Does attention alter appearance?

KEITH A. SCHNEIDER
University of Rochester, Rochester, New York
and Princeton University, Princeton, New Jersey

Abrupt onsets in the visual field can change the appearance of subsequent stimuli, according to one interpretation, by engaging an attentional mechanism that increases effective stimulus contrast. However, abrupt onsets can also engage capacity-unlimited and thus attention-independent sensory mechanisms. We conducted a series of experiments to differentiate the sensory and attentional accounts. Observers compared the contrasts of uncued low-contrast peripheral targets with simultaneous targets cued by one of three cue types with different sensory attributes: white or black peripheral abrupt onsets and central gaze direction cues devoid of sensory activity near the target locations. Each cue facilitated the perception of perithreshold targets; however, the white abrupt onsets increased the perceived contrast of suprathreshold targets, whereas the black abrupt onsets tended to reduce the perceived contrast, and the gaze direction cues had no significant effect. The effectiveness of the gaze direction cues in automatically orienting attention was demonstrated in a control experiment in which they consistently speeded response times. The results suggest that sensory interaction, and not attention, is responsible for changes in appearance.

A common feature of our nervous system is that the property of intensity—for example, the loudness of a tone, the luminance contrast of a light (its brightness relative to the background), or the strength of a muscular contraction—is encoded by the discharge frequency of neurons. Attention to a stimulus increases that stimulus's evoked firing rate, and, in the early visual system, attention ostensibly functions to increase the effective contrast of a stimulus, operating through what has become known as the *contrast gain model of attention*. For example, in neurons in areas V4 and MT of the macaque visual cortex, attention directed to a stimulus increases firing rates similar to an increase in the stimulus contrast (Martínez-Trujillo & Treue, 2002; Reynolds, Pasternak, & Desimone, 2000). In macaque V4, attention has an effect on orientation tuning curves of single neurons similar to that of contrast increments in the cat visual cortex, multiplicatively increasing the amplitude without changing the tuning width (McAdams & Maunsell, 1999; Sclar & Freeman, 1982; Skottun, Bradley, Sclar, Ohzawa, & Freeman, 1987).

The perceptual consequences of this apparent interchangeability between attention and contrast (the contrast gain model) in the early visual cortex are unclear. The independence of attention and the intensity of perception have been important questions in experimental psychology since the late nineteenth century (Newhall, 1921; Pillsbury, 1908; Titchener, 1908), but several methodological difficulties have hindered progress. First, conscious perception is difficult to study physiologically because its neural correlates remain unclear (e.g., Helekar, 1999; Markowitsch, 1995; Pollen, 1999; Rees, Kreiman, & Koch, 2002). Subjective comparisons between test and reference stimuli are the best we can do to study perception as a dependent variable. Second, to modulate attention as the independent variable within this paradigm, attention must be differentially allocated between the two stimuli. The difficulty of this was noted by Pillsbury (1908):

> It is impossible directly to compare an object attended to with one not attended to. There is an unavoidable impulse to attend to both before the judgment is made, and any results that should claim to be accurate on this point would be open to grave suspicion. (p. 4)

The problem has persisted because many modern methods of orienting attention, such as central arrows pointing toward locations in peripheral visual space (Posner, 1980), require volitional compliance; that is, observers must voluntarily shift their attention, and the cues may be easily ignored (Jonides, 1981). One method to circumvent this problem is to present the various test stimuli individually under different attentional conditions to be subsequently compared with the reference stimuli. Previous studies have used reference stimuli identical to the test stimuli (Hamlin, 1896; Münsterberg, 1894), a subjective scale (Newhall, 1923), exemplars (Tsal, Shalev,

Zakay, & Lubow, 1994, Experiments 1–3), or a physical scale (Prinzmetal, Nwachuku, Bodanski, Blumenfeld, & Shimizu, 1997). However, in these studies, observers were not obligated to utilize the reference directly while the targets were visible, which permitted the engagement of a confounding postperceptual process, such as memory.

A better solution is to present the test stimuli and the reference stimuli simultaneously and to compel observers to orient their attention to one of them using attentional cues that operate automatically, independent of the observers' intentions (Jonides, 1981; LaBerge, 1981). For example, abrupt visual onset cues (Eriksen & Hoffman, 1972; Posner & Cohen, 1984) involuntarily capture attention (Luck & Thomas, 1999; Müller & Rabbitt, 1989; Remington, Johnston, & Yantis, 1992; Yantis & Jonides, 1990), enhance the physiological activity of stimuli they cue (Hopfinger & Mangun, 1998, 2001), and may be ignored only when attention is tightly focused to a competing region of space (Yantis & Jonides, 1990). Three previous studies have explored the effects of abrupt onset cues on contrast perception but came to three different conclusions. One study demonstrated that abrupt onsets increased the perceived contrast of low- or medium-contrast target stimuli (Carrasco, Ling, & Read, 2004). Another study reported that the cues reduced response variability but did not alter perception of low- to high-contrast stimuli (Prinzmetal et al., 1997, Experiments 5–7). A third study reported that abrupt onset cues decreased the perceived contrast of high-contrast stimuli (Tsal et al., 1994, Experiment 4).

The discrepancy among these previous studies is difficult to explain in terms of an attentional phenomenon, since the abrupt onset cues they employed should be expected to engage the same attentional mechanisms. More likely, the discrepancy is due to differences in procedure and, as we investigated in the present study, visual stimuli. Although visual transients, such as abrupt onset cues, are advantageous in their ability to compel attentional orienting (e.g., Franconeri, Hollingworth, & Simons, 2005), they must appear in close spatial and temporal proximity to their targets, thereby introducing the collateral and confounding effects of sensory interaction. Abrupt onset cues have been reported in certain tasks to engage a mechanism that is capacity unlimited and therefore independent of attention (Schneider & Bavelier, 2003; Solomon, 2004). In a temporal order judgment task, abrupt onset cues shortened the time to perceive subsequent target stimuli even when 12 identical cues were presented simultaneously within the visual field (Schneider & Bavelier, 2003), a number that exceeds the capacity limitations of attention (Pylyshyn & Storm, 1988; Yantis & Johnson, 1990). Similarly, peripheral cues at as many as eight simultaneous locations enhanced the contrast threshold for orientation discrimination (Solomon, 2004).

The aim of the present study was to differentiate the contributions of attention from those of sensory interaction to the changes in appearance caused by abrupt onset cues. In a series of experiments, three types of attentional cues were used that differed in their sensory characteristics. In Experiment 1, white abrupt onset cues increased the perceived contrast of target stimuli; however, in Experiment 2, black abrupt onset cues did not affect the perception of readily detected targets. In Experiment 3, gaze direction cues without sensory activity in the vicinity of the targets also failed to modify the perception of targets above the threshold of detection. In Experiment 4, these cues were demonstrated to be effective in orienting attention and facilitating response times (RTs). The results suggest that while abrupt onsets can alter appearance, sensory and not attentional mechanisms are likely responsible.

EXPERIMENT 1

The purpose of the first experiment at the time it was conducted was to demonstrate that abrupt onset cues could increase the perceived contrast of subsequent target stimuli. Since then, Carrasco et al. (2004) have come to the same conclusion, and therefore Experiment 1 served to replicate those results using different stimuli, procedures, and analyses and to extend the range of stimulus contrasts studied. Two uniform disk target stimuli were presented simultaneously at pseudorandom locations within a thin annulus of peripheral eccentricity (Figure 1A). One of the targets was precued by a white ring stimulus at the same spatial location. The contrasts of the targets were chosen from a set that included those near the detection threshold (perithreshold) and those well above the detection threshold (suprathreshold). To control for response biases (Schneider & Bavelier, 2003), the observers were required, in separate sessions, to make two different types of judgments about the relative contrasts of the two targets: a comparative judgment (which was brighter) or an equality judgment (whether they were the same or not).

Method

Participants. Twelve observers (7 males, 5 females, 23–33 years old) participated, reported normal or corrected-to-normal visual acuity, were naive to the purpose of the experiment, gave their written and informed consent, and were paid for their participation. Data from 2 observers were discarded because their RTs were unusually rapid, and it appeared that they had disregarded the instructions and responded randomly.

Apparatus. The stimuli were presented in a dimly illuminated room. The experiment was controlled by MATLAB (The MathWorks, Natick, MA) computer program using Psychophysics Toolbox subroutines (Brainard, 1997; Pelli, 1997) on a Macintosh G3 computer (Apple Computer, Cupertino, CA). The stimuli were displayed on a Sony GDM-FW900 monitor (Sony Electronics, New York) with a refresh rate of 160.4 Hz, driven by an MP 850 video card (Village Tronic Computer, Sarstedt, Germany) and calibrated with a PR-650 photometer (Photo Research, Chatsworth, CA).

