

Dynamics of contrast adaptation in central and peripheral vision

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Adaptation aftereffects are generally stronger for peripheral than for foveal viewing. We examined whether there are also differences in the dynamics of visual adaptation in central and peripheral vision. We tracked the time course of contrast adaptation to binocularly presented Gabor patterns in both the central visual field (within 5°) and in the periphery (beyond 10° eccentricity) using a yes/no detection task to monitor contrast thresholds. Consistent with previous studies, sensitivity losses were stronger in the periphery than in the center when adapting to equivalent high contrast (90% contrast) patterns. The time course of the threshold changes was fitted with separate exponential functions to estimate the time constants during the adapt and post-adapt phases. When adapting to equivalent high contrast, adaptation effects built up and decayed more slowly in the periphery compared with central adaptation. Surprisingly, the aftereffect in the periphery did not decay completely to the baseline within the monitored post-adapt period (400 s), and instead asymptoted to a higher level than for central adaptation. Even when contrast was reduced to one-third (30% contrast) of the central contrast, peripheral adaptation remained stronger and decayed more slowly. This slower dynamic was also confirmed at suprathreshold test contrasts by tracking tilt-aftereffects with a 2AFC orientation discrimination task. Our results indicate that the dynamics of contrast adaptation differ between central and peripheral vision, with the periphery adapting not only more strongly but also more slowly, and provide another example of potential qualitative processing differences between central and peripheral vision.

Introduction

Differences between central and peripheral vision have long been noted (e.g., Wertheim, 1894). Since

then, many studies have characterized how visual perception and processing vary across the visual field (see Rosenholtz, 2016, and Strasburger, Rentschler, & Jüttner, 2011, for review). Performance decreases with eccentricity for many visual tasks such as contrast sensitivity (Rovamo & Virsu, 1979; Wright & Johnston, 1983), orientation discrimination (Paradiso & Carney, 1988), and face identification (Melmoth, Kukkonen, Makela, & Rovamo, 2000). These studies support the view that in some cases peripheral vision behaves like a degraded version of central vision and as such the differences are often interpreted as quantitative changes that might reflect differences in factors such as reduced neural sampling rates or larger receptive fields. Consistent with this, performance on some tasks can be equated by scaling the size of peripheral stimuli by a “cortical magnification factor” so that stimuli are sampled by an equivalent number of neurons (Azzopardi & Cowey, 1993; Carrasco & Frieder, 1997; Motter, 2009; Rovamo & Virsu, 1979; Virsu, Näsänen, & Osmoviita, 1987) though in others it cannot (e.g., Fendick & Westheimer, 1983; Harvey, Rentschler, & Weiss, 1985; Levi & Klein, 1986). However, there is increasing recognition that foveal and peripheral vision also often differ in qualitative ways (Rosenholtz, 2016). In particular, peripheral vision is much more susceptible to crowding, where objects are more difficult to recognize when flanked by nearby objects, and these crowding effects cannot be explained by the loss of spatial resolution in the visual periphery (Lettvin, 1976). Such results suggest that foveal and peripheral vision may be fundamentally different and optimized for different visual functions. For example, almost all of the field of view is peripheral vision, and thus this region may be the most useful for capturing the gist of a scene (Larson & Loschky, 2009).

Citation: Gao, Y., Webster, M. A., & Jiang, F. (2019). Dynamics of contrast adaptation in central and peripheral vision. *Journal of Vision*, 19(6):23, 1–13, <https://doi.org/10.1167/19.6.23>.

<https://doi.org/10.1167/19.6.23>

Received March 21, 2019; published June 28, 2019

ISSN 1534-7362 Copyright 2019 The Authors



In addition to crowding, foveal and peripheral vision also differ in other contextual effects such as simultaneous contrast gain control and successive contrast adaptation. For example, surround suppression is strongly amplified in the periphery (Xing & Heeger, 2000), as are pattern-selective contrast effects (Greenlee, Georgeson, Magnussen, & Harris, 1991; Over, Broerse, & Crassini, 1972). Similarly, many visual aftereffects increase in magnitude with eccentricity. These include tilt aftereffects (Harris & Calvert, 1985; Muir & Over, 1970), motion aftereffects (Castet, Keeble, & Verstraten, 2002; Wright, 1986), shape aftereffects (Gheorghiu, Kingdom, Bell, & Gurnsey, 2011; Suzuki & Cavanagh, 1998), and face aftereffects (Tangen, Murphy, & Thompson, 2011; Webster, Kaping, Mizokami, & Duhamel, 2004). Although the scaling of cortical magnification might explain the larger tilt aftereffect found in the periphery (Harris & Calvert, 1985), it cannot account for the eccentricity-dependent increase in the shape aftereffect, and Gheorghiu et al. (2011) suggested that the differences might instead reflect greater adaptation gain (i.e., larger post-adaptation sensitivity suppression) or an eccentricity-dependent decrease in the stimulus-selectivity of the adapted mechanisms.

Beyond magnitude, it is unclear whether adaptation in central vs peripheral vision differs in other important aspects such as temporal dynamic. Characterizing these dynamics and how they differ is important for understanding the types and timescales of information controlling sensitivity calibration in the fovea and periphery. Recent studies have revealed that visual adaptation can operate at multiple timescales, potentially to adjust to different rates of environmental variation (Bao & Engel, 2012; Bao, Fast, Mesik, & Engel, 2013; Fairhall, Lewen, Bialek, & de Ruyter van Steveninck, 2000; Vul, Krizay, & Macleod, 2008; Wark, Fairhall, & Rieke, 2009). Aftereffects at the different timescales involve distinct processes. For example, prolonged adaptation exhibits spontaneous recovery from a brief de-adapting stimulus, indicating at least two adaptation mechanisms operating at different rates. Specifically, the aftereffect from prolonged adaptation can be momentarily overruled by brief exposure to an opposing adapter, but then returns after the effect from the briefer adapter decays (Bao & Engel, 2012; Magnussen & Greenlee, 1986; Mesik, Bao, & Engel, 2013; Shadmehr, Smith, & Krakauer, 2010). Time courses may also vary with the level of visual processing (e.g., Mei, Dong, & Bao, 2017; Suzuki & Cavanagh, 1995). Whether there are also differences with eccentricity is not well understood, though the periphery is known to differ dramatically in adaptation effects like Troxler fading, in which stabilized images tend to fade from view (Clarke, 1960; Clarke, 1961; Clarke & Belcher, 1962; Troxler, 1804). Moreover, this

peripheral fading also occurs not just for static images but also for flickering stimuli (Anstis, 1996; Frome, MacLeod, Buck, & Williams, 1981; Harris, Calvert, & Snelgar, 1990; Schieting & Spillmann, 1987), pointing to large differences in adaptation to temporal contrast.

