

Metacontrast masking is specific to luminance polarity

Mark W. Becker^{a,*}, Stuart Anstis^b

^a Department of Psychology, Lewis and Clark College, 0615 SW Palatine Hill Road, Portland, OR 97219-7899, USA

^b Department of Psychology, University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0109, USA

Received 4 August 2003; received in revised form 7 May 2004

Abstract

A 1°-spot was flashed up on a screen, followed by a snugly fitting annular mask. We measured the amount of masking as a function of stimulus luminance. The surround was always mid-gray, the masking ring was either black or white, and the luminance of the spot target ranged from 0% to 100% of white in 4% steps. Observers reported the apparent lightness of the masked spot by adjusting a matching spot. *Results:* A black annular mask made all spots that were darker than the gray surround appear to be transparent, that is, of the same luminance as the surround (complete masking). The black ring had virtually no masking effect on spots that were lighter than the surround. Conversely, a white ring made all spots that were lighter than the gray surround look apparently the same luminance as the surround (complete masking), but had virtually no masking effect on spots that were darker than the surround. In summary, a black ring masked spatial decrements but not increments, whilst a white ring masked spatial increments but not decrements. Thus masking occurred only when the spot and the ring had the same luminance polarity. This same-polarity masking still occurred when the target spot was larger than the ‘donut hole’ of the masking ring, so that the target and ring partly overlapped. This ruled out simple edge-cancellation theories. Instead, masking disrupts the filling-in process that normally propagates inward from the edges of a spot [Vision Res. 31 (7–8) (1991) 1221]. We conclude that metacontrast masking occurs within, but not between, separate visual ON and OFF pathways.

© 2004 Elsevier Ltd. All rights reserved.

Keywords: Metacontrast; Masking; Luminance; ON channels; OFF channels

1. Introduction

Metacontrast masking is a useful tool for examining the time course of contour and brightness formation in the visual system. In metacontrast masking, a luminous spot is briefly flashed on a screen and followed, after an interval of 80–100 ms, by a briefly flashed luminous annulus whose inner diameter just fits the circumference of the spot (Werner, 1935). As a result, observers see the annulus but fail to see the spot. This form of backward masking, in which the target and mask share a contour, is known as metacontrast. It has attracted wide interest,

including several reviews (Breitmeyer & Ogmen, 2000; Enns & Di Lollo, 2000; Fox, 1978; Kahneman, 1968; Weisstein, 1972) and two books devoted solely to the topic (Bachmann, 1994; Breitmeyer, 1984).

The *timing* of metacontrast has been much studied. The effect of the visual mask stimulus on the perceptual strength of the target stimulus varies with the stimulus-onset asynchrony (SOA) between them. As SOA increases, the target percept first becomes weaker, bottoms out at an intermediate SOA in the order of 80 ms, and then increases for still larger SOAs (Reeves, 1982; Stoper & Banffy, 1977). As a result, a plot of target percept strength against SOA produces a U-shaped masking curve, with maximum masking at an intermediate SOA, as reviewed by Breitmeyer and Ganz, 1976 and by Breitmeyer (1984, chapter 4). Francis (1997, 2000)

* Corresponding author. Tel.: +1-503-768-7654; fax: +1-503-768-7658.

E-mail address: mbecker@lclark.edu (M.W. Becker).

reviews mathematical models of masking. His boundary contour model claims to account for nine key properties of metacontrast masking.

Metacontrast occurs dichoptically, that is, when the target is presented to one eye and the mask is presented to the other (Kolers & Rosner, 1960). Color also affects metacontrast. Bevan, Jonides, and Collyer (1970) have briefly noted that metacontrast is maximum when identical colors are used, is greatly reduced when complementary colors are used for the target and the mask, and is intermediate when differing but non-complementary colors are used. Kaloudis, Friedman, Vemuri, and von der Heydt (1998) also found that metacontrast was highly color selective, such that masking was strongest when the mask had the same color as the test, and fell off with color distance. Thus metacontrast depended on proximity in color space, which suggests that cortical color coding occurs in narrowly tuned channels. Beer, Becker and Anstis (unpublished results) reach similar conclusions.

