Microsaccades counteract perceptual filling-in

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Artificial scotomas positioned within peripheral dynamic noise fade perceptually during visual fixation (that is, the surrounding dynamic noise appears to fill-in the scotoma). Because the scotomas' edges are continuously refreshed by the dynamic noise background, this filling-in effect cannot be explained by low-level adaptation mechanisms (such as those that may underlie classical Troxler fading). We recently showed that microsaccades counteract Troxler fading and drive first-order visibility during fixation (S. Martinez-Conde, S. L. Macknik, X. G. Troncoso, & T. A. Dyar, 2006). Here we set out to determine whether microsaccades may counteract the perceptual filling-in of artificial scotomas and thus drive second-order visibility. If so, microsaccades may not only counteract low-level adaptation but also play a role in higher perceptual processes. We asked subjects to indicate, via button press/release, whether an artificial scotoma presented on a dynamic noise background was visible or invisible at any given time. The subjects' eye movements were simultaneously measured with a high precision video system. We found that increases in microsaccade production counteracted the perception of filling-in, driving the visibility of the artificial scotoma. Conversely, decreased microsaccades allowed perceptual filling-in to take place. Our results show that microsaccades do not solely overcome low-level adaptation mechanisms but they also contribute to maintaining second-order visibility during fixation.

Keywords: fixational eye movements, fading, scotoma, visibility, adaptation, texture

Introduction

Our visual system has a built-in paradox: we must fixate our gaze in order to inspect the minute details of the world, yet if our eyes were perfectly still, all stationary objects would fade from view. Although complete retinal stabilization is most easily achieved in the laboratory (Ditchburn & Ginsborg, 1952; Riggs & Ratliff, 1952; Yarbus, 1967), fading of stationary objects also occurs in normal vision. In 1804, Swiss philosopher Ignaz Paul Vital Troxler noted that deliberately focusing the gaze on something causes stationary images in the surrounding region to fade away gradually (Troxler, 1804). This fading happens to us every day, although we are usually unaware of it. In the late 1950s, Clarke made a connection between Troxler's fading and the fading of stabilized images in the laboratory (Ditchburn & Ginsborg, 1952; Riggs & Ratliff, 1952) and attributed both phenomena to neural adaptation (Clarke, 1957, 1960, 1961; Clarke & Belcher, 1962).

Troxler fading paradigms usually involve the perceptual disappearance of discrete, simple, low-contrast stationary peripheral targets. However, moving and flickering stimuli are also susceptible to Troxler-like fading (Cohen, 1965; Enoch, Johnson, & Fitzgerald, 1976; Hunzelmann & Spillmann, 1984; MacKay, 1982; Magnussen, Spillmann, Stürzel, & Werner, 2001; Schieting & Spillmann, 1987; Spillmann & de Weerd, 2003; Stürzel & Spillmann, 2001), as are foveally presented stimuli (Krauskopf, 1963; Pessoa & De Weerd, 2003; Spillmann & de Weerd, 2003). Recent experiments have moreover demonstrated Troxler fading of entire visual scenes. In this "scene fading," the entire visual scene fades to uniform hue and luminance (Simons et al., 2006).

An effect phenomenologically similar to Troxler fading can also be observed by positioning a small window, or artificial scotoma, within a field of dynamic noise. The term 'artificial' scotoma (coined by Gerrits & Timmerman, 1969) is used by analogy to 'naturally' occurring scotomas, whether pathological (i.e., due to retinal or cortical lesions) or physiological (such as the blind spot). During visual fixation, this artificial scotoma rapidly fades from perception; that is, the dynamic noise texture appears to fill-in the scotoma (De Weerd, Gattass, Desimone, & Ungerleider, 1995; Ramachandran & Gregory, 1991; Spillmann & Kurtenbach, 1992). When the dynamic noise is removed, a powerful texture after-image takes the place originally occupied by the scotoma. This after-image may be dynamic: the so-called Twinkle effect (Ramachandran & Gregory, 1991) or static (Spillmann & Kurtenbach, 1992; Stürzel & Spillmann, 2001).