In this study we compared the temporal dynamics of adaptation between central and peripheral vision. Specifically, we examined the effects of eccentricity on the time course of spatiotemporal contrast adaptation, following standard paradigms in which aftereffects are measured in brief test stimuli after intermittent exposure to an adapting pattern. The time course of these effects was tracked by measuring both the buildup and decay of the aftereffects. Contrast adaptation is thought to primarily reflect changes at a cortical site because the sensitivity losses are selective for the orientation and spatial frequency of the contrast changes and show strong interocular transfer. Our aim was to assess whether the dynamics of short-term contrast adaptation were consistent with a common form of adaptation at different loci, perhaps varying only in the strength of the adaptation; or whether there were qualitative differences in the time courses that might instead point to functionally distinct mechanisms.

General methods

Observers

Participants were students or postdoctoral researchers at the University of Nevada, Reno. All had normal or corrected-to-normal vision. Participation was with informed consent and followed protocols approved by the University of Nevada, Reno Institutional Review Board.

Several participants were involved in more than one experiment, but they were tested only once in each experiment. All were naïve except for author YG who participated Experiment 1. Data from a number of participants were excluded from analysis either due to missing eye-tracking data or due to large deviation from the fixation point ($>2^\circ$). The total number of participants excluded was two, three, and two, for the three experiments, respectively.

Apparatus and stimuli

Stimuli were displayed on a calibrated and gamma-corrected Display++ LCD monitor (Cambridge Research Systems, Rochester, UK). The mean luminance was 50.36 cd/m^2 and a CIE 1931 chromaticity of $x = 0.30$, $y = 0.31$, measured with a PR-655 spectropho-

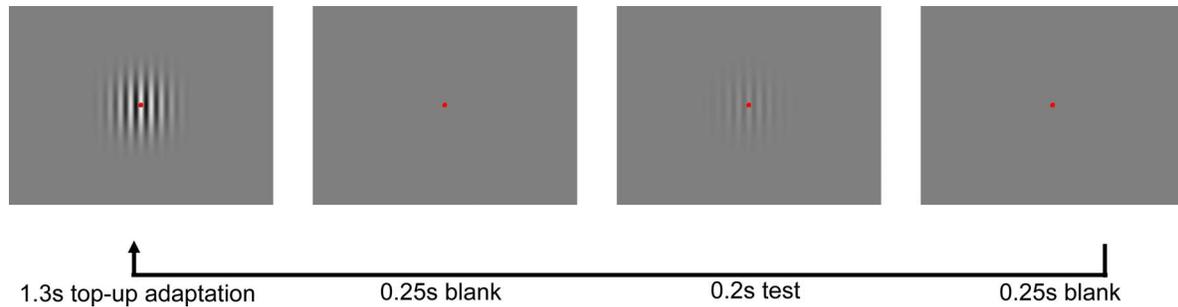


Figure 1. Example of a trial in the adaptation phase. Each trial started with a 1.3 s adapter, followed by a 0.25 s blank screen (with fixation only) and then a 0.2 s test stimulus was presented. Another 0.25 s blank screen (with fixation only) was presented before the next trial. In pre-adapt and post-adapt phases, the adapting stimulus was replaced by a blank screen with the same duration.

tometer (SpectraScan, Syracuse, NY). Participants were seated at a distance of 75 cm from the monitor, at which the monitor screen subtended $50^\circ \times 29^\circ$. LiveTrack Fixation Monitor (Cambridge Research Systems) was used throughout the experiment to make sure that participants were fixating at the center of the display.

Both adapter and test stimuli were Gabors with a spatial frequency of $1.5\text{ c}/^\circ$ unless otherwise stated. The diameter was 5° ($SD = 1.25^\circ$ of the Gaussian kernel) for the adapter and 4° ($SD = 1^\circ$) for the test stimulus unless stated otherwise. The adapter was counterphase flickered at 5 Hz. For the center condition, the stimuli were presented in the center of the screen. For the periphery condition, the closest edge of the adapters was 10° left or right to the central fixation. The center location of the test stimuli was the same as those of the adapters. A 0.25° red circle was presented as fixation point presented in the center of the monitor for both conditions. All stimuli were presented binocularly.

General procedure

We tracked the buildup and decay of contrast adaptation in both the center and periphery. The procedures were similar to those of Mei et al. (2017). Each session consisted of three phases: a 200 s baseline measurement, a 300 s adaptation phase, and a 400 s post-adapt. A “top-up” protocol was applied during the adaptation phase. Specifically, the adaptation phase included 150 trials, each consisting of a 1.3 s adapter, a 0.25 s blank gray screen (with fixation point only), and a 0.2 s test stimulus (see Figure 1). The test stimulus was accompanied by a beep throughout the experiment. Trials were separated by a 0.25 s blank gray screen (with fixation point only). In the pre-adapt and post-adapt phase, there was no top-up adaptation. Instead, a uniform gray screen was presented before the test stimulus. In this way, we were able to track threshold change before, during, and after adaptation phase.

Observers adapted to a single orientation but were tested at both the adapting orientation and the

orthogonal “control” orientation. In Experiments 1 and 2, either horizontal or vertical was chosen as the adapting orientation for each participant. This adapting orientation was counterbalanced across subjects and across sessions. Each participant was tested for one session in central vision and one session in peripheral vision. The order of adapting locations (center vs. periphery) was counterbalanced across participants.

Analysis

The baseline threshold was defined as the average of the last 10 reversals of the staircase during the pre-adapt phase. Maximum adaptation strength was defined as the average value of the last 40 s in the adaptation phase. To normalize the time course, the original time course was first interpolated every 2 s. Next, baseline for the control and adaptation orientation was subtracted from the corresponding time course. After baseline subtraction, the time course was then divided by the maximum adaptation strength. Finally, the normalized time course was fitted with three-parameter exponential function. Specifically, we used the formula: $Y = y_0(1 - e^{-t/\tau_1}) + y_t$ for the adaptation phase, and the formula: $Y = y_0e^{-t/\tau_2} + y_p$ for the post-adapt phase. y_0 represents the amplitude of the function, and τ_1 and τ_2 represent the time constants of the adaptation phase and post-adapt phase, respectively. y_t denotes the trough response in the rising phase and y_p denotes the plateau response in the decay phase.

