FUNDUS PIGMENTATION AND EQUILUMINANT MOVING PHANTOMS 1

JAMES M. BROWN

University of Georgia

Summary.—Visual phantoms are a perceptual completion illusion wherein contours and surfaces are seen where none physically exist. The visibility of moving phantoms was measured with equiluminant and near equiluminant chromatic inducing gratings for observers having a fundus classified as either darkly or lightly pigmented. Phantom visibility was greatest for observers with a lightly compared to a darkly pigmented fundus with the two groups showing differences in visibility as a function of background luminance. The results are discussed relative to equiluminant stationary phantom findings and a proposed relationship between phantom visibility and magnocellular pathway activity.

Fundus pigmentation has been shown to be related to differences in performance on a number of perceptual tasks including the WISC Block Design subtest (Mitchell & Pollack, 1974; Mitchell, Pollack, & McGrew, 1977), a spatial-geographical test (Jahoda, 1971), the Müller-Lyer illusion (Pollack & Silvar, 1967; Berry, 1971; Jahoda, 1971; Ebert & Pollack, 1972a, 1972b, 1973), and the perception of black and white, e.g., achromatic, moving phantoms (Brown, 1993). Together, these studies document a relationship between fundus pigmentation and differences in the processing of real and illusory contours and surfaces. The present study extends this area of inquiry to the perception of equiluminant moving phantoms.

Visual phantoms are a subjective completion phenomenon that fluctuates in visibility over time. A typical stimulus for producing visual phantoms is a vertical black and white inducing grating with a black horizontal occluder blocking out the middle of the grating. Phantoms can be produced with inducing gratings that are moving (Tynan & Sekuler, 1975), flickering (Genter & Weisstein, 1981), or stationary (Gyoba, 1983, 1994). When phantoms are not visible, the occluder appears in front of the inducing grating. When phantoms are visible, the black grating stripes appear complete with the occluder now appearing behind the completed phantom stripes. This reversible figure-ground illusion has been used to study figure-ground processing (Brown & Weisstein, 1988) and perceptual organization (Brown & Weisstein, 1991).

¹Thanks to Dr. Jiro Gyoba for helpful comments on an earlier draft of this manuscript. Please address correspondence to James M. Brown, Department of Psychology, University of Georgia, Athens, GA 30602-3013 or e-mail (jmbrown@uga.cc.uga.edu).

By manipulating stimulus variables and observing their effects on phantom visibility, this phenomenon gives us a glimpse into the processes normally operating during perceptual completion and figure-ground perception (Brown & Weisstein, 1991). A number of stimulus parameters have been investigated. For example, phantom visibility has been measured while the contrast (Mulvanny, Macarthur, & Sekuler, 1982) and the spatial (Tynan & Sekuler, 1975; Genter & Weisstein, 1981) and temporal (Genter & Weisstein, 1981) frequency of the inducing grating were varied. The lightness relationship between the occluder and the inducing grating has been studied (Brown & Weisstein, 1985; Sakurai & Gyoba, 1985) as well as the visible extent of the inducing grating relative to the height of the occluder (Tynan & Sekuler, 1975; Mulvanny, et al., 1982).

Gyoba (1994) recently noted that a number of studies have indicated phantom visibility to be best for stimuli with such spatiotemporal characteristics that "phantoms [may] have a close relationship to the magnocellular function" (p. 1004). For example, flickering phantom visibility is optimal for lower spatial frequency gratings which flicker at relatively higher temporal frequencies (Genter & Weisstein, 1981). Moving phantoms are visible with inducing gratings just barely above contrast threshold themselves (Mulvanny, et al., 1982). In addition, many phantom studies have used relatively low luminance-inducing stimuli usually in low mesopic luminance ranges (Genter & Weisstein, 1981; Gvoba, 1983; Sakurai & Gvoba, 1985; Brown & Weisstein, 1991; Brown, 1993). For example, stationary phantom visibility is greatly affected by inducing stimulus luminance, with visibility near 80% for low luminance (0.31 cd/m²) compared to less than 10% for high luminance (20 and 80 cd/m²) inducing gratings (Gyoba, 1994). Taken together, the results from many phantom studies suggest activity in the magnocellular pathway plays an important role in the perception of this illusion.