Unlike classical Troxler fading (Martinez-Conde, Macknik, Troncoso, & Dyar, 2006; Troxler, 1804), the perceptual vanishing of artificial scotomas cannot be easily explained by local first order adaptation to luminance edges: there is no average luminance difference

between the scotoma and the background, and moreover the dynamic background continually refreshes the edges of the fading stimulus on the retina (Ramachandran & Gregory, 1991; Spillmann & Kurtenbach, 1992). Interestingly, the dynamic noise helps to induce visual fading, which is not what one would expect from low-level adaptation mechanisms, as the edges of the scotoma are continuously refreshed by the kinetic border of dynamic noise (Spillmann & Kurtenbach, 1992). Rather, "the effect must be explained at least in terms of the extraction of the second-order characteristics (such as texture contrast) of the scene" (Welchman & Harris, 2001).

De Weerd, Desimone, and Ungerleider (1998) proposed that the filling-in of artificial scotomas takes place in a two-step process. The first step is the adaptation of the target-surround boundary between the scotoma and the surrounding dynamic background. Once the boundary adaptation is achieved, the neural propagation of the dominant representation (i.e., the surrounding dynamic-noise field) may invade the target (i.e., the scotoma), generating the filled-in percept. De Weerd et al. (1995) localized the neural correlates of this second step to extrastriate visual neurons in macaque area V3 (and to a lesser extent V2). Later studies have suggested that other extrastriate visual areas, such as area MT, may also be implicated (Welchman & Harris, 2001).

There has been a great deal of recent interest in the neural and perceptual mechanisms of filling-in (Cornelissen, Wade, Vladusich, Dougherty, & Wandell, 2006; De Weerd, 2006; De Weerd, Smith, & Greenberg, 2006; Hindi Attar, Hamburger, Rosenholtz, Gotzl, & Spillmann, 2007; Lleras & Moore, 2006; Mendola, Conner, Sharma, Bahekar, & Lemieux, 2006; Pessoa & De Weerd, 2003). However, the role of eye movements in the perception of filling-in has been neglected so far. Indeed, no previous studies have established a direct correlation between eye-movement dynamics and the perception of texture filling-in.

Microsaccades are rapid, small-magnitude involuntary saccades that occur during fixation (for a review of microsaccade parameters, see Martinez-Conde, Macknik, & Hubel, 2004). The oculomotor bases of microsaccade generation are largely unknown. However, a few studies point towards a common generator for both saccades and microsaccades (Otero-Millan, Troncoso, Macknik, & Martinez-Conde, in press; Rolfs, Kliegl, & Engbert, 2008; Rolfs, Laubrock, & Kliegl, 2006; Van Gisbergen, Robinson, & Gielen, 1981; Van Gisbergen & Robinson, 1977; Zuber & Stark, 1965).

Martinez-Conde et al. previously showed that microsaccades counteract classical Troxler fading and generate strong neural transients in the early visual system (Martinez-Conde, 2006; Martinez-Conde & Macknik, 2007; Martinez-Conde, Macknik, & Hubel, 2000, 2002; Martinez-Conde et al., 2006). Engbert and Mergenthaler (2006) subsequently found that microsaccades are optimized to counteract visual fading from an oculomotor perspective. Microsaccades may also be important in

binocular rivalry (Sabrin & Kertesz, 1983). Van Dam and Van Ee (2006) recently found a clear correlation between microsaccadic retinal image changes and perceptual alternations during binocular rivalry. Microsaccade rates and directions are moreover modulated by attention, and thus generate rich spatio-temporal dynamics (Engbert & Kliegl, 2003a, 2003b, 2004).

Martinez-Conde (2006) recently pointed out that the dynamic noise filling-in of artificial scotomas is facilitated by precise fixation by the observer, which suppresses microsaccades. Thus, microsaccades may counteract the perceptual filling-in of artificial scotomas by dynamic textures. This hypothesis has never been tested experimentally. Here we set out to determine the role of microsaccades in the perception of filling-in in an objective and quantified manner and to specifically find out whether microsaccades may counteract the filling-in of artificial scotomas during fixation.