Experiment 1

Methods

Eleven observers were tested in Experiment 1 (four female and seven male; mean age = 25 years, $SD = 4.2$). In Experiment 1, the adapting contrast was 90% in

both the center and periphery condition. Note that all the contrast levels used in this study were defined as Michelson contrast. Two 1-down 1-up staircases were used to track the contrast detection threshold to horizontal and vertical throughout the experiment, respectively. The minimum contrast of the test stimulus was set to 0.8%. The maximum contrast of the test stimulus was set to 40%. There were 69 levels between minimum and maximum contrast, spaced in constant logarithmic steps of 0.025. The first trial started from the 31st level and the initial jump was three steps, after three reversals the change was reduced to two steps, after another three reversals the change was fixed to one step. In each session, the testing sequence of each orientation (horizontal or vertical) was randomized. Other conditions were the same as described in General Methods. Throughout the experiment, subjects were asked to press the left-arrow key or right-arrow key on the keyboard to indicate whether they could see the test stimulus, respectively. Participants were asked to maintain the same criteria throughout the experiment.

Results

In Experiment 1, participants adapted to a 90% contrast Gabor in both the center and periphery condition. Baseline contrast thresholds averaged 1.35% in the center and 2.35% in the periphery. A two-way analysis of variance (ANOVA) of the thresholds showed that the interaction between adapting location (center vs. periphery) and orientation (adapting orientation vs. control orientation) was not significant, $F(1, 31) = 1.53$, $p > 0.25$. There was a main effect of adapting location, $F(1, 8) = 35.2$, $p < 0.0004$: the baseline threshold in the periphery was significantly higher than that in the center, $t(17) = 8.29$, $p < 0.0001$, all the t tests reported were paired two-tailed). There was no main effect of orientation, $F(1, 8) = 1.11$, $p > 0.32$.

Figure 2A shows the raw time course (without normalization) in the center and periphery. Adapting to 90% in the periphery induced significantly larger threshold elevation than adapting to the same contrast in the center, $t(8) = 2.99$, $p < 0.02$. The adaptation strength in the periphery was 3.8-fold that in the center. Note that this difference is still pronounced (2.3-fold) even when the threshold elevations are scaled in terms of multiples of the baseline threshold. This is consistent with previous studies showing stronger aftereffects in the visual periphery than in the center (Castet et al, 2002; Gheorghiu et al, 2011; Wright, 1986). We also tested whether there was a correlation across observers between the maximum strength of adaptation at the two eccentricities. However, this correlation was not significant ($r = -0.3$, $p > 0.42$), suggesting that there is not a strong coupling of “adaptability” at the two sites.

Figure 2B shows the time course normalized by the baseline threshold obtained in the pre-adapt phase and the maximum adaptation strength measured in the last 40 s during the adaptation phase. For the normalized time course, the time constant of the rising phase obtained from fitting the grand average with the exponential function was 52 s and 2,217 s in the center and periphery, respectively. Due to large individual variability in the parameter fits, parametric t test is not well suited to quantify the difference in the time constants estimated at individual levels. Instead, we used the Mann-Whitney U test to evaluate differences in the parameters obtained from the exponential fits. For the rising phase, the time constants in the periphery condition ($Mdn = 8.88 \times 10^7$) were marginally longer than in the center ($Mdn = 46$, $U = 14$, $p < 0.03$). The extreme range of time constants obtained for the exponential fits to the adaptation buildup in peripheral vision resulted because in some observers there was little evidence for the effect to saturate during the 300 s adaptation period, consistent with the large individual difference in time constants of the build-up and decay of adaptation revealed by Magnussen and Greenlee (1985). This further suggests that the dynamics of adaptation in peripheral vision might be very different from that in central vision. For each participant, we also determined the time point when adaptation strength reached 50% of the maximum. This was substantially longer for the periphery ($Mdn = 162$) than the center ($Mdn = 57$, $U = 7$, $p < 0.004$).

For the decay phase, the time constant obtained from fitting the grand average was 33 s and 50 s in the center and periphery, respectively. Adaptation effects decayed more slowly in the periphery ($Mdn = 48$) than in the center ($Mdn = 33$, $U = 5$, $p = 0.002$). To test whether the decay rate was independent of the maximum adaptation strength, we assessed the correlation between the half-life of the decay phase and maximum adaptation strength. Note that we chose half-life of the decay because it is free of the hypothetical model (Mei et al., 2017). There was no significant correlation between the half-life and maximum adaptation strength in both the center ($r = 0.46$, $p > 0.21$) and the periphery ($r = 0.55$, $p > 0.12$). Thus, the slower decay in the visual periphery was not strongly associated with a larger adaptation effect. However, due to our small sample size, we cannot exclude a weaker association.

As shown in Figure 2B, the thresholds for peripheral adaptation were also characterized by a long residual tail—where the thresholds did not return to the baseline level even 400 s after the adapter was removed. The post-adapt plateau estimated from the exponential fits was significantly higher than the baseline for the periphery ($Mdn = 0.11$, $U = 9$, $p < 0.007$) but not for the center ($Mdn = 0.05$, $U = 27$, $p > 0.25$). The plateau

