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The effect of perceptual contour orientation uncertainty on the tilt aftereffect

Gennady Erlikhman[a,*], Gurjyot Singh[b], Tandra Ghose[b], Zili Liu[a]

[a] *Department of Psychology, University of California, Los Angeles, United States*
[b] *Department of Psychology, Technical University of Kaiserslautern, Germany*

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ABSTRACT

The tilt aftereffect (TAE) occurs when, after adapting to an oriented line, a vertical line appears to be tilted in the opposite direction. The magnitude of the TAE has been shown to relate to the salience of the adapting stimulus (e.g., its contrast) as well as to the similarity between the adapting and testing stimuli. However, the relationship between TAE and orientation uncertainty – variability in the perceived orientation of the stimulus – of either the adapting or the testing stimulus and, more importantly, change in orientation uncertainty as a function of adaptation have not previously been explored. We manipulated stimulus salience by using a variety of contour types, including real and illusory contours. Tilt aftereffects were observed even for stimuli that had much weaker or invisible illusory contours. Orientation uncertainty of the adapting stimulus, as measured by the slope of a psychometric function in orientation discrimination, was positively correlated with TAE magnitude for real and illusory contours, but not for stimuli with weak contour percepts. On an individual subject level, orientation uncertainty increased post-adaptation and was correlated with pre-adaptation uncertainty. That is, individuals with more variability in their perception of orientation before adaptation showed increased variability in orientation discrimination following adaptation. This may account for some of the variability in TAE across individuals and stimulus types and is consistent with previous findings on increased orientation discrimination thresholds post-adaptation for nearby orientations.

1. Introduction

Accurately and reliably perceiving a basic visual attribute in the world such as the orientation of an object's contour is fundamentally important for functional vision. The perception of such visual features depends on the signal quality of the input stimulus, the spatial context in which the signal occurs, and the state of the visual system at the time of perception. This temporal dependence of perception on recent experience is perhaps best illustrated by visual adaptation. In the case of contour perception, after exposure to an oriented line that is tilted away from the vertical, a subsequently presented vertical line will be perceived as tilted in the opposite direction (Gibson & Radner, 1937). This is called the Tilt After Effect (TAE).

A TAE can be induced with a great variety of stimuli, including luminance-defined real contours, illusory contours (Berkley, Debruyn, & Orban, 1994; Bockisch, 1999; Paradiso, Shimojo, & Nakayama, 1989; Poom, 2000; Smith & Over, 1975, 1976), and contours defined by texture and motion (Cruickshank & Schofield, 2005; Hawley & Keeble, 2006; Larsson, Landy, & Heeger, 2006). Interestingly, TAEs can occur even when a contour is not perceived, e.g., for dots arranged symmetrically about some axis that is not explicitly drawn (Joung & Latimer, 2003; Joung, van der Zwan, & Latimer, 2000). Recent studies on tilt-adaptation have focused on two related questions: (1) The stimulus specificity of the TAE: is the TAE the same for self-adaptation (e.g., when both the adapting and test stimuli are real contours) as for cross-adaptation (e.g., between real and illusory adapting and testing contours)? Similarity in TAE magnitude between self- and cross-adaptation has been used to argue for shared representational mechanisms across contour types (e.g., Paradiso et al., 1989). That is, if both real and illusory contours produce the same TAEs, then this may be because there is a single contour mechanism by which both contour types are represented. (2) The role of contour salience in the TAE: in order for two stimuli to be compared in self- and cross-adaptation, which if any of their properties should first be equated so that the only difference between them is the stimulus type (Berkley et al., 1994; Bockisch, 1999)? For example, suppose that the TAE is stronger (i.e., vertical lines appear tilted to a greater degree) when the adapting stimulus is a real contour and the testing stimulus is also a real contour compared to when the

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[*] Corresponding author.
E-mail address: gennady@ucla.edu (G. Erlikhman).

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adapting stimulus is an illusory contour. One might argue that because these two adapting stimulus types produce different TAE magnitudes, then they must be engaging different representational mechanisms. However, because the two adapting contours are different, one may be more "salient" than another, resulting in lower orientation discrimination thresholds for real than for illusory contours. Without further consideration, it is therefore unclear whether differences in TAE magnitude are the result of differences in representational mechanism or uncontrolled stimulus properties.

Bockisch (1999) examined how stimulus salience affected TAE magnitude by measuring, in a separate experiment, orientation discrimination sensitivity as a function of stimulus luminance. Adapting and testing stimuli could then be matched on saliency by, for example, lowering the luminance of one stimulus until orientation discrimination performance was comparable to that of another. In his experiments, reducing the salience of the adapting stimulus was found to decrease TAE magnitude. Using a different way to manipulate salience, Berkley et al. (1994) found that adding noise to the testing stimulus increased TAE magnitude. Together, these results suggest that the less salient a test stimulus is, the larger the TAE; and that the less salient an adapting stimulus is, the smaller the TAE. However, when salience of real and illusory contours is equated, TAE magnitudes are still not the same, suggesting that real and illusory contours may be represented by distinct mechanisms that only share some features in common (Bockisch, 1999).

In the current study, in addition to examining how stimulus properties like stimulus saliency might affect TAE magnitude, we explored the effects of adaption on orientation uncertainty of the test pattern. Orientation uncertainty is quantified as the slope of the psychometric function fit to contour orientation discrimination. Bockisch (1999) used such discrimination to determine orientation sensitivity prior to adaptation, but not after. To our knowledge, few studies have examined the effects of adaptation from this perspective. In other domains, such as speed perception, perceived speed decreases following adaptation, but speed discrimination improves (Krekelberg, van Wezel, & Albright, 2006). In the visual orientation domain, TAE and orientation uncertainty are exact analogues to perceived speed change and speed discrimination post-adaptation (Clifford, 2002). However, whether or not tilt adaptation gives rise to similar changes in discriminability as in speed adaptation remains unknown. In one study that we are aware of, orientation uncertainty was shown to increase following adaptation, but this finding was never remarked upon since the study was looking at TAE magnitude as the main measure (von der Heydt, Machuda, & Qiu, 2005, Fig. 4).

