Available online at www.sciencedirect.com

ScienceDirect

Vision Research 46 (2006) 3823–3830

Vision Research

www.elsevier.com/locate/visres

Microsaccade directions do not predict directionality of illusory brightness changes of overlapping transparent surfaces

P.U. Tse *, G.P. Caplovitz, P.-J. Hsieh

Department of Psychological and Brain Sciences, Moore Hall, Dartmouth College, Hanover, NH 03755, USA

Received 17 January 2006; received in revised form 29 April 2006

Abstract

Tse (2005) recently introduced a new class of illusory brightness changes where shifts of attention lead to shifts in perceived brightness across overlapping, transparent figures, under conditions of visual fixation. In the absence of endogenous attentional shifts, illusory brightness changes appear to shift from figure to figure spontaneously, much as occurs in other multistable phenomena. The goal of the present research is to determine whether fixational microsaccades are correlated with perceived brightness changes. It has recently been demonstrated that microsaccades can reveal the direction of covert attentional shifts either toward (Engbert, R. & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research, 43*, 1035–1045; Hafed, Z. M. & Clark, J. J. (2002). Microsaccades as an overt measure of covert attention shifts. *Vision Research, 42*(22), 2533–2545) or away from (Rolfs, M., Engbert, R., & Kliegl, R. (2004). Microsaccade orientation supports attentional enhancement opposite a peripheral cue: commentary on Tse, Sheinberg, and Logothetis (2003). *Psychological Science, 15*(10), 705–707) a peripheral cue under certain circumstances. Others (Horwitz, G. D. & Albright, T. D. (2003). Short-latency fixational saccades induced by luminance increments. *Journal of Neurophysiology, 90*(2), 1333–1339; Tse, P. U., Sheinberg, D. L., & Logothetis, N. K. (2002). Fixational eye movements are not affected by abrupt onsets that capture attention. *Vision Research, 42*, 1663–1669; Tse, P. U., Sheinberg, D. L., & Logothetis, N. K. (2004). The distribution of microsaccade directions need not reveal the location of attention. *Psychological Science, 15*(10), 708–710) found no change in the distribution of microsaccade directions as a function of where attention is allocated, although changes in the rate of microsaccades were observed in all of these studies in response to the onset of attentional reallocation. It is therefore possible that the distribution of microsaccade directions will change as a function of which figure is perceived to darken, or that changes in this distribution predict which figure will subsequently darken. We find no correlation between this distribution and which figure undergoes the effect, and therefore conclude that microsaccade directionality is not influenced by and does not influence which figure undergoes the effect. Moreover, the directions of microsaccades that occur immediately prior to a perceptual switch are not correlated with the perceived position of the figure that undergoes the effect. However, we do find that the rate of microsaccades decreases upon a perceptual switch, signifying an attentional shift coincident with the perceptual shift. We conclude that microsaccade directionality does not determine, predict, or cause which figure will subsequently be perceived to undergo an illusory brightness change.

Keywords: Microsaccades; Brightness; Transparency; Attention

1. Introduction

A given patch of gray will appear brighter against a dark background and darker against a bright background. The earliest models of brightness perception attempted to explain such illusions in terms of lateral inhibition occurring in the retina (Cornsweet, 1970) or cortex, where the activation of one cell inhibits the activation of its neighbors. Such models failed to explain how higher level perceptual factors, such as inferred three-dimensional shape (Adelson, 1993), layout (Gilchrist, 1977), curvature (Kanill & Kersten, 1991), or transparency (Tse, 2005) could influence brightness perception. In particular, the visual system must

---

* Corresponding author.
E-mail addresses: peter.u.tse@dartmouth.edu (P.U. Tse), Gideon.Caplovitz@dartmouth.edu (G.P. Caplovitz), Po-Jang.Hsieh@dartmouth.edu (P.-J. Hsieh).

