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The eyes like their targets on a stable background

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In normal human visual behavior, our visual system is continuously exposed to abrupt changes in the local contrast and mean luminance in various parts of the visual field, as caused by actual changes in the environment, as well as by movements of our body, head, and eyes. Previous research has shown that both threshold and suprathreshold contrast percepts are attenuated by a co-occurring change in the mean luminance at the location of the target stimulus. In the current study, we tested the hypothesis that contrast targets presented with a co-occurring change in local mean luminance receive fewer fixations than targets presented in a region with a steady mean luminance. To that end we performed an eye-tracking experiment involving eight observers. On each trial, after a 4 s adaptation period, an observer's task was to make a saccade to one of two target gratings, presented simultaneously at 7° eccentricity, separated by 30° in polar angle. When both targets were presented with a steady mean luminance, saccades landed mostly in the area between the two targets, signifying the classic global effect. However, when one of the targets was presented with a change in luminance, the saccade distribution was biased towards the target with the steady luminance. The results show that the attenuation of contrast signals by co-occurring, ecologically typical changes in mean luminance affects fixation selection and is therefore likely to affect eye movements in natural visual behavior.

the local mean luminance, in order to efficiently signal local (temporal) contrast by means of their limited dynamic range (reviewed in Rieke & Rudd, 2009). The emphasis on change continues throughout the visual system. For example, on a level much higher than the photoreceptors, the focus of (covert and overt) visual attention is very effectively drawn by abrupt changes in stimuli (Castiello, Badcock, & Bennett, 1999; Todd & Van Gelder, 1979; Yantis & Jonides, 1990).

However, abrupt stimulus changes are not beneficial in every respect. For example, an abrupt change in local mean luminance is, as such, a powerful attention attractor (Ludwig, Davies, & Gegenfurtner, 2012; Theeuwes, Kramer, Hahn, & Irwin, 1998). At the same time, the luminance change may obscure relevant contrast-based information accompanying the change. This interaction occurs because already in the first processing step, namely the photoreceptors of the retina, the neural responses to the luminance change and the superimposed contrast stimuli are intermingled. When the luminance change and the contrast pattern reach the retina simultaneously, the photoreceptors and the subsequent retinal neurons have not had the time to adapt to the new local mean luminance (Rieke & Rudd, 2009). As a result, the contrast signal transmitted from each part of the retina is unavoidably attenuated by an abrupt luminance change in that retinal region. In other words, the local contrast information is swamped by the large responses to the luminance change. At the perceptual level, attenuation of contrast signals has been shown both at threshold (Poot, Snippe, & van Hateren, 1997) and suprathreshold (Kilpeläinen, Nurminen, & Donner, 2011) contrast levels.

The significance of an increase in detection threshold is relatively self-evident: a low contrast element will

Introduction

The human visual system places a strong emphasis on change. Already on the very first level of the visual system, the photoreceptors of the retina quickly adapt to

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remain unseen, if the change in the local mean luminance at the retinal region of the element attenuates the element's contrast signal. Yet, not much is known about the significance of attenuation at higher contrast levels, where the stimuli remain clearly visible, albeit perceptually weaker. One central visual function where the significance could surface is the selection of fixation targets. In free viewing of natural scenes, both high contrast and high local luminance are known to draw fixations (Rajashekar, Van der Linde, Bovik, & Cormack, 2007; however, see also Vincent, Baddeley, Correani, Troscianko, & Leonards, 2009). In addition, the abrupt onset of a high intensity stimulus draws fixations in a very effective manner, even if the stimulus is completely task irrelevant (Spehar & Owens, 2012; Theeuwes et al., 1998). It is therefore feasible that a suprathreshold contrast target presented on top of an abrupt increase in mean luminance would have more combined salience and hence draw more saccades than a target presented on a stable mean luminance. However, the exact opposite is predicted by the psychophysical study of Kilpeläinen et al. (2011), which showed that the contrast signal of a target is attenuated by a simultaneous change in local mean luminance, regardless of change direction (up vs. down). As a result, saccades should predominantly be directed towards the target with a *stable* mean luminance rather than the one with the change in mean luminance.

In the present study, we tested the above predictions using eye-tracking. We used the so-called global effect (Coren & Hoenig, 1972; Walker, Deubel, Schneider, & Findlay, 1997), which is the tendency for saccades to land in between two nearby targets. This setup is particularly suitable for the present purpose as it provides a continuous measure of the relative fixation attraction strengths of the two stimuli (cf. Deubel, Wolf, & Hauschke, 1984). Our results show that when one of the targets is presented with a simultaneous change in local mean luminance, the saccades tend to land away from that target, more towards the target presented in a region with steady mean luminance. The effect occurs both for upward and downward changes in mean luminance. The results have implications for the selection of contrast targets for fixation in natural visual behavior, where luminance changes frequently accompany contrast target onsets (e.g., Frazor & Geisler, 2006).