Methods

Subjects

Six subjects (2 females, 4 males) with normal or corrected-to-normal vision participated in this study. Each subject participated in 2 experimental sessions, of ~30 minutes each. Three of the subjects were naive (they were paid $15/session; numbered 4 through 6 in the figures). Experiments were carried out under the guidelines of the Barrow Neurological Institute's Institutional Review Board (protocol number 04BN039) and written informed consent was obtained from each participant.

Eye movement analyses and experimental design

Subjects rested their head on a chin rest, 57 cm from a linearized video monitor (Barco Reference Calibrator V, 75 Hz refresh rate). Eye position was acquired non-invasively with a fast video-based eye movement monitor (EyeLink II, SR Research). The EyeLink II system records fixational eye movements simultaneously in both eyes (temporal resolution 500 samples/s; instrument noise 0.01 deg RMS) in its off-the-shelf configuration.

We identified and removed blink periods as the portions of the EyeLink II recorded data where the pupil information was missing. We further added 200 ms before and after each period to also eliminate the initial and final parts of the blink, where the pupil is partially occluded. We moreover removed those portions of the data corresponding to very fast decreases and increases in pupil area (>50 units/sample) plus the 200 ms before and after. Such periods are probably due to partial blinks,

where the pupil is never fully occluded (thus failing to be identified as a blink by EyeLink II).

We identified microsaccades automatically with an objective algorithm (for details, see Engbert & Kliegl, 2003b). To reduce the amount of potential noise (Engbert, 2006), we considered only binocular microsaccades, that is, microsaccades with a minimum overlap of one data sample in both eyes (Engbert, 2006; Engbert & Mergenthaler, 2006; Laubrock, Engbert, & Kliegl, 2005; Rolfs et al., 2006). Additionally, we imposed a minimum intersaccadic interval of 20 ms so that potential overshoot corrections might not be categorized as new microsaccades (Møller, Laursen, Tygesen, & Sjølie, 2002). The microsaccadic main sequence is plotted in Figures 1C and 1D. Figure 1C shows the peak velocity–magnitude relationship for all microsaccades (n = 16,956 microsaccades; Zuber & Stark, 1965), and Figure 1D shows their duration-magnitude relationship (Evinger, Shaw, Peck, Manning, & Baker, 1984; Gruart, Blázquez, & Delgado-Garcia, 1995). Figure 1E

plots the distribution of microsaccade magnitudes (up to 3 deg; Engbert & Kliegl, 2003b). Of these, only microsaccades smaller than 1 deg (n = 16,252 microsaccades) were studied further (Rolfs et al., 2006) (equivalent results were obtained when using 2- or 3-deg thresholds; data not shown). Table 1 summarizes various microsaccade parameters for individual subjects and for the subject average.