0042-6989/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2006.05.007

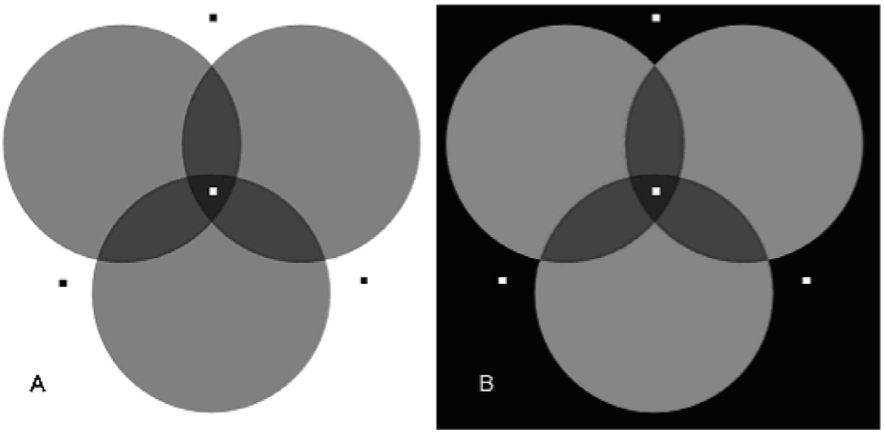

Fig. 1. Maintain fixation on any of the fixation spots in (A), while shifting attention from one disk to another. Notice that the attended disk appears to darken. Notice that even in the absence of voluntary shifts of attention, the darkening seems to pass from one disk to another. This effect depends on the disks being consistent with an interpretation of overlapping transparent layers. When the background is changed to black as in (B), a transparency interpretation is no longer possible, and the effect disappears.

determine what portion of a single luminance value detected at a location on the retina arises from each of several possible causes of that value in the world, such as surface coloring, shadow, illumination, or an intervening transparent layer. Models attempting to explain these effects have gone far beyond earlier models based solely on lateral inhibition among adjacent neurons. More recent models incorporate both low-level factors, such as lateral-inhibition, and mid-level factors, such as the global form analyses that may underlie the decomposition (Watanabe & Cavanagh, 1993) or 'scission' (Anderson, 1999, 2003) of the image into simultaneous contributions from reflectance, illumination, shadow, and transparency.

Tse (2005) recently introduced a new class of illusory brightness changes where shifts of attention lead to shifts in perceived brightness across overlapping, transparent figures, and under conditions of visual fixation. The effect can be seen when visually fixating any of the fixation spots in Fig. 1A while attending to any one of the gray disks. The attended disk appears to darken in the absence of eye movements. Shifting attention to another disk without breaking fixation decreases the brightness of this disk in turn. Of 16 observers tested on a version of this figure presented on a CRT screen (60 Hz refresh, 57 cm viewing distance, circle diameter 5.5°, white background ~89 cd/m^2 (~26 foot-lamberts), light gray ~46 cd/m^2 (~13.4 foot-lamberts), middle gray ~32 cd/m^2 (~9.3 foot-lamberts), and dark gray ~12 cd/m^2 (~3.5 foot-lamberts) as measured using Minolta CA-100), all said that they experienced the effect and said that they could "will" a chosen disk to darken by shifting attention to that disk ($p < .0001$, two-tailed under binomial test; Tse, 2005). This illusion appears to require that disks be interpreted as transparent surfaces occluding a background. The effect is very robust, and any combination of gray values seems to create the illusion, as long as the appearance of transparent layers is preserved. When such an interpretation is not possible, because key image cues for transparency (Metelli, 1974; Singh & Anderson, 2002) are absent, as in Fig. 1B, where the background alone has changed to black (<1 cd/m^2 (0.3 foot-lamberts)), perceived brightness is not modulated by attentional allocation (0 of 16 observers noted darkening with attentional shifts across disks; $p < .0001$).

While voluntary or endogenous attention is capable of specifying which disk darkens, the illusory darkening also flips automatically as in multistable figures generally (Leopold & Logothetis, 1999). Some bistable phenomena, such as the perceptual flipping that occurs in binocular rivalry, appear not to be modulated by selective attentional control, whereas others, such as the Necker cube, can be modulated by voluntary selective attention (Meng & Tong, 2004).

The main goal of the present research is to determine whether the directionality of microsaccades[1], which continue to occur under conditions of fixation, predict, cause, or are correlated with perceived brightness changes. Microsaccades are relevant to the understanding of an attentional effect, such as the one considered here, because it has recently been argued that microsaccades can reveal the direction of covert attentional shifts either toward (Engbert & Kliegl, 2003; Hafed & Clark, 2002) or away from (Rolfs, Engbert, & Kliegl, 2004) a peripheral cue under certain circumstances. Others (Horwitz & Albright, 2003; Tse, Sheinberg, & Logothetis, 2002, 2004) looked for but found no changes in the distribution of microsaccade directions as a function of where attention is allocated, although changes in the *rate* of microsaccades were observed in all of these

---

[1] In early work, microsaccades were sometimes called 'flicks' and were defined as saccades that occurred during fixation that were smaller than 10 min of arc in amplitude (e.g., Kowler & Steinman, 1979; Steinman, Cunitz, Timberlake, & Herman, 1967; Winterson & Collewijn, 1976). However, it has proven difficult to set an arbitrary upper limit on the amplitude of what is to count as a microsaccade because the amplitude of voluntary saccades can fall in the range that defines microsaccades (Martinez-Conde, Macknik, & Hubel, 2004). Here we use the term 'microsaccades' to mean the generally conjugate, fast (~25 ms) involuntary small saccades that occur during voluntary fixation, including those that are larger than 10 min of arc.

