# Binocular Rivalry with Isoluminant Stimuli Visible only via Short-wavelength-sensitive Cones*

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To test whether the binocular contour rivalry mechanism is tritanopic, we presented isoluminant, rival stimuli visible only via the short-wavelength-sensitive (S) cones. We stimulated only the S cones with violet gratings superimposed on a bright yellow field that adapted the responses of the middle- and long-wavelength-sensitive (M and L) cones. We found that an S-cone grating presented to one eye rivalled with an orthogonal grating presented to the other. Rivalry persisted over a range of luminances and contrasts of the S-cone stimuli, and was greater than could be accounted for by nonrival fading. The spatial spread of rivalry from S-cone stimuli is similar to that for the same stimuli when visible also to the M and L cones (luminance stimuli). We found that an S-cone stimulus would rival with a luminance stimulus, and exploited this to determine the equivalent luminance contrast of S-cone stimuli by putting them in a rivalry competition with luminance stimuli. For rivalry, the equivalent luminance contrast of isoluminant, S-cone stimuli is much less than their S-cone contrast. The existence of rivalry with isoluminant stimuli, along with earlier evidence that such stimuli can support stereopsis, challenges the view that an achromatic channel alone drives certain higher level functions such as depth perception. Copyright © 1996 Elsevier Science Ltd.

Binocular rivalry    S cones    Isoluminance    Spatial spread    Contrast    Equivalent luminance contrast

## INTRODUCTION

Binocular contour rivalry occurs when two different stimuli, for example orthogonal gratings, are presented one to each eye.§ Instead of the two gratings combining into a stable grid, first one, then the other grating is visible; this alternation continues for as long as one cares to look (e.g. Breese, 1899). Various models of rivalry have been proposed (e.g. Blake, 1989; Fox & Check, 1972; Lehky, 1988). Here we examine whether the mechanisms mediating binocular rivalry are tritanopic, that is, lack input from the short-wavelength-sensitive (S) cones. Reason to suppose this comes from two lines of evidence: one showing that blue stimuli only weakly initiate rivalry, the other showing that rivalry dispropor-

tionately affects the detection of blue stimuli presented to a suppressed eye.

Hollins and Leung (1978) measured rivalry between orthogonal, 6 c/deg, square-wave gratings illuminated by light of different, narrow bands of wavelengths. They found little rivalry when both gratings were 451 nm (blue). Moreover, they found no more rivalry when the gratings differed in colours that a tritanope would confuse. From these data, they suggested that S cones do not contribute to binocular rivalry.

Rogers and Hollins (1982) assessed the effects of differences in colour on rivalry between dichoptic orthogonal 3 c/deg square-wave gratings. In trichromats, they found that the larger the difference in the colour of the stimuli, the greater the rivalry. In red–green dichromats, however, Rogers and Hollins found no such effect, suggesting that such dichromats are essentially monochromats for rivalry. They concluded from this that S cones do not participate in rivalry.

Smith *et al.* (1982) and Ooi and Loop (1994) studied the effects of rivalry suppression on blue stimuli. Smith *et al.* produced binocular rivalry with dichoptically viewed, orthogonal gratings, and superimposed a small test flash on the grating in one eye to measure thresholds as a function of wavelength. These spectral sensitivity functions were distinctly different when the grating with the

superimposed test flash was visible, or *dominant*, in rivalry, from when that field was invisible, or *suppressed*, by rivalry. The spectral sensitivity function for rivalry dominance had three peaks reflecting the influence of opponent colour mechanisms. However, the spectral sensitivity function for rivalry suppression was unimodal, showing no evidence of the three peaks associated with opponent colour processing. Most relevant here was that the peak corresponding to the S cones had disappeared. Using a similar probe technique, Ooi and Loop (1994) confirmed that rivalry suppression effects are disproportionately large for blue stimuli.*

While the above studies suggest that S-cone signals are not nearly as effective as M- and L-cone, luminance signals in either initiating rivalry or in breaking rivalry suppression, they do not directly test whether S-cone signals alone are capable of initiating rivalry. The experiments described here are designed to do so.

To stimulate only the S cones we used gratings containing wavelengths <450 nm, superimposed on an intense, yellow field. The adapting field rendered the M and L cones insensitive to the violet gratings we used. As we will show later, our S-cone stimuli had negligible luminance contrast for the M and L cones, so they were essentially isoluminant. Isoluminant stimuli are supposed to be invisible to high-resolution pathways in the visual system processing luminance, and visible only via low-resolution chromatic pathways (e.g. Hurvich & Jameson, 1957; Boynton, 1979). Consequently, these stimuli allow us to ask whether the rivalry mechanism can be driven by chromatic contrast alone. Our technique is similar to that used by Grinberg and Williams (1985) and Wilson *et al.* (1988) when they studied other major components of binocular vision with S-cone input: stereopsis and fusion.

Grinberg and Williams (1985) showed that binocular fusion and perception of stereoscopic depth are possible with S-cone input. Consistent with the low spatial resolution of the S-cone input (e.g. Green, 1968), they found that the minimum disparity allowing crossed disparities to be discriminated from uncrossed disparities is about 40 sec arc, at least eight times larger than stereoacuity for luminance stimuli (i.e. stimuli visible also via the M and L cones). Grinberg and Williams also showed that perception of depth in random-dot stereograms is possible with only S-cone input, providing the dot size and disparity were large enough (20 min) so as not to defeat the low resolution afforded by the S cones.

Wilson *et al.* (1988) explored the limits of binocular fusion with S-cone input. Consistent with the low resolution of the chromatic system, they found it

impossible to measure fusion limits with fine stimuli (such stimuli were invisible). With coarse stimuli, however, the fusion limit from S-cone stimuli was similar to that from luminance stimuli. From that and other evidence on disparity scaling, Wilson *et al.* concluded that S-cone input had access to low but not high spatial frequency mechanisms for processing fusion.

Given that fusion and stereopsis are possible with S-cone stimuli, and given that stereopsis and rivalry are thought to be related (e.g. Blake, 1989; Livingstone & Hubel, 1987; O'Shea & Crassini, 1984; Shimojo & Nakayama, 1990), it would be surprising were binocular rivalry not to occur. Indeed Blake (personal communication) noticed rivalry during the above experiment. We wanted to confirm Blake's observation, and to study rivalry more systematically (Experiments 1 and 2).