Methods

Observers

Eight observers participated in the study. The observers were between 20 and 35 years of age and reported normal visual acuity. The study adhered to the principles of the Declaration of Helsinki. The observers practiced the task before the actual experiment.

Stimuli and apparatus

The context stimulus was a circular shape (radius 10° of visual angle), divided into 12 sectors (each 30° of polar angle). The screen around the circular shape and within 1° from the fixation cross (black cross hair, height 0.7°) contained the global mean luminance of 58 cd/m^2 . Local luminances of the sectors were assigned from four possible values (departing upwards or downwards by 14.5 or 43.5 cd/m^2 from the global mean luminance of 58 cd/m^2). Each local luminance was applied to three sectors (see Figure 1B, for examples). As a result, the global mean luminance of the context stimulus remained constantly equal to that of the unmodulated background. All edges of the context stimulus were blurred with a 2D Gaussian filter ($SD 0.2^\circ$). Three adjacent sectors of same luminance were precluded.

The target stimuli were sine wave gratings in circular apertures (2 cpd) with a 1° diameter, presented at 7° eccentricity and in the center of the underlying sector in polar angle direction. The Michelson contrast of the gratings was always 10%, the mean luminance the same as the underlying sector's. The orientations of the gratings were radial relative to fixation. The rightmost stimulus in Figure 1B presents an example of the context stimulus with the target stimuli added on it.

Stimuli were created and presented with the PsychoPy library (Peirce, 2007) operating within the OpenSesame experiment builder (Mathôt, Schreij, & Theeuwes, 2012). The stimuli were presented with a PC with an NVIDIA GeForce 220 video card and a 22" Samsung 2233RZ LCD monitor (for a test report, see Wang & Nikolić, 2011) with a spatial resolution of 1650×1050 and a 60 Hz refresh rate. Grayscale calibration was conducted with a Lacie BlueEye colorimeter and by correcting the look up table programmatically. Grayscale resolution was increased by controlling the green and red + blue components of the signal individually, but always within one level of each other (cf. Tyler, 1997). Our checkup measurements showed that the setup reproduced the luminance levels required by the gratings with a very good accuracy ($R^2 > 0.98$, regardless of mean luminance). Note that perfect accuracy is not critical for the main findings of the study because in any analyzed condition, the two targets were always *identical*. The only difference was the local luminance *before* target onset.

Eye movements were recorded with Eyelink 1000 (SR Research, Mississauga, Canada), a video based eye-tracker sampling at 1000 Hz. Both pupil and corneal reflection were used for tracking. The eye-tracker was controlled by the OpenSesame software. Saccades that landed within 2° of the central fixation, more than 45° in polar angle from either target (outside the target sectors or sectors adjacent to those), and saccades with latencies shorter than 100 ms or longer than 600 ms