A common method of exploring the contribution of the magnocellular pathway to perceptual processing has been to compare the differences in perception that occur under equiluminant and nonequiluminant conditions. The logic is that the magnocellular pathway's contribution to perception is reduced by using stimuli defined only by color differences because the magnocellular pathway has poor sensitivity to wavelength (Livingstone & Hubel, 1987). The perception of figure-ground (Koffka, 1935; Livingstone & Hubel, 1987), depth (Livingstone & Hubel, 1987), motion (Cavanagh, MacLeod, & Anstis, 1987), illusory contours (Brigner & Gallagher, 1974; Frisby & Clatworthy, 1975; Brussell, Stober, & Bodinger, 1977; Gregory, 1977), and green stationary phantoms (Gyoba, 1994) have all been reported to be adversely affected under equiluminant conditions (although see Treisman, Cavanagh, Fischer, Ramachandran, & von der Heydt, 1990). It is important to note that using equiluminant conditions is a way of manipulating relative activity

in the magnocellular pathway. The considerable variation across magnocellular cells in the luminance ratios effective at minimizing their activity indicates that at psychophysical equiluminance activity in the magnocellular pathway should be expected to be reduced, not eliminated (Logothetis, Schiller, Charles, & Hurlbert, 1990; Schiller, Logothetis, & Charles, 1990).

The present study examined how moving phantom visibility for observers with a lightly or darkly pigmented fundus was influenced by reducing activity in the magnocellular pathway using equiluminant conditions. While reducing activity in the magnocellular pathway at equiluminance can essentially eliminate the visibility of stationary phantoms (Gyoba, 1994), would similar influences be found on the visibility of moving phantoms? Previous work (Brown, 1993) indicated that phantom visibility should be greater for observers with a lightly compared to a darkly pigmented fundus; however, it was unknown how visibility would be effected for these groups at and near equiluminance.

Метнор

Participants

Eighteen introductory psychology students participated for course credit. All subjects had normal or corrected-to-normal vision and normal color vision. With race being a strong predictor of fundus pigmentation (Silvar & Pollack, 1967), the dark fundus group consisted of nine African Americans and the light fundus group nine Euro-Americans. Fundus readings were taken to verify this grouping (see below).

Stimuli and Apparatus

The stimuli were created and presented with a computer-controlled Data Translation 2862 Frame Grabber output to an NEC DM-2000P highresolution RGB monitor. According to manufacturer specifications the monitor's P-22 phosphors had CIE coordinates for red of x = .625, y = .318, and for green of x = .277, y = .587. The phantom inducing pattern was a 1-cpd square-wave grating moving continuously from left to right at 0.78 deg/sec. The monitor was viewed from 297 cm with room lights off. A black mask was placed in front of the monitor such that a 2.03° × 2.03° viewing area was visible in the middle of the monitor. An occluder subtending 0.675° (h) × 2.03° was centered within the viewing area with the inducing grating subtending 0.675° (h) × 2.03° above and below it. The grating was composed of alternating red and green stripes. The occluder was either red or green. The grating stripes the same color as the occluder were designated the phantom inducing color with the other color being the background color. Thus, the stimuli consisted of the phantom/background color combinations of red/ green with a red occluder and green/red with a green occluder.

Measures of fundus pigmentation were taken just to the left of the foveal depression using a Photovolt light meter connected to one eyepiece of a Bausch and Lomb binocular ophthalmoscope. A scale of reflectance was derived from the photometric scale (see Youn & Pollack, 1989). The range of reflectance varied from 1 unit, indicating dense or dark pigment, to 21 units, indicating a greater reflectance or light pigment. Each unit represents a photometric value of 5×10^{-7} footcandle. The nine participants making up the Darkly pigmented group had a mean fundus reading of 5.57 (SD=2.5). The Lightly pigmented group had a mean of 18.2 (SD=1.2). The broadspectrum wavelengths of the tungsten lamp used to make our fundus measurements peaked between 650 and 700 nm. Considering these peak wavelengths, our differences in fundus readings most likely reflect differences in choroidal melanin concentration (Hunold & Malessa, 1974; Weiter, Delori, Wing, & Fitch, 1986). These readings are consistent with differences in choroidal melanin concentration found between Caucasians and African Americans for both foveal (Hunold & Malessa, 1974; Weiter, et al., 1986) and peripheral retinal regions (Weiter, et al., 1986).