studies in response to the onset of attentional reallocation. It is therefore possible that the distribution of microsaccade directions will change as a function of which disk is perceived to darken, based on some past results (Engbert & Kliegl, 2003, 2004; Hafed & Clark, 2002), although other past work (Horwitz & Albright, 2003; Horowitz, Fine, Fencsik, Yurgenson, & Wolfe, 2006; Tse et al., 2002, Tse, Sheinberg, & Logothetis, 2004) suggests that there may be no evidence of this. We expect to see a change in microsaccade rate just before and after a perceptual switch if the perceptual shifts are driven by shifts in attentional allocation, whether or not microsaccade directions are correlated with which disk is perceived to darken, because all studies (Engbert & Kliegl, 2003, 2004; Hafed & Clark, 2002; Horwitz & Albright, 2003; Tse et al., 2002, 2004) agree that shifts of attention lead to changes in the rate of microsaccades.

2. Stimuli

Stimuli were arranged as depicted in Fig. 1A, but with only the central fixation spot present. The three outer fixation spots visible in Fig. 1A were not present. Each disk subtended 4 degrees visual angle, and the fixation spot subtended a very small 0.01° visual angle. The upper-right (upper-left) disk was centered 2° to the right (left) and 0.75° above the fixation spot. The lower disk was centered 1.75° below the fixation spot. The luminance of the non-overlapping portions of the disks was 20.1 cd/m^2 (5.9 foot-lamberts), and the luminance of the overlapping portions was 5.2 cd/m^2 (1.5 foot-lamberts). The background was a uniform white with a luminance of 102.8 cd/m^2 (30 foot-lamberts).

3. Methods

Eye movements were recorded using a SRresearch Eyelink2 system. Eye position was sampled at 250 Hz in the left eye. Three observers ran in one session each lasting 360 s. One subject, one of the authors, ran in two sessions, but since the data were indistinguishable, the second session was discarded. Thus, all data shown are pooled across three sessions obtained, respectively, from three subjects. Microsaccades and eyeblinks were located using the detection algorithms provided by SRresearch. Past analyses (Hsieh, Caplovitz, & Tse, 2006) found no difference in the results if the algorithms for microsaccade detection of Engbert and Kliegl (2003) are used instead, so the SRresearch algorithms were used here. Observers were required to maintain fixation on each trial. A miniature video camera, attached to an adjustable headband and bar, was fitted about 2 cm below the subject's left eye, and eye movements were calibrated to a dot that moved to nine positions on the screen in random order. Observers rested their chin in a stable rest. The head was not otherwise constrained, although observers were instructed to maintain their head perfectly still. Small head movements could be discounted online by the eye tracker software using the output of four cameras mounted on the monitor.

4. Results and discussion

Histograms of perceptual durations for the darkened disks over all subjects are shown in Fig. 2, pooled across data from the three disks. The mean perceptual duration for the "darkened disk" state was 3.13 s (SD = 2.81). The distribution of the perceptual durations was skewed toward the right, and can be approximated by a gamma distribution, as has been observed in other examples of perceptual bistability (Leopold & Logothetis, 1999; Meng & Tong, 2004). However, it must be noted that reaction times generally obey a gamma distribution rather than a normal distribution, for the simple reason that all reaction times must be greater than zero. While the occurrence of a gamma distribution is not itself evidence for multistability, the present illusion is another example of a multistable stimulus whose alternations among perceptual states resembles that of other multistable phenomena, including binocular rivalry and the Necker cube, because the median duration that a state is occupied is of a comparable duration to that observed in other multistable phenomena. This is at least indirect evidence that something similar may be going on across this and other multistable phenomena. For example, recent work suggests that voluntary shifts in perceptual multistability in general are mediated by shifts in spatial attention (Slotnick & Yantis, 2005).

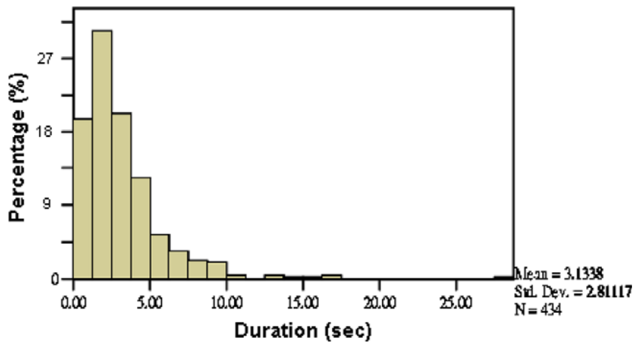

Fig. 2. Histogram of perceptual state durations (i.e., for staying in a perceptual state) where any one of the three disks appeared to darken.