Visual stimuli. Two 0.3° circular targets were simultaneously presented on a uniform gray background, 22.8 cd/m², for 100 msec at unpredictable positions located within an annulus centered at the fixation point with a radius of 6.5°–7.5°. The separation of the targets was constrained to be at least 7°. The cued targets were presented at gray-level contrasts (defined as

$$\frac{L - L_0}{L + L_0},$$

where L is the luminance of the target and L_0 is the luminance of the background) of 1.0%, 1.9%, 2.8%, 3.7%, 4.6%, 5.5%, and 6.3%,
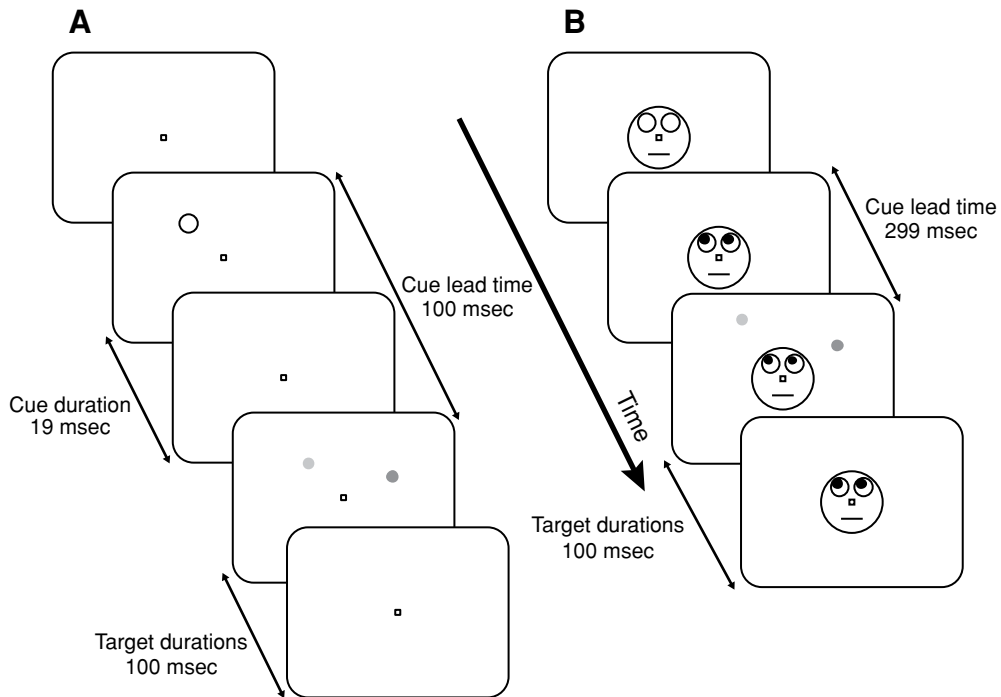
Figure 1. Stimuli. The typical frame sequences for the two types of cues used in separate sessions. (A) Abrupt onset cues. Each trial began with a uniform gray background with a fixation point. A white (Experiment 1) or black (Experiment 2) ring-shaped cue appeared for 19 msec, followed 100 msec later by the two simultaneous target stimuli that persisted for 100 msec, one of which was located in the same position. (B) Gaze direction cues (Experiment 3). A cartoon face without pupils was presented on a uniform gray background. The fixation point was the nose of the face. The pupils then appeared looking toward a point in the visual periphery, followed 299 msec later by the two target stimuli, one of which was located at the point of gaze. For each type of cue, the contrasts of the two targets varied, and the observers judged which target appeared brighter, or, in a separate session, whether the two targets appeared to be of equal brightness or not. The scale of the figure has been exaggerated for clarity.

corresponding to the incremental steps of the video display card. The contrast range was chosen to include target contrasts near or below the detection threshold and target contrasts well above the detection threshold. For each contrast level of the cued target, the paired uncued targets were presented at contrasts from three steps below (when possible) to three steps above the cued contrast level. The total range of all uncued target contrasts was 1.0%–8.8%. The lowest contrast cued target was also paired with an invisible (0% contrast) stimulus, but this condition was not included in the analysis.

The location of one target was cued by a white (113 cd/m², 66.4% contrast), thin 0.5° concentric ring that appeared 100 msec before the targets and persisted for 19 msec (Figure 1A). This cue lead time has been shown to produce the largest effects (Cheal & Lyon, 1991; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989; Posner & Cohen, 1984; Schneider & Bavelier, 2003).

Procedure. The observers were seated with their eyes level with and approximately 55 cm away from the monitor where they were instructed to maintain fixation. The observers' heads were not restrained, and their eye movements were not monitored. Although foveation of one target could enhance its perceived contrast relative to the other, eye movements were not likely to have confounded the results of this experiment. The targets appeared at unpredictable locations, and the lead time of the abrupt onset cues was too short (100 msec) to permit saccades to the target location (Crawford & Müller, 1992).

During separate sessions on different days, the observers performed one of two forced-choice tasks: an equality judgment or a comparative judgment. Since the targets were uniform in luminance and of positive contrast (brighter than the background), the more

familiar perceptual terminology of brightness was interchangeable with that of contrast and was used in the instructions to the observers. For the equality judgment, the observers were instructed to press one key if the two targets appeared equal in brightness and another key if the targets appeared to differ. For the comparative judgment, the observers were instructed to press a key indicating which of the two targets (the cued or the uncued) appeared brighter. In addition, the observers were instructed that if only one target was detected, then it should be regarded as the brighter one, and if no targets were visible, the observers were instructed to respond randomly. The observers were instructed to make their best guess when uncertain and, although their responses were not timed, to respond as quickly as possible while maintaining accuracy.

The method of constant stimuli was used to sample the psychometric functions. Each combination of cued and uncued contrast levels was repeated 25 times, with all conditions randomly interleaved. The experimental sessions lasted approximately 1 h, during which the observers were automatically allowed to rest and break fixation after every 50 stimuli presentations, resuming the experiment when ready.

Data analysis. We determined the equivalent contrasts of the cued targets by fitting the observers' responses to models (Schneider & Bavelier, 2003) through a global maximum likelihood optimization procedure. The comparative judgment data were fit to a cumulative normal distribution, $\Phi(0, \Delta c + \alpha, \sigma)$, where

$$\Phi(x, \mu, \sigma) \equiv \frac{1}{\sigma\sqrt{2\pi}} \int_{-\infty}^{x} e^{-(y-\mu)^2/2\sigma^2} dy,$$

and the equality judgment data to a difference of cumulative normal distributions, $\Phi(\kappa, \Delta c + \alpha, \sigma) - \Phi(-\kappa, \Delta c + \alpha, \sigma)$, where κ is the contrast difference threshold, Δc is actual difference in contrast between the cued target to the uncued target, α is the potential boost in perceived contrast of the cued target relative to the uncued target (the point where the psychometric function for the comparative judgment crosses 50%, and the peak point of the equality judgment function), and σ^2 is the response variance. Each parameter has units of logarithmic contrast and the perceived contrast $c' = ce^\alpha$ for each actual contrast level c of the cued target. The variances of the estimates of the model parameters were derived for each observer by assuming that the likelihood function is distributed in parameter space approximately normal near the optimal parameters (MacKay, 1992), and these variances were used to compute the weighted mean of each model parameter across observers (see Appendix A).

We obtained a more reliable assessment of whether an effect of the cue was necessary to explain the contrast perception data ($\mathcal{H}_1$: $\alpha \neq 0$ vs. $\mathcal{H}_0$: $\alpha = 0$) by using the Bayesian method of hypothesis testing (MacKay, 1992) to evaluate. This method of hypothesis testing ranks the models as the product of the evidence across observers, $P(\mathcal{D} \mid \mathcal{H}) = \int P(\mathcal{D} \mid \mathbf{w}, \mathcal{H}) P(\mathbf{w} \mid \mathcal{H}) d\mathbf{w}$, where $\mathcal{D}$ is the experimental data, $\mathcal{H}$ the model hypothesis, and $\mathbf{w}$ the model parameters. $P(\mathcal{D} \mid \mathbf{w}, \mathcal{H})$ is the likelihood function, and $P(\mathbf{w} \mid \mathcal{H})$ is the prior distribution of the parameters, which was assumed to be uniform. The likelihood functions were numerically integrated over the parameter space using adaptive quadrature to a fractional accuracy of 10^{-6} (d01fcc and d01ajc functions, Numerical Algorithms Group, Oxford). The results of the test were found to be insensitive to reasonable variations in the range of these priors.

Results

For each contrast level of the cued target, the responses to the range of contrasts of the paired uncued targets formed a distribution; the response distributions from a typical observer are shown in Figure 2. The comparative judgment yielded a sigmoid curve, as a function of the difference in contrast between the two targets, whereas the equality judgment yielded a bell-shaped curve. The perceptually equivalent contrast of each cued target contrast level was determined as the contrast of the uncued target from which it was least discriminable. This was the contrast at which the comparative judgment was maximally uncertain—the cued and uncued targets were equally likely to be reported as higher contrast—and the equality judgment was maximum—the targets were most likely to be reported of equal contrast. The weighted averages of the equivalent perceived contrasts across the group of observers are presented in Figure 3 (solid black line, with the gray area indicating the extent of the 95% confidence interval) for the comparative and equality judgments and each type of cue.

The equivalent perceived contrast was significantly greater ($p < .05$, two-tailed t test on the weighted mean) than the actual contrast at contrasts of 1.0%–3.7% for the comparative judgment (Figure 3A) and 1.0%, 1.9%, and 6.3% for the equality judgment (Figure 3B). In addition, there were marginally significant increases for the comparative judgment at the 4.6% contrast level ($p = .077$) and the equality judgment at the 2.8% contrast level ($p = .056$). The estimates of the cue effect did not significantly differ between the comparative and equality judgments at any of the contrast levels.