Macknik and Livingstone (1998) recorded neural responses from V1 in awake and anesthetized monkeys in response to masking stimuli. They found that stimuli that in humans produce forward masking (in which the mask precedes the target) suppressed the transient on-response to the target in monkey visual cortex. Those that produce backward masking (in which the mask comes after the target) inhibited the transient after-

discharge, the excitatory response that occurs just after the disappearance of the target. Their results suggest that the visibility of brief (maskable) targets is largely determined by the transient neuronal responses associated with onset and turning off of the target.

We used exclusively achromatic stimuli, and our concern in this paper is with the *relative luminance* of the target, the mask, and the surround. To anticipate, we find that masking occurs only when a target and mask have the same luminance polarity, with both being lighter than their surround, or with both being darker.

In our experiments, observers viewed a spot that was flashed up and then followed by a snugly fitting annular mask. The observer reported the apparent lightness of this masked spot by adjusting a nearby, unmasked matching spot, until the two spots appeared to match. The settings of apparent matches were recorded for later analysis. The observers were the two authors (MB, SA). In addition, our results have been repeatedly confirmed on other observers, both in our labs and elsewhere (J. Yellott, personal communication).

Fig. 1a shows two possible ‘ideal’ results. If the spots were always seen veridically, with no masking occurring, then all the datum points would lie along the line of unit slope. On the other hand, if there were complete masking on every trial the spot would always be invisible and would appear to have the same mid-gray as the surround. This possibility is shown by the horizontal line.

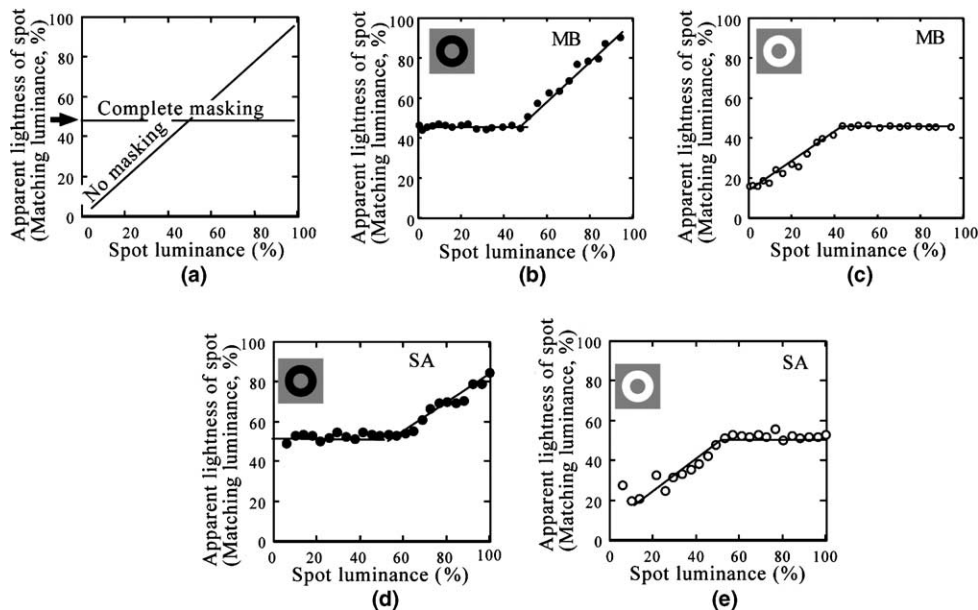


Fig. 1. (a) Possible results. If dots were seen veridically, all data points would lie along the line of unit slope, for which $y=x$. If dots were completely masked they would be indistinguishable from the surround and would lie along the horizontal line of luminance 45%. (c, e) Black annular mask on a mid-gray surround has no effect on spatial-increment spots that are lighter than the surround (right part of curve). But they make all spots that are darker than the surround become invisible and look the same mid-gray as the surround (horizontal left part of curve). (b, d) Conversely, white annular mask on a mid-gray surround has no effect on spatial-decrement spots that are darker than the surround (left part of curve). But they make all spots that are lighter than the surround become invisible and look the same mid-gray as the surround (horizontal right part of curve).