To address this question, we examined the correlations between changes in PSE (Point of Subjective Equality, which is the TAE here) and changes in slope (orientation uncertainty) as a result of adaptation. We also correlated those two measures with the orientation uncertainty of the adapting stimulus (i.e., orientation uncertainty prior to adaptation). We hypothesized that an adapting stimulus with lower orientation uncertainty (i.e., a steeper psychometric function) would give rise to a stronger adaptation effect, resulting in a greater TAE and a corresponding increase in the uncertainty of the test stimulus. We note that, due to our focus on correlational analyses, the issue of self- or cross-adaptation was of secondary importance to our goal. For the same reason, we used stimuli for which we expected to observe a range of orientation uncertainties, rather than stimuli with matched saliency.

A secondary aim of our study was to examine whether or not the subjective percept of a contour, or the lack of it, makes any difference in the presumed relationship between adaptor orientation uncertainty and TAE. Illusory contour strength, as measured by subjective ratings, was weakened by making minimal changes to the stimulus. These ratings were taken as an indirect measure of contour salience, at least from a phenomenological standpoint. We assumed that contour visibility would be reflected at some level of representation in the visual system. For example, a contour that elicits neural responses in the early visual cortices (V1 and V2) may be more likely to be subjectively visible, whereas a contour that does not elicit such early responses may be represented at higher levels in the brain. By testing whether subjective visibility has any influence to TAE magnitude or orientation uncertainty, we hoped to be able to make some inferences about the neural substrates where the orientation properties of such contours may be represented.

To anticipate the results, TAE increased when the testing contour was less clearly visible and decreased as the adapting contour visibility decreased. To the extent that stimulus visibility can be used as a proxy for stimulus salience, these results are consistent with previous findings on the relationship between salience and TAE magnitude (Berkley et al., 1994; Bockisch, 1999). Importantly, on an individual participant level, pre-adaptation orientation uncertainty was not only positively correlated with post-adaptation uncertainty, but uncertainty increased following adaptation. These effects on orientation uncertainty were present for all stimulus types, even including those in which illusory contours were greatly weakened or completely absent, suggesting that explicitly visible oriented contours are not necessary to recruit these mechanisms.

2. General methods

We first provide an overview of the experiments before describing details. The primary goal was to obtain psychometric functions of orientation discrimination for a testing stimulus pre- and post-adaptation and for an adapting stimulus, for each participant. The PSE and the slope of each psychometric function were then estimated, with TAE defined as the change of the PSE from pre- to post-adaptation for the test stimulus. Finally, correlations were analyzed between firstly, the psychometric function slope for the adapting stimulus (i.e., before adaptation) and the TAE for that stimulus, secondly, the psychometric function slope of the test stimulus (i.e., after adaptation) and its TAE, and finally, between psychometric function slopes of adapting and test stimuli (i.e., change in slope as a result of adaptation).

In all experiments, participants judged whether a test stimulus was tilted clockwise or counterclockwise relative to the vertical. They completed two sessions: the first without adaptation and the second with an initial adaptation phase to a stimulus that was tilted 15° clockwise or counterclockwise away from the vertical. The 15° tilt was chosen because adapting stimuli in the range of 10–20° had previously been shown to produce the largest TAEs (Paradiso et al., 1989; van der Zwan & Wenderoth, 1995). A number of experiments were separately run, primarily for logistical reasons, due to the number of stimuli used, the time-consuming nature of an adaptation experiment, and psychometric function measurement, as well as the availability of the participants. Although we will report the specific results from each experiment, our main focus will be on those three correlation analyses across experiments, as mentioned earlier.

We also examined whether or not there was any difference between perceivable and non-perceivable contours when used as either adapting or testing stimuli, or both. Participants adapted to either real or illusory contours (Experiment 1; a replication of Paradiso et al., 1989), or stimuli with perturbed (Experiments 2A and 2B), or ringed terminators (Experiment 3). All stimuli were Varin figures as used in Paradiso et al. (1989), composed of two sets of fives concentric half-circles whose ends or terminators defined the oriented edge (Fig. 1). In the perturbed conditions, the endings of the terminators of each half-circle were lengthened so that they could no longer be connected by a single straight line (Fig. 1B). Illusory contours are weaker or absent if they must form an inflection point to smoothly connect two terminators (Kellman & Shipley, 1991). In the ringed condition, small rings with random diameters were added on the ends of each terminator (Fig. 1C). Rounding of inducing edges also impairs illusory contour formation (Shipley & Kellman, 1990). These manipulations were meant to reduce contour salience by reducing perceived illusory contour strength.

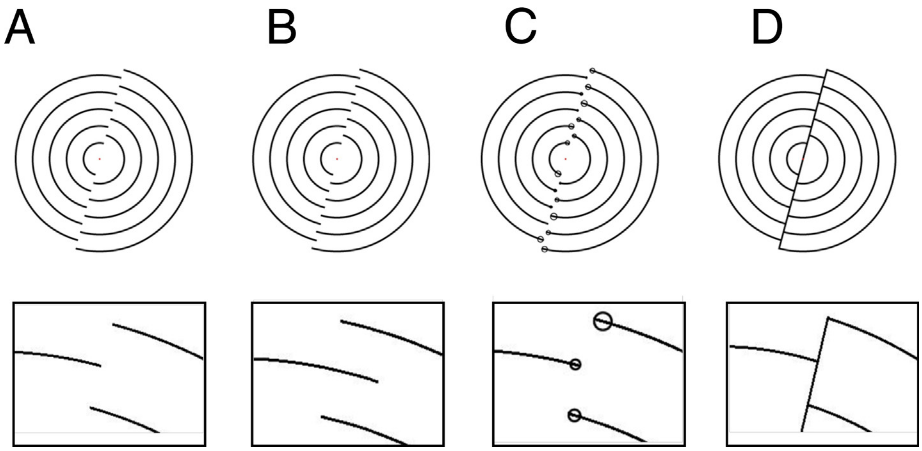

Fig. 1. Adaptor and test stimulus types used in the study. The second row depicts a zoomed in version of the terminators for each stimulus type. (A) Illusory contour (IC), similar to Paradiso et al. (1989). (B) Perturbed terminators (PT). (C) Ringed terminators (RT). (D) Real contours (RC). (Note: The stimuli in the first row are for illustration only. Their angular size in the experiments were very different from that viewed in this figure from a normal reading distance.)