Since the above statistics were performed on estimates of perceived contrast derived from model fits, a further,
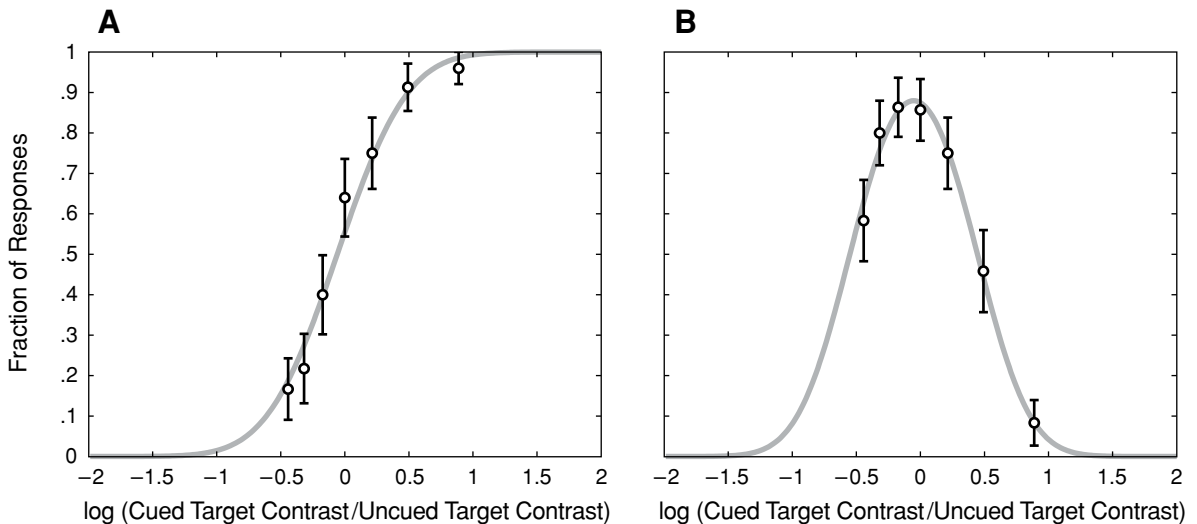

Figure 2. Typical responses from one observer. For each contrast level of the cued target (4.6% in this case), the uncued target was presented at a range of contrasts (1.9%–7.2%). The abscissa represents the natural logarithm of the ratio of contrast of the cued target to the contrast of the uncued target. The circular markers indicate the mean response for 25 repetitions, and the error bars depict the standard error of the mean. The solid gray lines indicate the model fits to the responses (see the Results section). The observers performed one of two judgments, in separate sessions. (A) In the comparative judgment, the observers decided which of the two targets was brighter; the ordinate represents the fraction of responses indicating that the cued target was brighter. The equivalent contrast of the cued target was determined to be 4.9% on the basis of the point at which the model function equaled 50%. (B) In the equality judgment, the observers decided whether the two targets were equally bright; the ordinate represents the fraction of affirmative responses. The equivalent contrast of the cued target was determined to be 4.8% on the basis of the point at which the model function was maximum.

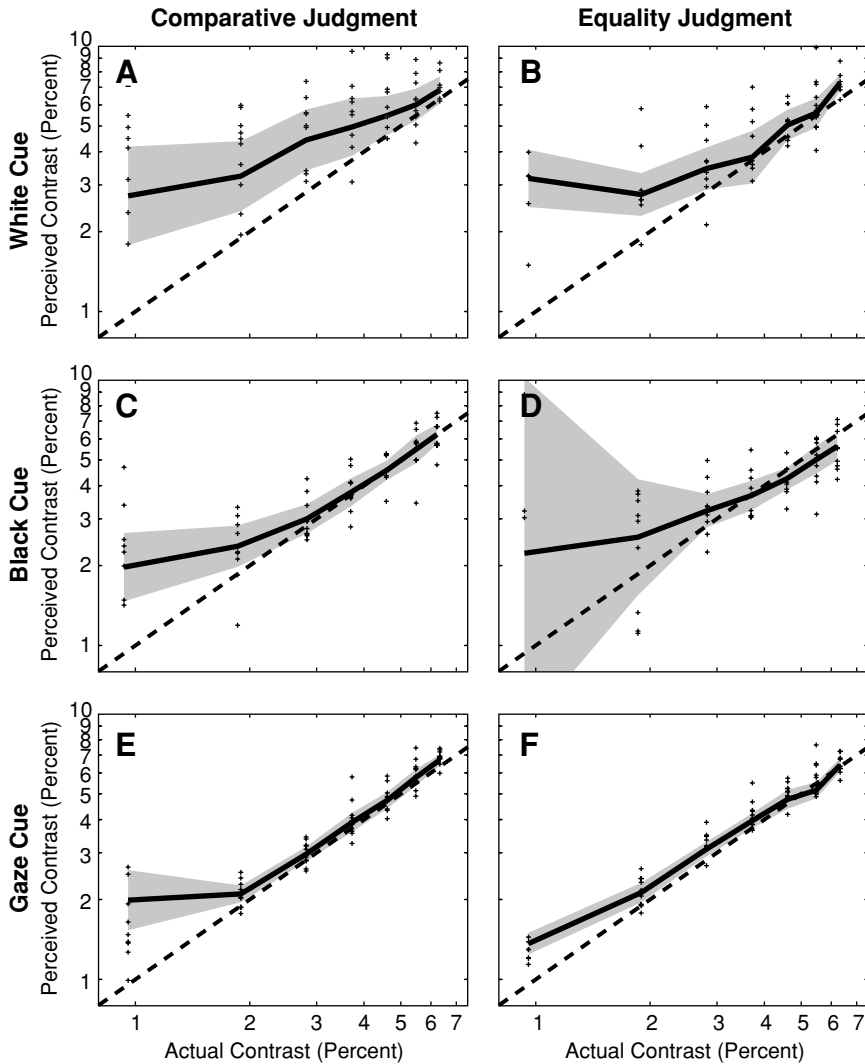**Comparative Judgment**   **Equality Judgment**

Figure 3. Equivalent contrast results for each cue type and judgment. The relationship between the actual contrast of the cued target and its perceived contrast was determined for the three types of cues and two different perceptual judgments. Each cross marker represents the perceived contrast of the cued target determined for a single observer. Several of these values lie beyond the graph boundaries. The solid line represents the weighted mean across the observers, and the gray shaded region marks the extent of the 95% confidence interval for the weighted mean. The dotted line indicates equality between actual and perceived contrast. (A) White abrupt onset cues (Experiment 1), comparative judgment. (B) White abrupt onset cues, equality judgment. (C) Black abrupt onset cues (Experiment 2), comparative judgment. (D) Black abrupt onset cues, equality judgment. (E) Gaze direction cues (Experiment 3), comparative judgment. (F) Gaze direction cues, equality judgment.

more reliable calculation was performed to test whether an additional model parameter was necessary to explain the experimental data. Two models were compared within a Bayesian framework (see the Method section). One model included a parameter to account for the hypothesized effect of the cue in changing the perceived contrast of the cued target. The other, null, model assumed that this parameter was zero and that the cue had no effect. The natural logarithm of the ratio of the evidence for each model across observers is plotted in Figure 4. When this

quantity is greater than zero, an additional model parameter is needed to explain the effect of the cue, and the more positive this quantity, the more robust the effect. An additional model parameter was necessary to explain the effect of the white abrupt onset cues on perceived contrast at all contrast levels tested. For the comparative judgment, the effect was most robust at the lowest contrasts tested and decreased for higher contrasts. For the equality judgment, the robustness of the effect peaked around a contrast of 3.7%.
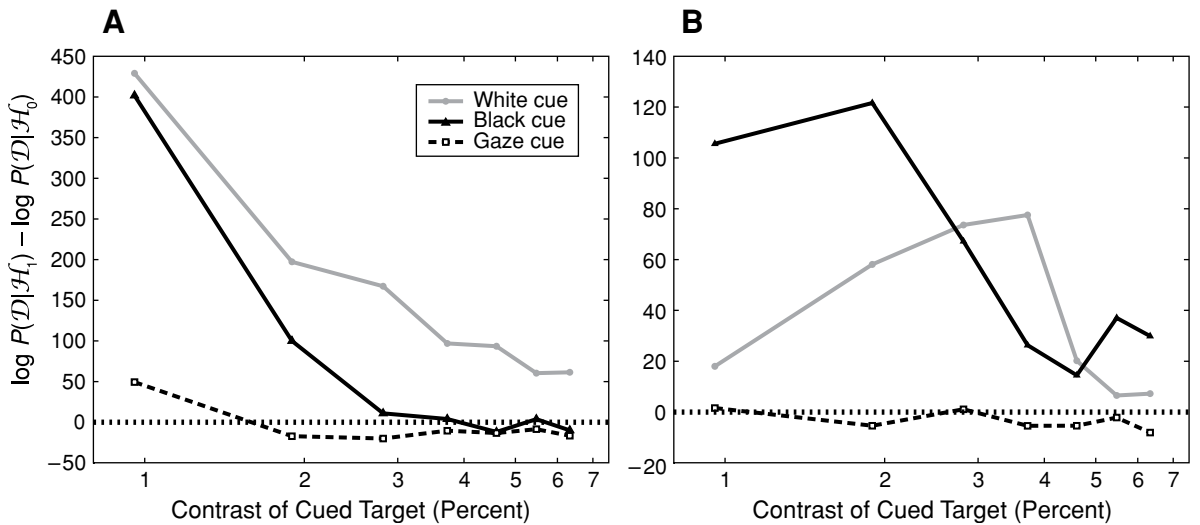
Figure 4. Hypothesis tests. For each type of cue, perceptual judgment, and contrast level of the cued target, a Bayesian inference hypothesis test was performed to determine whether an additional model parameter was necessary to account for any change in perceived contrast caused by the cue. The ordinate represents the logarithm of the ratio of the joint evidence across all observers for each model: $\mathcal{H}_1: \alpha \neq 0$ versus $\mathcal{H}_0: \alpha = 0$, where α is the contrast enhancement due to the cue (see the Method section). When the logarithm of the ratio is greater than zero, the cue was determined to have influenced contrast perception. (A) Comparative judgment. (B) Equality judgment.