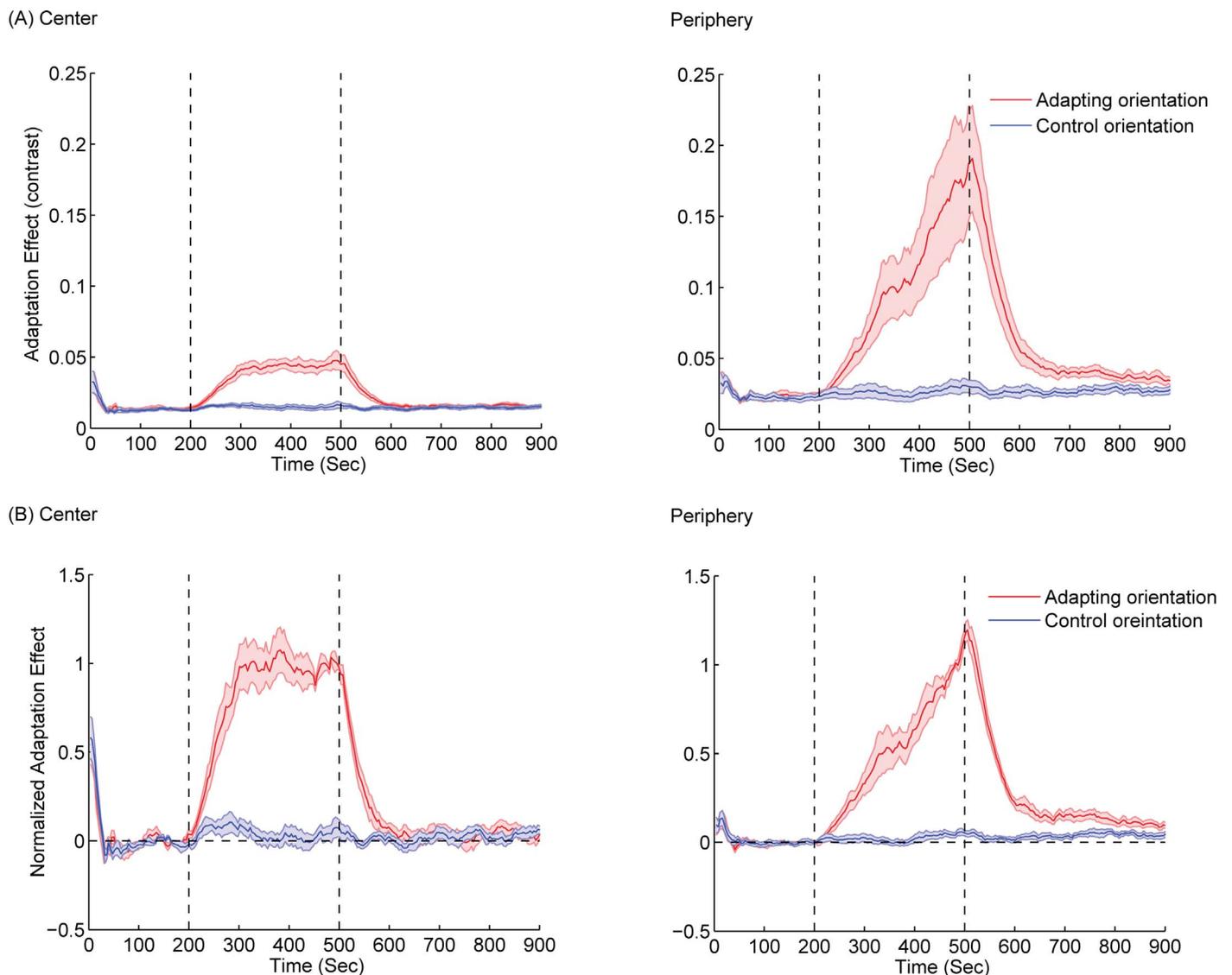


Figure 2. Results for Experiment 1 comparing adaptation to 90% contrast Gabors in the center (left panels) and periphery (right panels), showing raw time course (A) and time course after normalizing by the baseline and maximum adapt threshold (B). In all time course plots, thresholds at the adapting orientation were plotted in red, and thresholds at the orthogonal control orientation were plotted in purple. Solid line indicated the mean across the observers while the shaded area represented the standard error of the mean.

was marginally larger in the periphery than in the center ($U = 20$, $p > 0.07$). As a second measure we also averaged the threshold values for the last 60 s of the post-adapt phase. Similar to the estimates from fitting, the average residual threshold was higher than the baseline in the periphery, $t(8) = 6.47$, $p < 0.0002$, but not in the center, $t(8) = 1.3$, $p > 0.22$. The residual threshold was also significantly larger in the periphery compared with the center, $t(8) = 2.50$, $p < 0.04$.

To summarize, we found that adapting to 90% contrast induced a 3.8-fold greater threshold change in the periphery than in the center. Moreover, the periphery adapted not only more strongly, but also built up and decayed more slowly, and the decay of

adaptation asymptoted to a persistent residual threshold elevation. The different time constants suggest that adaptation in central and peripheral vision may rely on distinct mechanisms.

Experiment 2

Methods

Thirteen new participants were recruited for Experiment 2 (eight female and five male, mean age = 25

years, $SD = 4.8$). Another eight participants were recruited for the control experiment (four female and four male, mean age = 24 years, $SD = 3.4$). In Experiment 2 the adapting contrast was reduced to 30% in the periphery and remained at 90% in the center. Other experimental procedures were the same as those in Experiment 1.

In the control experiment of Experiment 2, the size of both adapter and test stimuli were reduced to 3° in the center and were magnified with a factor of 4.2 in the periphery (Rovamo & Virsu, 1979). The spatial frequency in the periphery in this case was also reduced to $0.36\text{ c}/^\circ$. Otherwise the stimuli were the same as described already.

Results

Because equal physical adapting contrasts produced much stronger adaptation in the periphery in Experiment 1, we examined whether the slower buildup and decay of adaptation in peripheral vision would persist if the adaptation magnitude was reduced. Specifically, we reduced the adapting contrast to 30% in the periphery while maintaining the adapting contrast at 90% in the center, and then re-measured the buildup and decay of the adaptation. In these sessions baseline thresholds averaged 1.13% in the center and 2.33% in the periphery. For baseline thresholds, a two-way ANOVA showed that the interaction between adapting location (center vs. periphery) and orientation (adapting orientation vs. control orientation) was again not significant, $F(1, 39) = 0.06$, $p > 0.80$. As in Experiment 1, there was a main effect of adapting location, $F(1, 9) = 22.21$, $p < 0.002$: with the peripheral thresholds significantly higher, $t(19) = 6.78$, $p < 0.0001$, and no main effect of orientation, $F(1, 9) = 0.02$, $p > 0.87$.

