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Adaptation-induced blindness is orientation-tuned and monocular

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Abstract

We examined the recently-discovered phenomenon of Adaptation-Induced Blindness (AIB) in which exposure to a rapidly flickering grating causes a gradually on-ramped static grating to remain invisible even as it reaches high contrast. We compared this approach to a more traditional paradigm measuring threshold elevation for low contrast stimuli after adaptation. Using very similar stimuli to those in the original experiment, we found post-adaptation threshold elevations were equivalent for both gradual and abruptly onset test stimuli, and both displayed orientation-tuned adaptation, with partial interocular transfer. Then, using full-contrast test stimuli with either abrupt or gradual onsets, we tested the 'disappearance' of these stimuli in a paradigm similar to that of the original AIB experiment. If, as the original authors suggested, AIB were a high-level (perhaps parietal) effect resulting from the 'gating' of awareness, we would not expect the effects of AIB to be tuned to the adapting orientation, and the effect should transfer between the eyes. Instead, we found that AIB (which was present only for the gradual onset test stimuli) was very tightly orientation-tuned and showed absolutely no interocular transfer. Our results therefore suggest a very early cortical locus for this effect.

Keywords

adaptation-induced blindness, thresholds, orientation tuning, awareness

Introduction

Neurons at the earliest stages of visual processing respond preferentially to retinal image movement (De Valois et al. 1982; Hubel and Wiesel 1962; Movshon and Newsome 1996). Not only does retinal motion inform us about the relative speeds and trajectories of objects in our visual environment (including our own bodies), it can capture our attention (Cass et al. 2011), break object camouflage, and can even inform us about the surface properties of objects (Doerschner et al. 2011).

Prolonged exposure to 'fast' (∼10 Hz) movement or flicker, however, can cause temporary problems for the visual system. Movement at a recently adapted retinal location appears slowed (Thompson 1981; see Hietanen et al. 2007 for an electrophysiological analogue of this effect). Under certain conditions, adaptation can even cause illusory reversals in perceived direction of motion (Arnold et al. 2014). Another casualty is contrast sensitivity, which is poorer at adapted locations, most significantly when adaptor and targets are similarly oriented (Campbell and Kulikowski 1966; Cass et al. 2012).

In 2010, Motoyoshi and Hayakawa introduced a compelling new illusion: Adaptation Induced Blindness (AIB) (Motoyoshi and Hayakawa 2010). Following exposure to ∼10 Hz motion, a test grating is then ramped on from zero to full contrast, with either a gradual or an abrupt temporal profile. The slope of this onset ramp has a profound effect on subsequent perception: whereas high contrast patterns with abrupt onsets are clearly visible, gradually presented patterns become temporarily 'invisible'. Motoyoshi and Hayakawa (2010) attributed this effect to relatively high-level processes, possibly parietal, suggesting that the visual transients associated with abrupt-onset stimuli are necessary to prompt visual awareness of the stimuli. They further suggest that even

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though the 'invisible' stimuli are not available to awareness, they can still cause low-level effects such as the tilt illusion, suggesting that there is some processing of the suppressed stimuli at lower (e.g., V1) levels.

Impressive as it is, is Motoyoshi and Hayakawa's effect really unique, or can current models of low-level visual processing predict it? One possible explanation relates to differences in the temporal frequency content of gradual and abrupt test stimuli. Abrupt targets introduce high temporal frequency energy not otherwise present under gradual onset conditions. Evidence derived using classical threshold methods shows that adapting to high frequency flicker ($\sim$10 Hz) impairs sensitivity to low frequency targets ($\sim$1 Hz), but not *vice versa* (Cass and Alais 2006). Might such an interaction underlie the inability to perceive gradually ramped targets in AIB?