Eye-tracking data show that 12.25 ± 4.04% of microsaccades and 21.89 ± 5.60% of eyeblinks took place in the 1000 ms prior to a button press indicating a perceptual shift (i.e., a shift of darkening from one circle to another). This result suggests that neither microsaccades nor eyeblinks are sufficient for generating perceptual switches. Conversely, 39.37 ± 3.06% of buttonpresses indicating a perceptual switch were preceded by a microsaccade within 1000 ms of a state onset (11.12 ± 2.84 % for eyeblinks). Because the baseline rate of microsaccades was roughly 0.92/s, this was less than might be expected to arise by chance. Indeed, examination of the running average for microsaccade rate (Fig. 3B) suggests that there is a decrease in microsaccade rate prior to the buttonpress indicating a perceptual switch. Even so, roughly 61% of the perceptual switches happened without being immediately preceded by a microsaccade (89% of switches were not preceded by an eyeblink) implying that neither microsaccades nor eyeblinks are necessary for generating perceptual switches to the 'see' condition.

Statistical analysis, described below, reveals that there is no difference between microsaccades that occur during the three different perceptual states (Fig. 4A), corresponding to the darkening of each of the three overlapping disks. This lack of change in the distribution of microsaccade directions implies that the directions and amplitudes of microsaccades are not correlated with the position of the perceptually darker disk. Since the direction and amplitude of each microsaccade could be decomposed into horizontal and vertical components, we first calculated the mean of the horizontal component (absolute value) of all microsaccades in each group, and then compared the three means from the three groups. Similar calculations were done for the vertical component. If the directions of microsaccades were correlated with the perceived position of the perceptually darker disk then, for example, we would expect those microsaccades that occurred while the bottom disk was perceived to be darker to have a bigger mean vertical component than the other groups. Statistical testing reveals that these means (of all microsaccades pooled across subjects) are not significantly different in either the horizontal component (ANOVA, $F(2,1054) = 0.782$, $p = 0.458$) or the vertical component (ANOVA, $F(2,1054) = 1.624$, $p = 0.198$), implying that the directions of microsaccades are not significantly predictive of the position of the perceptually darker disk. Similar lack of significance was found for individual subject data, implying that the present results were not an artifactual result of averaging across subjects' data. We conclude that microsaccade directionality is not influenced by and does not influence which of the three disks is perceived as darker at any given time.

Although microsaccades are not necessary for inducing perceptual switches and the directions of microsaccades during each perceptual state are not correlated with the position of the darker disk, those microsaccades that do occur within the 1000 ms prior to the perceptual switch ($21.57 \pm 0.57\%$ of total microsaccades, Fig. 4B) might be sufficient to bias which disk is subsequently perceived to be darker. The directions of these microsaccades might be correlated with the position of the darker disk. However, statistical analysis of this subset of microsaccades reveals that no significant differences exist when comparing among either horizontal (ANOVA, $F(2,150) = 0.88$, $p = 0.42$) or vertical microsaccade components (ANOVA, $F(2,150) = 0.78$, $p = 0.46$) for the three groups. Thus, the directions of microsaccades that do occur immediately prior to the perceptual switch are not correlated with the perceived position of the darker disk. We therefore conclude that microsaccade directionality does not determine, predict, or cause which disk will subsequently be perceived to darken.

5. General discussion

Which disk darkens is in part an attentional effect, because voluntarily attending to a given disk while maintaining fixation causes the attended disk to darken (Tse, 2005). Past researchers have reported that microsaccades can reveal the direction of covert attentional shifts either toward (Engbert & Kliegl, 2003; Hafed & Clark, 2002) or away from (Rolfs et al., 2004) a peripheral cue under certain circumstances. As such, it is possible that the distribution of microsaccade directions is