## EXPERIMENT 1: S-CONE RIVALRY AS A FUNCTION OF LUMINANCE–CONTRAST

We decided to measure rivalry of S-cone gratings varying over a wide range of visibilities. This is important for three reasons: first, it allows us to test whether S-cone rivalry is occurring within chromatic pathways. Whereas recent evidence suggests that S cones can have a small influence on luminance processing (e.g. Boynton *et al.*, 1985; Drum, 1983; Kaiser & Boynton, 1985), this occurs only close to S-cone detection threshold (Stockman *et al.*, 1991). If S-cone rivalry persists over a wide range of visibilities, it will confirm the involvement of chromatic mechanisms. Second, if S-cone rivalry does so persist, we can compare its relationship to visibility with that for similar variations of luminance stimuli. Third, we can choose an optimal value for our later experiments.

### Method

*Subjects.* There were two subjects, one of us (ROS), and another (OP) who volunteered for the experiment and was naive to its purposes. Each had at least 6/6 Snellen acuity in each eye (ROS needing correction for myopia), good stereoacuity and normal colour vision.

*Apparatus.* A schematic diagram of the apparatus is given in Fig. 1. Pairs of orthogonal sine-wave gratings were printed onto sheets of mylar drafting film and positioned on sheets of clear plexiglass. Subjects viewed the pairs of gratings through prisms that allowed one grating of each pair to be seen by the left eye and the other to be seen by the right eye with normal vergence and accommodation at 57 cm. The spatial frequency of the gratings was 2 c/deg, for optimum visibility via the S cones (Green, 1968). Gratings were masked by circular field stops with a diameter of 4 deg of visual angle.

We rear-illuminated the gratings with a Kodak Carousel projector containing Kodak Wratten filters 35 and 47, which produced violet light with less than about 4% transmittance of incident, visible light above 450 nm. Each grating was viewed with light reflected from a dichroic mirror (Oriel, part No. 66238) oriented at 45 deg to the optical axis. At this angle, these mirrors reflect 95% of the light between 350 and 450 nm and, in combination

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*Although these results suggest that rivalry suppression is particularly effective for S-cone stimuli, the authors of both studies agree that the mechanism is less direct, involving chromatic mechanisms, to which S cones exclusively project. Indeed, the same could be said for the weak ability of blue stimuli to initiate rivalry: this may occur via chromatic mechanisms that input only weakly (if at all) to the rivalry mechanism. We do not, however, want to emphasize this explanation, for, as we shall see, chromatic input can support rivalry.
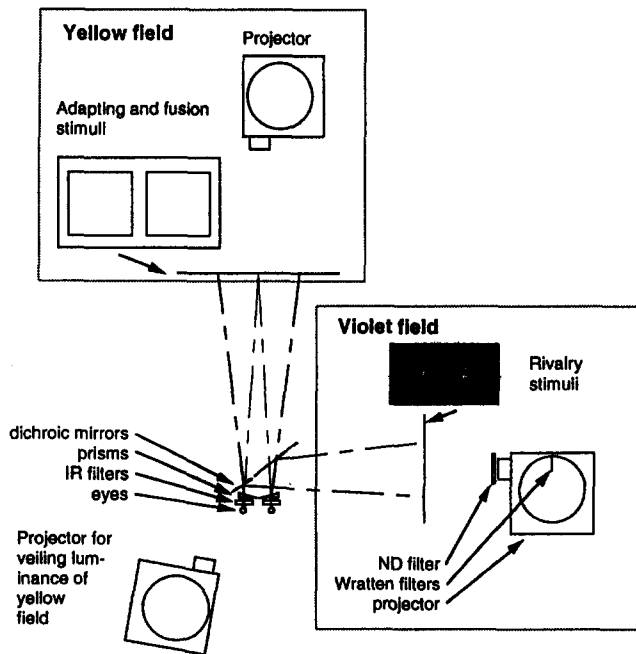
FIGURE 1. Schematic diagram of the apparatus. Dimensions of the apparatus and the stimuli are not to scale.

with the Wratten filters, reduced the light at wavelengths above 450 nm by more than a factor of 250.

The yellow background for isolating the S cones was a translucent card that could be rear- and front-illuminated by Kodak Carousel projectors. It was viewed with light transmitted through the dichroic filters. The filters transmit 85% of the light between 550 and 1000 nm, but almost no light <500 nm, creating a bright yellow field. The yellow field contained dark square borders designed to assist binocular alignment of the left-eye and right-eye fields. These squares had an internal side of 10.1 deg, and a line width of 0.35 deg. Contrast was 0.86. The yellow field was positioned in front of the eyes at 57 cm viewing distance.

The gratings were positioned at a distance of 36.5 cm to correct for the approx. 1 dioptre of longitudinal chromatic aberration for violet light with our experimental conditions (Brainard & Williams, 1993).

Luminances were measured through the observer's eyepiece with a Minolta Chromameter. The yellow field was set at a maximum luminance of 1070 cd/m$^2$. The violet field could take one of seven luminances shown in Table 1. The luminance contrast of the S-cone gratings, measured by themselves, was 0.79. We are confident that the violet gratings could be seen only via the S cones because their luminance contrast in the presence of the

yellow field was only about 0.002 at its highest value, which is less than the luminance–contrast threshold even under optimal conditions.

To calculate the contrast of our stimuli for the S cones, we used a Photo Research Spectracolorimeter (Chatsworth, CA model PR-650) to measure the spectral radiance of the gratings and of the background at 5 nm intervals from 380 to 780 nm. We then computed the integral of the product of the spectral radiances and the S-cone spectral sensitivity (Smith & Pokorny, 1975) to estimate the S-cone effectiveness of the gratings and the background. From this we calculated the Michelson contrasts of the combined grating and background for the S cones. These are listed in Table 1. We will refer to such contrasts as S-cone contrasts. S-cone contrast increases with luminance of the violet field because more effective light is being delivered to the S cones. The increase in contrast with luminance saturates, however, being proportional to the logarithm of luminance plus a constant (S-cone contrast = 0.4 log(luminance) + 0.41).