2.1. Participants

Participants in Experiments 1 ($n = 28$), 2A ($n = 17$), and 3 ($n = 14$) were students enrolled in the University of Kaiserslautern, Germany, aged 18–35. One of the authors, GS, was a participant in all three experiments; the remaining participants were naïve to the purpose of the study. All had normal or corrected-to-normal vision. Experiment 2B was performed at the University of California Los Angeles, where 46 undergraduate students participated for course credit. Participants provided informed, verbal consent. All experiments were carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Apparatus

Stimuli were programmed in Matlab version 7.13.0, using Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The experiments in Kaiserslautern were run on a PC with a 2.8 GHz hexa-core Intel Xeon processor, running Microsoft Windows XP Professional-SP3, and presented on a Sun Microsystems GDM-5510 monitor with a 21 in. screen with a pixel resolution of 1600 × 1200 and a refresh rate of 60 Hz. A headrest was used to help stabilize the head and participants sat at a distance of 2 m. The experiment at UCLA was run with matching parameters, except on a Dell PC.

2.3. Stimuli

In Experiment 1, adapting and test stimuli were either real or illusory contours. All stimuli consisted of two sets of five, white (56 cd/m^2) concentric half-circles of varying radii (0.448°–4.48°) on a black background (11 cd/m^2), centered on the screen. The sets of half-circles faced each other, but with their endings offset along a diagonal that defined the orientation of the adapting contour. In the illusory contour (IC) condition (Fig. 1A), the terminators of the half-circles were bare. In the real contour (RC) condition, a line was drawn connecting the ends of each half-circle (Fig. 1D). Both the real and illusory contour stimuli were used as adapting and testing stimuli, giving rise to 2 × 2 conditions. The adaptor stimulus was tilted by ± 15° from the vertical, where negative values mean counter-clockwise. This adapting stimulus orientation was counter-balanced between participants so that each participant only saw one of these two orientations. The test stimuli were tilted by ± 1, 1.5, 2, or 2.5° from the vertical and were the same for every participant. This range of testing values was selected based on previously observed TAE magnitudes from cross-adaptation studies (e.g., Bockisch, 1999; Paradiso et al., 1989).

For the perturbation experiments (Experiments 2A and 2B), the real contour stimulus was replaced with the perturbed stimulus. In Experiment 2A, the perturbed stimuli (PT) were created by extending the ends of the half-circles of the illusory contour stimulus by one additional angular degree of the circle. Because the radii of the circles varied, the length of the added segment that corresponded to one degree of the circle also varied. As a result, there was greater overlap between half-circles toward the outside of the stimulus than nearer to its center: For larger half-circles toward the outside of the stimulus, more pixels were added than for the smaller, inner half-circles. This is illustrated in the left panel of Fig. 2. Due to this manner of perturbation, the illusory contour may have been disrupted to a lesser extent toward the center of the stimulus. To make sure that the manipulation really did disrupt illusory contour perception, a second condition (Experiment 2B) was conducted in which a fixed amount of perturbation (5 pixels, 2.3 arcmin) was added to the end of each half-circle (PT2; right panel of Fig. 2).

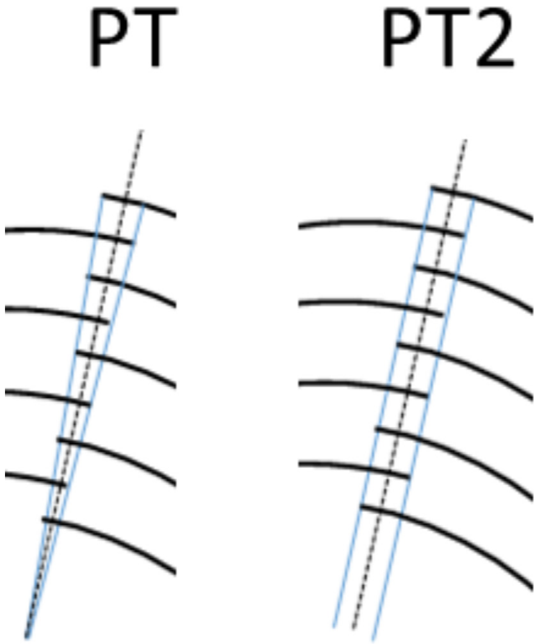

Fig. 2. The two types of perturbed terminators used in Experiment 2A (PT) and Experiment 2B (PT2). These are "zoomed-in" representations as in the second row of Fig. 1. The dashed line represents the contour orientation; the blue lines indicate the amount by which each terminator was extended (i.e., in the illusory contour (IC) condition, the terminators would have ended at the dashed line). PT stimuli were created by extending the length of each half-circle by one degree; this resulted in longer segments added to the outer circles than the inner ones (left). PT2 stimuli were created by extending each half-circle by an equal amount (right). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In Experiment 3, ringed terminator (RT) stimuli (Fig. 1C) and illusory contour stimuli identical to those used in Experiment 1 were used as adapting and testing stimuli. Each ring was a circle that was positioned on the terminators (i.e., ends of the half-circles) of the illusory contour stimulus. The ring diameter was determined randomly for each ring between 10 and 16 pixels (4.6–7.3 arcmin). In pilot work, we found that if the rings were all of the same size, a faint illusory contour could still be seen. Similarly, if the rings were centered on the terminators instead of passing through them, an illusory contour could also be seen through the rings connecting all of the terminators.