Subjects fixated on a small spot on the center of the monitor's screen, and simultaneously and continuously reported whether an artificial scotoma was visible (unfilled) or invisible (filled-in), via button press (Martinez-Conde et al., 2006). The fixation spot was a red dot (0.2 deg in diameter) placed on the center of the image. Subjects pressed a key and the stimulus, an artificial scotoma on a full-field dynamic noise background (Figure 1A) appeared on the screen. The artificial scotoma was a 1-deg wide 50% gray circle at 12 deg of eccentricity from the fixation spot. The dynamic noise background (De Weerd et al.,
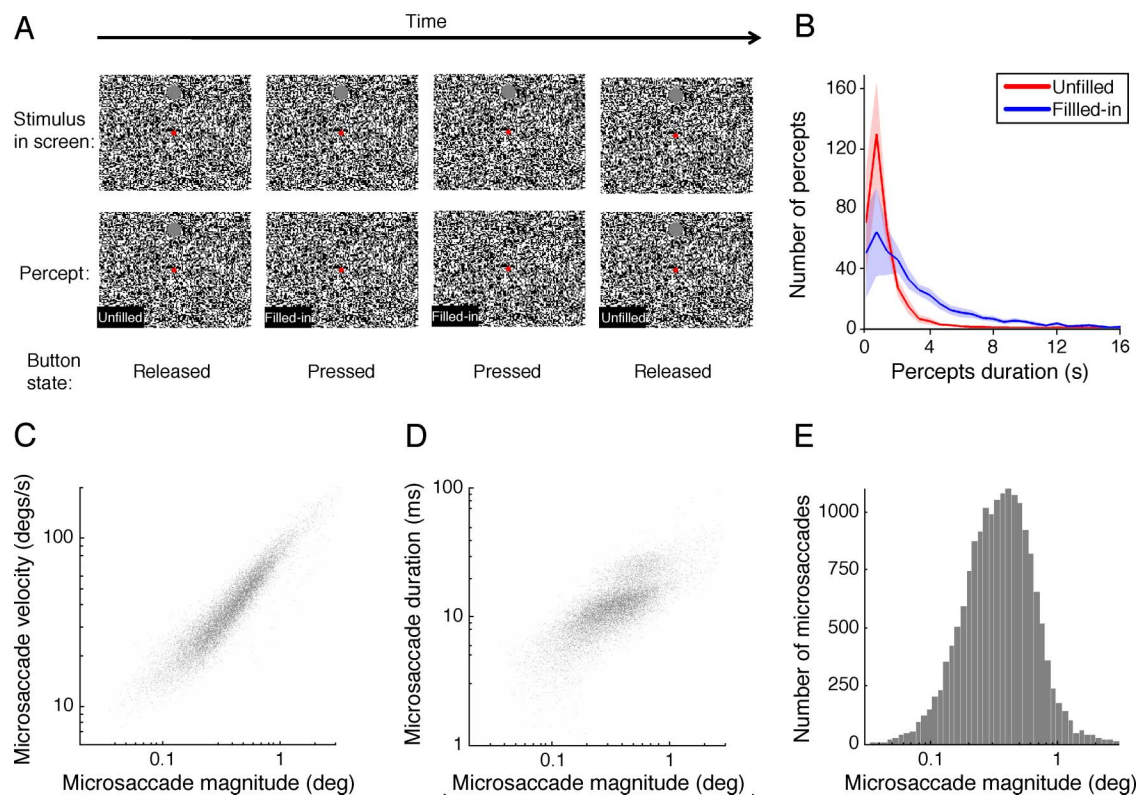

Figure 1. Filling-in of an artificial scotoma. (A) An epoch from a trial during the experiment. An artificial scotoma (a 50% gray circle) is positioned over a dynamic noise background (half black and half white 0.12 deg checks). On steady fixation, the scotoma tends to quickly fade and is filled-in by the "twinkling" noise from the surround (Ramachandran & Gregory, 1991; Spillmann & Kurtenbach, 1992). Movements of the eyes immediately bring back the perception of the scotoma. The top row shows the stimulus, which does not change over time (not to scale). The second row shows the percept of the stimulus: The artificial scotoma is intermittently invisible due to filling-in processes. The third row shows the subjects' report of their perception. (B) Distribution of "filled-in" (blue) and "unfilled" (red) periods during the experiment. Shaded red and blue areas indicate *SEM* between subjects (n = 6). (C–D) Main sequence: (C) velocity–magnitude relationship and (D) duration–magnitude relationship of all microsaccades (n = 16,956 microsaccades) up to 3 deg (Engbert & Kliegl, 2003b). Of these, only microsaccades smaller than 1 deg (n = 16,252 microsaccades) were studied further (Rolfs et al., 2006). However, equivalent results were obtained when using a 2- or 3-deg threshold. (D) Distribution of microsaccade magnitudes.