Figure 3A and 3B show the results for the raw and normalized time course of Experiment 2, respectively. Although adapting contrast was reduced to 30% in the periphery while remaining 90% in the center, adaptation strength was still much stronger than in the center, $t(9) = 3.88$, $p < 0.004$, paired t test. In fact, adapting to 30% contrast in the periphery induced almost the same magnitude of difference (2.9-fold increase relative to the center) as for the 90% contrast adapter. Again, no significant correlation was found between the maximum adaptation strength of center and periphery condition ($r = 0.48$, $p = 0.16$), suggesting that the adaptability at the two loci are not strongly linked. We also conducted auxiliary experiments with a range of adapting contrasts as low as 10%, yet surprisingly for none of these could we find a peripheral contrast that induced maximum threshold changes as weak as the high-contrast central adapter.

For the normalized time course, the time constant of the rising phase obtained from fitting the grand average was 89 s and 239 s in the center and periphery, respectively. A Mann-Whitney U test showed that the time constant in the periphery ($Mdn = 180$) was significantly larger than in the center ($Mdn = 84$, $U = 23$, $p < 0.05$). The time estimated for the periphery ($Mdn = 121.5$) to reach 50% of the maximum adaptation strength was also significantly larger than that in the center ($Mdn = 73$, $U = 14.5$, $p < 0.009$).

For the decay phase, the time constant obtained from fitting the grand average was 37 s and 47 s in the center and periphery. The time constant in the periphery ($Mdn = 45$) was significantly larger than in the center ($Mdn = 36$, $U = 15$, $p < 0.009$). No significant correlation was found between the half-life of the decay and the maximum adaptation strength in the periphery ($r = 0.55$, $p > 0.12$) or in the center ($r = 0.55$, $p = 0.12$). The post-adapt plateau estimated from exponential fitting in both center and periphery was significantly higher than the baseline (Center: $Mdn = 0.04$, $U = 20$, $p < 0.03$; Periphery: $Mdn = 0.09$, $U = 0$, $p < 0.0002$). The plateau also appeared to be stronger in the periphery than in the center, though the difference did not in this case reach significance ($U = 26$, $p > 0.07$). Moreover, the average residual threshold measured in the last 60 s of post-adapt was higher than the baseline in both center, $t(9) = 2.87$, $p < 0.02$, and periphery, $t(9) = 7.52$, $p < 0.0001$. And this residual threshold was significantly higher in the periphery compared with the center, $t(9) = 2.59$, $p < 0.03$.

In a further control experiment, we examined how scaling the stimuli by the cortical magnification factor would impact the differences in adaptation at the two loci. Experimental procedures were the same as Experiment 2, except that we reduced the size of the adapter and test to 3° in the center while magnifying the field by a factor of 4.195 in the periphery (Rovamo & Virsu, 1979). With this rescaling, baseline threshold averaged (1.74%) in the center and (1.77%) in the periphery. A two-way ANOVA showed no interaction between adapting location (center vs. periphery) and orientation (adapting orientation vs. control orientation), $F(1, 31) = 0.21$, $p > 0.66$. There was also no main effect of adapting location, $F(1, 7) = 0.01$, $p > 0.90$, and orientation, $F(1, 7) = 1.79$, $p > 0.22$. Thus, scaling by the cortical magnification factor effectively equalized baseline threshold in the center and periphery for our stimuli.

Figure 4A and 4B show the raw and normalized time course for these conditions. Although the baseline detection threshold was equated by cortical magnification between the center and periphery, adaptation strength remained significantly stronger (2.7-fold difference) in the periphery than that in the center, $t(7) = 3.26$, $p < 0.02$. No significant correlation was found