Procedure

First, observers were introduced to illusory contours and phantoms using pictures of white and black Kanizsa triangles (Kanizsa, 1979) and a black and white schematic diagram of a phantom-inducing display. The introduction familiarized them with the fluctuating, subjective nature of phantoms compared to illusory contours. Using the schematic, phantoms were described as when the black stripes appear complete from top to bottom in front of the black occluder.

Next, a flicker photometry procedure was used to set red and green to equiluminance. A fixed luminance (10.28 cd/m²) red square alternated with a variable luminance green square at 12 Hz. Each square subtended $2.03^{\circ} \times 2.03^{\circ}$. Observers made six settings adjusting the luminance of the variable green square to achieve minimal flicker with the red square. The mean of the last five settings was used as their equiluminant value.

Starting with the equiluminance setting of each observer, three additional luminance contrast conditions were created for the two color conditions by decreasing the luminance of the background stripes in three 1.03-cd/m² steps. Based on the fixed red value from the flicker photometry procedure, the red background in the green/red equiluminant condition was 10.28 cd/m² for every observer. This resulted in background stripe luminances for this color condition of 10.28, 9.25, 8.33, or 7.19 cd/m². Depending on an individual observer's equiluminant value for green, slightly different relative grating contrasts would result. For example, an observer who set the green to a lower luminance, e.g., 9.59 cd/m², than red when at equilumi-

nance would have a grating contrast of 3.45% at equiluminance with the red background slightly brighter. As the background luminance is decreased from equiluminance in 1.03-cd/m² steps, contrasts of 1.8%, 7.7%, and 14.3% would be produced with the green phantom inducing stripes being brighter than the red background stripes for all but the equiluminant contrast condition. Because the equiluminance setting was different across individuals, these grating contrasts were different too. When green was the background color in the red/green condition, the luminance of the green background stripes was either at the observer's equiluminant value or three smaller values decreasing in 1.03-cd/m² steps.

Before starting the experimental trials observers were instructed that they would be seeing red and green stripes with either a red or a green occluder. Phantoms were described when the colored stripes the same color as the occluder appeared as connected from top to bottom in front of the occluder. Whenever phantoms were visible they were to press and hold down the spacebar key on the computer keyboard. Observers viewed the displays in a darkened room and were instructed to keep their gaze directed towards the dim fixation point in the center of the occluder during each trial. The eight different color × luminance combinations were presented three times each for a duration of 30 sec. The first trial in each combination was eliminated in the analysis as a practice trial. The percentage of total viewing time was calculated from a total of 60 sec. per condition.

RESULTS

A 2 between (fundus: Lightly/Darkly pigmented) \times 2 within (color condition: red/green, green/red) × 4 within (contrast) analysis of variance on the percentage of total viewing time was significant for the main effect of fundus ($F_{1,16} = 5.78$, p < .03). The two-way interactions of fundus × color condition $(F_{1.16} = 7.53, p < .01)$ and color condition × contrast $(F_{3.48} = 4.49, p < .01)$.01), and the three-way interaction of fundus × color condition × contrast $(F_{3,48}=2.95, p<.04)$ were also significant. The Lightly pigmented group had significantly greater phantom visibility overall (32% vs 17%), a finding consistent with previous results for achromatic moving phantoms (Brown, 1993). Despite the 15% overall difference in visibility as a function of fundus pigmentation, the -3.09-cd/m² green/red condition, i.e., green occluder/ red background, is the first ever found producing similar phantom visibility for both fundus groups. Green/red visibility hovered near 20% across luminance conditions for the Darkly pigmented group. For the Lightly pigmented group, there was a significant decreasing linear trend (t=2.77, p<.05), with visibility decreasing from 40% to 20% as the luminance of the red background decreased (see Fig. 1). Curiously, when the phantom/background colors were reversed, i.e., the -3.09-cd/m2 red/green condition, phantom