To test whether the effects of the white abrupt onset cue agreed with the predictions of the contrast gain model of attention, the data were fit to two simple models, as shown in Figure 5. In the additive model, the perceived contrast of the cued target exceeds its actual contrast by a constant factor across the range of contrasts tested. The optimal value of this constant determined by a weighted least squares procedure was 0.98% (95% confidence interval [0.32, 1.6], $R^2 = .86$) for the comparative judgment and 1.0% ([0.55, 1.5], $R^2 = .88$) for the equality judgment. In the multiplicative model, the perceived contrast is proportional to the actual contrast, as is predicted by a contrast gain model of attention or the alternative response gain model in the low-contrast limit (see Appendix B).
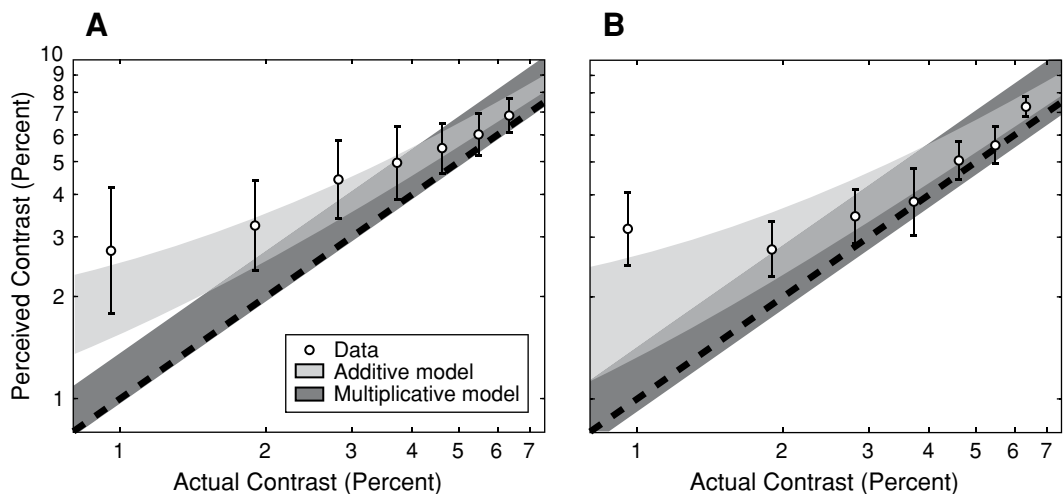
Figure 5. Additive versus multiplicative model fits. The data obtained with the white abrupt onset cues for the two perceptual judgments are presented with two single-parameter models. The shaded areas represent the range of each model over the 95% confidence interval of its optimal parameter. For the multiplicative model, equivalent to a contrast gain mechanism, the model parameter is a proportionality constant by which perceived contrast is scaled relative to the actual contrast. For the additive model, the model parameter is an additive constant by which perceived contrast exceeds the actual contrast. The error bars on the data points indicate the 95% confidence interval for the weighted mean. (A) Comparative judgment. (B) Equality judgment.

For this model, the data were best fit by a proportionality constant of 1.2 ([0.91, 1.4], $R^2 = .68$) for the comparative judgment and 1.2 ([0.97, 1.4], $R^2 = .62$) for the equality judgment. For both judgments, the additive model was a better fit and, in particular, provided a better account of the data at the lowest contrast levels.

Discussion

The results demonstrated that abrupt onset cues are able to increase the perceived contrast of subsequent stimuli. However, the effect of the white cue was best described as additive, independent of stimulus contrast. The inclusion of an additive factor in a model contrast response function (Appendix A) has the greatest consequences on the response at low contrasts. An additive effect is inconsistent with both the contrast gain model and the response gain model of attention and is suggestive of a simple luminance increment mechanism. Another possibility is that the effects are due to a perithreshold attentional mechanism, such as an increase in detectability. These possibilities were investigated further in the subsequent experiments.

EXPERIMENT 2

The contrast polarity of the cue was reversed in this experiment. If the mechanism of the perceptual effect is a simple luminance mechanism, then a black abrupt onset cue should decrease the perceived contrast of subsequent stimuli.

Method

Participants. Nine observers (3 males, 6 females, 23–31 years old) participated, reported normal or corrected-to-normal visual acuity, were naive to the purpose of the experiment, gave their written and informed consent, and were paid for their participation.

Apparatus. The experiment was controlled by a Macintosh G4 computer (Apple Computer, Cupertino, CA) and displayed on a Mitsubishi Diamond Pro 2070SB monitor (NEC-Mitsubishi Electronic Visual Systems Corp., Tokyo) with a refresh rate of 159.3 Hz, driven by an ATI Radeon 9000 Pro video card (ATI Technologies, Markham, Ontario, Canada) and calibrated with a Minolta CS-100 photometer (Konica Minolta Photo Imaging, Mahwah, NJ).

Stimuli. The stimuli were identical to those in Experiment 1 with the following exceptions. The contrast polarity of the cue was reversed so that it was black (0.2 cd/m^2, -98.3% contrast) instead of white as in Experiment 1. The cued targets were presented at contrast levels of 0.9%, 1.9%, 2.8%, 3.7%, 4.6%, 5.5%, and 6.2%, as close as possible to those in Experiment 1, using a different apparatus. For each of the contrast levels of the cued target, the paired uncued targets were presented at seven contrasts in the range of ± 1 (natural) logarithmic unit. The range of all uncued target contrasts was 0.6%–17.1%.

Procedure and Data analysis. The procedure and data analysis were identical to those in Experiment 1.

Results

The effects of the black abrupt onsets were reduced or eliminated relative to the effects of the white abrupt onset cues in Experiment 1. For the comparative judgment (Figure 3C), the black abrupt onsets significantly increased perceived contrast for the 1.0% and 1.9% contrast levels. The Bayesian hypothesis test indicated that

the effects were most robust for the lowest contrast levels (Figure 4). The effects were very small for the 3.7% and 5.5% contrast levels; for the 4.6% and 6.3% contrast levels, the hypothesis test indicated that no additional parameter was necessary to account for the cue effect. For the equality judgment (Figure 3D), the black abrupt onset cues did not significantly alter contrast perception at any of the contrast levels, although at 4.6%–6.3% contrast, the weighted means were marginally significant ($p \approx .1$), with the trend indicating a decrease in perceived contrast. The trends were substantiated as robust by the Bayesian hypothesis test, which indicated that an additional model parameter was necessary to account for the effects of the cues for all contrast levels, with the most robust effects occurring for the lowest contrast levels. For the comparative judgment, the effects of the black abrupt onsets were significantly smaller ($p < .05$, one-tailed t test) than the effects of the white abrupt onset cues at the 2.8%–4.6% contrast levels and marginally significantly smaller ($p = .061$) at the 1.9% contrast level. For the equality judgment, the effects of the black abrupt onset cues were significantly smaller than the effects of the white abrupt onset cues at the 4.6% and 6.3% contrast levels.

Discussion

The black abrupt onset cues increased perceived contrast of perithreshold targets but did not increase and even tended to decrease the perceived contrast of suprathreshold targets. It is clear that changing the sensory characteristics of the cue from white to black had a significant effect, particularly for the target stimuli in the suprathreshold contrast range. A simple luminance interaction mechanism is still plausible for the suprathreshold stimuli, but the persistent perithreshold effects suggest the presence of an additional independent process, perhaps an attentional mechanism that enhances detection, as will be discussed further in the General Discussion section. It is unlikely that the smaller effects of the black cues could be attributed to a lower salience of these cues, since the black cues had a larger absolute contrast, relative to the background, than did the white cues in Experiment 1 (98.3% vs. 66.4%); however, salience was not measured directly. Furthermore, a reduction in salience would not explain the trend toward a decrease in perceived contrast for the suprathreshold targets.

EXPERIMENT 3

If the effects of the abrupt onset cues observed in Experiments 1 and 2 were caused by sensory mechanisms and not by attention, as suggested by the sensitivity of the results to the sensory characteristics of the cues, then eliminating the sensory effects of the cues from the vicinity of the targets while retaining the attentional effects of the cue should eliminate the perceptual effects. In Experiment 3, we utilized gaze direction cues, a second type of automatic attentional cue, that were located remotely from the target location and therefore avoided cue–target sensory interactions (Figure 1B). Gaze direction cues, instan-

tiated as the gaze direction of cartoon or real faces, have been shown to operate counter to observers' intentions (Driver et al., 1999; Friesen & Kingstone, 1998; Langton & Bruce, 1999; Langton, Watt, & Bruce, 2000) and to enhance the physiological activity of targets (Schuller & Rossion, 2001). An additional benefit of the gaze direction cues is that, unlike the abrupt onset cues, they do not produce illusions of temporal order (Hikosaka, Miyauchi, & Shimojo, 1993; Schneider & Bavelier, 2003) that might bias contrast judgments.

Method

The 10 participants, the apparatus, stimuli, procedure, and analysis were the same as those in Experiment 1, with the exception of the cue stimuli. The cue used in this experiment was a cartoon face, 4º in diameter, with the fixation point as its nose (Figure 1B). Before the appearance of the target stimuli, the face was drawn to the screen with white eyes and no pupils. After 500–1,000 msec, the two black (0.78 cd/m^2) pupils, 0.3º in diameter, were presented within the eye whites, persisting and directing the gaze of the face toward the location where the cue target appeared 299 msec later. This cue lead time is optimal for this type of cue (Friesen & Kingstone, 1998; Schneider & Bavelier, 2003).