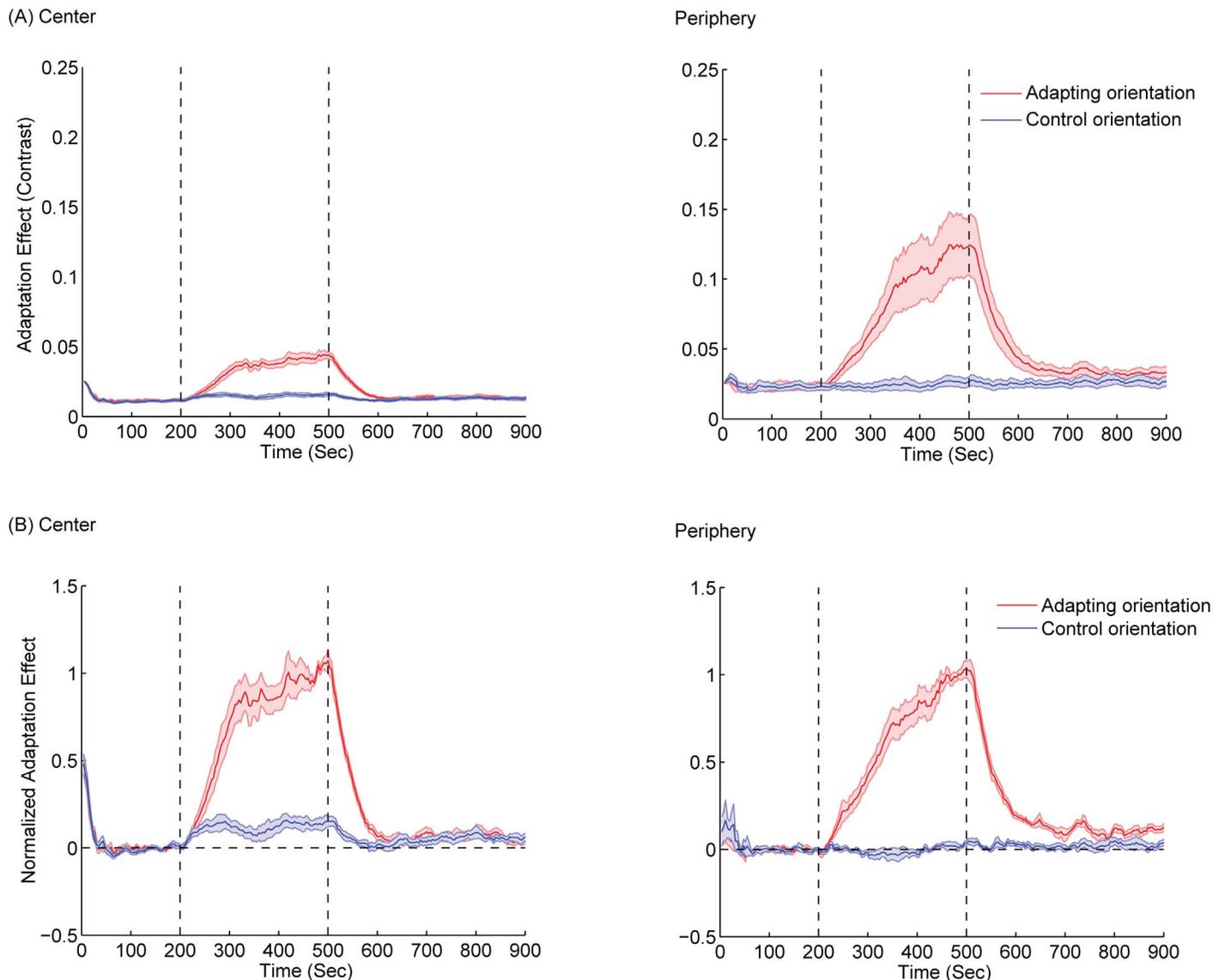


Figure 3. Results for Experiment 2 comparing 90% adapting contrast in the center and 30% contrast in the periphery. (A) Raw time course for the center (left panel) and periphery (right panel). (B) Normalized time course for center (left panel) and periphery (right panel).

between the maximum adaptation strength in the center and periphery, $r = 0.14$, $p > 0.74$.

For the normalized time course, the time constant of the rising phase obtained from fitting the grand average was 84 s and 860 s in the center and periphery, respectively. However, a Mann-Whitney U test did not reveal a significant difference between the periphery ($Mdn = 7.58 \times 10^7$) and the center ($Mdn = 77$, $U = 19.5$, $p > 0.20$) due to large individual variability. On the other hand, the time estimated to reach 50% of the maximum adaptation strength was significantly slower in the periphery ($Mdn = 168$) than in the center ($Mdn = 53$, $U = 10$, $p < 0.02$).

For the decay phase, the time constant obtained from fitting the grand average was 37 s and 47 s in the

center and periphery, respectively. The time constant in the periphery ($Mdn = 45$) was significantly larger than in the center ($Mdn = 34$, $U = 12$, $p < 0.05$). A significant correlation was found between the half-life of the decay and the maximum adaptation strength in the periphery ($r = 0.88$, $p < 0.005$) but not in the center ($r = 0.55$, $p = 0.12$).

The plateau obtained from exponential fitting was significantly larger than the baseline in the periphery but not in the center (Center: $Mdn = 0.13$, $U = 16$, $p > 0.10$; Periphery: $Mdn = 0.06$, $U = 0$, $p < 0.001$). However, these plateaus did not significantly differ between the center and periphery ($U = 28$, $p > 0.71$). Moreover, in this case the average threshold measured in the last 60 s of post-adapt was higher than the

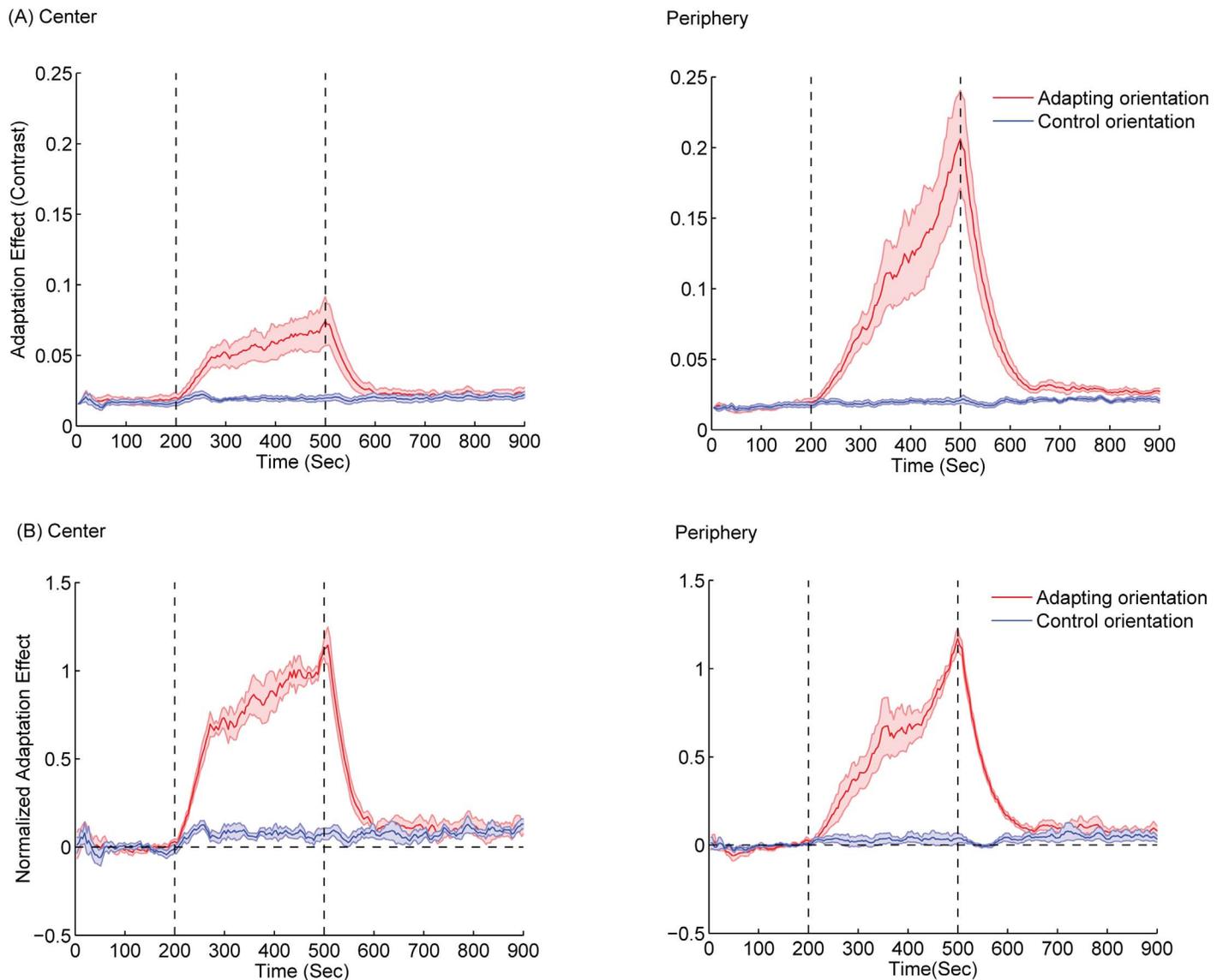


Figure 4. Results for stimuli rescaled by the cortical magnification factor. (A) Raw time course for the center (left panel) and periphery (right panel). (B) Normalized time course for center (left panel) and periphery (right panel).

baseline in both center, $t(7) = 2.65$, $p < 0.04$, and periphery, $t(7) = 2.79$, $p < 0.03$. The average threshold was not significantly different between the periphery and the center, $t(7) = 1.07$, $p > 0.31$.