In the event that AIB is the result of the same adaptation processes as those observed using classical methods, then AIB and threshold paradigms should show similar stimulus dependencies. It is well known that the reduction in contrast sensitivity that follows flicker adaptation is highly contingent upon the relative orientation of adaptor and test (Cass et al. 2012; Meese and Baker 2011), with most potent threshold elevation observed when adaptor and test are similar. Interestingly, this orientation-specific threshold elevation is evident regardless of whether one adapts and tests with the same eye or with different eyes. The finding that orientation-dependent adaptation transfers between the eyes suggests that the mechanism responsible for adaptation-induced threshold elevation occurs at a level of processing following the encoding of both orientation and binocularity, both of which are evident in neural responses as early as V1.

To our knowledge, the effects of adaptation on contrast sensitivity have not been measured using stimuli with identical target onset properties to those observed using AIB (gradual vs abrupt contrast ramps). Motoyoshi and Hayakawa (2010) attempted to measure contrast sensitivity, but stated that it became too low to measure for gradual test gratings (their Figure 1b). They reported that the proportion correct (for an 8AFC task) for full contrast gratings was 34%; however, since chance in this case would have been 12.5%, it is evident that some sensitivity remained, even though participants reported not being able to see the test stimuli. We aimed to further explore this puzzling discrepancy by measuring contrast thresholds for low-contrast test stimuli after adaptation to 10Hz flicker, at a range of test orientations, both in the adapted and in the unadapted eye. We also measured what we term 'disappearances': the proportion of full contrast test stimuli that were not seen after fast adaptation, measured (as in Motoyoshi and Hayakawa 2010) by proportion correct.

Based on previous work, for our first experiment (contrast thresholds), we predicted that adaptation would produce maximum threshold elevation when adaptor and test were similarly oriented, and that this orientation-contingent threshold elevation would be evident under both monocular and inter-ocular transfer (IOT) adaptation conditions (Cass et al. 2012).

In our second experiment ('disappearances'), we examined the orientation and eye-specificity of the AIB effect by presenting all test gratings at full contrast, again either to the adapted or unadapted eye, and either parallel or orthogonal to the adapting stimulus. We estimated the proportion that were seen by measuring proportion correct in a 4AFC task. If AIB is indeed the result of the same adaptation processes observed previously using the classic detection threshold paradigm, then the incidence of AIB would be predicted to be stronger when the orientation of adaptor and test patterns is more similar. Moreover, this orientation-dependent behaviour should be evident under both monocular and IOT conditions.

Methods

Participants

Five adults with normal or corrected-to-normal vision participated in the experiment. Three participants, including two of the authors, were experienced psychophysical observers, whilst the remaining participants were naive to the purposes of the study.

Apparatus and stimuli

Stimuli were programmed in MATLAB version 7.9 using the Psychophysics Toolbox version 3 (Brainard 1997; Pelli 1997). Visual stimuli were presented on a Sony Trinitron CPD-G500 22-inch CRT monitor with a screen resolution of 1024 x 768 pixels and a vertical refresh rate of 100 Hz. The monitor was gamma-corrected to ensure linear luminance output and was controlled by a quad core Mac Pro computer running Mac OS 10.8.2, connected to a Cambridge Research Systems Bits++ digital-to-analogue converter that provided 14-bit resolution for measurement of low contrast thresholds. Maximum and minimum luminances were 74.4 and 0.5 cd/m^2, and mean luminance was 33 cd/m^2. Participants sat in a darkened room with their head supported by a chin rest, and made responses on a standard keyboard.

The adapting stimuli were counterphasing gratings, each composed of two superimposed sine-wave gratings drifting

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leftwards and rightwards at a speed of 8 Hz, equal to the speed of the drifting gratings used by Motoyoshi and Hayakawa (2010), and was presented at full contrast. Counterphasing gratings were used as adaptors instead of drifting gratings because drifting gratings produce potentially confounding motion after-effects (Anstis et al. 1998; Glasser et al. 2011; Pantle and Sekuler 1969), and might reasonably be expected to induce saccades in the direction of the drift, thereby disrupting fixation and adaptation. A pilot experiment verified that drifting stimuli did not produce substantially differing effects. The spatial frequency and orientation of the adaptor was kept constant at 1.5 c.p.d and 0° (vertical) respectively. Each adaptor appeared in a circular aperture whose diameter subtended 2° of visual angle and was edge-blurred by a cosine ramp that transitioned from minimum to maximum over 0.78° of visual angle.