Results

The gaze direction cues caused small but significant increases in perceived contrast at contrast levels of 1.0%, 1.9%, and 6.3% for the comparative judgment (Figure 3E) and 1.0%–2.8% contrast for the equality judgment (Figure 3F). For the equality judgment, a marginally significant ($p = .088$) enhancement was present at the 3.7% contrast level. Of these effects, the Bayesian hypothesis test determined that an additional model parameter was necessary to account for the effect of the gaze direction cues at the 1.0% and 2.8% contrast for the equality judgment and at the 1.0% contrast level for the comparative judgment (Figure 4). The effects of the gaze direction cues were significantly smaller ($p < .05$, one-tailed t test) than those produced by the white abrupt onset cues at the 1.9% and 2.8% contrast levels for the comparative judgment and 1.0%, 1.9%, and 6.3% contrast levels for the equality judgment. Marginally significant smaller effects were found for the comparative judgment at the 3.7% ($p = .051$) and 4.6% ($p = .072$) contrast levels.

Discussion

The perithreshold effects remained in Experiment 3, employing gaze direction cues that contained no sensory component in the vicinity of the targets, but the suprathreshold effects caused by the black and white abrupt onset cues in Experiments 1 and 2 disappeared. The persistence of the perithreshold effects across attentional cue types suggests a common attentional mechanism in this contrast range, whereas the dependence of the suprathreshold effects on the sensory components of the cues suggests a sensory mechanism for the higher contrasts.

EXPERIMENT 4

Although the gaze direction cues in Experiment 3 significantly increased the perceived contrast of perithresh-

old stimuli, it is possible that the absence of effects for suprathreshold stimuli might reflect lack of effectiveness in orienting attention. Therefore, to verify the attentional automaticity of these cues within the stimulus configuration used in Experiment 3, we performed a control experiment to measure their ability to decrease RT, one of the hallmark effects of attentional cuing (e.g., Posner, 1980).

Method

Participants. Seventeen observers (8 males, 9 females, 23–36 years old) participated, reported normal or corrected-to-normal visual acuity, were naive to the purpose of the experiment, gave their written and informed consent, and were paid for their participation.

Apparatus. The apparatus was the same as that used in Experiment 2. In addition, the observers' eyes were monitored using an infrared eyetracking device (ASL Model 5000 control unit and standard Model 504 remote optics, Applied Science Laboratories, Bedford, MA), to ensure that they did not break fixation. The eyetracker was calibrated for each observer before the start of the experiment, and eye position data were acquired and recorded through a serial interface by the computer controlling the stimulus displays and timing. During some of the trials, a lag in the serial communication interfered with the precise timing of the stimulus; these trials were omitted from the analysis. All of the observers were under the impression that their eyes were being monitored; however, for 2 observers, it was impossible to acquire stable images of their pupil and corneal reflection, and their eye position data were not available.

Stimuli and Procedure. The cue and target stimuli were similar to those in Experiment 3, but only one target appeared, at a contrast level of 0.9%, 1.9%, 2.8%, 3.7%, 4.7%, 5.4%, or 6.3% (the same as those used in Experiment 2). In an equally likely condition, no target was presented. Two cue lead times, 53 and 306 msec, and two cue validity conditions were used. The 53-msec cue lead time was too quick for the gaze direction cues to become effective, whereas the cues were optimally effective for the 306-msec cue lead time (Friesen & Kingstone, 1998; Schneider & Bavelier, 2003). In half of the trials in which the target appeared, it appeared in the location indicated by the gaze of the cartoon face (valid cue). In the other half of the trials, the target appeared at a location at least 10º away from the cued location (invalid cue). Each contrast level, cue validity condition, and cue lead time was presented 40 times. The task of the observers was to maintain fixation and to press a key as quickly as possible on detection of the target, without regard to the validity of the cue. The observers were instructed not to respond if they did not detect a target. The observers were required to respond within 1,500 msec of the appearance of the target, after which time the pupils of the cartoon face disappeared. The next trial began after a pause of 500–1,000 msec. The distance between the observer and the visual display varied among observers to accommodate eyetracking, but the stimuli were scaled in size to match visual angles subtended by those in Experiment 3.

Data analysis. We estimated the contrast detection threshold for each cue lead time and cue validity condition by fitting the proportion of detections at each contrast level tested to a cumulative normal function. The threshold was defined as the contrast level at which each observer detected 50% of the targets. The detection thresholds and median RTs for each observer and each condition were compared using a general linear model and repeated measures design with the SPSS 11.5 statistical software (SPSS, Chicago).

Results

The RTs for each observer were analyzed for the target contrasts and cue conditions for which there were at least five detections. These included the six contrast levels of 1.9%, 2.8%, 3.7%, 4.7%, 5.4%, and 6.3% for all but 2 observers, for whom only the highest five contrast levels

were analyzed. The median RTs for each observer for each contrast level and cue condition were analyzed with a general linear model using a repeated measures design. The means across observers of the median RTs for each condition are illustrated in Figure 6. The main effect of cue lead time was significant [$F(1,15) = 30.4, p < .001$], with the RTs 13.9 ± 2.6 msec faster for the 306-msec cue than for the 53-msec cue. The main effect of cue validity was significant [$F(1,15) = 11.3, p = .004$] but there was also a significant interaction between cue lead time and cue validity [$F(1,15) = 6.2, p = .025$]. RTs were significantly faster by 12.6 ± 2.7 msec for the valid condition than for the invalid condition for the 306-msec cue [$t(100) = 4.6$, $p = .000012$, paired two-tailed t test], but there was no effect of cue validity for the 53-msec cue [$t(101) = 0.17$, $p = .86$]. The main effect of target contrast was significant in the multivariate test [$F(5,11) = 44.8, p < .001$]. RTs decreased with increasing target contrast. There was no significant interaction between contrast and either cue validity or cue lead time, suggesting that the benefit of the cues on RT was independent of target contrast.

Although the experiment was not designed to accurately determine the contrast detection threshold, the proportions of targets to which the observers responded were used to estimate the mean threshold to be $2.07\% \pm 0.12\%$ for the valid 53-msec cue, $2.17\% \pm 0.11\%$ for the invalid 53-msec cue, $2.08\% \pm 0.12\%$ for the valid 306-msec cue, and $2.09\% \pm 0.11\%$ for the invalid 306-msec cue. There was no significant effect of cue lead time on the detection threshold, and the main effect of cue validity was only marginally significant [$F(1,16) = 3.8, p = .069$].

Discussion

The gaze direction cues speeded RTs across the contrast range and were therefore demonstrated to be effective at orienting attention. The failure of these cues to modulate the perceived contrast of the suprathreshold targets in Experiment 4 cannot be attributed to ineffective attentional orienting. One possibility raised in the review of this paper was that the gaze direction cues simply might be too weak to manipulate perceived contrast, even though they were able to affect RTs. However, the cues were effective enough to alter the perception of perithreshold stimuli in Experiment 3, and their null effects for suprathreshold stimuli require no further explanation beyond the sensory interaction account—changing the cue contrast polarity between Experiments 1 and 2 almost completely reversed the cue effects for suprathreshold stimuli.

GENERAL DISCUSSION

The results of the four experiments suggest the presence of two distinct mechanisms that can appear to alter perceived contrast: (1) an attentional mechanism independent of the sensory nature of the cues that operated only on perithreshold stimuli and (2) a sensory interaction mechanism that also operated on suprathreshold stimuli.

Whether the visual cues altered the appearance of subsequent suprathreshold stimuli depended on the sensory attributes of the cue. In Experiment 1, white abrupt onsets increased the perceived contrast of the cued targets. The cues appeared in close temporal and spatial proximity to the targets they cued, thereby potentially evoking attention-independent sensory interactions and perhaps incorporating some aspect of the cue activity into the perception of the subsequent target (Helson, 1963). Supporting this, the effects of the white abrupt onset cues across the contrast range were more consistent with a constant additive contrast increment than with the multiplicative effect that is predicted by the contrast or response gain models of attention. Additional support for a simple stimulus interaction was found in Experiment 2, in which the contrast polarity of the cue was reversed. The black abrupt onsets eliminated and even tended to reverse the perceptual effects of the white cues for suprathreshold targets. In Experiment 3, the centrally located gaze direction cues, which avoided sensory interaction with the peripheral targets, did not affect the perceived contrast of the suprathreshold targets, even though they sped RTs to them in Experiment 4.

All three types of cues appeared to increase the perceived contrast of perithreshold targets. Attention has been demonstrated to improve sensitivity—detection and discriminability (Bashinski & Bacharach, 1980; Cameron,
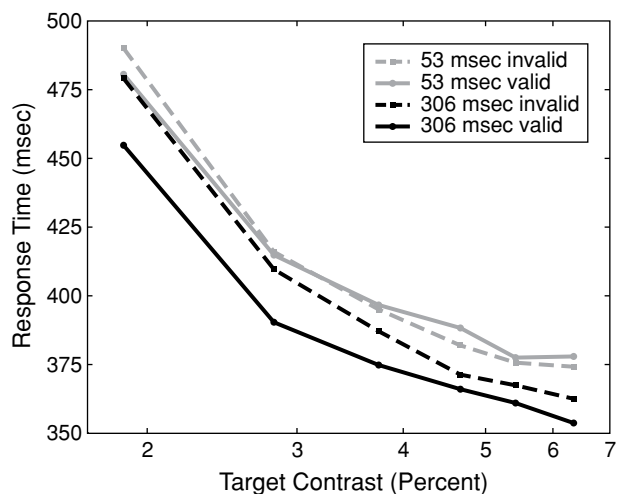

Figure 6. Verification of gaze direction cues. To verify the effectiveness of the gaze direction cues in orienting attention, the effects of these cues on the response times of the detection of single was measured in Experiment 4. The response times are shown for four different gaze direction cuing conditions and six different target contrast levels. For one half of the trials, the cue lead time was 53 msec; for the other half of the trials, the cue lead time was 306 msec. Independent of cue lead time, in half of the trials, the cues correctly indicated the target location (valid), whereas in the other half of the trials, the cues indicated a location separated by least 10º from the target location. The responses for the 306-msec cue lead time were significantly faster than for the 53-msec cue lead time across all contrast levels of the target stimuli. The effect of cue validity was significant for the 306-msec cue lead time but not the 53-msec cue lead time, significantly speeding the response time and demonstrating the effectiveness of the gaze direction cues in orienting attention.