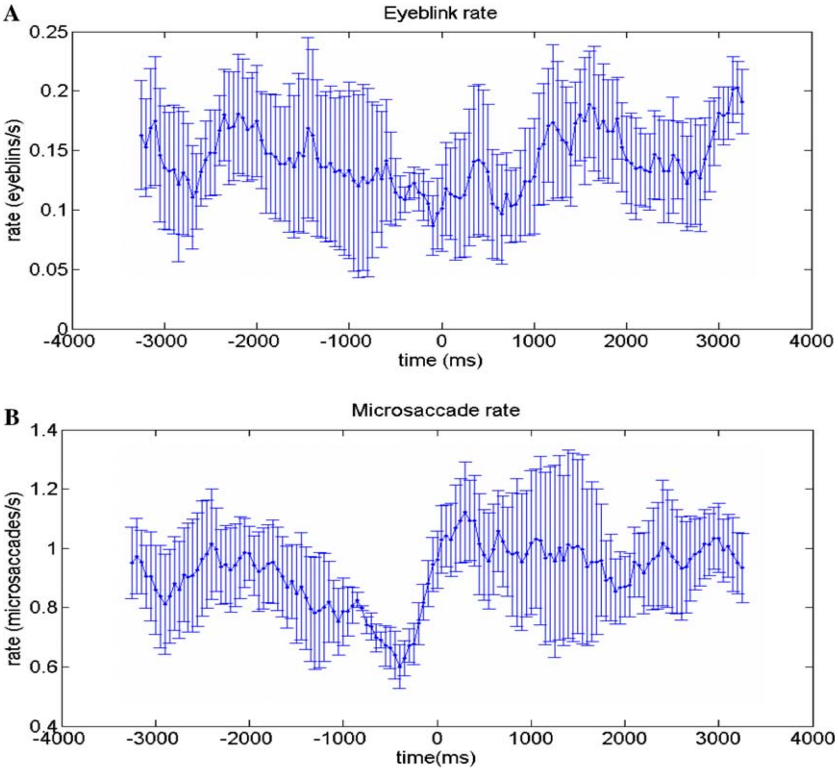

Fig. 3. Running average rate of (A) eyeblinks and (B) microsaccades per second before and after a perceptual switch indicated by a button press (time 0). Error bars represent standard errors of the mean.

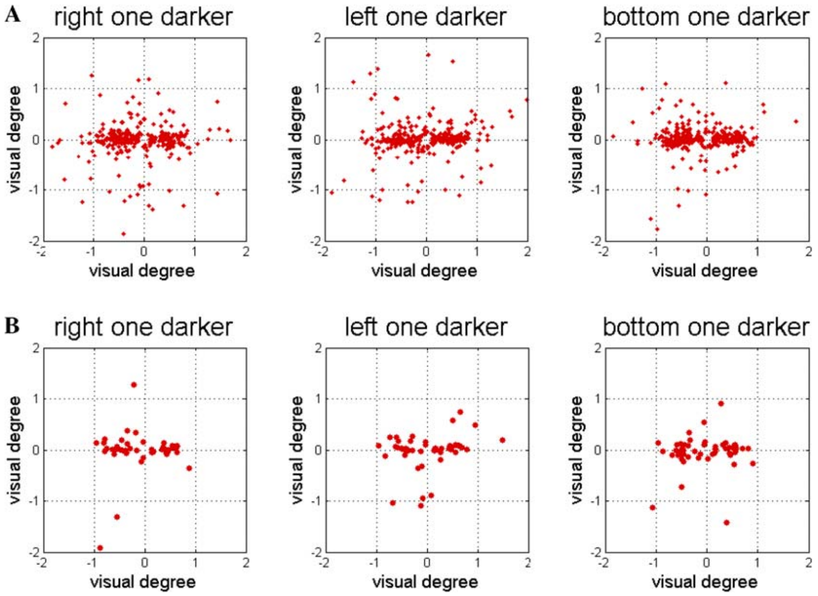

Fig. 4. The directions and amplitudes of microsaccades during three different perceptual states. (A) The directions and amplitudes (vertical and horizontal components in degrees of visual angle) of all microsaccades during three different percepts are plotted together for all subjects. The end position of each microsaccade was plotted as a dot on the x–y plane on which the zero point represents the fixation point that the subjects were fixating before making a microsaccade. For example, the leftmost subfigure shows the directions and amplitudes of all the microsaccades when the left disk was perceived to be darker. Each dot indicates the horizontal amplitude (x-axis) and vertical amplitude (y-axis) of each microsaccade. There is no significant difference between directions or amplitudes of microsaccades during the three different perceptual states. (B) There is no significant difference between the directions or amplitudes of those microsaccades that occur immediately before a perceptual switch during the three different perceptual states corresponding to the darkening of one of the three overlapping transparent disks. (See text for statistical details).