1.1. Method

1.1.1. Stimuli

Two spots were repetitively flashed up simultaneously for 33 ms on a computer-controlled monitor screen. Both spots were 1° in diameter, and their centers were located 1.8° above and 1.8° below a fixation point. The lower spot was followed after a 100 ms interstimulus interval (ISI) by an annular mask that was flashed up for 100 ms. This mask had an outer diameter 2° of visual angle, and an inner diameter (1° of visual angle) that was the same as the outer diameter of the test spot. The two spots were flashed repetitively every 700 ms, with only the lower spot being masked.

The luminances were as follows: The maximum screen luminance was 63.4 cdm^{-2} , which we designate as 100% (white). The surround was set to a mid-gray of 45%. The lower, masked spot was randomly set on each trial to a luminance between 0% and 100%, and maintained this luminance throughout a trial. On each block of trials the annular mask was set to either black or white, and maintained that luminance throughout the block.

1.1.2. Procedure

The lower test spot was preset on a trial-by-trial basis to one of 25 values, selected at random (0%, 4%, 8%, 12%, 16%, ..., 92%, 96%, 100%). The adjustable upper spot was set to a different random initial value on every trial, to reduce observer bias effects. The observer's task was to adjust the luminance of the upper spot, by striking a 'lightening' or a 'darkening' key, until it appeared to match the masked lower spot. Every 700 ms both spots were flashed up simultaneously for 100 ms, and the observer kept adjusting the upper spot until s/he was satisfied that the two spots matched. S/he then pressed the space bar. This automatically recorded the settings of the upper and lower spot for later analysis. The lower spot was then set to another randomly chosen luminance value, and the process was repeated, until matches had been made for all 25 luminance values.

1.2. Results

Results for conditions which had a white masking ring on a mid-gray (45%) surround are plotted for both observers separately in Fig. 1 panels c and e. Note that if masking made no difference to the appearance of the test spot, the results would lie along the line of unit slope. If masking made the test spot look lighter (or darker), this would push the data points above (or below) the line of unit slope.

In Fig. 1c and e, the datum points lay along the line of unit slope for spots that were darker than the surround, but then leveled out and lay along a horizontal line for spots that were lighter than the surround. The

height of this horizontal line indicates that these light spots were seen as the same gray as the surround, that is, they were invisible to the observer. This implies that a white ring masked light spots almost completely, but had virtually no masking effect on dark spots.

This state of affairs was reversed when the surround was gray and masking ring was black (Fig. 1b and d). Now the datum points lay along a horizontal line for spots that were darker than the surround, indicating that these spots were invisible. However, for spots that were lighter than the surround the data lay along the line of unit slope, showing that they were not masked at all by the black ring. This implies that a black ring masked dark spots almost completely, but had virtually no masking effect on light spots.

In sum, on a mid-gray surround of 45%, the annular mask had almost no effect on the appearance of the test spot, provided that the spot and the masking annulus were of opposite luminance polarities (one being a spatial increment, the other a spatial decrement). However, when the spot had the same luminance polarity as the annulus it was fully masked and appeared transparent, so that it looked the same luminance as the surround. Thus when the annular mask was black, all dark spots, from mid-gray down to black, became invisible and looked the same mid-gray as the surround. However, light spots, from mid-gray up to white, were unaffected by the black mask and were seen veridically. Conversely, when the annular mask was white, all light spots, from mid-gray up to white, became invisible and looked the same mid-gray as the surround. However, dark spots, from mid-gray down to black, were unaffected by the white mask and were seen veridically.

Fig. 2 shows a cartoon of the results. A white spot followed by a white annular mask is invisible (fully masked) and so is a black spot followed by a black annular mask. However, no masking occurs when a white spot followed by a black mask, or a black spot is followed by a white mask.