	SMC (Mean ± *SD*)	SLM (Mean ± *SD*)	JOM (Mean ± *SD*)	Subject 4 (Mean ± *SD*)	Subject 5 (Mean ± *SD*)	Subject 6 (Mean ± *SD*)	Average (Mean ± *SE*)
Average microsaccade parameters							
Rate (N/sec)	0.82	0.50	0.20	0.66	1.04	1.19	0.7 ± 0.1
Magnitude (deg)	0.48 ± 0.18	0.50 ± 0.22	0.48 ± 0.13	0.32 ± 0.17	0.45 ± 0.19	0.24 ± 0.11	0.41 ± 0.04
Duration (ms)	16.1 ± 6.5	15.9 ± 5.1	13.5 ± 4.5	9.8 ± 3.4	12.6 ± 5.9	10.7 ± 3.8	13 ± 1
Peak velocity (deg/s)	45 ± 14	43 ± 16	46 ± 14	35 ± 13	51 ± 17	26 ± 9	41 ± 3
Average parameters of perceptual reports							
"Filled-in" period duration (s)	1.7 ± 1.5	2.2 ± 1.4	3.1 ± 2.6	8.8 ± 6.9	5.0 ± 3.1	4.3 ± 3.1	4 ± 1
"Unfilled" period duration (s)	0.99 ± 0.64	1.9 ± 1.6	2.3 ± 1.6	1.1 ± 0.5	1.5 ± 1.1	1.2 ± 0.5	1.5 ± 0.2
% Time spent in "filled-in" periods	65	57	62	92	81	81	73 ± 5
% Time spent in "unfilled" periods	35	43	38	8	19	19	27 ± 6

Table 1. Microsaccade and perceptual parameters for individual subjects and for the subject average.

1995; Ramachandran & Gregory, 1991; Spillmann & Kurtenbach, 1992) was made up of a full screen of checks (half white and half black), each 0.12 deg in size and flickering dynamically at 7.5 Hz. Thus, the artificial scotoma had the same average luminance as the surrounding dynamic noise background. The scotoma was positioned randomly at one of the 8 points of the compass each trial, to control for effects of contrast adaptation across trials.

Subjects were asked to fixate on the fixation spot and press a button if the scotoma's visibility was decreasing (i.e., the scotoma was filling-in) and to release the button if the scotoma's visibility was intensifying (i.e., the scotoma was becoming unfilled).

After 30 s, all stimuli disappeared and the trial ended. To disregard the potential effect of the initial stimulus-onset transient at the start of each trial, we conducted analyses only on those data recorded after the first button press. Each experimental session included 40 trials, pseudo-randomly ordered.

Stimuli parameters were chosen so as to maximize perceptual filling-in of the artificial scotoma (De Weerd et al., 1998, 1995; Spillmann & Kurtenbach, 1992). The distribution of "filled-in" vs. "unfilled" periods for the average of all subjects is plotted in Figure 1B. Table 1 summarizes the average parameters of the perceptual reports for individual subjects and for the subject average.

Event-triggered averages

Event-triggered averages (Figures 2 and 3) were calculated by averaging a multi-second window of data around (Figure 2) or after (Figure 3) the trigger event (the perceptual transition in Figure 2, or the microsaccade onset in Figure 3). Thus, the event-triggered averages in Figure 2 represent the average microsaccade rate at any given time during the 6-second window plotted. If there were less than 6 seconds of data around a trigger event (due to the edge of the recording time during that specific trial), the 6-second window was dynamically reduced to fit

the available data. Each subject's event-triggered averages (Figures 2 and 3, bottom panels) were calculated individually using a 100-ms sliding window that advanced 1 data sample (2 ms) at a time. For each subject, calculations were made separately for each eye and then averaged between the two eyes. The population average and *SEM* error bars were then calculated across subjects. We performed one-sample one-tailed paired *t*-tests to establish statistical significance on a bin-by-bin basis ("unfilled" vs. "filled-in" event-triggered averages; bin size = 2 ms).

In interpreting the graphs in Figure 2, one should keep in mind that a large number of the perceptual periods for each subject (and for the subject average) were shorter than 2.5 s (for details, see Figure 1B and Table 1). Both red and blue lines meet the baseline at about −2.5 s, as for latencies longer than −2.5 s, the influence of previous perceptual transitions towards "filled-in" and "unfilled" percepts averages out.

It should also be noted that the delay between microsaccade onset and button press is not equivalent to traditional reaction time measurements. Traditional reaction times indicate the delay between a physical change in the stimulus and the subject's report; however, the delay between microsaccade onset and button press combines two different latencies: (a) the delay between microsaccade onset and perceptual change and (b) the delay between perceptual change and the subject's report (Martinez-Conde et al., 2006; van Dam & van Ee, 2005).