The test stimulus was a static Gabor with equal spatial frequency to the adaptors but had variable orientation (0 or 90°) and temporal onset. Test stimuli were equal in diameter to the adaptors at 2° of visual angle. Gradually onset test stimuli were ramped on by a temporal Gaussian with a standard deviation of 200ms and peak amplitude at 1000ms, while abruptly onset targets were presented within a rectangular temporal window of 300 ms duration.

To ensure that participants had sufficient stereoacuity to support interocular transfer (Mitchell and Ware 1974; Movshon et al. 1972), an Optec 2500 Vision Tester capable of testing down to 20 seconds of arc was used to test participants' depth perception. Published thresholds for normal stereoacuity range from 40 to 60 seconds of arc (Adams et al. 2008; Romano et al. 1975). A mid-range cut-off of 50 seconds of arc was chosen because substantial interocular transfer is still observed for this level of ability (Mitchell and Ware 1974). All participants had better stereoacuity than the cut-off (M = 29, SD = 12.8).

To maximise the potential for interocular transfer, participants' ocular dominance was determined behaviourally by a standard finger pointing measure. Each participant pointed to a coin glued to a wall and observed how far their finger appeared to deviate when viewing with their left eye closed compared to when their right eye was closed. The closed eye that caused the greatest deviation was judged to be dominant. Using this method, three participants were identified as right-eye dominant and two as left-eye dominant. The adaptor was always presented to the dominant eye.

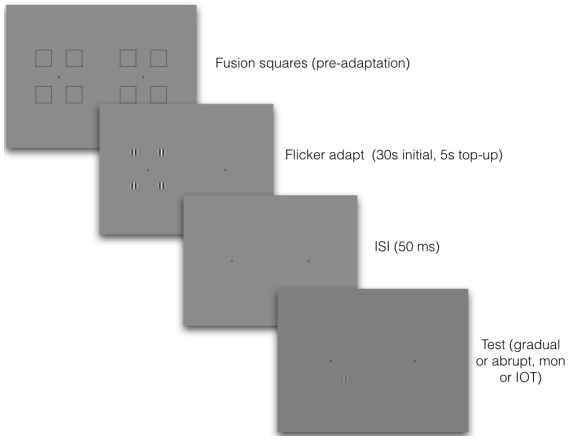

Figure 1. A schematic illustration of the procedure for both experiments. Observers first adjusted the stereoscope using the fixation squares, which then disappeared; they adapted to four counterphasing high-contrast gratings in one eye, and then were tested either in the same or in the other eye, with gradual or abrupt test gratings. For the threshold elevation experiment, the contrast of the test grating was modulated by QUEST; for the disappearance experiment, test gratings were always at full contrast, and the number of incorrect judgments was recorded. Responses were always 4AFC (what was the location of the test grating?).

Procedure

Observers viewed all stimuli through a mirror stereoscope with a total reflection path of 57 cm. Prior to the adaptation period, each eye was presented with four fusion-locking squares of 4.5 degrees of visual angle surrounding a central fixation cross, presented on a grey background of mean luminance (33.5 cd/m^2). After each trial was initiated, the fusion squares disappeared and the adaptation stimuli appeared in the centre of the location of each square, which was 5.9 degrees from the central fixation cross. See Figure 1 for a schematic illustration.

Participants adapted to counterphasing stimuli presented to either the left or right eye. In monocular conditions, the adapting stimulus was presented to the non-dominant eye. In order to maximise the potential for interocular transfer to occur, participants had their dominant eye adapted in the interocular conditions. This meant that the target was always presented to the non-dominant eye, regardless of ocular condition.