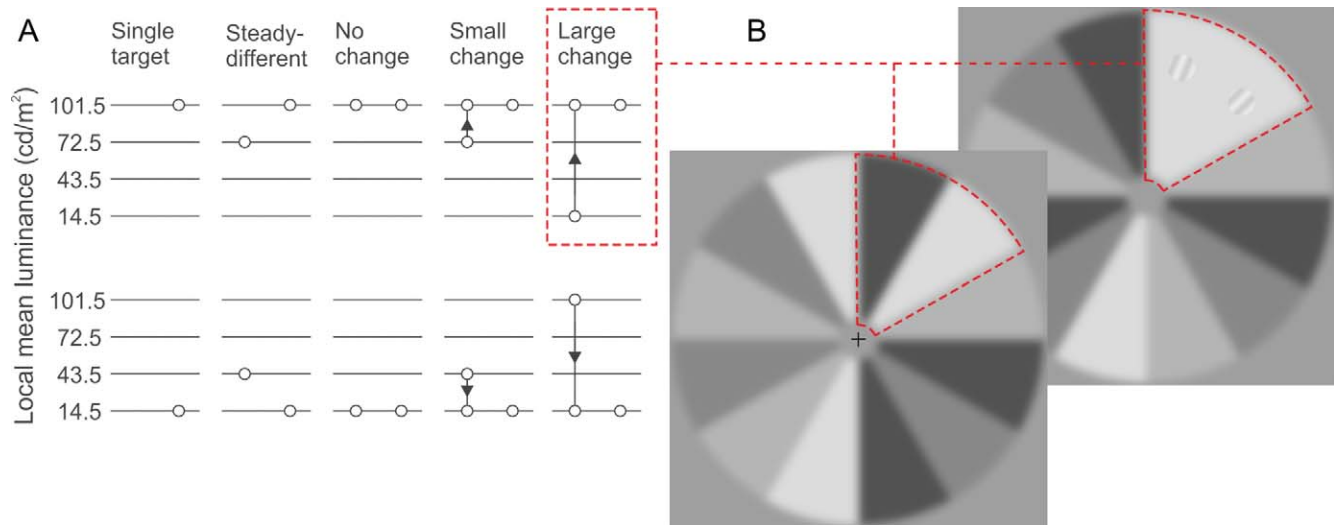


Figure 1. (A) The different stimulus conditions of the experiment. Circles show the mean luminance of the sector under each target stimulus. An arrow indicates the direction and magnitude of a transition from one mean luminance to another (the circles connected by the arrow), occurring at the moment of target onset. Upper and lower rows of diagrams correspond to high and low local mean luminances in target sectors, respectively. (B) Examples of the stimuli: Left, the combination of a context stimulus and a fixation cross hair, which were presented during the adaptation phase. Right, the target display. As soon as the fixation cross hair was extinguished, observers had to make as quickly as possible a saccade to one of the two target gratings. In this example (of the *Large change* condition), one target grating is presented in a sector of steady (high) mean luminance, the other at a sector where the local mean luminance steps from a low to high level simultaneously with the onset of the target gratings.

were excluded from the analyzes. The exclusion criteria led to a 16% loss of trials which was mainly due to relatively small amplitude saccades that occurred near stimulus presentation, probably because of the long (4000 ms, the adaptation period) fixation required before target stimulus appearance.

Procedure

Each trial proceeded as follows. First, a context stimulus and the central fixation cross hair appeared (the leftmost stimulus in Figure 1B). Then the observer had to fixate and press a button. Once fixation was stable, a 4000 ms adaptation period commenced, during which the stimulus remained unchanged and the observer fixated on the cross hair. After a 4000 ms adaptation period, the stimulus display changed abruptly: the fixation cross hair was extinguished, sector luminances changed, and the target gratings were presented (see Figure 1B). The observer's task was to make a saccade to either one of the targets as quickly as possible after the disappearance of the fixation cross. The stimulus with the targets was presented for 1000 ms, followed by 500 ms of blank grey screen, and then the next trial. On a few trials, only one target grating appeared in which case the observer made a saccade to the single target grating. The sectors at which the targets appeared were randomized. In order to achieve a sufficient number of relevant luminance transitions,

the luminances of the sectors of the context stimulus were pseudorandomized. Different types of trials were presented in a mixed order.

Figure 1A presents the different trial types of the experiment. Note that the *Steady-different* condition was included in order to increase the probability of a target appearing in a sector with an intermediate local luminance, and the data of those trials was not analyzed. The example in Figure 1B illustrates a trial where one of the targets is presented in a sector of steady (high) mean luminance, but the other target, in a sector where the mean luminance steps from a low to high simultaneously with the onset of the targets. For most observers, the eight conditions involving two targets were repeated 36 times, the two single target conditions 24 times (Figure 1A). For two observers (S1, S2), the corresponding numbers were 30 and 15, respectively. The data of those two observers did not differ from the others.

Results

Saccades deviate away from the target with a changing background luminance

For analysis and presentation, saccade directions were normalized so that the steady target is at -15° , the