*Procedure.* Trials of at least 1 min duration began when the subject pressed a key to signal the first episode of exclusive visibility. Subjects depressed one response button with the left index finger to signal exclusive visibility of vertical, and another button with their right index finger to signal exclusive visibility of horizontal. They pressed neither button if a composite of the two gratings was visible, or if both gratings became invisible. If a button were depressed when the trial duration reached 60 sec, the trial concluded when the subject released the button, that is, when that particular period of exclusive visibility terminated. Otherwise, the trial finished after 60 sec.

Our procedure gives three measures of rivalry. Rivalry *rate* is the number of episodes of rivalry dominance per minute (i.e. the number of times one and the other button is pressed during 1 min). Cumulative *exclusive visibility* is the amount of time that one and the other rival stimulus were exclusively visible (i.e. the total time that the buttons are held down during 1 min). Rivalry *period* is the average time for episodes of exclusive visibility (i.e. cumulative exclusive visibility for each eye divided by rivalry rate for the respective eye and then averaged over the two eyes).

Trials were separated by at least 1 min. Trials were run in blocks of 14, in which each luminance was tested twice in a random order. Orientation of the grating viewed by the left eye was alternated over trials; the right eye always viewed an orthogonally oriented grating. Testing continued over three sessions, with at least 24 hr between sessions.

TABLE 1. Photometric luminances (in cd/m$^2$) and S-cone contrasts for S-cone stimuli

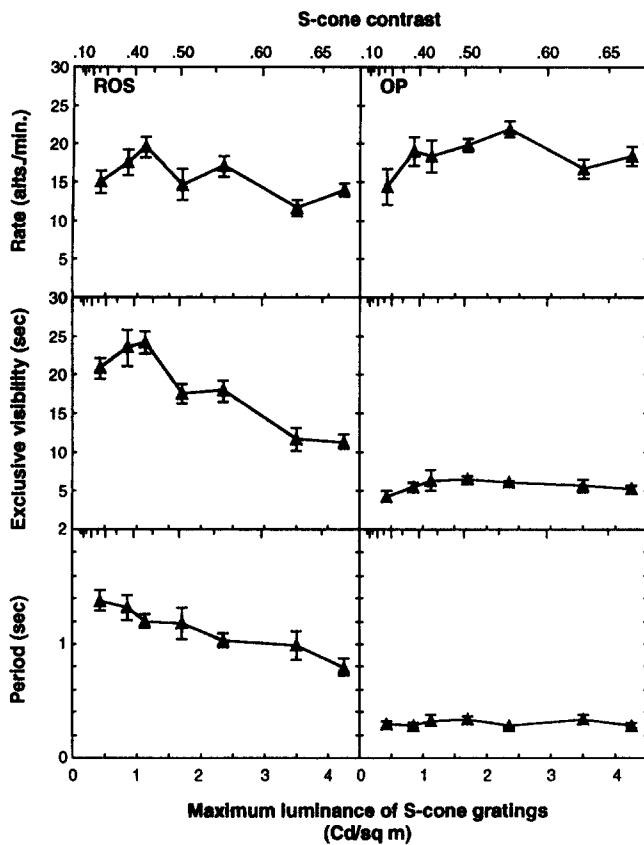| | Experiment 1 | | | | | | | Experiment 2 |
|---|---|---|---|---|---|---|---|---|
| Photometric luminance | 0.42 | 0.85 | 1.13 | 1.69 | 2.35 | 3.50 | 4.26 | 1.37 |
| S-cone contrast | 0.25 | 0.38 | 0.44 | 0.51 | 0.57 | 0.63 | 0.65 | 0.47 |

FIGURE 2. Rivalry rate, cumulative exclusive visibility and period plotted as a function of contrast and luminance of S-cone rivalry stimuli for ROS and OP. Each point is the mean of 12 observations (2 eyes × 2 eye-orientations × 3 sessions). Error bars show 1 SEM.

## Results and discussion

Both subjects experienced binocular rivalry. One of us (ROS) has had considerable experience in viewing rivalry; he found it to be qualitatively similar to rivalry from luminance stimuli, although with briefer periods and more instances of composites than with luminance stimuli.* Quantitative results for ROS and OP are graphed in Fig. 2, as a function of luminance and S-cone contrast of the gratings. For both subjects, the rivalry, indexed by all three measures, is significantly greater than zero; for ROS, all $t$s (6) > 9.26, all $P$s < .0001; for OP, all $t$s > 19.74, all $P$s < .0001. That is, rivalry endures over more than a 10-fold range of luminances and more than a 2.5-fold range of contrasts of S-cone stimuli. This suggests that rivalry is occurring

*We make a direct contrast between S-cone rivalry and luminance rivalry in Experiment 2.

†ROS also showed significant linear declines for rate and cumulative visibility with increasing S-cone luminance and contrast, $F$s = 5.03, 50.35, both $P$s < 0.05.

‡When we were pilot testing this experiment, we erroneously put enough light through the violet field to stimulate the M- and L-cones. There was a qualitative change in the appearance of the violet gratings such that they abruptly appeared nearer, in much more detail and with much greater apparent contrast. The highest luminance we used in the experiment approached this value we used during piloting by about 0.2 log units.

within the chromatic pathways and not because S cones can input to the luminance pathway over a small range of visibilities near threshold (Stockman et al., 1991).

Both rivalry rate and exclusive visibility tend to show inverted U-shaped functions of luminance and contrast for both ROS and OP. Although ROS's quadratic trend for rate fell short of conventional significance, $F(1,35) = 2.03$ $P < 0.2$, the same trend for exclusive visibility was clear: $F = 4.84$ $P < 0.05$.†

For OP there were significant quadratic trends for rate and exclusive visibility, $F(1,35) = 6.07$ and 4.58 respectively, $P$s < 0.05. In this respect, S-cone rivalry is similar to rivalry of photopic luminance stimuli (Hollins, 1980; O'Shea et al., 1994).