Participants pressed a key to initiate trials and were presented with four counterphasing adaptor gratings, one appearing in each aperture. Adaptors were displayed for 30 s for the initial two trials, with 5 s 'top-ups' for subsequent trials. (Pilot testing with 60s initial adaptation and 10s top-ups indicated that the shorter adaptation times produced identical results). Following offset of the adaptors, a spatial four-alternative forced-choice task required observers to use

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a standard keyboard to indicate which aperture the test appeared in. Conditions were blocked by test orientation, temporal onset of the test (gradual versus abrupt), and tested eye (monocular vs. IOT conditions). The order of completion was counterbalanced to ameliorate practice effects.

Detection thresholds were estimated by two randomly interleaved adaptive QUEST staircases (Watson and Pelli 1983) containing 25 trials each. Baseline contrast thresholds corresponding to each of the test conditions were obtained by having participants perform the same spatial location task but without an adaptation period at the beginning of each trial. Baselines were collected before test blocks and were not obtained if the participant had completed a test block at some point during the day. For each participant, the initial two control and test blocks were discounted as practice. Participants completed at least one control and one test per condition. The initial 2 trials in each staircase were dummy trials, and QUEST estimations were jittered throughout by a random offset of $\pm$ 1dB, to expand the range of contrasts tested. The threshold estimate was the contrast level at which responses were correct 62.5% of the time, halfway between chance-level responding and perfect responding for a 4AFC task. This was The dependent variable was contrast threshold elevation expressed in decibels (dB), where A refers to the magnitude of threshold elevation and T refers to contrast detection threshold:

$$A = 20\log_{10}\left(\frac{T_{adapted}}{T_{unadapted}}\right) \quad (1)$$

Thresholds were then estimated by fitting cumulative Gaussian functions to the data produced by QUEST, using custom MATLAB code. An example of this is shown in Figure 2.

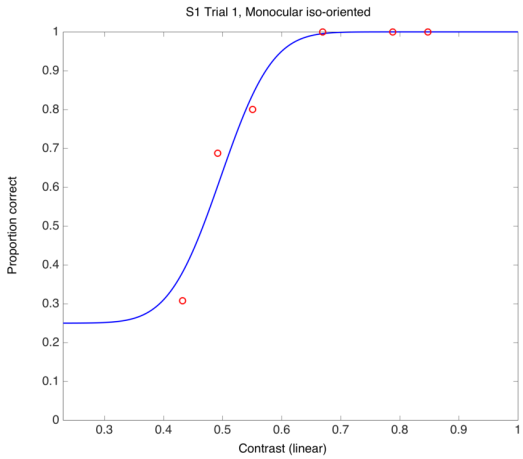

Figure 2. An example of the cumulative Gaussian fit to the data for a single subject, for a trial in the monocular, parallel adaptation condition where the highest threshold elevations were found. As can be seen, participants did reach 100% correct on trials where the contrast of the test stimulus was high enough, though thresholds were much higher in the gradual test condition than in other conditions.

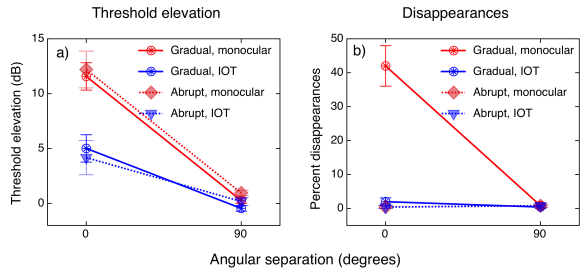

Figure 3. Threshold elevation (a) and percentage of disappearances of full contrast test stimuli (b) after adaptation to counterphasing gratings, for test stimuli which were either 0 degrees or 90 degrees of angular separation from the adapting stimuli, with either gradually onset (solid lines) or abrupt (dotted lines) test stimuli, tested either in the same eye as the adapting stimulus (red) or in the other eye (blue). Error bars show $\pm$1 standard error. All five subjects completed this condition.