Mean luminance in both target sectors at target onset
101.5 cd/m² 14.5 cd/m²

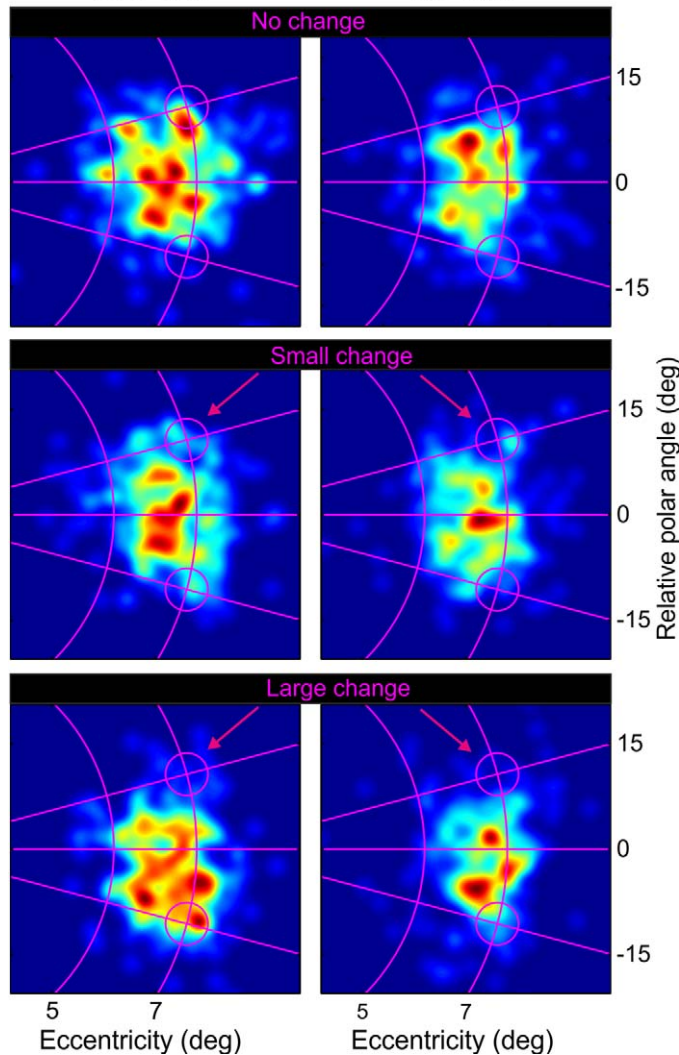


Figure 2. Heat maps of all saccades (for all observers) when both targets were presented with identical, steady mean luminance (top), when one of the targets (the upper magenta circle) was presented with a small (middle) or large (bottom) simultaneous change in local mean luminance. At the moment of target onset, the local mean luminance in both target sectors was 101.5 cd/m² (left) or 14.5 cd/m² (right). The heat maps were created by filtering the saccade landing point map with a 2-D Gaussian filter ($SD\ 0.2^\circ$).

step target at +15° (see Figure 2), and the angular midpoint is at 0° (except in the single target condition 0° is the center of the target). In the *No change* condition, where two targets were presented in sectors with a steady low (14.5 cd/m²) or high (101.5 cd/m²) luminance, saccades landed on and around the midpoint between the two targets, demonstrating the classical global effect (top panels in Figure 2). However, when one of the targets was presented in a sector where the mean luminance changed simulta-

Mean luminance in target sectors (cd/m²)

	101.5	14.5
No change	1.1 (10.1)	−0.1 (10.4)
Small change	1.0 (10.1)	−0.5 (10.2)
Large change	−3.8 (10.1)	−2.6 (10.8)
Single target	−0.8 (7.2)	0.1 (8.2)

Table 1. Average saccade directions (and *SDs*) over all saccades (pooled over observers) in the different conditions. Zero refers to the angular midpoint between the two targets, −15 to the steady target; except in the single target condition, zero refers to the center of the target.

neously with target presentation (upper magenta circles in the bottom panels of Figure 2), saccades mostly deviated away from that target (henceforth the *step target*) and landed closer to the other target, which was presented on a steady background luminance (henceforth the *steady target*). The *Small change* condition (middle panels) had little, if any, effect. In a repeated measures ANOVA with the normalized saccade direction relative to the targets as dependent variable, the effect of luminance change magnitude (No-Small-Large) was statistically significant, $F(2, 14) = 17.1, p < 0.01$. The effect of luminance level and the interaction effect (magnitude \times level) were not significant ($p > 0.2$). The average saccade directions (and *SDs*) in all conditions are presented in Table 1.

Inspection of Table 1 reveals that when two targets were presented (without luminance change), the saccade landing points are roughly as close to the midpoint between the two objects as they are to the midpoint of one object in the single target condition, but slightly more dispersed. The heat maps for the condition where a single target was presented on a steady mean luminance are shown for reference in

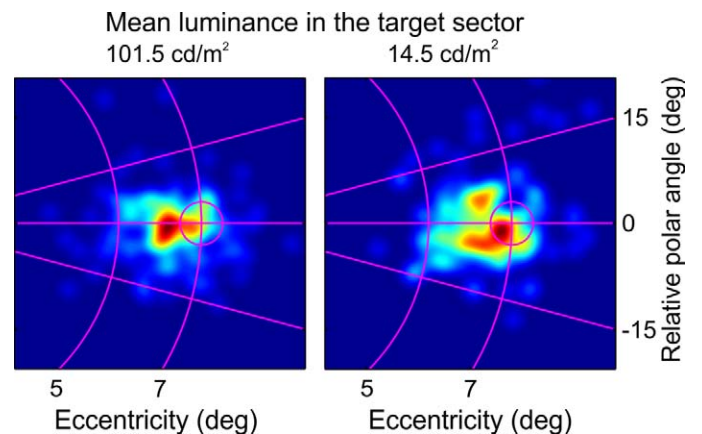


Figure 3. Heat maps of all saccades (for all observers) in the condition where a single target was presented in a sector with a steady mean luminance (left: 101.5 cd/m², right: 14.5 cd/m²).