Rivalry periods decline as luminance and contrast increase for ROS, $F = 24.41$, $P < 0.01$, again similar to luminance rivalry (Hollins, 1980; O'Shea et al., 1994), whereas there is no systematic relationship for OP. At lower luminances than those tested, the S-cone grating does approach detection threshold. At higher luminances, we run the risk of exceeding threshold for the L and M cones. The slight upturn in the rate for both subjects at the maximum luminance may be evidence of the influence of M and L cones.‡

It would seem that S-cone stimuli can engage in binocular rivalry similar to that from photopic luminance stimuli. Peak rivalry occurs around an S-cone contrast of about 0.47 (we use this value in Experiment 2). However, we have to rule out other explanations for the alternate disappearances of our rival stimuli. There are phenomena, other than rivalry, in which suprathreshold, monocular stimuli alternately disappear and reappear [e.g. fading of stabilized retinal images; Riggs, Ratliff, Cornsweet & Cornsweet (1953) and fading of nonstabilized peripheral stimuli, Troxler's fading; Wade & Wenderoth (1978)]. Such monocular fading could simulate binocular rivalry. We shall refer to such fading as nonrival fading.

### Is S-cone binocular rivalry caused by nonrival fading?

We have used the term nonrival fading to distinguish it from rivalry, and to encompass any sort of fading mechanism other than rivalry; we are agnostic about the mechanism of such nonrival fading. S-cone stimuli are supposed to fade often (see Williams et al., 1981), so such fading could simulate rivalry. What distinguishes rivalry from nonrival fading is that nonrival fading in one eye would be independent of the sort of stimulus viewed by the other, whereas dependence on the stimulus viewed by the other eye is a hallmark of rivalry (Levelt, 1968).

To obtain estimates of the amount of nonrival fading, we asked both subjects to view an S-cone grating (S-cone contrast of 0.47) with the left eye, while the right eye viewed a uniform field showing violet light of 1.37 cd/m². Subjects pressed the left-hand button whenever contours could be seen over the whole field, using the same criterion as for Experiment 1. If the contours became invisible over the whole field, the right-hand
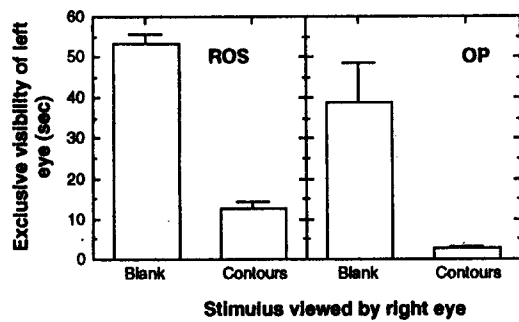
FIGURE 3. Cumulative exclusive visibility resulting from pairing an S-cone grating to the left eye with a blank field to the right eye (blank: leftmost bars) and with a rival grating (contours: rightmost bars). Error markers show SEMs based on four observations for the blank condition, and 12 observations for the contours condition.

button was to be pressed. Neither button was to be pressed if contours faded only partially.

Cumulative time of visibility of contours from the above control condition is plotted in Fig. 3. The left panel shows ROS's results and the right shows OP's. Also plotted are the cumulative times of exclusive visibility for the left eye of each subject from the similar conditions in Experiment 1, in which the right eye viewed rival contours. It is quite clear that exclusive visibility in nonrival conditions is much greater than in rival conditions. The slight nonrival fading that reduced the exclusive visibility from the maximum (60 s) cannot account for all of the disappearances of the same stimulus under rival conditions. We can safely conclude that any nonrival fading has a minimal role in producing exclusive visibility during rivalry of S-cone stimuli.*

The results of Experiment 1 show that S-cone input can support rivalry. We can, therefore, add rivalry to the other major binocular phenomena supported by S-cone input: stereopsis (Grinberg & Williams, 1985) and fusion (Wilson et al., 1988).

## EXPERIMENT 2: SPATIAL SPREAD OF S-CONE RIVALRY

### Spatiotemporal resolution allowed by S-cone input

Studies of the spatial contrast sensitivity of the S-cone system suggest that it is essentially low pass and falls off more quickly with spatial frequency than that for luminance gratings, reaching an acuity of about 10

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*This control condition was rather more extensive than we have described it. We counterbalanced orientation and which eye viewed the contours. We also used a second 'nonrival' condition, in which the eye not viewing contours was presented with a gray patch of the same space-averaged luminance as the grating. For all of these conditions the conclusions were the same: nonrival fading was far less than needed to account for the fading from rivalry in Experiment 1. We also measured nonrival fading for two types of luminance gratings, one of 0.31 contrast and another of 0.10 contrast. Surprisingly, the amount of nonrival fading with the low-contrast luminance grating was similar to that from the S-cone grating.

c/deg instead of 60 (e.g. Green, 1968; Sekiguchi et al., 1993). Similarly, the temporal modulation sensitivity for S-cone stimuli has a lower critical flicker fusion limit of about 20 c/sec or less instead of 60 or more (Green, 1969; Wisowaty & Boynton, 1980).

### Rivalry with other low-resolution subsystems

O'Shea et al. (1994) found that the area over which rivalry will spread when input is restricted to the low-spatiotemporal-resolution rod system is much greater than when all cones are stimulated too. Moreover, Blake et al. (1992) found that rivalry would spread over larger areas when the stimuli were presented to the lower-resolution periphery than to the high-resolution fovea. Blake et al. have modelled photopic rivalry as involving a cooperative process between local cortical regions whose retinal areas are inversely proportional to their resolutions (operationalized as the cortical magnification factor). As the S cones are a low-resolution system, one might predict that rivalry via S cones should spread over larger areas than via the achromatic subsystem. We wanted to test this idea (Experiment 2).

To assess the spread of rivalry, it is necessary to measure rivalry over a range of areas of rival stimuli. With luminance stimuli, rival gratings of small area, say 0.5 deg in diameter, alternate crisply and completely. As the gratings are increased in area, there is an increase in the duration of perception of composites of the two eyes' views (Breese, 1899). With relatively large rival targets, for example, 10 deg diameter, composites are seen often; exclusive visibility is therefore substantially reduced. As the size of rival stimuli increases, all three measures of rivalry—rate, exclusive visibility, and period—typically decrease (Breese, 1899). With low-resolution subsystems, the decrease in the three rivalry measures with increasing diameter is less than for central photopic vision, showing that rivalry will spread over larger areas in such subsystems. In other words, if spatial spread of rivalry is greater with S-cone than with luminance stimuli, we can predict that the slope of the function relating rivalry to stimulus diameter will differ for S-cone and luminance stimuli.