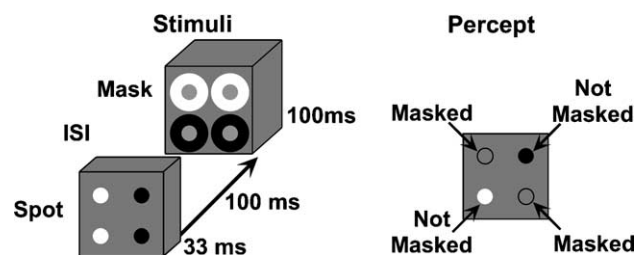


Fig. 2. Cartoon of (a) stimulus. Time is not shown to scale; and (b) results. Four spots are flashed up, followed by four masks. Complete masking occurs if both spot and mask are white, or if both spot and mask are black. No masking occurred if spot is black and mask is white, or vice versa.

2. Experiment 2: area masking or edge cancellation?

Why should a light ring mask only light spots, and a dark ring mask only dark spots? There are two possibilities. Either masking occurs only when the target and mask are of the same polarity, or else the edges cancel at the junction where the target spot meets the target. Note that when the spot and the ring have the same polarity, the edges where they meet have opposite polarities. Reading outward from the center of a white spot on a gray surround, the edge is white (spot) to gray (surround), in other words light to dark. Reading outwards from the center of a white ring on the same gray surround, the edge is gray (the ‘hole in the donut’) to white (the ring), in other words dark to light. So perhaps a light to dark edge presented first is masked when it is followed by a dark to light edge. There is recent evidence that visual neurons in areas V1, V2, and V4 of awake behaving monkeys can encode edges, their luminance polarity, and their border ownership (Zhou, Friedman, & von der Heydt, 2000). Such neurons could plausibly support edge cancellation.

In Experiment 2 we tested whether successive edges of opposite polarity might cancel out, by varying the relative size of the spot and the hole in the mask. (In the previous experiment these were of the same size.) The logic was as follows. If masking is caused by edge cancellation, it should work optimally only when the edges of the target and mask abut, that is when the target spot is exactly the same size as the hole in the annular mask. So if masking proves to be still present when the target is appreciably larger or smaller than the hole in the mask, this will rule out edge cancellation as the sole mechanism of masking.

2.1. Methods

Two conditions were run: In one condition the target and mask were both white, and in the other condition they were both black. (Both conditions gave strong masking in Experiment 1.) The surround was mid-gray

(45% of white). The mask was always the same size, with an inner diameter of 1° and an outer diameter of 3° . The size of the target was either 0.5° , 0.75° , 1° , 1.25° , 1.5° or 1.75° , and a size was picked randomly on each trial. It follows that the ratio of the spot size to the mask-hole size was 0.5, 0.75, 1, 1.25, 1.5 or 1.75. In all other respects the procedure was the same as in Experiment 1.

2.2. Results

Results are shown in Fig. 3. Data for white spots masked by a white ring are shown as open circles, and data for black spots masked by a black ring are shown as filled circles. Fig. 3a shows hypothetical ‘ideal’ results: If there were no masking at all, the perceived brightness of all the white targets would be 100% and of the black targets would be 0%. If there were complete masking then all the targets, black and white alike, would have a perceived brightness equal to the surround luminance of 45%. In fact, Fig. 3b and c shows that small targets, half the size of the mask hole, showed almost no masking. Targets three-quarters the size of the mask hole showed partial masking. Targets that were the same size or larger than the mask hole were masked almost completely. Results were symmetrical for black and white targets.

In summary, our results show that if the spot was made progressively smaller than the hole in the mask, then masking was progressively reduced and the spot remained visible. However, if the spot was the same size as the hole or larger then masking was almost complete (datum points lay along a horizontal line at 45%), even though the edges of the spot and the mask no longer coincided. So the edges of the target and the mask did not need to abut for masking to occur. We did not find that masking reached a local maximum when the target and hole coincided, falling off symmetrically if the target were either larger or smaller than the mask hole. Such a finding would have given a V-shaped plot in Fig. 3, with the V’s vertex at a target/hole size ratio of 1. Instead, the datum curve was asymmetrical. Masking did fall off