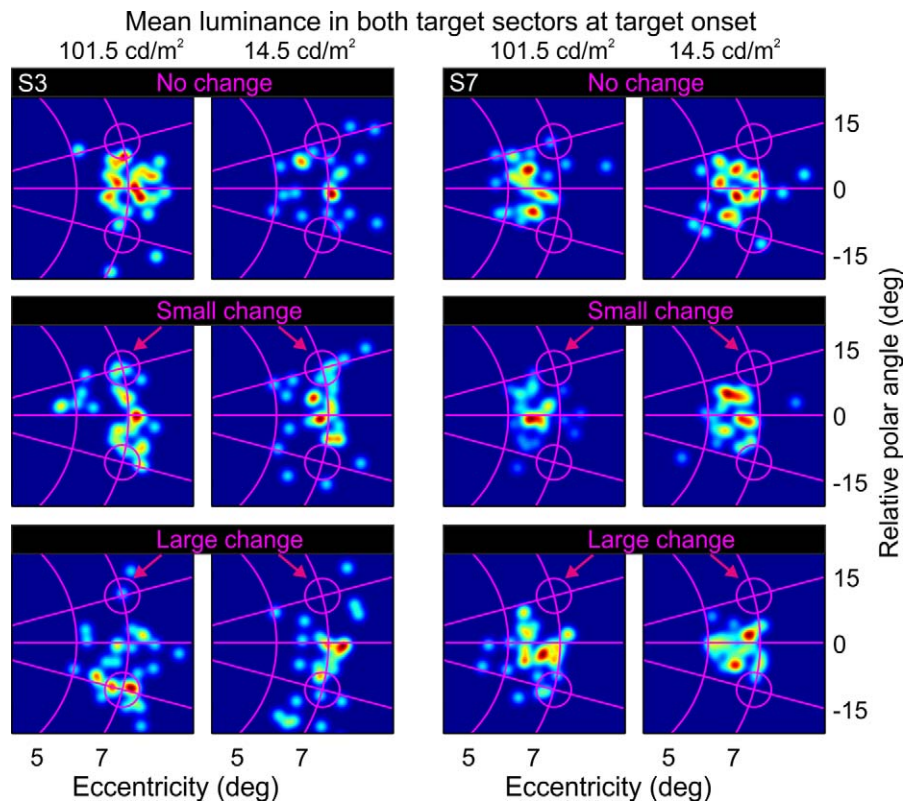


Figure 4. Heat maps for two representative observers. Order of panels as in Figure 2.

Figure 3. It is important to note that even in the *Large change* condition, the peak of the landing point distribution lies between the two targets. The distribution is not centered on the steady target, as it is in the single target conditions (compare bottom panel of Figure 2 with Figure 3). This pattern of results indicates that although the relevant perceptual response of the step target is attenuated, it still plays a role in saccade guidance.

Figure 4 presents heat maps for two representative observers. The figure shows that the effect of the luminance change is discernible even in single-observer data. Individual variation in the strength of the effect is also apparent in the figure (compare bottom panels of S3 and S7). Importantly, however, the large luminance change in the location of the step target shifted the average saccade direction towards the steady target *in all eight observers*.

Saccades towards high luminance targets have shorter latencies

Saccades had shorter latencies, when the targets were presented on a background with high (101.5 cd/m^2) rather than low (14.5 cd/m^2) mean luminance, across luminance change conditions (see Figure 5). In a

repeated measures ANOVA with latency as dependent variable, the effects of luminance level, $F(1, 7) = 73$, $p < 0.01$, and change magnitude, $F(2, 14) = 4.5$, $p < 0.05$, were significant, as was their interaction effect, $F(2, 14) = 4.3$, $p < 0.05$. We examined whether the effect of change magnitude was simply a consequence of longer latencies in saccades directed towards the step target ($\pm 10^\circ$ in polar angle), but latencies of saccades towards both targets increased equally.

Control experiment: The effect of luminance change without a target

The main finding of the experiment presented above is that when two identical targets are presented in adjacent sectors, saccades are biased away from the target presented in an area of changing mean luminance, towards the target presented in an area of stable luminance. It is possible, however, that the luminance change as such had a repelling or attracting effect on saccade direction, regardless of how the luminance change affected the superimposed target. We tested this possibility in a control experiment.

The main conditions of the control experiment were identical to the *Large change* condition of the main experiment (Figure 1A), except that only one target was

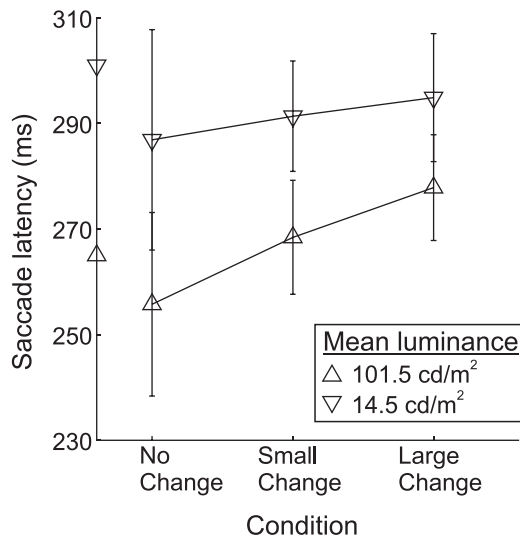


Figure 5. Average saccade latency (\pm SD, over all observers) in the different luminance change conditions, separately for high and low mean luminance at the moment of target onset (see legend). The markers on top of the y-axis represent the single target trials.