### Method

The subjects and apparatus were similar to those of Experiment 1. The S-cone contrast of the gratings was 0.47. We also made measurements of rivalry with two luminance stimuli, visible to the achromatic subsystem. These were produced by placing transparencies of orthogonal gratings in the yellow field and turning off the violet field. There were two such gratings: a high-contrast grating (contrast of 0.31), and a low-contrast grating (contrast of 0.10), produced by projecting a veiling luminance. These stimuli will be referred to as the *luminance high-contrast gratings* and the *luminance low-contrast gratings*. For all three sorts of gratings, field sizes could be 2, 4, 6, 8, or 10 deg of visual angle in diameter. There were two eye-orientation arrangements: vertical to the left eye and horizontal to the right (VH)
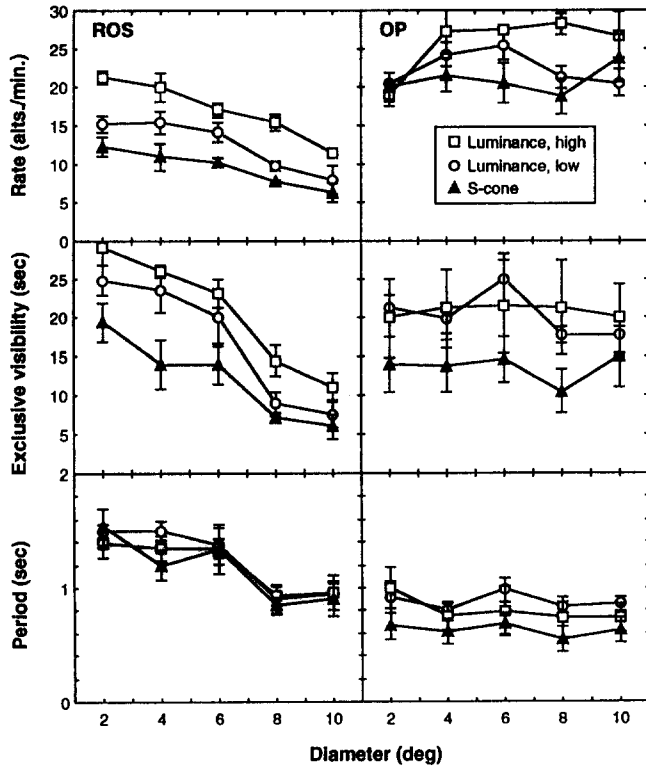
FIGURE 4. Rivalry rate, cumulative exclusive visibility and period plotted as a function of diameter of the rivalry stimuli for ROS and OP. Each point is the mean of eight observations (2 eyes × 2 eye-orientations × 2 sessions). Error bars show 1 SEM.

and the opposite (HV). Testing continued until there were two observations for each of the conditions formed by the full factorial combination of the above factors.

## Results and discussion

The experimental design was analyzed separately for each subject using analyses of variance with sessions as replicates. We have plotted mean rivalry rates, exclusive visibilities and periods in Fig. 4.

For ROS, all three measures of rivalry declined as stimulus diameter increased. Linear trend analyses for the high-contrast luminance stimuli found $F(1,15) = 46.23$, 66.28, 12.76 for rate, exclusive visibility and period respectively, all $Ps < 0.01$. For the low-contrast luminance stimuli, the $F$s were 23.83, 41.76, 12.76 respectively; and for the S-cone stimuli the $F$s were 23.83, 22.80, 11.54 respectively, all $Ps < 0.01$. This decline in rivalry measures with increasing stimulus diameter shows the classic pattern (e.g. Breese, 1899) in which

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*We do not know why OP did not show the classical pattern of a decline in rivalry rate and time with increasing stimulus diameter. One possibility, suggested by Blake (personal communication) is that OP's criterion for reporting exclusive visibility involved only a small area of the stimulus field (say between 2 and 4 deg in diameter) and hence was uninfluenced by larger increases in the actual field size.

dominance by one or the other rival stimuli is supplanted by increasing incidence of composites.

There was also a difference between the two luminance gratings for ROS: at each field size, the high-contrast pair showed greater rate and exclusive visibility than the low-contrast pair. The main effect of contrast between the two sorts of luminance stimuli was significant for rate and exclusive visibility, but not for period, $F(1,20) = 40.50$, 5.93 ($Ps < 0.05$), and 0.50, respectively. This also is consistent with previous research (e.g. Hollins, 1980).

S-cone gratings rivalled less often and for less time at all field diameters than luminance gratings. For example, when the low-contrast stimuli were compared with the S-cone stimuli, $F(1,20) = 15.44$, 9.77 ($Ps < 0.05$), and 0.81 for rate, exclusive visibility, and period respectively.

Critically, there were no significant differences in the slopes of the functions among the S-cone and luminance gratings for any of the three measures of rivalry for ROS. The slopes were derived by linear regression on diameter. For rate, the slopes were $-1.20$, $-1.01$, and $-0.76$ for high-contrast luminance stimuli, low-contrast luminance stimuli, and S-cone stimuli, respectively. The slope for high-contrast luminance stimuli was compared with that for S-cone stimuli using the $z$ test based on Fisher's $r$ to Z transformation [see Glass & Hopkins (1984) pp. 304–309]. It yielded $z = 1.12$, $P = 0.26$. For exclusive visibility, the respective slopes were $-2.40$, $-2.46$, and $-1.68$ for a $z = 1.24$, $P = 0.22$. For period, the respective slopes were $-0.03$, $-0.05$, and $-0.03$ for a $z = 0.03$, $P = 0.94$.

OP had generally more variable data, yet the functions relating rivalry to diameter were similar for the three lighting conditions. Over field diameter, OP showed little change in any measure, except for a slight increase from 2 to 4 deg for rivalry rate. For the difference between 2 and 4 deg diameter stimuli, $F(1,12) = 5.86$ ($P < 0.05$), 0.00, 1.24 for rate, exclusive visibility and period, respectively.* The effect of contrast on rivalry of luminance gratings was also more muted for OP, being significant only for the rate measure. The main effect of contrast between the two sorts of luminance stimuli was significant for rate but not for exclusive visibility or period, $F(1,20) = 6.73$ ($P < 0.05$), 0.03, and 0.83, respectively.