In order to confirm that illusory contour strength was disrupted by these manipulations, a separate group of 10 individuals provided subjective contour clarity ratings for the stimuli used in these studies for all conditions except for PT2. Ratings were on a scale of 0 (lowest) to 10 (highest). A real contour was included as a baseline which received the highest rating (9.5). Contours were shown at different orientations corresponding to those used in the adaptation study. The ratings were: 9.5 for real contours, 5.6 for illusory, 4.8 for perturbed, and 3.9 for ringed terminators. There was a main effect of stimulus type (Friedman's test, $\chi^2 = 26.84$, $p < 0.001$). Post-hoc, pair-wise comparisons using Wilcoxon signed rank test found a significant difference between median subjective ratings for all pair-wise comparisons (all p's < 0.004, Bonferroni corrected for multiple-comparisons) except for between perturbed and ringed terminator stimuli ($p = 0.065$).

2.4. Procedure

Participants in Experiments 1, 2A, and 3 completed two experimental sessions each. One session used the illusory contour stimulus as the adaptor and the other used real (Experiment 1), perturbed (Experiment 2A), or ringed stimuli (Experiment 3). In both sessions, both types of stimuli were used as the testing stimuli. The order of the two sessions was counterbalanced across participants. Sessions could be run on the same day or with a break of several days in between. The break was at least two hours long. The adapting stimulus orientation ($-15°$ or $15°$) was the same across both sessions for each participant, but was random across participants.

Each experimental session was divided into two blocks. In the first block, only the testing stimuli were presented with no adapting stimulus to form a no-adaptation baseline. Each testing stimulus was presented for 50 ms. A short presentation for the test stimulus was used because it has been shown that short presentation times increase the size of the tilt aftereffect (Wolfe, 1984) and because this was the timing used in Paradiso et al. (1989). The participants had at most 30 s after stimulus offset to make a response. The actual duration of each trial was 7.5 s on average. The next trial began 1 s after the participants made a response.

In the second block of an experimental session, presentations alternated between adapting and test stimuli. On each trial, an adapting stimulus was presented for 1.5 s, followed by a 100 ms blank screen, and then a test stimulus for 50 ms (this sequence matches the timing parameters in Paradiso et al. (1989)). After a response from the participants, the adapting stimulus was shown again (i.e., top-up). A red fixation disk (0.08° of visual angle) was shown in the middle of the adapting stimulus and a green fixation disk in the middle of the test stimulus to help participants distinguish between adapting and testing portions of a trial. Participants were instructed to keep their eyes fixed at the fixation disk and to avoid eye and head movements as much as possible. A combination of the 8 testing stimulus orientations × 2 testing stimulus types × 20 repetitions of each trial resulted in 320 trials per block. A short break was given between the blocks. A single experimental session, consisting of the two blocks, lasted approximately 40 min.

Experiment 2B was identical to the other experiments, except that the sessions were run between participants (i.e., each participant completed one session using only one of the stimuli as the adapting stimulus) because it was more difficult to recruit participants to come back for a second session at UCLA.

2.5. Data analysis

For each adaptor-test pair and for the baseline no-adaptor condition, the proportion of "clockwise" responses were fit with a cumulative Gaussian function using iterative least squares estimation with the *nlinfit* function from the Statistics Toolbox in Matlab. A cumulative Gaussian was used to fit the data because the standard deviation (sigma or σ) of the function is the inverse of the slope, which is readily interpretable as orientation uncertainty of the test stimulus (see, e.g., Hawley & Keeble, 2006). The cumulative Gaussian function relates proportion of "clockwise" responses, P("clockwise"), to the test stimulus orientation θ by

$$P(\text{“clockwise”}) = \frac{1}{2}\left(1 + erf\left(\frac{\theta - \mu}{\sqrt{2\sigma}}\right)\right)$$

where *erf* is the error function, and μ is the midpoint (50%) or the point of subjective equality (PSE). The TAE was defined as the change in PSE following adaptation. This difference corresponds to the change in orientation at which the stimulus appeared to be vertical. Intuitively, one can think of this shift of the PSE as a change, after adaptation, in how much the test stimulus needs to be tilted for it to appear vertical. Because some participants adapted to a stimulus that was tilted clockwise and others to a stimulus that was tilted counter-clockwise, the unsigned magnitude of the TAE was used. TAE effects were tested by performing Wilcoxon signed rank tests comparing median TAE to zero. Nonparametric tests were used because some experiments had a lesser number of participants and because some conditions produced outlier TAE values.

In addition to looking at the magnitude of the TAE, it was also informative to examine the change in the slope ($1/\sigma$) of the psychometric function. The slope can be taken as a measure of uncertainty in the tilt estimation process. For a fixed mean (μ), a large or steep slope (small σ) corresponds to precise estimates of orientations: tilting the stimulus only slightly to the right will generate clockwise responses nearly 100% of the time. In contrast, a small or shallow slope (large σ) corresponds to noisy orientation estimates such that tilting the stimulus to the right from the perceived vertical will not greatly change the proportion of clockwise responses. Another way to think of this is that when the slope is large, there is a clearer discriminatory boundary between stimuli tilted clockwise and counter-clockwise; when the slope is small, the distinction is fuzzier and it is more difficult to tell them apart. For ease of interpretation, we present the data in terms of sigma (σ) instead of slope. Large sigma values correspond to greater variability in the perceived tilt. These values were computed separately for psychometric functions in pre- and post-adaptation, respectively.