Mean luminance in the target sector at target onset
101.5 cd/m² 14.5 cd/m²

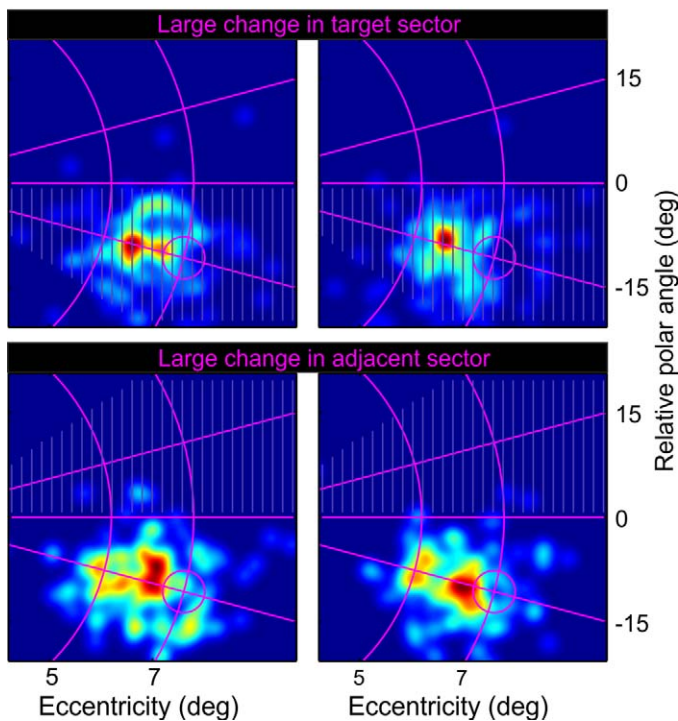


Figure 6. Heat maps of all saccades (for all three observers) when a single target (magenta circle) was presented with a simultaneous change in local mean luminance at the target sector (top) or the adjacent sector (bottom). Texture represents the area where luminance change occurred.

presented, either in the steady luminance sector or in the changing luminance sector. Figure 6 presents the heat maps for those conditions. Texture in the heat maps represents the area where the luminance change occurred. A condition where the single target was presented on a steady, moderate mean luminance (72.5 or 43.5 cd/m²), and with both adjacent sectors also steady (43.5 cd/m² when target sector was 72.5 cd/m², and vice versa), was also included, mainly to balance the a priori probabilities of target locations. The heat maps of that condition are provided for reference (Figure 7). There were three observers (one of them the first author, the others naïve). There were 48 trials per condition per observer. The same data exclusion criteria as in the main experiment were applied in the control experiment (see Methods), which led to a loss of 9% of trials. The lower rejection rate in this experiment is probably due to more experienced observers and a shorter measurement session.

The data strongly suggest that there is little, if any, difference in saccade directions between the case where a luminance change occurs in the sector of a single target and the case where the change occurs in the adjacent sector (see Table 2). More specifically, a luminance change in the target sector does not seem to repel saccades away from the target (upper panels of Figure 6). In addition, a luminance change in the adjacent sector does not draw the saccades away from the target (lower panels of Figure 6).

On the basis of this control experiment, we conclude that in the main experiment the concurrent luminance changes did not directly affect saccade direction, but rather interacted with the target contrast such that saccades were biased towards targets presented on a stable background.

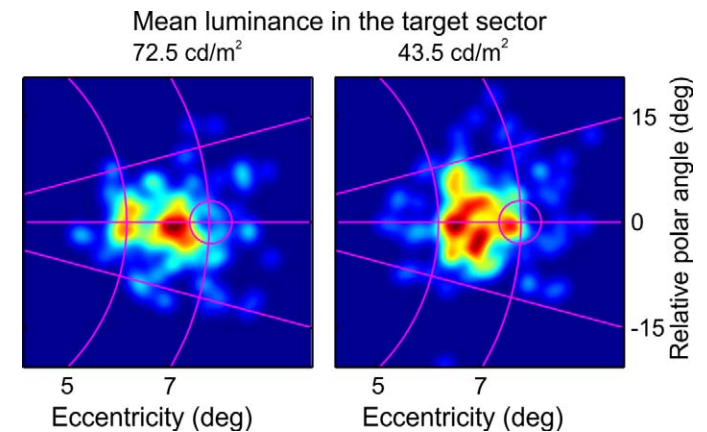


Figure 7. Heat maps of all saccades (for all three observers) in the condition where a single target was presented in a sector with a steady mean luminance (left: 72.5 cd/m², right: 43.5 cd/m²). Both sectors adjacent to the target sector also had a steady mean luminance (left: 43.5 cd/m², right: 72.5 cd/m²).