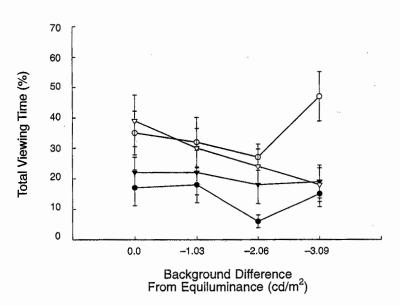


Fig. 1. Visibility of moving phantoms for observers with a darkly and a lightly pigmented fundus for green-red and red-green phantom/background color conditions as a function of the background difference from equiluminance. Phantom/Background color and fundus: (\(\Delta \)) Green/Red - Light, (\(\Delta \)) Red/Green - Dark

visibility across all luminance conditions was now significantly greater for the Lightly compared to the Darkly pigmented group and for the Lightly pigmented in all but the two equiluminant conditions (Newman-Keuls, all p < .05).

Phantom visibility for the Darkly pigmented group in the red/green -2.06-cd/m² condition was significantly less than all conditions for the Lightly pigmented group except the -3.09-cd/m² green/red condition (Newman-Keuls, all p < .05). While different in overall magnitude, the shape of the red/green curves for both fundus groups are quite similar. Visibility decreased from equiluminance to a minimum at a difference in background luminance of -2.06 cd/m² followed by an increase in visibility as the difference in background luminance increased further to -3.09 cd/m². These quadratic trends were significant for both the Lightly (t = 2.71, p < .05) and Darkly pigmented groups (t = 2.61, p < .05). Thus, the significant three-way interaction is due to the difference between the red/green and green/red curves for the two fundus pigmentation groups as a function of background luminance.

Whatever the reasons are for the fundus-related differences in phantom visibility, they are not due to differences in equiluminance settings between

the groups. Mean equiluminant settings across fundus-pigmentation groups were not significantly different (t_{16} =1.38, p>.19, two-tailed). Mean contrast at equiluminance was 2.65% (SE=3.2, i.e., red slightly brighter) for the Darkly pigmented and -2.96% (SE=2.5, i.e., green slightly brighter) for the Lightly pigmented group. In addition, during debriefing, observers in both groups noted how the gratings seemed to "move funny," as though they were slowing down and nearly stopping sometimes. These observations indicate the inducing gratings were at or very near equiluminance.

Discussion

What does the classification as darkly or lightly pigmented mean? As mentioned earlier, the fundus readings most likely reflect a difference in choroidal melanin concentration (Hunold & Malessa, 1974; Weiter, et al., 1986) with lower, i.e., darker, readings indicating greater concentration. Why a greater concentration of choroidal melanin should lead to a decrement in the magnitude of geometric, i.e., Müller-Lyer (Pollack & Silvar, 1967; Berry, 1971; Jahoda, 1971; Ebert & Pollack, 1972a, 1972b, 1973), and filling-in type, i.e., phantom, illusions is still unclear. One possibility is that absolute light levels are lower for observers with a darkly pigmented fundus. Brown irises transmit approximately one hundred times less light than blue or blue-green irises (van den Berg, Ijspeert, & de Waard, 1991). All observers in our Darkly pigmented group had brown irises and all except one in the Lightly pigmented group had blue or blue-green irises. Researchers might test this idea by comparing the visibility of phantoms for blue-eyed observers with a lightly pigmented fundus under natural viewing conditions and under conditions simulating the reduction in transmitted light for brown irises.