Cumulative Gaussian functions could not be fit properly for several participants. These participants pressed the same response key for a majority of trials in one or more of the adaptation conditions. As a result, these participants had large response biases even in the no-adaptor blocks. These biases were often in opposite directions across the two sessions (i.e., responding "clockwise" nearly 100% of the time in one block and 0% of the time in another, when only the test stimuli with no adaptation was shown), suggesting that they may not have been doing the task properly. When functions were fit to their data, the resulting parameter estimates of the psychometric function were extreme (e.g., mean of 10,000°). We therefore felt justified in excluding them from all subsequent analyses. In order to remove these extreme values, we excluded all estimates that were more than three standard deviations away from the mean. This led to the exclusion of five participants from Experiment 1, two from Experiment 2A, six from Experiments 2B, and one participant from Experiment 3.

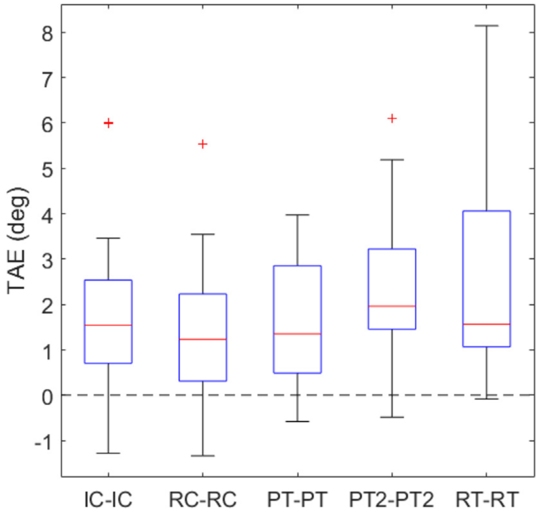

Fig. 3. The TAE magnitude median values across for all same adaptor-test stimulus pairs. IC – illusory contour, RC – real contour. PT –arc-length perturbation of terminators. PT2 –pixel-based perturbation of terminators. RT – ringed terminators. The IC-IC data are aggregated across all experiments, whereas the other four conditions come from Experiments 1, 2A, 2B, and 3, respectively. The dashed line indicates where TAE = 0°. The red lines are the median, the extent of the boxes are the 25th and 75th percentiles, and whiskers extend to most extreme points that are not outliers, which are marked with +'s. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

We first briefly consider the effects of stimulus type on TAE magnitude, to demonstrate that we successfully replicated the results of Paradiso et al. (1989) and that adaptation did, in fact occur. We then examine orientation uncertainty (slope of the psychometric function), both before and after adaptation, and the relationship between this uncertainty and TAE. The analyses are split by within-stimulus effects (i.e., the same adapting and testing stimulus type) and cross-adaptation effects (i.e., different adapting and testing stimuli). We use a two-term notation like IC-IC to denote the type of adapting and testing stimuli that were used. For example, IC-RC is the condition in which the adapting stimulus was an illusory contour (IC) and the test stimulus was a real contour (RC).

3.1. Within-stimulus adaptation effects

The median TAE magnitudes for within-stimulus adaptation pairs (e.g., real adapting and test stimuli, RC-RC) are shown in Fig. 3. Because all experiments had an illusory contour condition, the data were combined across experiments for IC-IC. A TAE was observed for illusory, real, perturbed (PT), and ringed contours (all p's < 0.001), but not for the PT2 contour ($p = 0.85$). However, overall median TAE magnitudes observed in our experiment (1–2°) were lower than those in Paradiso et al. (1989) (2–3°). For some participants, the TAE magnitudes were near-zero or in the opposite direction. Such variability is not unusual (see, e.g., Bockisch, 1999). There was no difference in median TAE magnitude across stimulus types (Kruskal-Wallis, $H(4) = 5.32$, $p = 0.26$).

Bockisch (1999) had found that the TAE magnitude was affected by the contrast of the adapting contours and whether or not they were masked with random noise dots. The orientation uncertainty was quantified as the sigma (σ) estimate from the fit of the psychometric function. The left panel of Fig. 4 plots the pre-adaptation sigma against the TAE magnitude across all stimulus types. Because some participants took part in multiple experiments, the data shown here are only from unique participants so that each point corresponds to a single person. Since all experiments had the IC-IC condition, the corresponding points (pink) display data from all experiments. The pre-adaptation sigma was positively correlated with the TAE magnitude for real contours (RC: Spearman's $\rho = 0.55$, $p = 0.009$) and was marginally significant for illusory contours ($\rho = 0.27$, $p = 0.057$). However, there was no such relationship for stimuli with either perturbed (PT: $\rho = -0.19, p = 0.50$; PT2: $\rho = 0.17$, $p = 0.47$) or ringed terminators (RT: $\rho = 0.34$, $p = 0.26$). It appears, therefore, that there was a positive correlation between pre-adaptation sigma and TAE only for the real and illusory contour adaptor and test stimuli. The rest of the contours that were not subjectively visible showed no such correlations.

We also examined the effects of adaptation on stimulus orientation uncertainty by comparing pre- and post-adaptation sigmas (Fig. 4, right panel). A majority of the points lie above the 45° dashed line, suggesting that sigma or orientation uncertainty increased after adaptation. This was confirmed by comparing sigma values before and after adaptation across all conditions (Wilcoxon signed rank test, $Z = 7.13$, $p < 0.001$). Collapsing across stimulus types, there was an overall positive correlation between pre- and post-adaptation sigma ($\rho = 0.57$, $p < 0.001$). Looking at individual trends for each contour type, a positive correlation was present for real contours ($\rho = 0.56$, $p = 0.008$) and for illusory contours ($\rho = 0.63$, $p < 0.001$). The correlations between pre- and post-adaptation sigmas for ringed and both types of perturbed terminator stimuli were positive, but not significant. In short, for stimuli whose contours were visible (real and illusory), the TAE and orientation uncertainty increased following adaptation, and, on an individual-participant level, did so to a greater extent as a function of that individual's pre-adaptation orientation uncertainty.