Tai, & Carrasco, 2002; Carrasco et al., 2004; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Foley & Schwarz, 1998; Hawkins et al., 1990; Huang & Dobkins, 2005; Lu & Dosher, 1998; Morrone, Denti, & Spinelli, 2002; Pestilli & Carrasco, 2005; Solomon, 2004; Solomon, Lavie, & Morgan, 1997), producing the largest effects at low contrasts (Cameron et al., 2002; Carrasco et al., 2004). The perithreshold effects demonstrated the attentional effectiveness of the cues and can be explained in terms of an increased probability of detection: When the observers detected only one target, they indicated that it was the brighter one. Another possibility is that attention intensified only very weak stimuli (Stumpf, 1890, p. 293). Even though attention may influence the detection threshold and therefore which stimuli enter awareness, attention does not seem to alter the subjective impressions of readily perceived stimuli.

Abrupt onset cues have been posited to invoke different and independent processes from those invoked by gaze direction and other central cues. For example, gaze direction cues, unlike abrupt onset cues, do not produce inhibition of return at the target location (Friesen & Kingstone, 2003; though see Frischen & Tipper, 2004). The effects of other central cues have been shown to be consistent with a process of external noise exclusion, whereas the effects of peripheral abrupt onset cues occur in the absence of external noise and have been shown to be consistent with stimulus enhancement or, equivalently, an internal additive noise reduction (Cameron et al., 2002; Carrasco et al., 2000; Lu & Dosher, 2000).

The exact sensory mechanism responsible for the suprathreshold effects of the abrupt onset cues is not clear. One possibility, given the differential effects of the black and white cues, is simple luminance assimilation, which could be tested by displaying the cues subsequent to the targets (Gobell & Carrasco, 2005). More likely, the stimulus interaction mechanism is temporally dependent and perhaps involves the spreading region of subthreshold cortical activation that is evoked by abrupt onsets and other dynamic stimuli (Jancke, Chavane, Naaman, & Grinvald, 2004). Motion binding mechanisms may be involved—the spatiotemporal properties required for short-range apparent motion match the effective range of abrupt onset cues (e.g., Braddick, 1974; Henderson & Macquistan, 1993; Nakayama & Mackeben, 1989; Schneider & Bavelier, 2003; Yantis & Gibson, 1994). Supporting this, motion and motion onset can reflexively capture attention (Abrams & Christ, 2003; Franconeri & Simons, 2003).

The findings of the present study may help to explain the discrepant results of previous studies that investigated the effects of abrupt onset cues on the perception of contrast (Carrasco et al., 2004; Prinzmetal et al., 1997; Tsal et al., 1994). Even though there were significant differences between the stimuli used in the two studies, the results of Experiment 1 confirm the results of Carrasco et al. (2004) that abrupt visual onsets can alter the appearance of subsequent stimuli. The cues in the Carrasco et al. (2004) study were large black dots located directly above the targets, which were Gabor gratings that included areas brighter

and darker than the background with contrasts of 6% or 22%. The targets always appeared in the same two spatial locations. Observers performed a comparative judgment, reporting both the location and orientation (45º to the left or right) of the higher contrast target. In the present study, in comparison, the abrupt onset cues were white (Experiment 1) or black (Experiment 2) circles surrounding the target, and the target stimuli were uniform disks brighter than the background. The targets could appear anywhere within an annulus of fixed eccentricity, and the observers performed, in separate sessions, both comparison and equality judgments. Although Carrasco et al. (2004) performed control experiments to eliminate response bias as an explanation for the effects they observed, they did not completely control for sensory interactions. In the present study, we also controlled for response bias by utilizing both comparative and equality judgments (Schneider & Bavelier, 2003); in addition, we tested the dependence of the results on sensory factors by manipulating the sensory attributes of the cues in Experiments 2 and 3. Simply reversing the contrast polarity of the cue in Experiment 2 significantly affected the results, and eliminating the sensory interactions altogether while maintaining the attentional effects in Experiment 3 eliminated the perceptual effects. These results demonstrate that the perceptual effects of abrupt onset cues depend on sensory factors and suggest that the increases in perceived contrast observed in Carrasco et al. (2004) were sensory effects and not, as they concluded, a general property of attention.

Considering the trend of the black abrupt onset cue in the present study to decrease the perceived contrast of suprathreshold targets, it might seem surprising that Carrasco et al. (2004) reported that a black abrupt onset cue increased perceived contrast. However, Carrasco et al. used a Gabor patch stimulus, which consists of a grating with dark and light stripes convolved with a Gaussian envelope rather than the uniform luminance stimuli used in the present study. If a dark cue decreased the overall luminance of the stimulus, subtracting from both the dark and light areas, then the overall contrast of the stimulus would be increased. To make this clearer, let the original contrast of the Gabor stimulus be

$$C = \frac{L_1 - L_2}{L_1 + L_2},$$

where L_1 and L_2 are the maximum and minimum luminances within the stimulus. If the cue caused a decrease in overall luminance by an amount ε, then $L_1' = L_1 - \varepsilon$, $L_2' = L_2 - \varepsilon$, and

$$C' = \frac{L_1 - L_2}{L_1 + L_2 - 2\varepsilon} > C.$$

According to this theory, a white cue would be predicted to decrease the perceived contrast of Gabor targets.

Prinzmetal et al. (1997) used two different types of abrupt onset cues, including a red square that appeared 133.3 msec before the onset of the target and persisted with no offset (Experiments 5 and 6) and a set of dots

that moved from the fixation point to the peripheral targets (Experiment 7). The target stimuli were high contrast (97%–99.5%) on a dark background or medium to high contrast (-8.3% to -73%; negative contrasts were darker than the background) on a bright background. Neither type of cue significantly altered the appearance of the target stimuli, although there was a trend for the dot cue to decrease perceived contrast.

Tsal et al. (1994) claimed that attention reduced perceived contrast. Although Prinzmetal et al. (1997) discussed procedural differences that could account for these findings, sensory effects may have also been important. Tsal et al. used two slightly different high contrasts, either 88% or 90% contrast targets on a black background (Experiment 4A) or -32% or -44% contrast targets on a white background (Experiment 4B). One important difference from the present study was the timing of the cue and the targets. One of the two square targets was cued by a series of thin horizontal lines that appeared for 150 msec and were followed immediately by targets that appeared for 30 msec. The offset cue, a contrast decrement, was therefore coincident with the onset of the cued target, a contrast increment. Offset transients, like onset transients, have also been shown to capture attention (e.g., Miller, 1989). In comparison, we (in Experiment 1 of the present study) and Carrasco et al. (2004) observed an increase in perceived contrast, respectively, using a cue duration of 19 msec followed by an 81-msec gap and then the 100-msec duration target or a 67-msec cue, 53-msec gap, and 40-msec target. The observed reduction in the apparent cued target contrast in the Tsal et al. study could be a consequence of a sensory interaction between the cue offset and the target onset. The results of the present study and the discrepancy among previous studies suggest that the precise sensory characteristics of the cue and target stimuli, including their temporal dynamics and relative contrasts, play an important role in determining whether the cue stimuli can alter perception.

Although the results of the present study suggest that attentional cues without visual transient components do not affect perceived contrast, the results of a study by Tse (2005) have demonstrated that voluntary attention, in the absence of visual transients, may modify perceived brightness by changing contextual information. In Tse's study, attention indirectly modified the perceived brightness of surfaces by changing the grouping properties of neighboring surfaces and thereby influencing lightness illusions.

Although attention appears to operate through a contrast gain mechanism in the early visual cortex, this model fails to account for many other experimental results and cannot obtain throughout the visual system. For example, according to the contrast gain model, attention to high-contrast stimuli should produce no benefit (see Appendix A); 100% contrast is by definition the maximum possible, but we are clearly able to covertly orient our attention to one of multiple high-contrast stimuli present within our visual fields—for example, in visual search tasks (e.g., Treisman & Gelade, 1980)—and attention speeds RTs to high-contrast stimuli (e.g., Posner, 1980). Although the alternative response gain model predicts attentional benefits at high contrast, neither it nor the contrast gain model predicts any attentional benefit at zero contrast—when no target is present (Appendix A)—but physiological and brain imaging studies have demonstrated an increase in baseline activity when attention is directed to an empty region of the visual field (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Luck, Chelazzi, Hillyard, & Desimone, 1997). Psychophysical orientation discriminations demonstrate attentional effects for low-contrast stimuli consistent with the contrast gain model (Cameron et al., 2002), but simple contrast discriminations require additional response gain effects (Huang & Dobkins, 2005).

An absence of attention-induced perceptual changes in contrast would need to be reconciled with the known contrast gain effects in early visual cortex. First, even though an increase in the intensity of a stimulus may cause an increase in the firing rate of neurons encoding it, the causation need not be bidirectional. The communication bandwidth of the visual system allows the independent encoding of attention and intensity signals. An increased firing rate may simply indicate an increase in amount of information available about a perceptual quality of a stimulus without necessarily indicating a change in that quality. Second, the similarity between the effects of attention and contrast on the responses of single neurons is exaggerated by simply counting the total number of action potentials, because the effects are not constant throughout the duration of the response. For example, Reynolds et al. (2000) found that in macaque V4 neurons, for high-contrast stimuli, attentional effects did not occur until approximately 100 msec after the initial neural response, whereas for low- and subthreshold-contrast stimuli, attentional effects began immediately. Attentional effects in macaque MT neurons are similarly delayed (Seidemann & Newsome, 1999). Since the neural correlates of conscious perception have not been identified, the importance of the features of the temporal response is not clear. Our perceptions could conceivably depend only on activity that is not modulated by attention, such as early phases of the neural response or activity in particular neural populations. A third possibility is that, even if attentional signals of central origin do directly alter the contrast intensity code in early visual processing, veridical perception could be preserved through a compensatory signal, such as efferent copy (Evarts, 1971; von Holst, 1954).