	Mean luminance in target sectors (cd/m ²)	
	101.5	14.5
Change in adjacent sector	−0.5 (8.4)	−0.6 (8.5)
Change in target	−0.1 (8.5)	−1.6 (9.1)

Table 2. Average saccade directions (and *SDs*) over all saccades (pooled over observers) in the single target conditions, where the luminance change occurred either in the sector of the target or the adjacent one. Zero refers to center of the target.

Discussion

When two physically identical, equally relevant target stimuli appear simultaneously, observers move their gaze towards a target with a stable mean luminance rather than a target presented with a simultaneous change in background luminance. The transient change in mean luminance appears to decrease the salience of a target at the location of the change, an observation which is in line with earlier reports of attenuation of contrast percepts by a simultaneous change in mean luminance. Such attenuation is well explained by known properties of retinal neurons.

Target selection is biased by local mean luminance changes

Attending to changes in the visual field is potentially more important for survival than is the meticulous scrutiny of unchanging features. In that light, the strong fixation attraction ability of an individual transient change in the visual field is not a surprise (Theeuwes et al., 1998; Todd & Van Gelder, 1979). When multiple transient changes occur simultaneously, however, the direction of the first saccade becomes much less predictable (reviewed in Findlay & Walker, 1999). One intriguing property of stimulus-driven saccade guidance is the so-called global effect, where saccades tend to land roughly at the centre of gravity of two equally relevant, simultaneously appearing stimuli (Coren & Hoenig, 1972; Walker et al., 1997). The proportion of such averaging saccades and the precise location and shape of their spatial distribution depends, among other aspects, on the size, the intensities, and the spatial arrangement of the two stimuli (Deubel et al., 1984; Van der Stigchel, Heeman, & Nijboer, 2012; Van der Stigchel, Meeter, & Theeuwes, 2007).

In this study, we used the global effect to probe the perceptual significance of the earlier observed attenuation effect of mean luminance changes. When both targets were presented with identical, steady mean

luminance, saccades predominantly landed in the area between the two targets, with very few saccades landing at the location of either target. However, when one of the targets (the step target) was presented with a simultaneous change in local mean luminance, saccades deviated away from that. The magnitude of the effect was roughly equal for upward and downward luminance changes. It is important to keep in mind that at the moment of target presentation, the two target sectors (including the targets themselves) are identical. The sectors only differ regarding their mean luminances immediately before target onset.

Saccade guidance starts in the retina

Why did the saccades predominantly land closer to the target with the steady mean luminance (the steady target)? The short answer (expanded below) is that the contrast signal of the step target becomes weaker than the signal of the steady target and thus gets a lower (but nonzero) weight in the averaging process that determines the saccade direction.

The attenuation of a contrast signal by a simultaneous change in the local mean luminance has been psychophysically observed in threshold and supra-threshold stimuli (Hayhoe, Benimoff, & Hood, 1987; Kilpeläinen et al., 2011; Poot et al., 1997). Such attenuation is an unavoidable consequence of retinal light adaptation principles (reviewed in Rieke & Rudd, 2009). Cone photoreceptors and subsequent retinal neurons adjust their relatively narrow dynamic range according to the local mean light level falling in their retinal region. As a result, their contrast responses are nearly linear to contrasts around the adaptation level, but increasingly compressed to contrasts around a mean far from the adaptation level (for a more detailed discussion, see Kilpeläinen, Nurminen, & Donner, 2012). In the *Large change* condition of the current experiment, the steady target consists of light levels close to the adaptation level (set by the steady local mean luminance of the sector), whereas the same light levels of the step target are far from the adaptation level (set by the *immediately preceding* local mean luminance of that sector, as adaptation is not instantaneous). On the level of retinal output, then, the contrast response to the step target is *weaker* than the response to the steady target, and saccade accumulation closer to the steady target is to be expected.

Why did the saccades not go directly to the steady target? The superior colliculus (SC), currently considered the main hub of oculomotor command integration, does not operate in such a winner-takes-all manner. Instead, the stimulation of two retinotopic SC locations produces a saccade that corresponds to a vector average weighted according to the intensities of

the two stimuli (Katnani & Gandhi, 2011; Robinson, 1972; Van Opstal & Van Gisbergen, 1989). It is currently unclear whether a single peak of activity anywhere in the SC actually determines the direction of the averaging saccade (Edelman & Keller, 1998; Katnani & Gandhi, 2011), and what is the role and specific neural implementation of lateral inhibitory connections in the process (Arai & Keller, 2005; Meeter, Van der Stigchel, & Theeuwes, 2010; Trapenbergh, Dorris, Munoz, & Klein, 2001). Nevertheless, human and primate behavioral data on averaging saccades are well predicted by the vector averaging account (Deubel et al., 1984; Edelman & Keller, 1998). Also the current result where the distribution of saccades is biased away from the step target is understandable in this context. The contrast signal of the step target is attenuated in the retina, but remains above threshold. This is well illustrated by the control experiment: saccades land in the sector of the *single* target very accurately even when the target is presented in a sector with a change in mean luminance (Figure 6). As a result, the step target signal affects the vector average in the global effect setting, although with a lower weight, and saccades land closer to the steady target, but rarely quite on it.