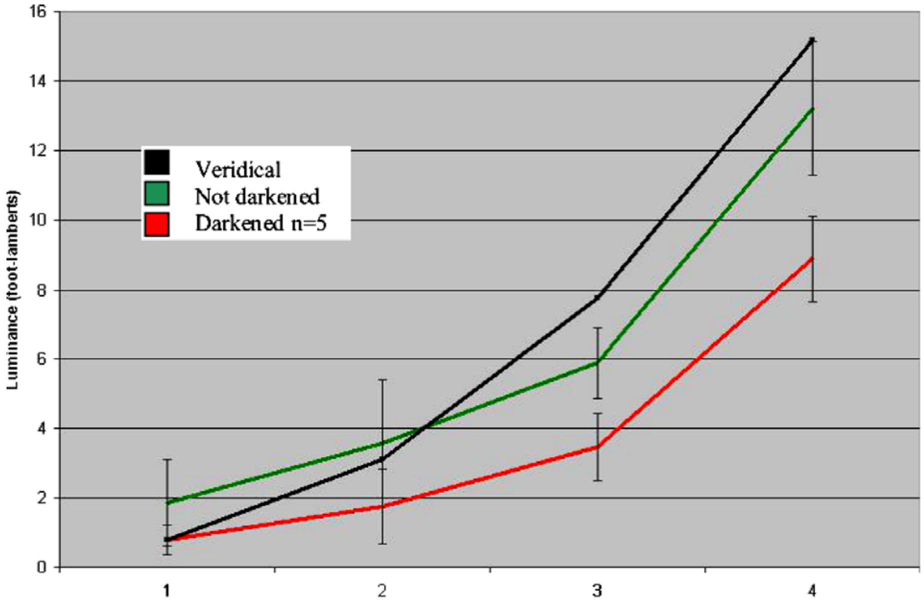

Fig. 5. Psychophysical results demonstrate that the disk that appears to darken does indeed darken, while the apparent brightness of the remaining disks remains unchanged. The x-axis is not labeled because luminances were chosen arbitrarily to span a wide range of values, but were not chosen at regular luminance intervals. The particular shape of the black curve is therefore arbitrary. Error bars represent standard errors of the mean.

correlated with which disk is perceived to darken. Others (Horwitz & Albright, 2003; Tse et al., 2002, 2004) found no change in the distribution of microsaccade directions as a function of where attention is allocated, although changes in the running rate of microsaccades were observed in all of these studies as a function of attentional shifts. The present results support the findings of the latter group of researchers (i.e., Horwitz & Albright, 2003; Tse et al., 2002, 2004; Horowitz et al., 2006) in that the distribution of microsaccade directions is not affected by perceptual switches to (or from) any particular disk, either during a perceptual state, or just prior to a perceptual state switch.

Early microsaccade researchers (e.g., Kowler & Steinman, 1979; Steinman et al., 1967; Winterson & Collewijn, 1976) concluded that microsaccades play no functional role in vision whatsoever. And yet, that microsaccades are typically conjugate implies that there is a central command that triggers them. The current consensus, in contrast, is that microsaccades play at least a functional role in blocking the onset of the perceptual fading that would occur under conditions of perfectly motionless fixation because of neuronal adaptation in the retina (e.g., Cornsweet, 1956; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006). Although we find that microsaccade directions play no role in determining the direction of the illusory darkening effect examined here, our data do not imply that microsaccades play no functional role in vision in general.

Our data imply that the brightness change effect is not an artifact introduced by eye movements. It does not imply that the darkening effect is not an attentional effect. Indeed, the pattern of change in the rate of microsaccades is very similar to that reported by Engbert and Kliegl (2003). They report that approximately 100–150 ms after the onset of a cue that triggers an attentional shift, the rate of microsaccades decreases, and then increases above baseline at about 250–350 ms after cue onset. Our microsaccade rate data are therefore consistent with the possibility that an attentional shift occurs starting approximately 500–750 ms prior to the button press indicating that a new one of the disks has darkened. It appears that attention drives both the darkening transparency effect of Tse (2005), and also drives changes in the rate of microsaccades.

It remains an open and important question why shifts of attention should alter the rate of microsaccades. One possibility is that attentional shifts inhibit or activate some of the same circuits that generate microsaccades, momentarily blocking the generation of microsaccades. The attentional system is thought to have at least two subsystems, one involved in automatic and rapid shifts of “exogenous” attention to abrupt onsets (Irwin, Colcombe, Kramer, & Hahn, 2000; Jonides & Yantis, 1988; Remington, Johnston, & Yantis, 1992; Theeuwes, 1994; Yantis & Hillstrom, 1994; Yantis & Jonides, 1990), and the other subsystem involved in volitional shifts of “endogenous” attention. The bottom-up subsystem is thought to involve circuitry in the superior colliculus (SC), and the top-down subsystem is thought to involve circuitry in the frontal lobe (Mesulam, 1981; Posner & Petersen, 1990). Similarly, saccade generation involves at least two parallel subsystems. A sub-cortical pathway involving the SC generates reflexive, orienting saccades, and a cortical pathway involving the frontal eye fields generates voluntary saccades via top-down input into the SC (e.g., Everling & Munoz, 2000; Hanes, Patterson, & Schall, 1998; Schall, 1995). Because microsaccades are small involuntary conjugate saccades made while voluntarily fixating, their generation can safely be assumed to involve processing within at least the SC pathway. Both the abrupt attentional shift system and the abrupt eye movement system appear to recruit some of the same circuitry in the SC, one to move the direction of gaze and the other to move the focus of processing without necessarily moving the eyes (Corbetta et al., 1998; Kustov & Robinson, 1996; Rizzolatti et al., 1994; Robinson & Kertzman, 1995). If attentional shifts and saccades require processing within overlapping circuitry, then a shift in attention may momentarily activate this circuitry and preclude this same circuitry from generating a microsaccade. Indeed, attentional circuitry may actively inhibit saccade circuitry during an attentional shift. If this is correct, then the brief rise in microsaccade rate above baseline after an attentional shift (seen here and in the data of Engbert & Kliegl, 2003) may result from release from inhibition. In future work it will prove interesting to determine whether changes in the microsaccade rate differ for voluntary versus involuntary shifts in attention.