Results

Threshold elevations

Using traditional measures of threshold elevation following adaptation to counterphasing gratings, we found that elevations were strongly orientation-dependent regardless of the waveform (gradual or abrupt onset) of the test stimulus, and showed some (but not complete) interocular transfer of this orientation-dependent adaptation. Threshold elevation was very similar for abrupt and gradual onset targets, and was higher when adaptor and tests were presented in the same eye relative to different eyes.

The threshold elevation results were tested using a separate $2 \times 2 \times 2$ repeated-measures ANOVA with onset type (gradual vs. abrupt), eye tested (adapted vs. unadapted) and test orientation (parallel vs. orthogonal) as factors. There were significant main effects of test orientation, $F(1, 4) = 318.74$, $p < .001$, and eye tested (monocular vs IOT), $F(1, 4) = 16.43$, $p = .015$, and a significant interaction between test orientation and eye tested, $F(1, 4) = 13.84$, $p = .020$, but no significant main effect of onset type, $F(1, 4) = .297$, $p = .615$, no interaction between onset type and either eye, $F(1, 4) = .711$, $p = .447$ or orientation $F(1, 4) = .026$, $p = .881$, and no significant three-way interaction, $F(1, 4) = 1.17$, $p = .340$ (see Figure 3a).

Target disappearances

Using a method more similar to the original methods introduced by Motoyoshi and Hayakawa (2010), we presented all the target stimuli in the 4AFC paradigm at

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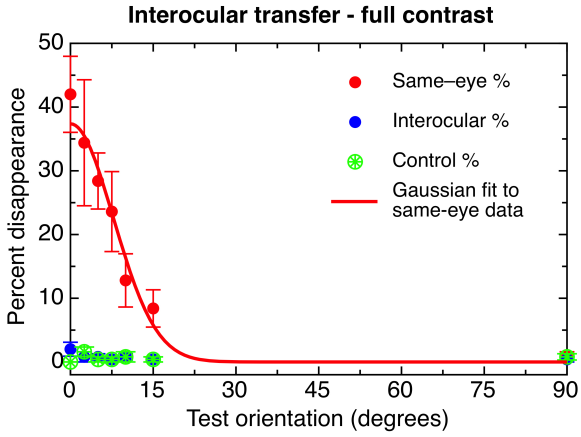

Figure 4. A more detailed examination of the orientation tuning of disappearances (measured by error rates) at full contrast. Red data points show percent disappearances for stimuli presented in the same eye as the adapting stimuli; blue points show those presented in the unadapted eye, and green show the control stimuli presented without adaptors. The solid line shows a Gaussian fit to the data, fitted in ProFit Version 6.2.11, using a Leverburg-Marquardt algorithm; the fit was given two free parameters (amplitude and bandwidth), with a fixed mean of 0 and baseline of 0. Standard deviation of the fit was 7.76 degrees, with an amplitude of 37.4%.

full contrast, either ramped up gradually or with abrupt onset, and measured the proportion of times the observers failed to correctly identify the location of the target grating. Participants' subjective reports indicated that in many instances, the gradual onset targets were simply not seen, even though they were ramped up to full contrast. This is shown clearly in the data (see Figure 3b); most interestingly, though, the pattern is very different from that seen in the threshold data. As for the threshold elevation data, the target disappearances are strongly orientation-tuned; however, there was absolutely no interocular transfer of the effect. In addition, abruptly presented targets never disappeared (perhaps unsurprisingly, since they were at full contrast).