Considering earlier eye-tracking findings, the finding that an abrupt increase in the luminance of a region *reduces* the number of saccades towards a target in that sector may, despite the explanation presented above, still appear surprising. Firstly, transient stimulus onsets (and offsets) strongly attract saccades, even if the stimulus onsets are irrelevant to the task (Ludwig, Ranson, & Gilchrist, 2008; Theeuwes et al., 1998). Secondly, both local luminance and contrast attract (although modestly) fixations in natural image viewing (Rajashekar et al., 2007). One might thus expect a transient luminance step within a region to add to the salience of the contrast target presented in that region, and *increase* the number of saccades towards that target. The ineffectiveness of the luminance step as saccade attractor was probably caused by the stimulus setup. In any given trial, large luminance steps could occur in any sector(s) of the background stimulus, and using the sector luminances for saccade decisions would lead to a very poor performance on the task. Instead, there were virtually no saccades towards random locations in the current experiment, indicating that observers were able to base saccadic decisions on the contrast signals alone. The results of the control experiment support this interpretation: When a single target was presented in a sector of steady mean luminance, saccades were not drawn to the adjacent sector with large step in mean luminance (Figure 6). Whereas the data do not allow us to rule out *beyond any doubt* that in the global effect setting the luminance change under one target could

have simultaneously attenuated the saliency of the contrast signal and drawn saccades with a luminance change signal, it is clear that the attenuation effect is the more potent one.

Saccades towards high luminance targets have shorter latencies

Saccades towards targets presented with high mean luminance had consistently shorter latencies, across the luminance change conditions, which is in agreement with faster *manual* reaction times at higher background luminance (e.g., Mollon & Krauskopf, 1973). This effect can be explained by the fact that photoreceptor responses to a fixed contrast rise to a certain (low) criterion level faster with higher background luminance (Donner & Fagerholm, 2003; Donner, Hemilä, & Koskelainen, 1998). Saccades also had longer latencies in the conditions involving luminance change than in the *No chance* condition. Somewhat unexpectedly, this increase in latencies concerned all saccades towards both targets, not only those towards the step target. The analysis is complicated by the fact that in the *Large change* condition, there were hardly any saccades directed, even approximately, towards the step target (see bottom panels of Figure 4). One possible explanation for such a general increase in latencies is that in the *Large change* condition, one of the target signals (and hence the combined strength of the two targets) is weakened by the luminance change. This idea is supported by the fact that the average latency in the *Large change* condition is comparable with the latency in the single target condition (markers on the *y*-axis in Figure 5).

The relevance of the current study regarding natural vision

Abrupt changes in the visual field are likely to become increasingly prominent in modern, manmade environments. In comparison to completely natural environments, manmade environments contain more light sources and glossy surfaces as well as a more spatially discrete luminance distribution (Hansen & Gegenfurtner, 2009; Torralba & Oliva, 2003). In addition, the speed of travel through the environment is often much higher than in natural environments. Finally, an increasing amount of time is spent viewing various dynamically illuminated digital displays.

In any environment, except possibly for some highly dynamic simulated environments, a predominant cause for changes in the retinal image will always be saccadic eye movements. We believe the current results are likely to be relevant concerning those changes as well.

However, although the neural responses to contrast stimuli brought to a receptive field by saccades and abrupt stimulus transitions are quite similar in the primary visual cortex (Gawne & Woods, 2003; Kagan, Gur, & Snodderly, 2008; MacEvoy, Hanks, & Paradiso, 2008), differences could arise on later processing stages. Thus, it will be necessary to study the effect of local mean luminance changes that are caused by actual, observer-initiated, saccades (see e.g., Ludwig et al., 2012). Secondly, the images need to be more complex natural images and the saccades more under the observer's control. We would like to emphasize, though, that although the stimuli of the current study are far from natural, the target contrast, the luminance step magnitudes, and the required saccade amplitudes are very typical in natural visual behavior (Frazor & Geisler, 2006; Land & Hayhoe, 2001; Tatler, Baddeley, & Vincent, 2006). If the current results are supported by data from such, more naturalistic studies, the luminance change effect provides a novel factor for eye-movement prediction: saccades are more likely to be drawn by contrast targets at locations where the previous saccade (or another cause) did not lead to a large luminance transition. Such a factor could, for example, be implemented into salience based saccade prediction models (Itti, Koch, & Niebur, 1998), and the models' currently modest predictive power could be improved (Schütz, Braun, & Gegenfurtner, 2011; Tatler, Hayhoe, Land, & Ballard, 2011).

Keywords: averaging saccades, eye movements, eye-tracking, retina, light adaptation, luminance, contrast, abrupt onset

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