus described in Pulos and Makous (1982). Backgrounds were always presented to the left eye. Test stimuli were presented either to the left eye (monocular conditions) or the right eye (dichoptic conditions). Two observers served in all conditions: observer EP was highly experienced but observer LS had no prior experience in setting dichoptic thresholds. Thresholds were estimated by means of a four-alternative forced-choice staircase procedure used by Pulos and Makous (1982) that estimated thresholds at about the 50% level, with chance performance at the 25% level. The indicated thresholds are the means of four replications, each of which is based on the mean of eight reversals of the staircase.

Initial tests indicated that backgrounds of less than 1° diameter could not be tested dichoptically because our observers could not keep them aligned with the test stimulus. One degree backgrounds produced greater monocular interaction than larger backgrounds, so they were selected for more detailed study.

When test and 1° -background stimuli were presented monocularly, 0.3–0.6 log unit of rod–cone interaction was observed as shown at the top of each panel of Fig. 1. That is, test thresholds were 0.6 (EP) or 0.3 (LS) log unit higher when measured at the midpoint of the 490-nm background interval (-0.75 sec) compared to those measured at the midpoint of the 630-nm background interval (0.75 sec). LS also showed an additional threshold elevation of 0.2 log unit at 0.1 sec, just after the transition to the 630-nm background. This magnitude of interaction is consistent with that usually obtained for these conditions (Buck *et al.*, 1979; Buck and Makous, 1981). These timing values were chosen because they have efficiently characterized transitory and maintained monocular interaction in past work (Buck *et al.*, 1984).

When these same test and background stimuli were presented dichoptically, there was no measurable elevation of test thresholds above the absolute threshold level (data not shown). Thus, the backgrounds that produced 0.3–0.6 log unit of monocular interaction produced no dichoptic rod–cone interaction. Indeed, they failed to produce any measurable elevation of test thresh-

olds in the dichoptic condition. No other background diameter up to 8° , the largest tested, produced any measurable dichoptic interaction.

We then raised the background illuminances to 2.0 log scot td, the maximum that our apparatus could produce while maintaining the scotopic match. Data for this condition are shown in the lower portion of Fig. 1. At this background level, dichoptic thresholds were raised no more than 0.3 log unit above absolute threshold, shown by the dashed line. The rod–cone interaction produced was small and idiosyncratic. LS showed 0.3 log unit of interaction between the midpoints of the background intervals, but in the opposite direction to that observed monocularly. EP showed no interaction between the midpoints and 0.15 log unit interaction in the usual direction 0.1 sec after the transition to the 630-nm background. These small threshold elevations may truly represent rod–cone interaction, but they are clearly different from the monocular interactions usually studied.

The results imply that the rod–cone interaction that has been studied monocularly with overlapping backgrounds is a property of monocular but not binocular pathways. The one previous test of the dichoptic properties of rod–cone interaction was conducted by Foster and Mason (1977) in the metacontrast paradigm, with large, brief, nonoverlapping test and background (mask) stimuli. They found dichoptic interactions of about 0.2 log unit at

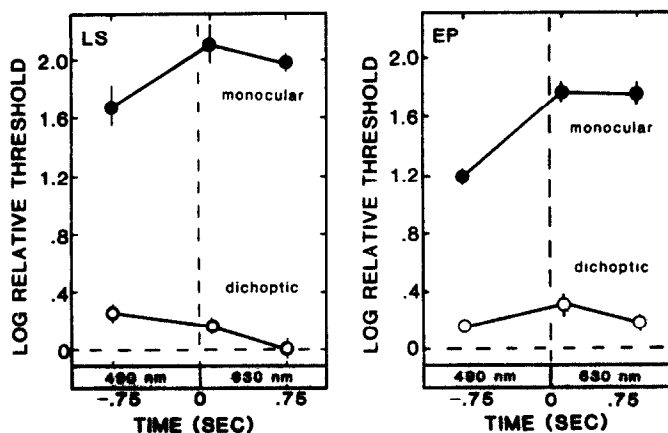


Fig. 1. Threshold elevations obtained in monocular (solid symbols) and dichoptic (open symbols) conditions for two observers. The dashed line at 0 on the ordinate indicates absolute threshold for detection of the test stimulus alone. Rod–cone interaction is shown by differential elevation of threshold on scotopically matched 490 and 630-nm backgrounds exchanged over time (abscissa). The interaction shown here for the monocular condition is absent in the dichoptic condition (data not shown) at the moderate background levels typically used for monocular testing. The small threshold elevations and interaction shown here for the dichoptic condition were obtained at background levels about 2 log units higher. Error bars represent ± 1 SE of the mean of 4 sessions and are smaller than the symbol size if not shown.

50 msec and again at 350 msec after presentation of a 10-msec mask. This type of interaction appears to be fundamentally different from that reported here. The meta-contrast interaction has been studied too little to determine the reason for the differences but candidates include the much larger test field, the very brief (10-msec) duration of the mask, and the nonoverlapping mask and test fields.

Most observers including the present ones, show somewhat more monocular interaction on 0.4–0.6° backgrounds than on 1° backgrounds. Nevertheless the magnitude of monocular interaction obtained here on 1° backgrounds (up to 0.6 log unit) is substantial. Thus, the tendency for smaller backgrounds to produce more interaction is unlikely to explain our failure to find dichoptic interaction.

These observations were not designed to compare rigorously rod–cone interactions with isolated scotopic or photopic vision. However, a general observation can be made. In isolated scotopic or photopic vision, dichoptic background presentation influences threshold more at background onset (transient conditions) than under steady-state conditions (e.g. Boynton, 1961; Battersby *et al.*, 1964; Markoff and Sturr, 1971; Fiorentini *et al.*, 1972; Sturr and Teller, 1973). For rod–cone interaction, we find no threshold elevation nor spatial sensitization for dichoptic presentation, although both are found with monoptic presentation (Buck *et al.*, 1984). However, we have not tested the dichoptic properties of the isolated scotopic and photopic systems by means of the present stimuli.

The present results do help to disentangle competing explanations for the findings by Sturr and Teller (1973) of large, transient spatial sensitization under dichoptic conditions. Their stimulus conditions, which were generally comparable to ours, allow their result to be explained by purely scotopic processing, by rod–cone interactions, or by both. The present failure to find transient spatial sensitization attributable to rod–cone interaction supports the explanation of dichoptic transient spatial sensitization in terms of purely scotopic processing.

The finding that the present type of rod–cone interaction is a property of monocular pathways does little to constrain the possible loci of interacting signals. There may be multiple sites of interaction and one or all may still be central to the retina. However, a variety of psychophysical results (e.g. Buck, 1981, 1985; Bauer *et al.*, 1983a,b) and at least one physiological study

in humans (Sandburg *et al.*, 1981) suggest that important spatial and temporal properties of the interactions are determined early in the visual pathways, presumably in the retina. Certainly, physiological and anatomical studies in other species have identified a variety of retinal interactions between signals originating in rods and cones (e.g. Nelson, 1977; Raviola, 1976; Gouras and Link, 1966; Whitten and Brown, 1973; Hood, 1972). Nevertheless, definitive identification of the locus or loci of rod–cone interactions in humans awaits further investigation.

Acknowledgements—This research was supported by PHS grant EY03221 awarded to S. Buck. We thank D. Leo Stefurak for serving as an observer and Angela Brown and Roger Knight for comments on the manuscript.

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