For the disappearance data, there were significant main effects of onset type (gradual vs. abrupt), $F(1, 4) = 58.82$, $p = .002$, eye tested (monocular vs. IOT), $F(1,4) = 35.36$, $p = .002$, and angular separation (0 vs. 90 degrees), $F(1,4) = 50.69$, $p = .002$. There were also significant two-way interactions between onset type and eye tested, $F(1,4) = 35.36$, $p = .004$, onset type and angular separation, $F(1,4) = 68.48$, $p = .001$, and eye tested and angular separation, $F(1,4) = 32.83$, $p = .005$. In addition, there was a significant three-way interaction between onset type, eye tested and angular separation, $F(1,4) = 32.83$, $p = .005$. In summary, the only case in which adapting to the flickering pattern caused disappearance of the target was in the monocular condition where the gradually presented target was parallel to the adaptor, as can be clearly seen from Figure 3b.

We further measured the orientation tuning of the disappearance effect in more detail (see Figure 4), since orientation tuning of this effect was not reported in the original paper. Here it is clear that there is tight orientation tuning of the effect, which is well fitted by a Gaussian function with a standard deviation of 7.76 and an amplitude of 37.4.

The fitted amplitude of the function (37.4%) is very close to the approximate percentage of target disappearances at 0 degrees, on average, across participants. We note that this is also very close to the reported percentage of incorrect responses (34%) in the original paper (Motoyoshi and Hayakawa 2010). It should be noted that the actual percentage of targets not seen in our experiment (and in Motoyoshi's, in fact) would probably be higher, given that the 4AFC paradigm would result in a 25% guess rate, on average. Of further interest is the narrowness of the tuning curve for the disappearances; however, it is important to note here the divergence of the results from Experiment 1 (threshold elevations), in that the orientation-tuned component of this effect showed no IOT at full contrast. The implications of this difference will be covered in the Discussion.

Discussion

This study was designed to determine whether the AIB phenomenon recently reported by Motoyoshi and Hayakawa (2010), might be explained solely in terms of established adaptation-induced contrast sensitivity loss. To achieve this we conducted two adaptation experiments: one measuring classical sensitivity via the derivation of detection thresholds (Experiment 1) and the other; high contrast disappearances, as used by Motoyoshi and Hayakawa (2010) (Experiment 2); from which we were able to compare stimulus dependencies associated with each measure of performance.

Consistent with previous findings, threshold elevation (Experiment 1) was strongly dependent upon the relative orientation of adaptor and test. This was characterized by significant elevation at 0° angular separation and no elevation at 90°, which is what we would expect using the spatial frequency employed in this study (1.5 c.p.d.) (Cass et al. 2012; Baker and Meese 2012). Also consistent with these previous studies is the finding that thresholds were greater overall when adapting and testing in the same eye than in different eyes, an effect which was most prominent when adaptor and test were similarly oriented (Cass et al. 2012;

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Baker and Meese 2012). Importantly, we found for the first time that the effects of adaptation on detection thresholds were identical for abrupt and gradual onset targets, both overall and as a function of angular separation and eye tested.

A very different set of stimulus contingencies was observed for detection at full contrast (Experiment 2). Unlike contrast thresholds, subjects rarely, if ever, failed to correctly locate targets with abrupt temporal profiles. This was the case regardless of the angular distance between target and test. Perceptual disappearances were, however, commonplace (occurring on up to 50% of trials) when targets were presented with gradual onset profiles, but *only when their orientation was similar to that of the adaptor*. This propensity to miss gradual but not abrupt full contrast gratings following flicker adaptation (which we observed only at small angular separations) effectively replicates Motoyoshi and Hayakawa's (2010) original AIB effect.

Another dissociation concerns interocular transfer of flicker adaptation. Experiment 1 showed that, whilst thresholds were maximally elevated when adaptor and test stimuli were presented to the same eye (and at a similar orientation), strong and significant threshold elevations were nonetheless evident when adapting and testing in different eyes, regardless of their onset profile. This is very different to what we observed in Experiment 2, in which perceptual disappearances were exclusively contingent upon the adaptor and (gradual) target stimuli being presented to the same eye, with no evidence of any interocular transfer at any level of angular separation.