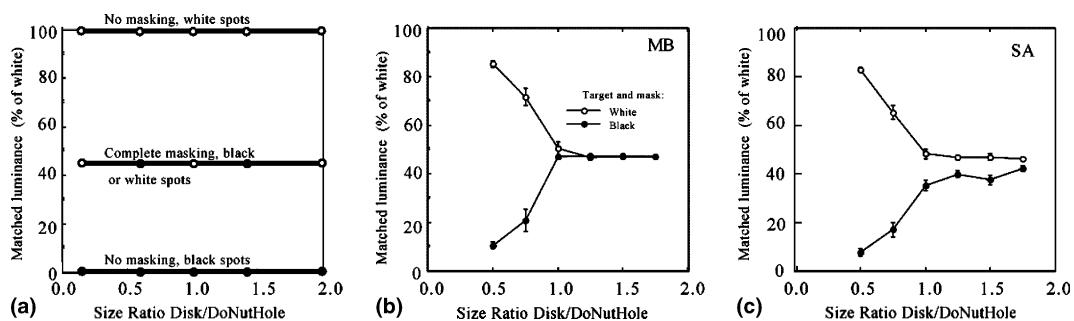


Fig. 3. Effect of spot size: (a) hypothetical results; (b) and (c) for both observers, small spots that did not overlap the mask were not much masked, but larger spots that overlapped the inner part of the mask were strongly masked. Results attribute masking to matching polarities of test spot and mask, not to edge interactions between spot and mask.

monotonically as the target was made smaller than the hole, as if the edges of a mask exercised a masking influence that fell off spatially as the target-mask separation increased. But when the target was made progressively larger than the hole, so that the mask overlapped the target, masking did not fall off at all but in fact stayed at the maximum possible. This experiment offers strong evidence that an edge cancellation model alone cannot explain metacontrast masking.

We conclude that local cancellation of opposite-polarity edges is not the sole explanation for masking. Instead, masking is contingent upon the areas of the spot and the ring having the *same* luminance polarity.

3. Discussion

3.1. Our results differ from others

We have found no other published reports that masking is polarity specific. [Breitmeyer \(1978\)](#) used black or white spots on a medium gray surround, which were masked by spatially surrounding rings that again could be either black or white on gray. He found only a minimal increase in masking when the target and mask had the same polarity. [Sherrick, Keating, and Dember \(1974\)](#) masked both black and white targets with either black or white masks on a gray surround, and they also reported little or no effect of luminance polarity. Neither [Breitmeyer's results \(1978\)](#) nor those of [Sherrick et al. \(1974\)](#) are really consistent with ours. Although we cannot fully account for these differences, they may arise from differences in methods.

[Sherrick's](#) exposure times were much briefer than ours—we used a stimulus duration of 33 ms, an ISI of 100 ms, and a mask duration of 100 ms, compared with their values of 15, 0, and 100 ms. Thus the SOA for their study was 15 ms, while ours was 133 ms. Masking at longer SOAs may follow different rules than masking at extremely short SOAs.

[Breitmeyer's](#) task was different from ours. His observers had to detect a truncation or flat on the target disk, whereas we looked directly at the effect of masking on perceived brightness. His geometrical task and our brightness task may follow different rules, but it is not clear why this should make such a difference. We have confidence in our results, which were clean and robust and have been informally confirmed on a dozen other observers, as well as by independent investigators elsewhere ([J. Yellott](#), personal communication).

We conclude that the masking of spots by annuli takes place independently for spatial increments and for spatial decrements, with little or no interaction between them. This implies that metacontrast masking occurs independently within *ON* pathways and within *OFF* pathways ([Schiller, 1982, 1984, 1992](#)), but that little or

no masking occurs between *ON* and *OFF* pathways. [Schiller \(op. cit.\)](#) reported that the *ON* and *OFF* pathways are processed separately until the early visual cortex. At the cortical level there is evidence of an interaction between the two pathways ([Bowen, 1995](#); [Edwards & Badcock, 1994](#); [Harris & Parker, 1995](#); [Schechter & Hochstein, 1990](#)).