This led us to consider whether TAE magnitude correlated with the *change* in orientation uncertainty as a result of adaptation. In other words, if an individual became comparatively more uncertain about orientation as a result of adaptation, were they also more likely to perceive contours as more tilted? We refer to change in orientation uncertainty following adaptation as the "Uncertainty Aftereffect," which is simply the difference between post-adaptation and pre-adaptation sigmas. There was a positive correlation between the Uncertainty Aftereffect and TAE when collapsing across all stimulus types ($\rho = 0.37$, $p < 0.001$). Looking at each stimulus type individually, there was a positive correlation between the Uncertainty and Tilt Aftereffects for the PT2 stimuli ($\rho = 0.58$, $p = 0.005$), a marginal effect for real ($\rho = 0.37$, $p = 0.09$), ringed ($\rho = 0.52$, $p = 0.07$), and PT stimuli ($\rho = 0.46$, $p = 0.09$), and no correlation for illusory stimuli ($\rho = 0.11$, $p = 0.46$). This provides tentative evidence for simultaneous shifting and broadening of psychometric functions as a result of tilt adaptation and that the amount of change in one property is predictive of the amount of change in the other.

3.2. Cross-adaptation effects

In the above analyses, the adapting and testing stimuli were always the same (e.g., RC-RC and IC-IC). Differences across stimulus types could have therefore been either the result of differences in the adapting stimulus, the testing stimulus, or both. To compare the effects of adapting or testing stimulus type on TAE magnitude or post-adaptation sigma or to examine the effects of pre-adaptation sigma, we examined the trials in which either the adapting or the testing stimulus was the illusory contour (IC-X and X-IC, where X represents stimulus type, e.g., RC or RT).

Fig. 5 depicts the cross-adaption TAE magnitude for all conditions across all experiments. Regardless of whether the illusory contour (IC) was the adapting or testing stimulus, a TAE was observed for all pairings (all p's < 0.05) except for the IC-RC condition. The median TAE magnitudes were comparable or a little larger than the within-adaptation conditions (1–2° for most conditions). This pattern of results was qualitatively similar to those observed in Paradiso et al. (1989) for 15°

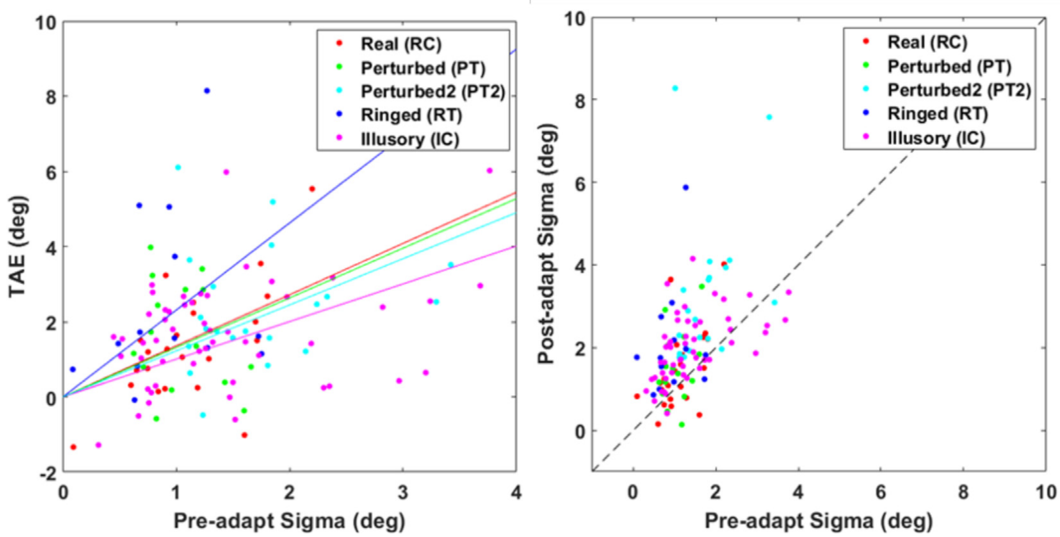

Fig. 4. Left: Scatter plot depicting the relationship between the pre-adaptation sigma (σ) and TAE magnitude for the following adaptor types: real contours (RC, red), perturbed terminators (PT, green), perturbed terminators of equal length (PT2, cyan), ringed terminators (RT, blue), and illusory contours (IC, pink). Colored lines represent linear regression fits. Right: Scatter plot depicting the relationship between pre-adaptation stimulus orientation uncertainty (pre-adapt sigma) and post-adaptation stimulus orientation uncertainty (post-adapt sigma). Sigma is the inverse slope of the fitted psychometric function for each observer. The dashed line has a slope of one and passes through the origin. Points below the line indicate a lower sigma post-adaptation; points above the line indicate an increase in sigma post-adaptation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

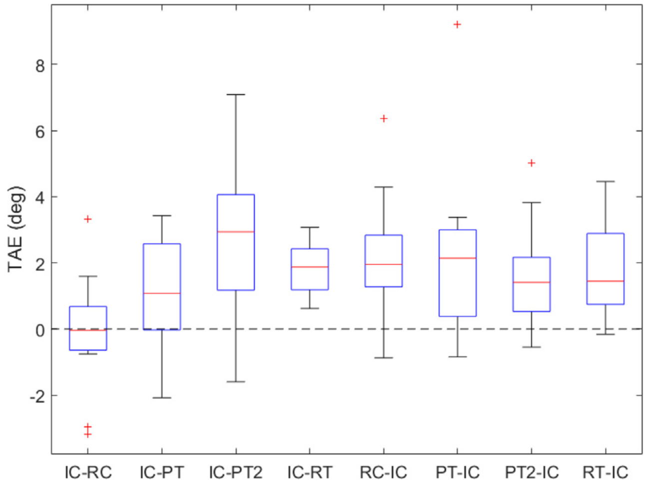

Fig. 5. The baseline-subtracted TAE magnitude median values for cross-adaptations. IC – illusory contour, RC – real contour, PT –arc-length perturbation of terminators, PT2 –pixel-based perturbation of terminators, and RT – ringed terminators. The horizontal dashed line indicates where TAE = 0°. The red lines are the median, the extent of the boxes are the 25th and 75th percentiles, and whiskers extend to most extreme points that are not outliers, which are marked with +'s. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

adaptors: the largest adaptation effects were found for real-illusory (RC-IC) and illusory-illusory (IC-IC) conditions, intermediate TAE (for three of the four participants in Paradiso et al., 1989) for real-real (RC-RC) adaptor-test pairs, and the weakest TAE for the illusory-real (IC-RC) condition.