One mechanism by which spatial attention could enhance the detection threshold of a stimulus without altering its appearance is through differential modulation of the various parallel information channels in the primate visual system. For example, the magnocellular and parvocellular streams originate in the retinal ganglion cells, are segregated in the lateral geniculate nucleus (LGN) and remain relatively segregated in the visual cortex (Lennie, 1980; Merigan & Maunsell, 1993). The magnocellular stream exhibits transient responses to stimuli and is sensitive to low-contrast stimuli, ideal for signaling the presence and spatial location of a stimulus. The parvocellular stream exhibits more sustained responses, encodes a larger dynamic

range of contrasts, and is color opponent, ideal for encoding the form and appearance of stimuli. A prominent role of the magnocellular stream in attentional selection has been suggested by the findings that normal visual search requires only a small luminance contrast (Cheng, Eysel, & Vidyasagar, 2004) and that the activity in the magnocellular but not parvocellular layers of the LGN is enhanced by a spatial versus featural attention task (Vanduffel, Tootell, & Orban, 2000). The magnocellular stream may also be responsible for the attention-independent sensory facilitations caused by abrupt onset cues, since the impairments to temporal resolution caused by these cues (Yeshurun & Levy, 2003) are reduced when using isoluminant stimuli (Yeshurun, 2004).

In summary, the findings of the present study are consistent with the hypothesis that attention enhances detection and salience but does not alter appearance (Blaser, Sperling, & Lu, 1999) and are consistent with the results of Schneider and Bavelier's (2003) study showing that the perceptual effects of abrupt onset cues can largely be explained by sensory and not attentional factors. Sensory interference can alter the appearance of stimuli, but attention acts primarily to influence which stimuli are perceived, without, in the process, misinforming the visual system about their attributes.

REFERENCES

Abrams, R. A., & Christ, S. E. (2003). Motion onset captures attention. *Psychological Science*, **14**, 427-432.

Bashinski, H. S., & Bacharach, V. R. (1980). Enhancement of perceptual sensitivity as the result of selectively attending to spatial locations. *Perception & Psychophysics*, **28**, 241-248.

Blaser, E., Sperling, G., & Lu, Z.-L. (1999). Measuring the amplification of attention. *Proceedings of the National Academy of Sciences*, **96**, 11681-11686.

Braddick, O. (1974). A short-range process in apparent motion. *Vision Research*, **14**, 519-527.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, **10**, 433-436.

Cameron, E. L., Tai, J. C., & Carrasco, M. (2002). Covert attention affects the psychometric function of contrast sensitivity. *Vision Research*, **42**, 949-967.

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, **7**, 308-313.

Carrasco, M., Penpeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: Support for signal enhancement. *Vision Research*, **40**, 1203-1215.

Cheal, M., & Lyon, D. R. (1991). Central and peripheral precuing of forced-choice discrimination. *Quarterly Journal of Experimental Psychology*, **43A**, 859-880.

Cheng, A., Eysel, U. T., & Vidyasagar, T. R. (2004). The role of the magnocellular pathway in serial deployment of visual attention. *European Journal of Neuroscience*, **20**, 2188-2192.

Crawford, T. J., & Müller, H. J. (1992). Spatial and temporal effects of spatial attention on human saccadic eye movements. *Vision Research*, **32**, 293-304.

Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition*, **6**, 509-540.

Eriksen, C. W., & Hoffman, J. E. (1972). Temporal and spatial characteristics of selective encoding from visual displays. *Perception & Psychophysics*, **12**, 201-204.

Evarts, E. V. (1971). Central control of movement: V. Feedback and corollary discharge: A merging of the concepts. *Neurosciences Research Program Bulletin*, **9**, 86-112.

Foley, J. M., & Schwarz, W. (1998). Spatial attention: Effect of position uncertainty and number of distractor patterns on the threshold-versus-contrast function for contrast discrimination. *Journal of the Optical Society of America A*, **15**, 1036-1047.

Franconeri, S. L., Hollingworth, A., & Simons, D. J. (2005). Do new objects capture attention? *Psychological Science*, **16**, 275-281.

Franconeri, S. L., & Simons, D. J. (2003). Moving and looming stimuli capture attention. *Perception & Psychophysics*, **65**, 999-1010.

Friesen, C. K., & Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. *Psychonomic Bulletin & Review*, **5**, 490-495.

Friesen, C. K., & Kingstone, A. (2003). Abrupt onsets and gaze direction cues trigger independent reflexive attentional effects. *Cognition*, **87**, B1-B10.

Frischen, A., & Tipper, S. P. (2004). Orienting attention via observed gaze shift evokes longer term inhibitory effects: Implications for social interactions, attention, and memory. *Journal of Experimental Psychology: General*, **133**, 516-533.

Gobell, J., & Carrasco, M. (2005). Attention alters the appearance of spatial frequency and gap size. *Psychological Science*, **16**, 644-651.

Hamlin, A. J. (1896). Attention and distraction. *American Journal of Psychology*, **8**, 3-66.

Hawkins, H. L., Hillyard, S. A., Luck, S. J., Mouloua, M., Downing, C. J., & Woodward, D. P. (1990). Visual attention modulates signal detectability. *Journal of Experimental Psychology: Human Perception & Performance*, **16**, 802-811.

Helekar, S. A. (1999). On the possibility of universal neural coding of subjective experience. *Consciousness & Cognition*, **8**, 423-446.

Helson, H. (1963). Studies of anomalous contrast and assimilation. *Journal of the Optical Society of America*, **53**, 179-184.

Henderson, J. M., & Macquistan, A. D. (1993). The spatial distribution of attention following an exogenous cue. *Perception & Psychophysics*, **53**, 221-230.

Hikosaka, O., Miyauchi, S., & Shimojo, S. (1993). Focal visual attention produces illusory temporal order and motion sensation. *Vision Research*, **33**, 1219-1240.

Hopfinger, J. B., & Mangun, G. R. (1998). Reflexive attention modulates processing of visual stimuli in human extrastriate cortex. *Psychological Science*, **9**, 441-447.

Hopfinger, J. B., & Mangun, G. R. (2001). Tracking the influence of reflexive attention on sensory and cognitive processing. *Cognitive, Affective, & Behavioral Neuroscience*, **1**, 56-65.

Huang, L., & Dobkins, K. R. (2005). Attentional effects on contrast discrimination in humans: Evidence for both contrast gain and response gain. *Vision Research*, **45**, 1201-1212.

Jancke, D., Chavane, F., Naaman, S., & Grinvald, A. (2004). Imaging cortical correlates of illusion in early visual cortex. *Nature*, **428**, 423-426.

Jonides, J. (1981). Voluntary versus automatic control over the mind's eye's movement. In J. B. Long & A. D. Baddeley (Eds.), *Attention and performance IX* (pp. 187-203). Hillsdale, NJ: Erlbaum.

Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, **22**, 751-761.

LaBerge, D. (1981). Automatic information processing: A review. In J. B. Long & A. D. Baddeley (Eds.), *Attention and performance IX* (pp. 173-186). Hillsdale, NJ: Erlbaum.

Langton, S. R. H., & Bruce, V. (1999). Reflexive visual orienting in response to the social attention of others. *Visual Cognition*, **6**, 541-567.

Langton, S. R. H., Watt, R. J., & Bruce, V. (2000). Do the eyes have it? Cues to the direction of social attention. *Trends in Cognitive Sciences*, **4**, 50-59.

Lennie, P. (1980). Parallel visual pathways: A review. *Vision Research*, **20**, 561-594.

Lu, Z.-L., & Dosher, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research*, **38**, 1183-1198.

Lu, Z.-L., & Dosher, B. A. (2000). Spatial attention: Different mechanisms for central and peripheral temporal precues? *Journal of Experimental Psychology: Human Perception & Performance*, **26**, 1534-1548.

LUCK, S. J., CHELAZZI, L., HILLYARD, S. A., & DESIMONE, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, **77**, 24-42.

LUCK, S. J., & THOMAS, S. J. (1999). What variety of attention is automatically captured by peripheral cues? *Perception & Psychophysics*, **61**, 1424-1435.

MACKAY, D. J. C. (1992). Bayesian interpolation. *Neural Computation*, **4**, 415-447.

MARKOWITSCH, H. J. (1995). Cerebral bases of consciousness: A historical view. *Neuropsychologia*, **33**, 1181-1192.

MARTÍNEZ-TRUJILLO, J., & TREUE, S. (2002). Attentional modulation strength in cortical area MT depends on stimulus contrast. *Neuron*, **35**, 365-370.

MCADAMS, C. J., & MAUNSELL, J. H. R. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *Journal of Neuroscience*, **19**, 431-441.

MERIGAN, W. H., & MAUNSELL, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, **16**, 369-402.

MILLER, J. (1989). The control of attention by abrupt visual onsets and offsets. *Perception & Psychophysics*, **45**, 567-571.

MORRONE, M. C., DENTI, V., & SPINELLI, D. (2002). Color and luminance contrasts attract independent attention. *Current Biology*, **12**, 1134-1137.

MÜLLER, H. J., & RABBITT, P. M. A. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception & Performance*, **15**, 315-330.