The S-cone stimulus alternated less frequently and for less time than the luminance stimuli. Moreover the periods of dominance of the S-cone stimulus were consistently briefer than for the luminance stimuli. For example, when the low-contrast stimuli were compared with the S-cone stimuli, $F(1,20) = 1.01$ ($P > 0.05$), 10.37, and 13.39 ($Ps < 0.01$) for rate, exclusive visibility, and period, respectively.

As OP showed essentially flat functions of all three rivalry measures against diameter, it is evident that, similar to ROS's results, slopes were similar for the S-cone, and for the two luminance, gratings.

In conclusion, the results of Experiment 2 provide no evidence that spatial spread of rivalry with S-cone stimuli is greater than for luminance stimuli. Rivalry measures

with S-cone stimuli were less at all diameters than for luminance stimuli. We suspect that this is because the S-cone stimuli had lower effective contrast than the luminance gratings. As contrast of luminance stimuli decreases, so does rivalry (Hollins, 1980; Liu *et al.*, 1992). We attempt to assess effective contrast of our S-cone stimuli next.

## EXPERIMENT 3: EQUIVALENT LUMINANCE CONTRAST OF S-CONE RIVALRY STIMULI

Although we have computed S-cone contrast of our isoluminant stimuli, we do not know how effective this contrast is for the rivalry mechanism. We can define effective contrast as contrast equal to that from similar luminance stimuli. Cavanagh and Anstis (1991) call this "equivalent luminance contrast" (p. 2109). Agonie and Gorea (1993) have reviewed various techniques by which luminance and chromatic stimuli can be compared directly. These usually pit a luminance stimulus against a chromatic stimulus in some task, such as using a luminance stimulus to mask a chromatic stimulus (e.g. De Valois & Switkes, 1983), using luminance flicker to mask chromatic flicker (e.g. Stromeyer, Cole & Kronauer, 1990), or using a moving luminance stimulus to null the apparent movement of an oppositely moving chromatic stimulus (e.g. Cavanagh & Anstis, 1991). In the case of movement, for example, the equivalent luminance contrast of a moving chromatic stimulus is defined as equal to the luminance contrast of the nulling luminance stimulus. We propose to add rivalry to the techniques by which equivalent luminance contrast of chromatic stimuli can be estimated by pitting an isoluminant, S-cone stimulus against a luminance stimulus in a rivalry 'competition'.

As far as we can ascertain, Hollins and Leung (1978) originated the idea of varying the "strength" of one stimulus in rivalry to find perceptual equivalence with another (luminance) stimulus that differed in chromaticity. The first to apply this technique to isoluminant stimuli was Flanagan (1991), who studied *monocular* rivalry. Rivalry has the advantage over the other techniques reviewed by Agonie and Gorea (1993), of allowing estimation of equivalent luminance contrast of stationary, suprathreshold, stimuli.

When rival luminance stimuli are of very different contrasts, the higher-contrast stimulus has more episodes of dominance, is exclusively visible for more of a trial, and its period is longer, than the lower-contrast stimulus (e.g. Levelt, 1968). As one stimulus is altered to be more similar in contrast to the other, the differences in these three aspects of rivalry diminish, until when the two stimuli are equal in contrast, the three measures are equal for the two stimuli.

We propose to estimate the equivalent luminance contrast of the S-cone stimuli for rivalry by adjusting its

contrast while in rivalry with a luminance stimulus of known contrast. When we find an S-cone contrast at which the two stimuli are equally dominant in rivalry, the equivalent luminance contrast of the S-cone stimulus should be equal to that of the luminance stimulus, at least as far as rivalry is concerned.

Our method of varying the contrast of our S-cone stimuli, by varying the luminance of the stimuli as we did in Experiment 1, raises the problem of whether contrast or luminance is the critical variable in attaining equality of rivalry between an S-cone and luminance stimulus. We prefer to think contrast is critical for two reasons. First, although the fields containing the S-cone grating and the luminance grating differ in luminance, the difference is very small, <0.4% for the largest difference. Second, for rivalry with luminance stimuli, contrast is a much more important component of stimulus strength than luminance (Whittle, 1965). To determine whether contrast or luminance is critical, however, we decided to use two luminance gratings having contrasts of 0.31 and 0.10 but equal in luminance. If luminance is critical, the same S-cone contrast would be required to attain equality in rivalry with the higher-contrast luminance grating as with the lower-contrast luminance grating. If however, contrast is critical, a higher S-cone contrast would be required to attain equality in rivalry with the higher-contrast luminance grating than with the lower-contrast luminance grating.

### Method

The subjects and apparatus were similar to those of Experiment 1, except that an S-cone grating was visible to one eye,* and an orthogonal, luminance grating visible to the other. Field size was fixed at 4 deg diameter. S-cone contrast of the S-cone gratings was varied over the same range as used in Experiment 1 by varying the luminance of the S-cone gratings. Contrast of the luminance grating was either 0.31 or 0.10. Four sessions were run.

In one session, one eye always received the S-cone stimulus and the other eye received the luminance stimulus. This eye-colour arrangement (i.e. violet to the left eye and yellow to the right eye, VY and YV) was alternated over sessions. Within sessions, there were four blocks of trials, made up of the factorial combination of eye-orientation (i.e. VH and HV) and contrast of the luminance grating. Blocks were presented in a random order over sessions. Within blocks, the seven contrasts of the S-cone grating were also presented in random order.

### Results and discussion

Results are presented separately for the competition between S-cone stimuli and low- and high-contrast luminance stimuli, in Figs 5 and 6, respectively. The first thing to note, and this is critical for our aims, is that an S-cone, isoluminant grating will indeed rival with a luminance grating.