The relationship between pre-adaptation sigma of the adapting stimulus and TAE magnitude when the IC contour was used as a test stimulus is shown in Fig. 6 (left panel). The IC-IC data are the same as in the previous section and are included here for comparison. Overall, collapsing across stimulus types, there was a positive correlation between adaptor sigma and cross-adaptation TAE magnitude ($\rho = 0.28$, $p = 0.019$). The IC-IC condition was not included in this analysis. When looking at individual stimulus types, only when the adapting stimulus was visible (RC-IC: $\rho = 0.48$, $p = 0.026$; marginal for IC-IC: $\rho = 0.27$, $p = 0.057$) was there a positive correlation between the two variables (all other p's > 0.05). This is the same pattern of results as for within-stimulus adaptation. In particular, when the adapting stimulus was a real contour, irrespective of the type of test stimulus (RC or IC), TAE magnitude was correlated with the orientation uncertainty of the real contour. No such relationship was observed for any other stimulus type except for the illusory contour.

We also examined how orientation uncertainty of the IC stimulus changed following adaptation as a function of the adapting stimulus type. As for within-stimulus adaptation, orientation uncertainty for the IC stimulus was greater following adaptation (i.e., when it was used as a testing stimulus) compared to pre-adaptation. This general pattern can be seen from the fact that a majority of the points lie above the dashed line in the right panel of Fig. 6. Collapsing across stimulus type, there was a positive correlation between pre- and post-adaptation sigma ($\rho = 0.64$, $p < 0.001$). The IC-IC condition was not included in this analysis. There was a positive correlation between pre- and post-adaptation sigma for the IC stimulus for PT (PT-IC: $\rho = 0.82$, $p < 0.001$) and RT stimuli (RT-IC: $\rho = 0.63$, $p = 0.025$), a marginal one for real contours (RC-IC: $\rho = 0.38$, $p = 0.08$), and none for PT2 stimuli ($\rho = 0.27$, $p = 0.24$).

In order to further explore this relationship, we fit linear regression models to both sets of data and compared the fitted slopes across adapting stimulus types. The fitted lines were forced to pass through the origin. The data are shown in Tables 1 and 2. The slope of the regression lines indicates how much TAE or post-adaptation sigma changed as a function of pre-adaptation sigma, or orientation uncertainty. No obvious pattern can be seen from the fitted slopes between pre-adapt and TAE. However, an interesting relationship emerges in the sequence of slopes of lines fitted to the pre- and post-adaptation sigma. In particular, the slopes are ordered inversely with respect to average contour clarity ratings of the adapting stimuli: RC, IC, RT, PT (note that there were no clarity ratings collected for PT2). That is, orientation uncertainty for the IC stimulus increased more following adaptation to stimuli with less clearly visible contours (RT and PT) than when the adapting stimulus had visible contours (RC and IC). Subjective stimulus saliency ratings, therefore, predicted the degree of *change* of orientation uncertainty following adaptation. We note again that this analysis was

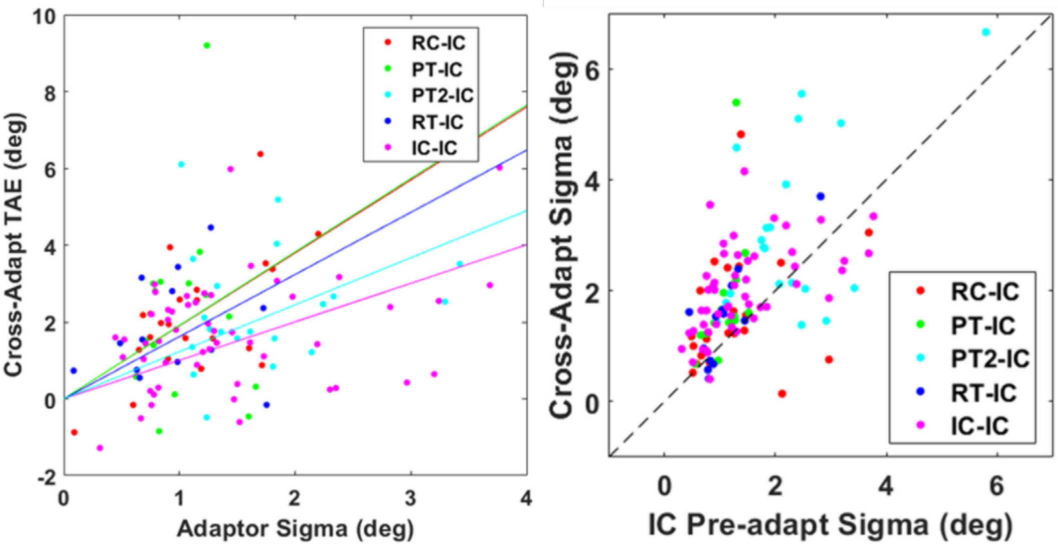

Fig. 6. Left: Relationship between pre-adaptation sigma for each adapting stimulus and TAE magnitude when the illusory contour (IC) was the test stimulus. Colored lines represent linear regression fits. Right: Relationship between pre- and post-adaptation sigmas for the IC as a function of the adapting stimulus. The IC-IC points are the same as in Fig. 4 and are included here for ease of comparison.