What do the interactions of fundus pigmentation with the visibility of achromatic and chromatic moving phantoms suggest? The effects of color and luminance on phantom visibility found in the present study suggest differences in perception related to fundus may be due to differences in the response of color- and luminance-sensitive mechanisms. In addition to the possibility of absolute differences in light level discussed above, the overall greater visibility of achromatic and chromatic phantoms for those with a light pigmented fundus might be attributed to light scatter, i.e., a lighter fundus might create relatively greater stray-light and thus, possibly, greater visibility of phantoms. This might seem plausible considering interocular straylight has been shown to be greater for blue-eyed Euro-Americans compared to brown-eved African Americans (Ijspeert, de Waard, van den Berg, & de Jong, 1990; van den Berg, et al., 1991). However, it is unlikely that a straylight account is the main reason for the group differences in the magnitude of the illusion for two reasons. First, such an account is contradicted by the finding that the visibility of red phantoms was so much greater than green

for the Light pigmented group at -3.09-cd/m² difference. The longer wavelength red light should produce less scatter than green, yet it produced the greater illusion magnitude. Second, it is important to note that optical factors can not account for the phantom illusion. The configural properties of phantoms related to perceived depth (Weisstein, Maguire, & Williams, 1982; Brown & Weisstein, 1991), the production of dichoptic phantoms (Tynan & Sekuler, 1975), the reduced visibility of stationary phantoms under high illumination conditions (Gyoba, 1994), and the findings of phantom dots (Tynan & Sekuler, 1975) and columns of X's (Weisstein & Maguire, 1978) all argue strongly against any low-level, stray-light account of the phantom phenomenon.

A comparison of equiluminant moving and stationary phantom visibility indicates some interesting similarities and differences. Visibility of green-red stationary phantoms fluctuates as a function of grating contrast. It is low, e.g., less than 40%, for contrasts near equiluminance, decreasing to near zero at equiluminance (Gyoba, 1994). While this low and fluctuating illusion magnitude near equiluminance is similar to that found for red-green moving phantoms (described above), particularly for the darkly pigmented fundus group, the point of least visibility was not at equiluminance. Strangely, the visibility of green/red moving phantoms did not vary across contrast for observers with a darkly pigmented fundus and showed a decreasing function across contrast for those with a lightly pigmented fundus. At present it is not clear why the two color conditions produced differences in visibility for the two groups across contrast. It is also uncertain if the differences in the visibility of equiluminant moving and stationary phantoms could be related to differences in fundus pigmentation between the populations tested, i.e., Euro-Americans and African Americans in the moving phantom studies and Japanese in the stationary phantom studies.

The relative contributions of the magnocellular and parvocellular pathways to the phantom illusion are still unknown. As noted earlier, magnocellular pathway contributions have been implicated from the relationships found between phantom visibility and the spatial and temporal frequency characteristics of the stimuli. The greater visibility of moving compared to stationary equiluminant phantoms might seem to contradict this idea. However, a number of movement related factors may have contributed to this difference. First, the stimulus motion and the variability of responses in the magnocellular pathway at and near equiluminance (Logothetis, et al., 1990; Schiller, et al., 1990) may have contributed to relatively greater magnocellular pathway activity. Second, although disturbances in perceived motion were reported consistent with equiluminant conditions, collinearity and common fate cues were still available from the synchronous movement of the inducing grating above and below the occluder. Third, illusory contours and sur-

faces are difficult to see under stationary equiluminant conditions (Brigner & Gallagher, 1974; Frisby & Clatworthy, 1975; Brussell, Stober, & Bodinger, 1977; Gregory, 1977), vet kinetic illusory contours and surfaces (Kellman & Cohen, 1984) are vividly seen when only motion information defines the inducing elements relative to the background, i.e., there are no luminance differences between inducing elements and the background (Kellman & Loukides, 1987). Thus, it may be that the addition of motion information facilitates the visibility of equiluminant illusory contours and phantoms. Finally, it may be informative to consider the greater visibility of equiluminant moving phantoms from the perspective of Grossberg's FACADE, i.e., Form-And-Color-And-DEpth) theory (Grossberg & Mingolla, 1993; Grossberg, 1994). The nature of FACADE's parvocellular boundary contour system (BCS) and feature contour system (FCS), and magnocellular motion boundary contour system, are such that, if the color contrast information and any extraneous luminance information was sufficient to activate boundary contour system and motion boundary contour system processing, then phantoms could be filled in by the feature contour system.