For both subjects, an S-cone contrast can be found at which the S-cone grating will be equal in rivalry

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*A small amount of unpatterned violet light would have also fallen on the field containing the luminance grating.
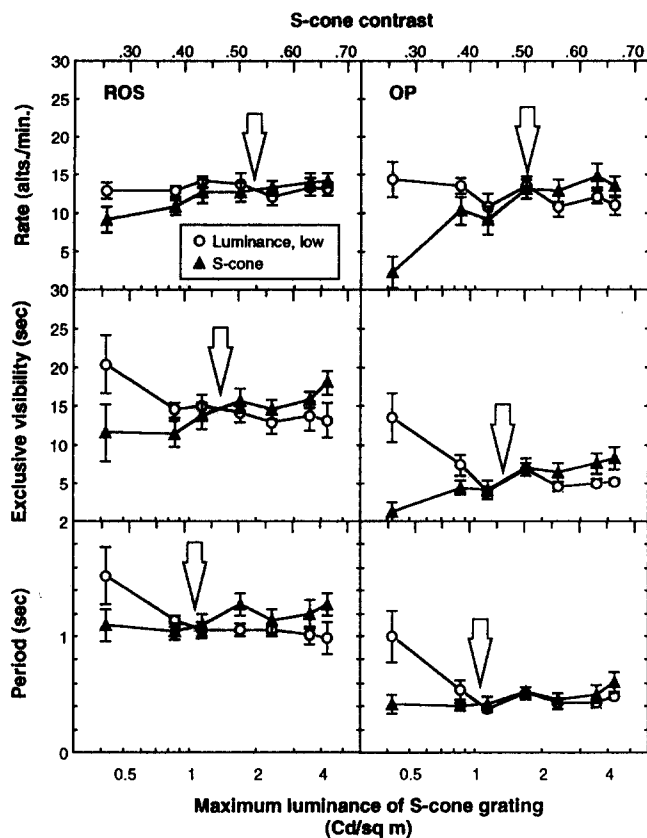
FIGURE 5. Rivalry rate, cumulative exclusive visibility and period for rivalry between an S-cone stimulus and a low-contrast luminance stimulus. Data have been plotted as a function of contrast and luminance of S-cone rivalry stimuli for ROS and OP. Each point is the mean of eight observations (2 eye-orientations × 4 sessions). Error bars show 1 SEM. Points at which the functions for S-cone and luminance stimuli cross are arrowed.
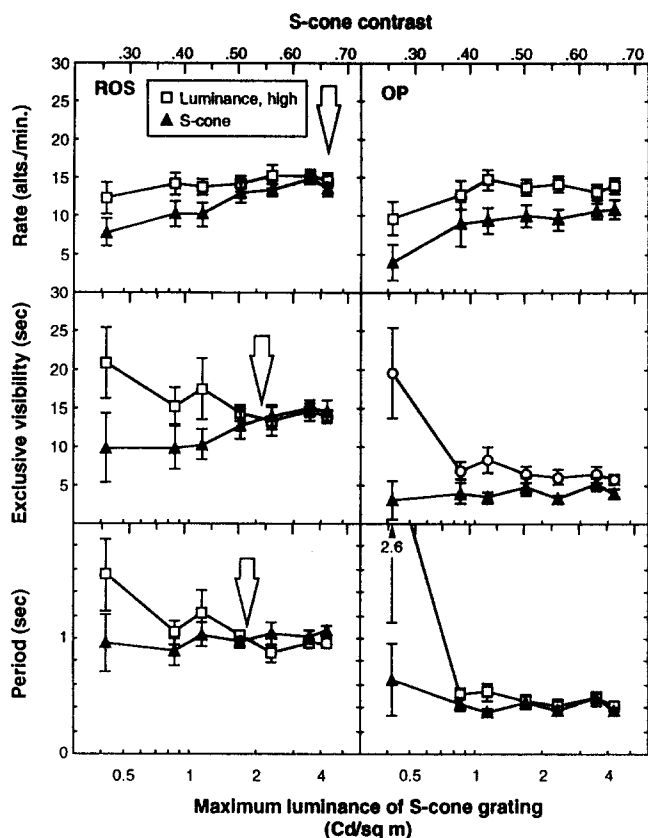
FIGURE 6. Rivalry rate, cumulative exclusive visibility and period for rivalry between an S-cone stimulus and a high-contrast luminance stimulus. Data have been plotted as a function of contrast and luminance of S-cone rivalry stimuli for ROS and OP. Each point is the mean of eight observations (2 eye-orientations × 4 sessions). Error bars show 1 SEM. Points at which the functions for S-cone and luminance stimuli cross are arrowed.

dominance to the low-contrast luminance grating. For example, for ROS, the rate functions for an S-cone grating and the low-contrast luminance grating (upper left panel of Fig. 5) cross (arrowed) at an S-cone contrast of about 0.52. Interestingly the functions for exclusive visibility (middle left panel) do not cross at the same value, but at about 0.46. The crossing point for the measure of period (lower left panel) also differs: it is at about 0.42. We decided simply to take the average of the crossing points of the three measures: for ROS, this is 0.47. At approximately this contrast of the S-cone grating, it has an effective contrast equal to that of the luminance grating, that is 0.10. Going through a similar process for OP shows that he needed a slightly lower S-cone contrast, 0.45 to attain an effective contrast equal to 0.10. That is, an S-cone contrast of about 0.46 has an equivalent luminance contrast of 0.10 in rivalry.

When we set up a rivalry competition between the high-contrast luminance grating and the S-cone stimulus, ROS's rivalry functions for S-cone and luminance gratings also cross (Fig. 6). ROS needed an S-cone contrast of about 0.58 to attain equality in rivalry to the luminance grating having a luminance contrast of 0.31. OP's rivalry functions for S-cone and luminance gratings

do not cross within the range of contrasts we studied, although extrapolation suggests that they cross at some higher value. Whereas these results do not allow us to estimate the equivalent luminance contrast of our S-cone stimuli with any great precision, they do show that S-cone stimuli require a higher contrast to achieve equality with a high-contrast luminance grating than with a low-contrast luminance grating. As the high-contrast luminance grating is the same luminance as the low-contrast grating, this shows that the critical determinant of equality in rivalry is the contrast of the S-cone stimulus, rather than its luminance. This agrees with the effects of contrast and luminance on predominance in conventional rivalry (e.g. Whittle, 1965).

While our data are not extensive enough to map out the complete function relating S-cone contrast to its effective contrast, we can make two points:

1. The effective contrast of S-cone stimuli, indexed by their ability to achieve equality in a rivalry competition with luminance stimuli, is much less than what we compute from spectroradiometry. For example, for an S-cone grating to have an effe contrast of about 0.10, its S-cone contrast be about 0.46.