3.2. *ON* and *OFF* pathways

There is a wealth of physiological and psychophysical evidence for the existence of separate *ON* and *OFF* pathways. [Schiller \(1982, 1984, 1992\)](#) reviews the physiological evidence. There are also chemical differences: DL-2-amino-4-phosphonobutyric acid (APB) reduces the sensitivity of *ON* and *OFF* responses in goldfish retina, although the *ON*-responses are reduced significantly more than the *OFF*-responses ([Bilotta, Demarco, & Powers, 1995](#)), whilst kainic acid selectively destroys *OFF*—rather than *ON*—bipolar cells in chickens, and also destroys amacrine cells ([Dvorak & Morgan, 1983](#)).

In a series of papers, [Bowen](#) and others have found psychophysical evidence for separate *ON* and *OFF* pathways. [Bowen \(1995, 1997\)](#) and [Bowen and de Ridder \(1998\)](#) reported facilitatory and inhibitory interactions between *ON* and *OFF* pathways when they masked a bar with a flashed grating. [Bowen, Pokorny, and Smith \(1989\)](#) and [Bowen, Pokorny, Smith, and Fowler \(1992\)](#) found that temporal contrast sensitivity to temporal increments and decrements in light level was mediated by separate *ON* and *OFF* visual mechanisms. [Anstis \(1967\)](#) and [Arnold and Anstis \(1993\)](#) found that following adaptation to a gradually brightening (or dimming) gray patch that was modulated by a 1 Hz repetitive temporal sawtooth, a subsequently viewed steady patch showed an aftereffect of apparent dimming (or brightening). They attributed this to selective adaptation of neural pathways selective for gradual temporal increase (or decrease) of luminance, in other words *ON* and *OFF* pathways. Such adaptation produced threshold elevations, both for gradual brightening and dimming ([Hanly & MacKay, 1979](#)), and conversely, for detecting the *fast* phase of a fast-on or fast-off temporal sawtooth ([Krauskopf, 1980](#)). Our experiments add a further quantum to the growing pile of evidence that *ON* and *OFF* pathways are not only traceable by physiological techniques, but are also separable in many psychophysical tasks.

3.3. *Not magno—parvo mismatch*

[Breitmeyer \(1984\)](#) proposed that masking resulted from a mismatch between the magno (*M*) and parvo (*P*) visual pathways. Our results do not favor this model for the following reasons. We find that masking is highly sensitive to luminance polarity, and there is independent

evidence for ON and OFF channels within both magno and parvo pathways (Schiller, 1984). However, a magno–parvo mismatch story would need to add complexity in which cross-pathway inhibition would be restricted within a single polarity channel; and we know of no independent evidence for this.

Our results can also be extended to color. In further experiments together with Dirk Beer (being prepared for publication), we find that a red mask will mask red spots but not green spots, and a green mask will mask green spots but not red spots. This implies that masking is selective both for luminance polarity, a property of the M pathways, and for hue opponence, a property of the P pathways (Derrington & Lennie, 1984; Lennie, Krauskopf, & Sclar, 1990; Livingstone & Hubel, 1987; Wiesel & Hubel, 1966). An M–P mismatch model would have trouble in explaining how separate properties of the M and P pathways can combine so smoothly to yield very similar masking curves for luminant and chrominant stimuli.

3.4. Filling-in theories

Our results on spot size in Experiment 2 lead us to conjecture that the contour of the mask hole might be interfering with a brightness filling-in process within the target spot. This filling-in was first proposed by Paradiso and Nakayama (1991), who flashed up a large white spot followed by a masking white outline circle, concentric with the spot but of smaller radius. They found that the mask had a large (up to 2 log unit) suppressive effect on the brightness of the target, but only inside the radius of the mask. They also found that the latest time at which masking was effective was correlated with the distance between the edge of the target stimulus and the contour in the mask, and they concluded that the masking contour was interfering with the propagation of a brightness signal traveling inwards from the target's border. However, it is not at all clear why such an interference with filling-in would be so extremely sensitive to polarity.