MÜNSTERBERG, H. (1894). The intensifying effect of attention. *Psychological Review*, **1**, 39-44.

NAKA, K. I., & RUSHTON, W. A. (1966). S-potentials from luminosity units in the retina of fish (*Cyprinidae*). *Journal of Physiology*, **185**, 587-599.

NAKAYAMA, K., & MACKEBEN, M. (1989). Sustained and transient components of focal visual attention. *Vision Research*, **29**, 1631-1647.

NEWHALL, S. M. (1921). The modification of the intensity of sensation by attention. *Journal of Experimental Psychology*, **4**, 222-243.

NEWHALL, S. M. (1923). Effects of attention on the intensity of cutaneous pressure and on visual brightness. *Archives of Psychology*, **61**, 5-75.

PELLI, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, **10**, 437-442.

PESTILLI, F., & CARRASCO, M. (2005). Attention enhances contrast sensitivity at cued and impairs it at uncued locations. *Vision Research*, **45**, 1867-1875.

PILLSBURY, W. B. (1908). *Attention*. New York: Macmillan.

POLLEN, D. A. (1999). On the neural correlates of visual perception. *Cerebral Cortex*, **9**, 4-19.

POSNER, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, **32**, 3-25.

POSNER, M. I., & COHEN, Y. (1984). Components of attention. In H. Bouma & D. G. Bouwhuis (Eds.), *Attention and performance X: Control of language processes* (pp. 531-556). Hillsdale, NJ: Erlbaum.

PRINZMETAL, W., NWACHUKU, I., BODANSKI, L., BLUMENFELD, L., & SHIMIZU, N. (1997). The phenomenology of attention: Part 2. Brightness and contrast. *Consciousness & Cognition*, **6**, 372-412.

PYLYSHYN, Z. W., & STORM, R. W. (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision*, **3**, 179-197.

REES, G., KREIMAN, G., & KOCH, C. (2002). Neural correlates of consciousness in humans. *Nature Reviews Neuroscience*, **3**, 261-270.

REMINGTON, R. W., JOHNSTON, J. C., & YANTIS, S. (1992). Involuntary attentional capture by abrupt onsets. *Perception & Psychophysics*, **51**, 279-290.

REYNOLDS, J. H., PASTERNAK, T., & DESIMONE, R. (2000). Attention increases sensitivity of V4 neurons. *Neuron*, **26**, 703-714.

SCHNEIDER, K. A., & BAVELIER, D. (2003). Components of visual prior entry. *Cognitive Psychology*, **47**, 333-366.

SCHULLER, A., & ROSSION, B. (2001). Spatial attention triggered by eye gaze increases and speeds up early visual activity. *NeuroReport*, **12**, 2381-2386.

SCLAR, G., & FREEMAN, R. D. (1982). Orientation selectivity in the cat's striate cortex is invariant with stimulus contrast. *Experimental Brain Research*, **46**, 457-461.

SEIDEMANN, E., & NEWSOME, W. T. (1999). Effect of spatial attention on the responses of area MT neurons. *Journal of Neurophysiology*, **81**, 1783-1794.

SKOTTUN, B. C., BRADLEY, A., SCLAR, G., OHZAWA, I., & FREEMAN, R. D. (1987). The effects of contrast on visual orientation and spatial frequency discrimination: A comparison of single cells and behavior. *Journal of Neurophysiology*, **57**, 773-786.

SOLOMON, J. A. (2004). The effect of spatial cues on visual sensitivity. *Vision Research*, **44**, 1209-1216.

SOLOMON, J. A., LAVIE, N., & MORGAN, M. J. (1997). Contrast discrimination function: Spatial cuing effects. *Journal of the Optical Society of America A*, **14**, 2443-2448.

STUMPF, C. (1890). *Tonpsychologie* (Vol. 2). Leipzig: Hirzel.

TITCHENER, E. B. (1908). *Lectures on the elementary psychology of feeling and attention*. New York: Macmillan.

TREISMAN, A. M., & GELADE, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, **12**, 97-136.

TSAL, Y., SHALEV, L., ZAKAY, D., & LUBOW, R. E. (1994). Attention reduces perceived brightness contrast. *Quarterly Journal of Experimental Psychology*, **47A**, 865-893.

TSE, P. U. (2005). Voluntary attention modulates the brightness of overlapping transparent surfaces. *Vision Research*, **45**, 1095-1098.

VANDUFFEL, W., TOOTELL, R. B., & ORBAN, G. A. (2000). Attention-dependent suppression of metabolic activity in the early stages of the macaque visual system. *Cerebral Cortex*, **10**, 109-126.

VON HOLST, E. (1954). Relations between the central nervous system and the peripheral organs. *British Journal of Animal Behaviour*, **2**, 89-94.

YANTIS, S., & GIBSON, B. S. (1994). Object continuity in apparent motion and attention. *Canadian Journal of Experimental Psychology*, **48**, 182-204.

YANTIS, S., & JOHNSON, D. N. (1990). Mechanisms of attentional priority. *Journal of Experimental Psychology: Human Perception & Performance*, **16**, 812-825.

YANTIS, S., & JONIDES, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception & Performance*, **16**, 121-134.

YESHURUN, Y. (2004). Isoluminant stimuli and red background attenuate the effects of transient spatial attention on temporal resolution. *Vision Research*, **44**, 1375-1387.

YESHURUN, Y., & LEVY, L. (2003). Transient spatial attention degrades temporal resolution. *Psychological Science*, **14**, 225-231.

APPENDIX A
t Tests for Weighted Means

The weighted mean of n measurements x_i, each with weights w_i, is

$$\hat{\mu} = \frac{\sum\limits_{i=1}^{n} w_i x_i}{\sum\limits_{i=1}^{n} w_i}.$$

The weights $w_i = \sigma_i^{-2}$, the reciprocal of the variance associated with each measurement, minimize the weighted variance

$$\hat{\sigma}^2 = \frac{\left(\sum\limits_{i=1}^{n} w_i\right)\sum\limits_{i=1}^{n} w_i\left(x_i - \hat{\mu}\right)^2}{\left(\sum\limits_{i=1}^{n} w_i\right)^2 - \sum\limits_{i=1}^{n} w_i^2}.$$

To compare the weighted mean to zero, the t statistic

$$\frac{\hat{\mu}}{\hat{\sigma}/\sqrt{f}} \sim t_{n-1}$$

with $n-1$ degrees of freedom may be used, where

$$f = \frac{\left(\sum\limits_{i=1}^{n} w_i\right)^2}{\sum\limits_{i=1}^{n} w_i^2}$$

is the effective sample size. To compare two weighted means $\hat{\mu}_x$ and $\hat{\mu}_y$, the t statistic

$$\left(\hat{\mu}_x - \hat{\mu}_y\right)\Big/\sqrt{\hat{\sigma}_x^2/f_x + \hat{\sigma}_y^2/f_y} \sim t_d$$

may be used, with

$$d = \frac{\left(\hat{\sigma}_x^2/f_x + \hat{\sigma}_y^2/f_y\right)^2}{\dfrac{\hat{\sigma}_x^4/f_x^2}{n_x - 1} + \dfrac{\hat{\sigma}_y^4/f_y^2}{n_y - 1}}$$

degrees of freedom.

APPENDIX B
Models of Attentional Contrast Modulation

A model of the neural response R as a function of stimulus contrast C is given by

$$R = \frac{R_{max}C^n}{C^n + C_{50}^n} + M,$$

where R_{max} is the maximum response and C_{50} is the contrast at which the response is half maximum (Martínez-Trujillo & Treue, 2002; Naka & Rushton, 1966). Under the contrast gain model, attention modulates the parameter C_{50} to C_{50}', causing an equivalent change in R as does changing the contrast to $C' = (C_{50}/C_{50}')C$—that is, a multiplicative change. Under the response gain model, attention modulates the parameter R_{max}. For low contrasts, $C \ll C_{50}$, changing R_{max} to R_{max}' also causes an equivalent change in R as does a multiplicative change in contrast, $C' \approx (R_{max}'/R_{max})^{1/n}C$. The effects of adding or multiplying C by a constant factor are illustrated in Figure A1. The additive factor affects the response at low contrasts, whereas the multiplicative factor shifts the response function in parallel across the contrast range, equivalent to a change in C_{50}.
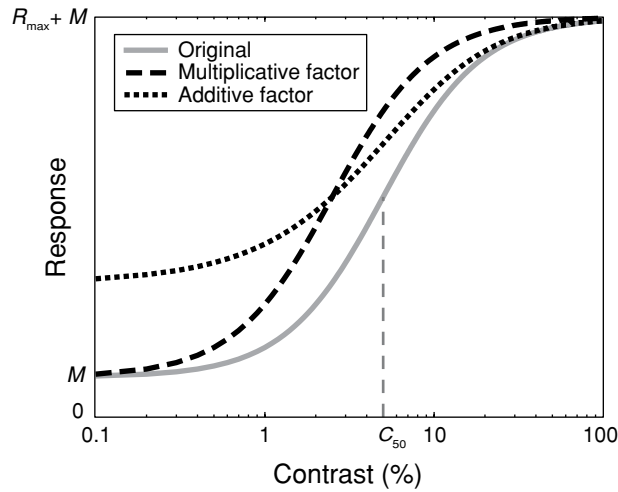

Figure A1. The effects of additive and multiplicative factors on a model contrast response function. The function

$$R = \frac{R_{max}C^n}{C^n + C_{50}^n} + M,$$

with typical parameters is shown in the solid gray line. The effects of an additive (dotted black line, most prominent at low contrasts) and a multiplicative (dashed black line, a parallel shift equivalent to a change in C_{50}) are also shown.