2. There appear to be individual differences in the gain of the function relating effective and S-cone contrast.

It would be premature to make a detailed comparison of our estimate of equivalent luminance contrast of S-cone stimuli with those found from other studies for at least three reasons:

1. The individual differences limit our estimate's precision.
2. The early state of research into the equivalent luminance contrast of S-cone stimuli from other approaches means there is little to compare our estimate to.
3. The dependence on the sort of technique, and even psychophysical method, for estimating equivalent luminance contrast (Agonie & Gorea, 1993) would make such comparison simplistic.

Nevertheless, these other techniques all seem to agree that the equivalent luminance contrast of chromatic stimuli is quite low, similar to what we found for S-cone stimuli.

## GENERAL DISCUSSION

In Experiment 1, we showed evidence that S-cone stimuli can engage in rivalry that cannot be accounted for by nonrival fading. Can we rationalize our finding of rivalry from S-cone stimuli with those of Hollins and Leung (1978) and Rogers and Hollins (1982), who argued that the S cones do not participate in rivalry? We should point out that our S-cone stimuli had a higher luminance than those used in either study. Also, we have taken pains to ensure that M and L cones do not contribute, whereas their displays stimulated all cone types. It may well be that, especially at low luminances, the input through both (Hollins & Leung, 1978) or one of the M and L cones (Rogers & Hollins, 1982) is sufficient to mask any contributions the weakly stimulated S cones make. Moreover, we used sine-wave gratings with spatial frequencies at an optimal part of the contrast-sensitivity function for the S cones (2 c/deg), whereas Hollins and Leung (1978) used square-wave gratings of 6 c/deg and Rogers and Hollins (1982) used square-wave gratings of 3 c/deg. These stimuli, with their abundance of high-spatial frequency edge information, would be expected to stimulate the M and L cones much more than the S cones. Our results show that when S cones are isolated they can support binocular rivalry.

The results of Experiment 2 suggest that the spatial spread of S-cone rivalry is similar to that for photopic, central, luminance gratings. This makes the S-cones an exception to the low-resolution systems of the rods (O'Shea et al., 1994) and the periphery (Blake et al., 1992), in which spatial spread of rivalry is greater. Without doing more work, it may be premature to speculate on why there is this difference between S cones and the other subsystems. However, we do note that Wilson et al. (1988) found that the upper limit of binocular fusion with S-cone stimuli was similar to that for luminance gratings. Moreover, while the lower limits of stereopsis with S-cone stimuli have been assessed (Grinberg & Williams, 1985), its upper limits have not. They may well prove to be the same as for luminance stimuli, in which case rivalry would be the rule, rather than the exception. That is, for all the major binocular phenomena, spatial spread with S-cone stimuli, indexed by spreading of rivalry, and the upper limits of fusion and stereopsis, may be similar to that from luminance stimuli.

What is clear from Experiment 2 is that while rivalry occurs between S-cone stimuli, its alternations are fewer or briefer than for the luminance stimuli we tested. This may be because the effective contrast of S-cone stimuli is low. When the contrast of luminance stimuli is reduced, their rivalry alternations also decline in frequency and duration, until, near threshold none seem to be reported (Liu et al., 1992).

The seemingly low effective contrast of S-cone stimuli was also evident in Experiment 3, in which we pitted an S-cone stimulus against a luminance stimulus in a rivalry competition. At low contrasts of the S-cone stimulus, the luminance stimulus is dominant in rivalry much more often, and for much longer. As the contrast of the S-cone stimulus is increased, it can be made to have approximately equal dominance to that of the luminance stimulus, and even to "win" the rivalry competition, but it never wins by very much.

The results of our three experiments show that rivalry is possible with S-cone, isoluminant stimuli. This has at least two theoretical ramifications:

1. It extends our knowledge of binocular interactions possible within chromatic pathways of the visual system. S-cone, chromatic pathways can support all of the major binocular phenomena: rivalry, stereopsis (Grinberg & Williams, 1985), and fusion (Wilson et al., 1988). Isoluminant stimuli produced by gratings modulated only in chromaticity also can support the same phenomena: rivalry (Flanagan, personal communication), stereopsis and fusion (Simmons & Kingdom, 1994).
2. The existence of rivalry, fusion and stereopsis with isoluminant stimuli challenges the notion that there is a clean segregation between chromatic processing and other perceptual functions such as form, motion and depth (e.g. Livingstone & Hubel, 1987). Form perception is possible with S-cone stimuli (Green, 1968; Humanski & Wilson, 1992, 1993). Motion perception is possible with S-cone stimuli (Cavanagh & Anstis, 1991). As well as the stereoscopic phenomena reported above, pictorial depth perception is possible with S-cone stimuli (e.g. Rabin et al., 1992). The major limitation on demonstrating the perceptual "abilities" of the chromatic system seems to be in the low effective contrast of chromatic stimuli.

Spatial ability of the chromatic system is to be expected if De Valois and Switkes' (1983) analysis of

the important role of colour in natural spatial vision is accepted: They note that a shadow falling across an object will create a major luminance step that the luminance system would detect as a (nonexistent) discontinuity. The same shadow, however, will make only a minimal change in chromaticity, leaving the chromatic system to signal the integrity of the object. Moreover, Gur and Akri (1994) have recently shown that the spatial properties of the chromatic system can be revealed more clearly when chromatic and luminance stimuli are combined. They suggest that the chromatic and luminance systems cooperate in spatial perception.

In conclusion, isoluminant, S-cone stimuli can engage in binocular rivalry with each other and with luminance stimuli. It appears that S cones provide an input to the binocular rivalry mechanism. The spatial spread of S-cone rivalry seems similar to that for luminance rivalry; this is consistent with the similarity of the upper limit of fusion for S-cone and luminance stimuli. Binocular rivalry offers a way of quantifying the effective contrast of S-cone stimuli. In a rivalry competition with luminance stimuli, S-cone stimuli have an equivalent luminance contrast of about four times less than their spectroradiometrically computed contrast. It may well be this low effective contrast that accounts for the fewer, briefer rivalry alternations of S-cone stimuli compared with luminance stimuli.

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