Paradiso and Nakayama suggest that when a uniform luminance spot is viewed, the luminance information 'fills in', or propagates inward from the edge. This theory offers two opportunities for masking to occur within a metacontrast experiment. First, interrupting or degrading the edge signal (edge cancellation) would reduce the amount of energy that could propagate. Second, if the target's edge was unmasked, the brightness information from that edge would propagate inward from that edge. If the mask contained a second edge with the opposite polarity and this edge appeared within the area of the target, this second edge may serve as a terminating point of the propagation. So we conjecture that when a snugly fitting annulus masks a target spot (Experiment 1) the mask interrupts or degrades the

perimeter of the target. This attenuates the edge signal so that it cannot propagate into the spot from that edge, and thus the target is masked. If however, the target's edge is not in the same location as the mask's inner edge, the mask now fails to affect the edge signal of the target spot, thus luminance information from the target's edge begins to propagate inward filling in the target. If the inner edge of the mask is flashed up before the filling-in process reaches it, then the mask's edge serves as a stopping point for the target's filling-in process. Thus the target itself becomes something of an annulus with no filling in of the inner part of the target. In other words, if the donut hole in a mask is smaller than the target spot, it stops the propagation in its tracks, but if it is the same size as the target spot it nips the propagation in the bud.

Acknowledgements

Supported by a grants from the UCSD Academic Senate and Department of Psychology to SMA.

References

- Anstis, S. M. (1967). Visual adaptation to gradual change of luminance. *Science*, *155*, 710–712.
- Arnold, K., & Anstis, S. (1993). Properties of the visual channels that underlie adaptation to gradual change of luminance. *Vision Research*, *33*, 47–54.
- Bachmann, T. (1994). *Psychophysiology of visual masking: The fine structure of conscious experience*. Nova Science Publishers.
- Bevan, W., Jonides, J., & Collyer, S. C. (1970). Chromatic relationships in metacontrast suppression. *Psychonomic Science*, *19*, 367–368.
- Bilotta, J., Demarco, P. J., & Powers, M. K. (1995). The contributions of ON- and OFF-pathways to contrast sensitivity and spatial resolution in goldfish. *Vision Research*, *35*(1), 103–108.
- Bowen, R. W. (1995). Isolation and interaction of ON and OFF pathways in human vision: Pattern-polarity effects on contrast discrimination. *Vision Research*, *35*, 2479–2490.
- Bowen, R. W. (1997). Isolation and interaction of ON and OFF pathways in human vision: Contrast discrimination at pattern offset. *Vision Research*, *37*, 185–198.
- Bowen, R. W., & de Ridder, H. (1998). Dynamic contrast perception assessed by pattern masking. *Journal of Optical Society of America A—Optics Image Science and Vision*, *15*, 570–578.
- Bowen, R. W., Pokorny, J., & Smith, V. C. (1989). Sawtooth contrast sensitivity: Decrements have the edge. *Vision Research*, *29*(11), 1501–1509.
- Bowen, R. W., Pokorny, J., Smith, V. C., & Fowler, M. A. (1992). Sawtooth contrast sensitivity: Effects of mean illuminance and low temporal frequencies. *Vision Research*, *32*, 1239–1247.
- Breitmeyer, B. G. (1978). Metacontrast with black and white stimuli: Evidence of inhibition of on and off sustained activity by either on or off transient activity. *Vision Research*, *18*, 1443–1448.
- Breitmeyer, B. G. (1984). *Visual masking: An integrative approach*. Oxfordshire/New York: Oxford/Clarendon Press/Oxford University Press.
- Breitmeyer, B. G., & Ganz, L. (1976). Implications of sustained and transient channels for theories of visual pattern masking, saccadic