In conclusion, our data are not consistent with the claim that the distribution of microsaccade directions is altered by the shifts in attention that generate the darkening effect reported by Tse (2005). And our data rule out that the darkening effect is predicted by, caused by, or correlated with the directions of fixational eye movements.

Appendix A

Here, the results of an experiment are described that quantifies the direction and strength of the basic effect for the first time. In particular, it has yet to be shown empirically whether disks darken or lighten when they appear to change brightness. Although the attended disk appears to subjectively darken when it is attended, no empirical test characterizing this most basic aspect of the effect has yet been carried out. When the brightness of one of the disks appears to decrease, it could be that it darkens in absolute terms, or it could be that it darkens only in relative terms. For example, it may be that its perceived brightness remains constant and that of the other disks lightens. To characterize this basic property of the effect, observers adjusted the luminance of two abutting square patches, one indicating the perceived brightness of the darkened disk regardless of which one was darkened, and the other indicating the brightness of the non-darkened disk.

Appendix B. Methods

Four sets of three overlapping gray disks on a constant white ($102.8\,\text{cd/m}^2$ (30 foot-lamberts)) background were used (same configuration as Fig. 1A). Subjects manipulated the luminance of two abutting two degree solid gray square patches located at the bottom of the monitor using the up-down arrow keys for one patch, and the left-right arrow keys for the other patch. One patch was to be manipulated to have the same appearance as the non-overlapping portion of the darkened disk, and the other the appearance of the non-overlapping portion of the non-darkened disk. The luminance of two grayscale square patches was initially always the same, and identical to that of the non-overlapping portion of the disks. Observers were allowed to manipulate the luminance of the patches for as long as necessary, and to make eye movements to the patches. When the perceived brightnesses were accurately specified, the grayscale values were recorded. Each observer carried this out three times per condition, and values were averaged within subject before averaging across subjects. After all five subjects had run in this experiment, luminance values were measured using a Spectra® Spotometer® (Photo Research, Chatsworth, CA, USA) at a distance of 18 cm to determine the actual luminance of the specified gray values.

Appendix C. Results

The actual luminance (in units of foot-lamberts; values in cd/m^2 are given by foot-lamberts × 3.43) of the non-overlapping portion of each disk is indicated in black in Fig. 5. These luminances were chosen arbitrarily to span a large range of brightnesses, so there is no particular significance to the shape of the black curve in Fig. 5. The adjusted luminance corresponding to the non-darkened circles is indicated in green, and that of the darkened circle is indicated in red. The darkened values are significantly different than the non-darkened values ($F(3,40) \ll .0001$). The brighter values do not differ from the real value at luminance level 1 ($p = 0.07$) or level 2 ($p = 0.50$), but do differ significantly from the real value at luminance level 3 ($p = 0.004$) and level 4 ($p = 0.04$). The darker values do not differ from the real value at luminance level 1 ($p = 0.99$), but do differ significantly from the real value at luminance level 2 ($p = 0.02$), level 3 ($p < 0.0001$), and level 4 ($p < 0.0001$), assessed using a two-tailed t-test.

Appendix D. Discussion

These results imply that the one disk that appears to darken in this illusion darkens in absolute, not just relative terms. The disks that do not appear to darken, do not in fact darken at all, but remain constant.

References

Adelson, E. (1993). Perceptual organization and the judgment of brightness. *Science, 262*, 2042–2044.

Anderson, B. L. (2003). The role of occlusion in the perception of depth, lightness, and opacity. *Psychological Review, 110*(4), 785–801.

Anderson, B. L. (1999). Stereoscopic surface perception. *Neuron, 24*(4), 919–928.

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., et al. (1998). A common network of functional areas for attention and eye movements. *Neuron, 21*(4), 761–773.

Cornsweet, T. N. (1970). *Visual perception*. New York: Academic Press.

Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research, 43*, 1035–1045.

Everling, S., & Munoz, D. P. (2000). Neuronal correlates for preparatory set associated with pro-saccades and anti-saccades in the primate frontal eye field. *Journal of Neuroscience, 20*(1), 387–400.

Gilchrist, A. L. (1977). Perceived lightness depends on perceived spatial arrangement. *Science, 195*, 185.

Hafed, Z. M., & Clark, J. J. (2002). Microsaccades as an overt measure of covert attention shifts. *Vision Research, 42*(22), 2533–2545.

Hanes, D. P., Patterson, W. F., & Schall, J. D. (1998). Role of frontal eye fields in countermanding saccades: visual, movement, and fixation activity. *Journal of Neurophysiology, 79*(2), 817–834.