The relationship between fundus pigmentation and perception poses an interesting challenge for future studies. The present study provides additional evidence of differences in illusory contour and surface processing related to fundus pigmentation. Studies using different spatial and temporal measures may help us to understand better the differences in perceptual processing related to fundus pigmentation.

REFERENCES

BERRY, J. W. (1971) Mueller-Lyer susceptibility: culture, ecology or race? International Journal of Psychology, 6, 193-197.

BRIGNER, W. L., & GALLAGHER, M. B. (1974) Subjective contours: apparent depth or simultaneous brightness contrast? Perception and Motor Skills, 38, 1047-1053.

Brown, J. M. (1993) Moving phantom visibility as a function of fundus pigmentation. Perception & Psychophysics, 53, 367-371.

BROWN, J. M., & WEISSTEIN, N. (1985) Flickering phantoms: a figure/ground approach. Proceedings and Abstracts of the Annual Meeting of the Eastern Psychological Association, 57, 38

Brown, J. M., & Weisstein, N. (1988) A phantom context effect: visual phantoms enhance target visibility. Perception & Psychophysics, 43, 53-56.

Brown, J. M., & Weisstein, N. (1991) Conflicting figure-ground and depth information reduces moving phantom visibility. *Perception*, 20, 155-165.

BRUSSELL, E. M., STOBER, S. R., & BODINGER, D. M. (1977) Sensory information and subjective contour. American Journal of Psychology, 90, 145-156.

CAVANAGH, P., MACLEOD, D. I. A., & ANSTIS, S. M. (1987) Equiluminance: spatial and temporal factors and the contribution of blue-sensitive cones. *Journal of the Optical Society of America*, 4, 1428-1438.

EBERT, P. C., & POLLACK, R. H. (1972a) Magnitude of the Mueller-Lyer illusion as a function of hue, saturation, and fundus pigmentation. *Psychonomic Science*, 26, 225-226.

EBERT, P. C., & POLLACK, R. H. (1972b) Magnitude of the Mueller-Lyer illusion as a function of lightness contrast, viewing time, and fundus pigmentation. Psychonomic Science, 26, 347-348.