To summarize, reducing the adapting contrast in the periphery to 30% relative to the center (90%) still led to much stronger aftereffects in the periphery. Moreover, the time course of the peripheral aftereffects again showed slower buildup and decay with a larger residual threshold elevation, replicating the findings of Experiment 1. After cortical magnification, we still found stronger adaptation strength and slower buildup and decay in the periphery, while the differences in residual threshold in the post-adapt phase was diminished.

Experiment 3

Methods

Experiment 3 included eleven participants (six female and five male, mean age = 24, $SD = 4.1$). In Experiment 3, we extended the testing procedures to suprathreshold test contrasts by using the tilt aftereffect. The tilt aftereffect was measured in a similar way as in Experiments 1 and 2. Adapting contrast was 90% in the center and 30% in the periphery. The contrast of the test stimuli was the same as that of the adapter. The adaptation orientation was 15° leftward or rightward relative to vertical. The orientation of the test stimulus

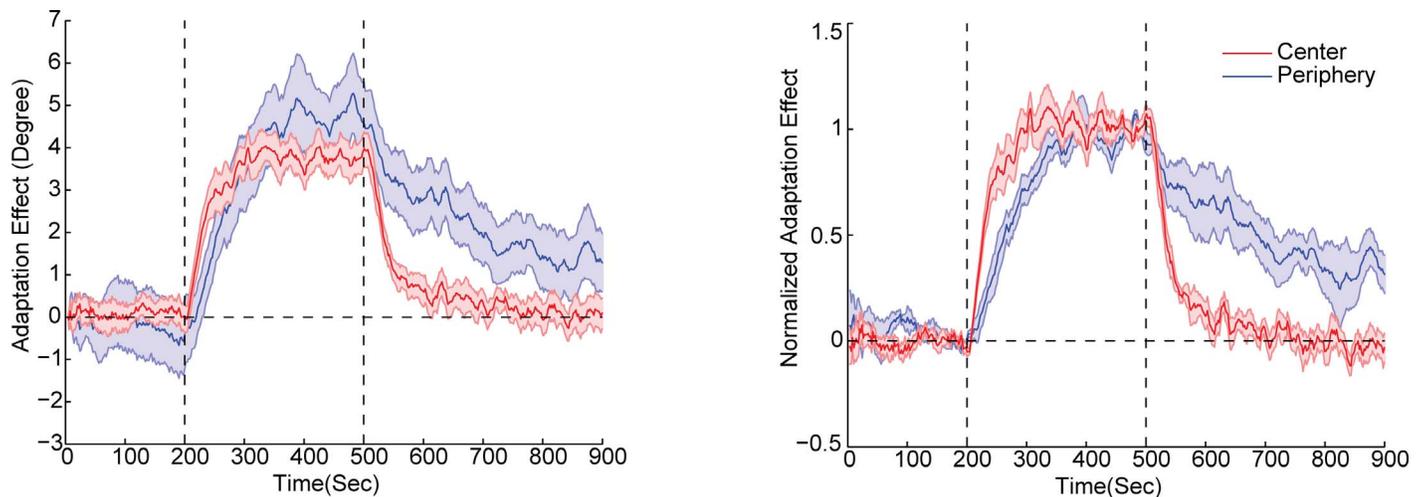


Figure 5. Raw (left panel) and normalized (right panel) time course for the tilt aftereffect in Experiment 3.

started at vertical and the step size was 0.14° . The staircase initially jumped three steps, after three reversals it jumped two steps, after another three reversals the change was fixed to one step. Participants pressed the left arrow key or right arrow key to indicate if the test stimulus was tilted left or right relative to vertical. The adapting orientation was counterbalanced across participants but remained the same for the two eccentricities tested for each participant.

Results

In Experiments 1 and 2, we found that adaptation changed contrast sensitivity in very different ways in central and peripheral vision. In the final experiment, we tested whether these differences persist at higher, suprathreshold contrasts, by measuring the time course of tilt aftereffect (TAE) induced in the Gabor patterns. Figure 5 shows the original and normalized time course for these conditions. The baseline point of subjective equality (PSE) for vertical did not significantly differ between the center and periphery, $t(8) = 0.04$, $p > 0.96$. The average maximum aftereffects also did not differ significantly, $t(8) = 1.46$, $p > 0.18$. Larger TAEs in the periphery have been reported in previous studies (Harris & Calvert, 1985; Muir & Over, 1970; Over et al., 1972). In our study the adapting contrast was 90% in center and 30% in periphery, and this may be one reason for the similar aftereffects we observed. No significant correlation was found between the maximum adaptation strength of center and periphery condition ($r = 0.04$, $p = 0.91$).

The time constant of the rising phase fitted from the grand average was 31 s and 76 s in the center and periphery, respectively. These time constants were significantly larger in the periphery ($Mdn = 79$) than in the center ($Mdn = 40$, $U = 57$, $p < 0.02$). It also took

longer for the peripheral aftereffect to reach 50% of the maximum adaptation strength than in the center ($U = 10$, $p < 0.006$).

The time constant from fitting the grand average in the decay phase was 39 s and 192 s in the center and periphery, respectively. The decay time constant for the periphery ($Mdn = 95$) was significantly larger than the center ($Mdn = 39$, $U = 10.5$, $p < 0.006$). No significant correlation was found between the half-life and maximum adaptation strength in both adapting locations (center: $r = -0.43$, $p = 0.25$; periphery: $r = -0.53$, $p > 0.14$). The final plateaus for the center ($Mdn = 0.02$) and periphery ($Mdn = 0.11$) did not differ from the pre-adaptation baselines (center: $U = 36$, $p > 0.72$; periphery: $U = 36$, $p > 0.72$). Moreover, the fitted plateaus were not statistically different between the center and the periphery ($U = 34$, $p = 0.60$). However, as shown in the right panel in Figure 5, the tilt aftereffect in the periphery did not reach an asymptote within our 400 s post-adapt, suggesting that the exponential function provided a poor fit in this case. The average threshold of the last 60 s of the post-adaptation phase was significantly larger than baseline in the periphery, $t(8) = 3.90$, $p < 0.005$, but not in the center, $t(8) = -0.70$, $p > 0.5$. Clearly, the baseline shift was much higher in the periphery than in the center, $t(9) = 3.42$, $p < 0.01$.