Probability of perceptual transitions triggered by microsaccade onsets

Only microsaccades produced during a "filled-in" period may possibly trigger a transition to an "unfilled" period. Conversely, only microsaccades produced during an "unfilled" period may trigger a transition to a period of "filling-in." Thus, to calculate the probability of transitions to "unfilled" scotomas after microsaccade onsets, we only considered those microsaccades that were produced during the previous "filled-in" period (as determined by the subject's report). Likewise, to calculate the probability of transitions to "filling-in" after microsaccade onsets, we only
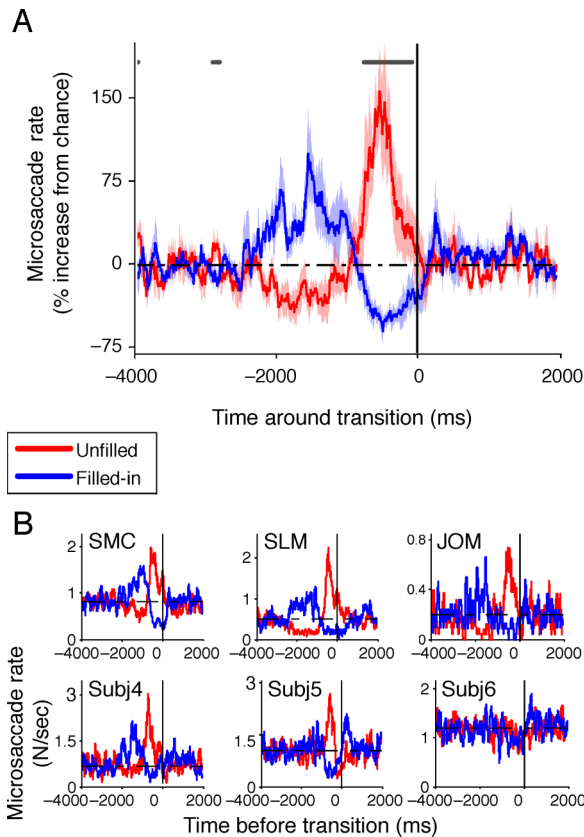
A

B

Figure 2. Microsaccade dynamics before perceptual transitions towards "unfilled" versus "filled-in" scotomas. Average rate of microsaccades before transitions towards "unfilled" (red) versus "filled-in" (blue) scotomas. Horizontal black lines indicate average rate of microsaccades during the recording session. (Top panel) Average of all subjects. Shaded red and blue areas indicate SEM between subjects. The gray dots at the top of the graph indicate the bins where the "unfilled" averages are significantly different from the "filled-in" averages (one-sample one-tailed paired t-test, $p < 0.05$). (Bottom panel) Data from individual subjects. Naive subjects are numbered from 4 through 6.

considered those microsaccades that occurred during the previous "unfilled" period. Therefore, Figure 3 cannot be directly derived from Figure 2 (because the microsaccades included in Figure 3 are only a subset of those in Figure 2).

To ensure that any results obtained would not be due to chance correlations between the dynamics of microsaccades and those of perceptual transitions, we repeated the above calculations, this time replacing microsaccades with the same number of events, now randomly distributed in time, for each subject. We then repeated this randomization by a factor equal to the number of microsaccades measured for each subject. We thus obtained a baseline for each subject, from which we calculated the percent increase in the probability of perceptual transitions following actual microsaccades. This analysis is comparable to the "cross-correlogram shuffling" often used to rule out spurious correlations between potential pre- and post-synaptic neurons (Alonso & Martinez, 1998; Martinez & Alonso, 2001).