- EBERT, P. C., & POLLACK, R. H. (1973) The effect of lightness contrast, tachistoscopic duration and fundus pigmentation on the magnitude of the Mueller-Lyer illusion. *American Journal of Optometry and Archives of American Academy of Optometry*, 50, 872-879.
- Frisby, J. P., & Clatworthy, J. L. (1975) Illusory contours: curious cases of simultaneous brightness contrast? *Perception*, 4, 349-357.
- GENTER, C. R., & WEISSTEIN, N. (1981) Flickering phantoms: a motion illusion without motion. Vision Research, 21, 963-966.
- GREGORY, R. L. (1977) Vision with isoluminant color contrast: a projection technique and observation. Perception, 6, 113-119.
- GROSSBERG, S. (1994) 3-D vision and figure-ground separation by visual cortex. Perception & Psychophysics, 55, 48-121.
- Grossberg, S., & Mingolla, E. (1993) Neural dynamics of motion perception: direction fields, apertures, and resonant grouping. *Perception & Psychophysics*, 53, 243-278.
- GYOBA, J. (1983) Stationary phantoms: a completion effect without motion or flicker. Vision Research, 22, 119-134.
- GYOBA, J. (1994) Disappearance of stationary visual phantoms under high luminant or equiluminant inducing gratings. Vision Research, 34, 1001-1005.
- HUNOLD, W., & MALESSA, P. (1974) Spectrophotometric determination of the melanin pigmentation of the human ocular fundus in vivo. Ophthalmic Research, 6, 355-362.
- IJSPEERT, J. K., DE WAARD, P. W. T., VAN DEN BERG, T. J. T. P., & DE JONG, P. T. V. M. (1990) The interocular straylight function of 129 healthy volunteers: dependence on angle, age, and pigmentation. Vision Research, 30, 699-707.
- JAHODA, G. (1971) Retinal pigmentation, illusion susceptibility and space perception. International Journal of Psychology, 6, 199-208.
- Kanizsa, G. (1979) Organization in vision. New York: Praeger.
- Kellman, P. J., & Cohen, M. H. (1984) Kinetic subjective contours. Perception & Psychophysics, 35, 237-244.
- Kellman, P. J., & Lourides, M. G. (1987) An object perception approach to static and kinetic subjective contours. In S. Petry & G. E. Meyer (Eds.), *The perception of illusory contours*. New York: Springer-Verlag. Pp. 151-164.
- Koffka, K. (1935) Principles of Gestalt psychology. New York: Harcourt Brace.
- LIVINGSTONE, M., & HUBEL, D. (1987) Psychophysical evidence for separate channels for the perception of form, color, movement and depth. *Journal of Neuroscience*, 7, 3416-3468.
- LOGOTHETIS, N. K., SCHILLER, P. H., CHARLES, E. R., & HURLBERT, A. C. (1990) Perceptual deficits and the activity of the color-opponent and broad-band pathways at isoluminance. Science, 247, 214-217.
- MITCHELL, N. B., & POLLACK, R. H. (1974) Block-design performance as a function of hue and race. Journal of Experimental Child Psychology, 17, 377-382.
- MITCHELL, N. B., POLLACK, R. H., & McGrew, J. F. (1977) The relation of form perception to hue and fundus pigmentation. *Bulletin of the Psychonomic Society*, 9, 97-99.
- Mulvanny, P., Macarthur, R., & Sekuler, R. (1982) Thresholds for seeing visual phantoms and moving gratings. *Perception*, 11, 35-46.
- POLLACK, R. H., & SILVAR, S. D. (1967) Magnitude of the Mueller-Lyer illusion in children as a function of pigmentation of the fundus oculi. *Psychonomic Science*, 8, 83-84.
- Sakurai, K., & Gyoba, J. (1985) Optimal occluder luminance for seeing stationary visual phantoms. Vision Research, 25, 1735-1740.
- SCHILLER, P. H., LOGOTHETIS, N. K., & CHARLES, E. R. (1990) Functions of the color-opponent and broad-band channels of the visual system. *Nature*, 343, 68-70.
- SILVAR, S. D., & POLLACK, R. H. (1967) Racial differences in pigmentation of the fundus oculi. Psychonomic Science, 7, 159-160.
- TREISMAN, A., CAVANAGH, P., FISCHER, B., RAMACHANDRAN, V. S., & VON DER HEYDT, R. (1990) Form perception and attention: striate cortex and beyond. In L. Spillman & J. S. Werner (Eds.), Visual perception: the neurophysiological foundations. New York: Academic Press. Chap. 11. Pp. 273-316.
- TYNAN, P., & SEKULER, R. (1975) Moving visual phantoms: a new visual completion effect. Science, 188, 951-952.

- Van den Berg, T. J. T. P., IJSPEERT, J. K., & DE WAARD, P. W. T. (1991) Dependence of intraocular straylight on pigmentation and light transmission through the ocular wall. Vision Research, 31, 1361-1367.
- Weisstein, N., & Maguire, W. (1978) Computing the next step: psychophysical measures of representation and interpretation. In A. L. Hanson & E. M. Riseman (Eds.), Computer vision systems. New York: Academic Press. Pp. 243-260.
- WEISSTEIN, N., MAGUIRE, W., & WILLIAMS, M. C. (1982) The effect of perceived depth on phantoms and the phantom motion aftereffect. In J. Beck (Ed.), Organization and representation in perception. Hillsdale, NJ: Erlbaum. Pp. 235-249.
- WEITER, J. J., DELORI, F. C., WING, G. L., & FITCH, K. A. (1986) Retinal pigment epithelial lipofuscin and melanin and choroidal melanin in human eyes. *Investigative Ophthalmology & Visual Science*, 27, 145-152.
- YOUN, G., & POLLACK, R. H. (1989) The magnitude of the Mueller-Lyer illusion as a function of hue, saturation, fundus pigmentation, and simulated aging. *Experimental Aging Research*, 15, 19-25.

Accepted April 24, 2000.