Horwitz, G. D., & Albright, T. D. (2003). Short-latency fixational saccades induced by luminance increments. *Journal of Neurophysiology, 90*(2), 1333–1339.

Horowitz, T.S., Fine, E.M., Fencsik, D.E., Yurgenson, S., & Wolfe, J.M. (2006). Fixational eye movements are not an index of covert attention. Psychological Science, in press.

Hsieh, P.-J., Caplovitz, G.P., & Tse, P.U. (2006). Microsaccades reveal that motion-induced blindness is not due to sensory adaptation. Neuroreport, in press.

Irwin, D. E., Colcombe, A. M., Kramer, A. F., & Hahn, S. (2000). Attentional and oculomotor capture by onset, luminance and color singletons. *Vision Research, 40*, 1443–1458.

Jonides, J., & Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. *Perception & Psychophysics, 43*, 346–354.

Kanill, D., & Kersten, D. (1991). Apparent surface curvature affects lightness perception. *Nature, 351*, 228.

Kowler, E., & Steinman, R. M. (1979). The effect of expectations on slow oculomotor control. I. Periodic target steps. *Vision Research, 19*(6), 619–632.

Kustov, A. A., & Robinson, D. L. (1996). Shared neural control of attentional shifts and eye movements. *Nature, 384*(7), 74–77.

Leopold, D., & Logothetis, N. K. (1999). Multistable phenomena: changing views in perception. *Trends in Cognitive Sciences, 3*(7), 254–264.

Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2004). The role of fixational eye movements in visual perception. *Nature Reviews Neuroscience, 5*, 229–240.

Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Dyar, T. A. (2006). Microsaccades counteract visual fading during fixation. *Neuron, 49*, 297–305.

Meng, M., & Tong, F. (2004). Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. *Journal of Vision, 4*(7), 539–551.

Mesulam, M. M. (1981). A cortical network for directed attention and unilateral neglect. *Annals of Neurology, 10*, 309–325.

Metelli, F. (1974). The perception of transparency. *Scientific American, 230*(4), 91.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience, 13*, 25–42.

Remington, R. W., Johnston, J. C., & Yantis, S. (1992). Involuntary attentional capture by abrupt onsets. *Perception & Psychophysics, 51*, 279–290.

Rizzolatti, G. et al. (1994). In C. Umilta & E. M. Moscovitch (Eds.), *Attention and Performance XV* (pp. 231–265). Cambridge: MIT.

Robinson, D. L., & Kertzman, C. (1995). Covert orienting of attention in macaques. III. Contributions of the superior colliculus. *Journal of Neurophysiology, 74*(2), 713–721.

Rolfs, M., Engbert, R., & Kliegl, R. (2004). Microsaccade orientation supports attentional enhancement opposite a peripheral cue: commentary on Tse, Sheinberg, and Logothetis (2003). *Psychological Science, 15*(10), 705–707.

Schall, J. D. (1995). Neural basis of saccade target selection. *Reviews in the Neurosciences, 6*(1), 63–85.

Singh, M., & Anderson, B. L. (2002). Toward a perceptual theory of transparency. *Psychological Reviews, 109*(3), 492–519.

Slotnick, S. D., & Yantis, S. (2005). Common neural substrates for the control and effects of visual attention and perceptual bistability. *Brain Research Cognitive Brain Research, 24*(1), 97–108.

Steinman, R. M., Cunitz, R. J., Timberlake, G. T., & Herman, M. (1967). Voluntary control of microsaccades during maintained monocular fixation. *Science, 155*, 1577–1579.

Theeuwes, J. (1994). Stimulus-driven capture and attentional set: selective search for color and visual abrupt onsets. *Journal of Experimental Psychology: Human Perception & Performance, 20*(4), 799–806.

Tse, P. U. (2005). attention modulates the brightness of overlapping transparent surfaces. *Vision Research, 45*(9), 1095–1098.

Tse, P. U., Sheinberg, D. L., & Logothetis, N. K. (2002). Fixational eye movements are not affected by abrupt onsets that capture attention. *Vision Research, 42*, 1663–1669.

Tse, P. U., Sheinberg, D. L., & Logothetis, N. K. (2004). The distribution of microsaccade directions need not reveal the location of attention. *Psychological Science, 15*(10), 708–710.

Watanabe, T., & Cavanagh, P. (1993). Surface decomposition accompanying the perception of transparency. *Spatial Vision, 7*(2), 95–111.

Winterson, B. J., & Collewijn, H. (1976). Microsaccades during finely guided visuomotor tasks. *Vision Research, 16*(12), 1387–1390.

Yantis, S., & Hillstrom, A. P. (1994). Stimulus-driven attentional capture: evidence from equiluminant visual objects. *Journal of Experimental Psychology: Human Perception & Performance, 20*(1), 95–107.

Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception & Performance, 16*(1), 121–134.