To summarize, while the adaptation strength of the tilt aftereffect was similar between the center and periphery for the adapting contrasts we used (90% in center and 30% in periphery), the dynamics continued to be very different between the two adapting locations, replicating the slower rising and decay of adaptation in the periphery observed in the two threshold experiments. In fact, if anything, these differences in dynamics appear more pronounced in the supra-threshold aftereffects.

Discussion

The current study compared temporal dynamics of contrast adaptation in central versus peripheral vision. We found that contrast adaptation in the periphery was not only stronger, but also rose and decayed in a slower fashion, providing evidence for central and peripheral differences in temporal properties. Though the baseline threshold can be equated between the center and periphery by cortical magnification, the larger threshold elevation after adaptation, and slower buildup and decay in the periphery, remained robust. Moreover, the slower dynamics in the peripheral vision were replicated with the suprathreshold appearance task. Together, these results suggest that adaptation in central and peripheral vision may involve fundamentally different temporal processes.

Central and peripheral differences in visual adaptation were first noticed by Troxler (1804) who found that a stimulus gradually disappears from perception under steady fixation and that this phenomenon only occurs in peripheral vision. Later studies showed that adapting to peripheral flicker drastically elevates thresholds for flashed spots or gratings (e.g., Frome et al., 1981) and that the fading effects tend to be stronger for faster flicker (e.g. Anstis, 1996; Schieting & Spillman, 1987). In our study the top-up adapter was presented for 1.3 s flickered at 5 Hz, and alternated with the test stimulus presented as a static 0.2 s pulse. Thus, our adapting stimulus had comparable flicker to stimuli that induce strong Troxler-like fading. However, there are a number of results that distinguish our effects. First, fading would be expected to lead to more rapid adaptation in the periphery, whereas we found the buildup and decay to be slower. Second, the sensitivity losses from fading show specificity for size and spatial frequency but not for orientation and eye (Frome et al., 1981), while the threshold elevation found in our study was orientation specific. Third, while the time needed for adaptation to peripheral flicker can be compensated by cortical magnification (Anstis, 1996; Schieting & Spillman, 1987), yet the slower buildup and decay of the contrast adaptation effect we found cannot be corrected by this scaling. Thus, while perceptual fading and associated flicker habituation (Frome et al., 1981) may have contributed to our effects, they cannot explain our findings completely, and nor can eccentricity-dependent dynamics of light adaptation (Barrionuevo et al, 2018; Gloriani et al, 2016; Osaka, 1980).

Greenlee et al. (1991) compared the time course of decay after adapting to a grating at various eccentricities. They found stronger adaptation after 100 s adaptation at 10° than at 0° in one of the two participants. The recovery of threshold with increasing eccentricity resembled the result of increasing adapting

duration, instead of increasing contrast. This was consistent with our findings that reducing adapting contrast in the periphery did not affect the slower decay and larger adaption magnitude in the periphery. However, based on the larger adaptation magnitude in the periphery, they speculated that the periphery may saturate earlier compared with the center, which differs from our results, in which the adaptation effects saturated earlier in the central visual field. Moreover, threshold elevations for the contrast detection task in the peripheral vision showed no sign of saturation within our 300-s adaption period. Thus again for our conditions contrast adaptation in peripheral vision built up and decayed in a much slower fashion, and the residual threshold change asymptoted at a higher level.

The differences in time course could also reflect differences in the adaptive properties of different pathways or cell types in the visual system. For example, while we cannot easily relate our conditions to different subsystems, it is notable that retinal and geniculate cells in the more peripherally- oriented magnocellular pathway are thought to exhibit stronger contrast adaptation than cells in the more foveally-oriented parvocellular pathway (Solomon, Peirce, Dhruv, & Lennie, 2004) (though this distinction is not clearly manifest in fMRI adaptation; Chang, Hess, and Mullen, 2016).

Our findings of different timescales for adaptation at different eccentricities complement work pointing to multiple timescales at the same loci. These multiplexed dynamics have been revealed in adaptation across a variety of visual levels (Bao & Engel, 2012; Bao et al., 2013; Fairhall et al., 2000; Wark et al., 2009) as well as across various cognitive functions (Colagiorgio, Bertolini, Bockisch, Straumann, & Ramat, 2015; Kim, Ogawa, Lv, Schweighofer, & Imamizu, 2015; Körding, Tenenbaum, & Shadmehr, 2007; Ulanovsky, Las, Farken, & Nelken, 2004), and these have been tied to different functional demands. Similarly, different timescales for central and peripheral vision may indicate functional or information-theoretic significance. In particular, the different rates of adaptation in foveal and peripheral vision could be influenced by differences in the level of noise at the two loci. The timescales of visual adaptation have been found to be dependent on the variance of the stimulus distribution and the discriminability of changes in the distribution (Wark et al., 2009). Stimuli presented in the periphery are noisier and thus have higher variance (Levi, 2008; Mareschal, Bex, & Dakin, 2008; Wardle, Bex, Cass, & Alais, 2012). Moreover, the visual periphery has less ability to separate incoming signals (Hansen, Pracejus, & Gegenfurtner, 2009; Träschütz, Zinke, & Wegener, 2012), making it harder to discriminate rapid changes in the stimulus distribution. To ensure that adaptation occurs to real changes instead of noise, peripheral

processing may need to collect evidence for changes in the environment over a longer period of time. Thus, neurons responding to peripheral signals may have a longer encoding time window (Panzeri, Brunel, Logothetis, & Kayser, 2009), and these differences may also apply to network dynamics (Whitmire & Stanley, 2016). As a result, peripheral adaptation may accumulate evidence over longer timescales in order to recalibrate to changes in the same visual environment.

Keywords: visual adaptation, temporal dynamics, peripheral vision

Acknowledgments

The research was supported by EY023268 to Fang Jiang, EY010834 to Michael A. Webster.

Commercial relationships: none.

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