- suppression, and information processing. *Psychological Review*, 83, 1–36.
- Breitmeyer, B. G., & Ogmen, H. (2000). Recent models and findings in visual backward masking: A comparison, review, and update. *Percept Psychophysics*, 62, 1572–1595.
- Derrington, A. M., & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurons in lateral geniculate nucleus of macaque. *Journal of Physiology*, 357, 219–240.
- Dvorak, D. R., & Morgan, I. G. (1983). Intravitreal kainic acid permanently eliminates off-pathways from chicken retina. *Neuroscience Letters*, 36(3), 249–253.
- Edwards, M., & Badcock, D. (1994). Global motion perception: Interaction of the ON and OFF pathways. *Vision Research*, 34, 2849–2858.
- Enns, J., & Di Lollo, V. (2000). What's new in visual masking?. *Trends in Cognitive Science*, 9(4), 345–352.
- Fox, R. (1978). Visual masking. In R. Held, H. W. Leibowitz, & H.-L. Teuber (Eds.), *Handbook of sensory physiology. Vol. 8: Perception*. Heidelberg: Springer-Verlag.
- Francis, G. (1997). Cortical dynamics of lateral inhibition: Metacontrast masking. *Psychological Review*, 104(3), 572–594.
- Francis, G. (2000). Quantitative Theories of Metacontrast Masking. *Psychological Review*, 107(4), 768–785.
- Hanly, M., & MacKay, D. M. (1979). Polarity-sensitive perceptual adaptation to temporal sawtooth modulation of luminance. *Experimental Brain Research*, 35(1), 37–46.
- Harris, J., & Parker, A. (1995). Independent neural mechanisms for bright and dark information in binocular stereopsis. *Nature*, 374, 808–810.
- Kahneman, D. (1968). Metacontrast: Methods, findings and theory in studies of visual masking. *Psychological Bulletin*, 70, 404–425.
- Kaloudis, P., Friedman, H., Vemuri, C., & von der Heydt, R. (1998). Color selectivity of metacontrast masking. *Investigative Ophthalmology and Visual Science*, 39, S407.
- Kolers, P. A., & Rosner, B. S. (1960). On visual masking (metacontrast): Dichoptic observations. *American Journal of Psychology*, 73, 2–21.
- Krauskopf, J. (1980). Discrimination and detection of changes in luminance. *Vision Research*, 20(8), 671–677.
- Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience*, 10(2), 649–669.
- Livingstone, M. S., & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *Journal of Neuroscience*, 7(11), 3416–3468.
- Macknik, S. L., & Livingstone, M. S. (1998). Neuronal correlates of visibility and invisibility in the primate visual system. *Nature Neuroscience*, 1(2), 144–149.
- Paradiso, M. A., & Nakayama, K. (1991). Brightness perception and filling-in. *Vision Research*, 31(7–8), 1221–1236.
- Reeves, A. (1982). Metacontrast U-shaped functions derived from two monotonic processes. *Perception*, 11(4), 415–426.
- Schechter, S., & Hochstein, S. (1990). ON and OFF pathway contributions to apparent motion perception. *Vision Research*, 30, 1189–1204.
- Schiller, P. H. (1982). Central connections to the retinal ON- and OFF-pathways. *Nature*, 297, 580–583.
- Schiller, P. H. (1984). The connections of the retinal ON- and OFF-pathways on the lateral geniculate nucleus of the monkey. *Vision Research*, 24, 923–932.
- Schiller, P. H. (1992). The ON and OFF channels of the visual system. *Trends in Neurosciences*, 15, 86–92.
- Sherrick, M. F., Keating, J. K., & Dember, W. N. (1974). Metacontrast with black and white stimuli. *Canadian Journal of Psychology*, 28, 438–445.
- Stoper, A. E., & Banffy, S. (1977). Relation of split apparent motion to metacontrast. *Journal of Experimental Psychology: Human Perception and Performance*, 3, 258–277.
- Weinstein, N. (1972). Metacontrast. In Jameson, D., & Hurvich, L. M. (Eds.), *Handbook of sensory physiology: Visual psychophysics* (Vol. VII/4). New York: Springer-Verlag.
- Werner, H. (1935). Studies on contour: I. Qualitative analysis. *American Journal of Psychology*, 47, 40–64.
- Wiesel, T. N., & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *Journal of Neurophysiology*, 29(6), 1115–1156.
- Zhou, H., Friedman, H. S., & von der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *Journal of Neuroscience*, 20(17), 6594–6611.