Results

Subjects were asked to fixate on a small spot while continuously reporting on the visibility of a peripheral artificial scotoma (Figure 1A) via button press. They indicated whether the scotoma was perceptually faded/fading ("filled-in" scotoma; button pressed) versus visible/intensifying ("unfilled scotoma"; button released). Their eye movements were simultaneously recorded with high precision. Figure 1A describes a typical epoch during a trial. As previously described in filling-in paradigms (Spillmann & Kurtenbach, 1992), subjects reported that the perception of the artificial scotoma appeared to oscillate between the "filled-in" and the "unfilled" states (not unlike
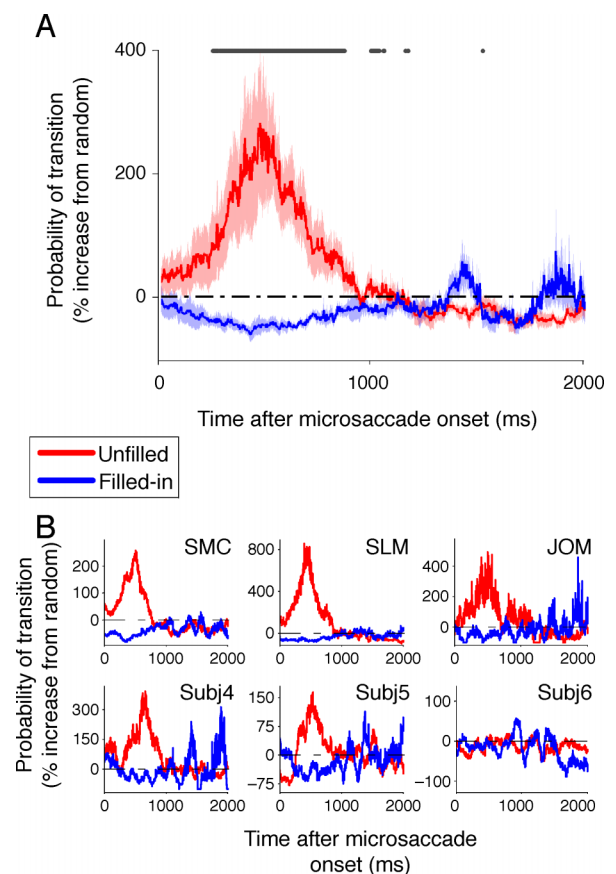
A

B

Figure 3. Microsaccades counteract the perception of filling-in. Blue: Average probability of transitions to "filled-in" periods after microsaccade onset. Red: Average probability of transitions to "unfilled" periods after microsaccade onset. The results are expressed as the percent increase over a correlation where microsaccades happened at random times. (Top panel) Average of all subjects. Shaded red and blue areas indicate SEM between subjects. The gray dots at the top of the graph indicate the bins where the "unfilled" averages are significantly different from the "filled-in" averages (one-sample one-tailed paired t-test, $p < 0.05$). (Bottom panel) Data from individual subjects. Naive subjects are numbered from 4 through 6.

the oscillations of rivalrous and other bistable stimuli; Martinez- Conde et al., 2006; van Dam & van Ee, 2005).

We identified microsaccades and correlated them to the time of the subject-indicated perceptual transitions (total number of microsaccades for all subjects: 16,252; see also Table 1 for a summary of various microsaccade parameters). The results show a clear positive relationship between the rate of microsaccades and the perception of the scotoma: before transitions to an "unfilled" period, microsaccade rates increased (Figure 2, red lines). Before transitions to a "filled-in" period, microsaccade rates decreased (Figure 2, blue lines). These findings reveal, for the first time, a direct quantitative link between suppression of microsaccades and the perception of texture filling-in.

To further establish the causal role of microsaccades in driving the perceptual transitions, we calculated the average probability of transitions to "unfilled" vs. "filled-in" percepts after microsaccade onsets (Figure 3). The results show that microsaccade onsets are followed by an increased probability of transitions to "unfilled" periods and a decreased probability of transitions to "filled-in" periods (a peak 250% increase and a peak 58% decrease from random, respectively). Thus, our results are compatible with a causal relationship between suppression of microsaccades and the perception of filling-in. At the very least, we cannot exclude a causal role of microsaccades in counteracting and overcoming filling-in processes.

Equivalent results were found in both naive and non-naive subjects (Figures 2 and 3). Equivalent results were moreover obtained when microsaccades were identified with a different algorithm (Martinez-Conde, 2006; Martinez-Conde & Macknik, 2007; Martinez-Conde et al., 2000, 2002, 2006) (data not shown).