These dissociations strongly suggest that AIB is mediated by mechanisms distinct from those responsible for classical adaptation-induced elevations in detection threshold. Interestingly, Motoyoshi and Hayakawa (2010) drew a similar conclusion, proposing that AIB is mediated at a level processing beyond that of primary visual cortex, possibly post-parietal. Our results imply a very different interpretation, however.

Firstly, AIB fails to transfer interocularly. This implies that this form of adaptation is dependent upon neurons which receive input from a single eye. The human visual pathway is constituted entirely of monocularly responsive neurons up to and including the earliest input layers of primary visual cortex. Ascending the visual pathway, neurons rapidly become ocularly ambivalent and are driven to some extent by stimulation to either eye Howarth et al. (2009). The complete absence of any interocular transfer for AIB, but not threshold elevations, suggests that AIB is mediated at a level of processing preceding mechanisms responsible for threshold adaptation.

Curiously, when AIB does occur, it is always within a very narrow angular range (adaptor orientation within 9.1° half width at half height of the test); far narrower than what is generally found when measuring contrast thresholds for orientation (∼30°; Cass et al. 2012, 2009). Again, from a neurophysiological point of view, this is interesting, as orientation tuning selectivity emerges at the earliest stages V1, and becomes broader at higher levels (Blasdel and Fitzpatrick 1984; Fitzpatrick et al. 1985).

This combination of zero interocular transfer and narrow orientation selectivity points to AIB being mediated at the earliest stages of visual cortical processing. Simple cells found in initial layer 4Cβ are not only highly orientation-selective but many are also monocular (Ringach et al. 2002). This particular set of dependencies is quite unique in the primate visual cortex. Cells in all other visual areas are ambivalent about which eye receives a given image (assuming normal visual function).

By contrast, the combination of strong interocular transfer and broader orientation-selectivity for adapted thresholds (Experiment 1) strongly suggests that these may be mediated elsewhere, and probably at a higher stage of the visual processing hierarchy. Our inference that AIB occurs at the earliest stages of visual cortical processing is at odds with Motoyoshi and Hayakawa's (2010) interpretation which is high-level and post-parietal, citing some compelling evidence showing that the tilt illusion occurs regardless of whether or not the tilt-inducing stimulus is rendered invisible by flicker.

Assuming that the mechanisms responsible for the tilt illusion have an extrastriate locus and receive input from local orientation filters in V1, this is difficult to reconcile with our evidence which points to a very early cortical stage for AIB. One possible explanation is that AIB and the tilt illusion may occur in parallel; in other words, the neuronal processes which underlie the tilt illusion may not be (entirely) dependent on input from neurons associated with AIB.

A curious paradox remains. Given that AIB is observed using full contrast stimuli, how is it then that contrast detection threshold estimates are even possible following exposure to high frequency flicker? One possibility may be that AIB is a contrast-gated process, such that the manifestation of adaptation itself is dependent upon a critical level of target contrast, or perhaps on similarity between adaptor and target contrast (see Figure 5). This question may be addressed in future studies by systematically varying adaptor and target contrast, from threshold to full contrast.

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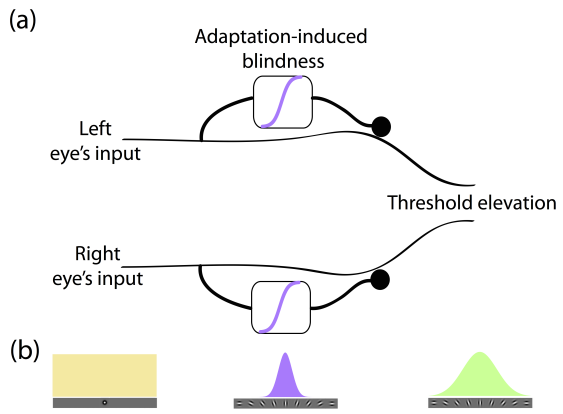

Figure 5. a) A model of how adaptation-induced blindness might differ from threshold elevation in terms of neural input. b) The orientation tuning bandwidth at each stage.

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