Discussion

Much, if not most, of our visual experience occurs during fixation (Martinez-Conde, 2006). Therefore, understanding the dynamics responsible for overcoming visual fading and filling-in during fixation is of utmost importance to our understanding of vision as a whole. Here we examined the relationship between microsaccade dynamics and stimulus visibility during dynamic noise filling-in of an artificial scotoma. This filling-in effect cannot be explained by simple low-level (i.e., first order) adaptation to luminance edges: first, the artificial scotoma is equiluminant with the surrounding background (see Methods section for details), and second, low-level adaptation would be expected to fail for kinetic edges. Our results indicate that microsaccades counteract dynamic noise fading and the filling-in that ensues. Thus, microsaccades do not merely overcome low-level adaptation mechanisms, such as those presumably involved in classical Troxler fading (Martinez-Conde et al., 2006), but

they also contribute to maintaining second-order visibility during fixation.

Our results are consistent with De Weerd et al.'s (1998) proposal that perceptual filling-in is accomplished in two stages: adaptation of target-background boundaries followed by the virtually instant spreading or propagation of the background properties into the target's area (an idea proposed originally by Walls, 1954, and subsequently by Gerrits & Vendrik, 1970). Our results also agree with the observation that microsaccades increase spiking rates in visual neurons by displacing their receptive fields over the edges of stationary objects (Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002). Microsaccades produced during the presentation of an artificial scotoma continuously refresh the neural representation of the local boundary. Thus, the initial adaptation stage fails, as well as the subsequent propagation of the background properties to the scotoma region. With the target-background boundary firmly in place, no neural signals can cross from the surround.

Conversely, when microsaccades are suppressed, the remaining fixational eye movements (drifts and/or tremor) fail to prevent the adaptation of the target-background boundary. In the absence of such boundary, the target area rapidly takes on the properties of the surrounding dynamic noise field. A similar albeit more dramatic phenomenon may underlie the fast filling-in of physiological scotomas, for which no boundary representations must be previously adapted. Examples of physiological scotomas include the blind spot (Spillmann, Otte, Hamburger, & Magnussen, 2006; Walls, 1954)—although the filling-in across the blind spot may result from a specialized, more hardwired mechanism (De Weerd et al., 1998; Spillmann & de Weerd, 2003); the foveal blue scotoma (Magnussen et al., 2001; Magnussen, Spillmann, Stürzel, & Werner, 2004); and the shadows from retinal vasculature (i.e., *angioscotomas*) (Sharpe, 1972). The virtually instantaneous filling-in of such physiological scotomas is also typical of pathological retinal scotomas (Gerrits & Timmerman, 1969; Safran, 1997; Zur & Ullman, 2003).

The necessity of *active* neural filling-in mechanisms (i.e., as proposed by De Weerd et al., 1998 and Ramachandran & Gregory, 1991) has nevertheless been debated. For instance, observers may simply fail to notice scotomas not because of active filling-in but due to the lack of neural signals following a period of adaptation (Churchland & Ramachandran, 1996; Dennett, 1991, 1996; O'Regan, 1998; Pessoa, Thompson, & Noë, 1998; Spillmann & de Weerd, 2003). Macknik, Martinez-Conde, & Haglund (2000) and Magnussen et al. (2001) have proposed that if perceptual filling-in can be counteracted, this would indicate the existence of an active neural process (such as in the "Unfilled Flicker" illusion; see an interactive demonstration at http://macknik.neuralcorrelate.com). Active neural filling-in mechanisms are also supported by the occurrence of filled-in afterimages, such as the Twinkle effect (Ramachandran & Gregory, 1991; Spillmann & Kurtenbach, 1992; Stürzel & Spillmann, 2001). Our current results are compatible with

the active neural filling-in hypothesis. Here we show that microsaccades prevent the filling-in of dynamic textures and propose that this deterrence likely takes place at the boundary adaptation stage. Future studies should determine whether microsaccade dynamics may also counteract, or modulate, filling-in processes at the propagation stage.

Conclusions

We found that increases in microsaccade production counteract the perception of dynamic-noise filling-in and drive the visibility of artificial scotomas during visual fixation. Conversely, decreased microsaccades allow perceptual filling-in to take place. Our results show that microsaccades do not solely overcome low-level adaptation mechanisms (as in classical Troxler fading) but they also contribute to maintaining second-order visibility during fixation.

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