Table 1
Slope of linear regression fits for left panel of Fig. 6.

Pre-adaptation sigma and TAE	slope	SE	*t*	*p*
RC-IC	1.89	0.22	8.77	< 0.001
PT-IC	1.91	0.58	3.24	0.006
PT2-IC	1.22	0.20	6.00	< 0.001
RT-IC	1.62	0.40	4.09	0.002
IC-IC	1.00	0.12	8.35	< 0.001

Table 2
Slope of linear regression fits for right panel of Fig. 6.

Pre- and post-adaptation sigma	slope	SE	*t*	*p*
RC-IC	0.99	0.17	5.86	< 0.001
PT-IC	1.66	0.23	7.22	< 0.001
PT2-IC	1.26	0.13	9.74	< 0.001
RT-IC	1.34	0.11	11.7	< 0.001
IC-IC	1.18	0.08	14.6	< 0.001

only possible in cross-adaptations such that one of the two stimuli could vary while the other remained constant.

Similar analyses were carried out when the IC stimulus was the adapting, not the testing stimulus. Fig. 7 shows the relationship between pre- and post-adaptation orientation uncertainties of the testing stimulus. For all testing stimulus types, the adapting stimulus was the illusory contour. Recall that the orientation uncertainty increased following adaptation for within-stimulus adaptation as well as cross-adaptation when the testing stimulus was the IC contour. When combined together, there was a positive correlation between pre- and post-adaptation sigma ($\rho = 0.74, p < 0.001$). This correlation was found for all stimulus types (IC-RC: $\rho = 0.61$, $p = 0.003$; IC-PT: $\rho = 0.67$, $p = 0.008$; IC-PT2: $\rho = 0.52$, $p = 0.024$; IC-RT: $\rho = 0.58$, $p = 0.040$). Taken together, considering all combinations of adaptor and test types, orientation uncertainty increased following adaptation.

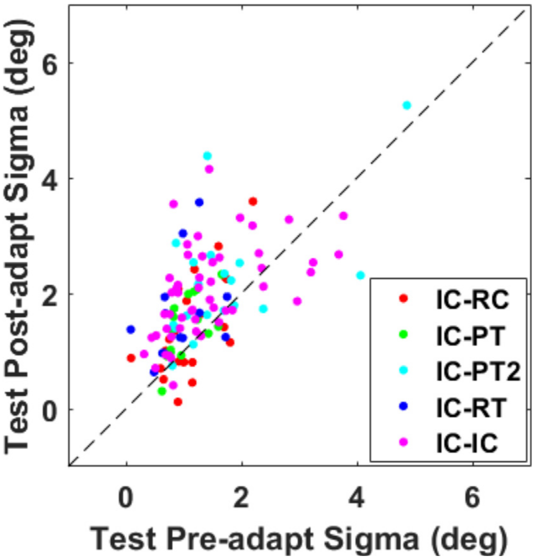

Fig. 7. Relationship between pre- and post-adaptation sigma of the testing stimulus, when the adaptor was always the illusory contour. The dashed line has a slope of one.

4. Discussion

A tilt aftereffect was observed when adapting and testing with real (i.e., luminance-defined) and illusory contours, confirming previous findings regarding TAEs and cross-adaption between real and illusory contours (Berkley et al., 1994; Bockisch, 1999; Hawley & Keeble, 2006; Paradiso et al., 1989; Smith & Over, 1975). A TAE was also produced when the adapting stimuli were two novel stimulus types – perturbed (PT and PT2) and ringed terminators (RT) that contained neither real nor illusory contours. This is in agreement with several recent studies that have found a TAE for stimuli that contain no extended contours whatsoever, such as symmetrical dot patterns (Joung & Latimer, 2003; Joung et al., 2000), translational Glass patterns (Pavan, Hocketstaller, Contillo, & Greenlee, 2016), and for images of buildings (Ismail, Solomon, Hansard, & Mareschal, 2016). The tilt aftereffect may therefore be more general and reflect adaptation at many visual processing stages or, alternatively, a common substrate, perhaps in early visual cortex, for the perception of contours, symmetry, and Glass patterns (Otswald, Lam, Li, & Kourtzi, 2008; Rainville & Kingdom, 2000; Smith, Bair, & Movshon, 2002; van der Zwan, Leo, Joung, Latimer, & Wenderoth, 1998).

Importantly, we observed that TAEs for some contour types were predicted by their orientation uncertainty. Contour orientation uncertainty was characterized by the sigma parameter estimates of cumulative Gaussian functions fitted to orientation discrimination psychometric functions. Larger values of sigma correspond to small slopes of the function and greater uncertainty in the orientation of the stimulus; smaller values of sigma correspond to large slopes and greater certainty in the orientation. A positive relationship was found between orientation uncertainty before adaptation and the magnitude of the tilt aftereffect for real and illusory contours, but not for contours with perturbed or ringed terminators. To the extent that stimulus salience may affect orientation uncertainty, these results are consistent with previous findings that TAE magnitude decreases with the saliency of the adapting stimuli (Berkley et al., 1994; Bockisch, 1999). Of greatest interest, however, was not the magnitude of the TAE effect, which others had previously shown to be quite variable depending on stimulus saliency and type, but, the relationship between pre- and post-adaption orientation uncertainty. For both within- and cross-adaptation, orientation uncertainty increased following adaptation (Figs. 5–7).

Previously reported effects of adaptation on detection and discrimination of orientation and other stimulus properties have been mixed. Contrast discrimination, for example, has sometimes been found to improve after adaptation (Abbonizio, Langley, & Clifford, 1998; Greenlee & Heitger, 1988), and sometimes it has been found to remain unchanged (Maatanen & Koenderink, 1991; Ross, Speed, & Morgan, 1993). Orientation discrimination likewise has been shown to improve (Regan & Beverley, 1985), remain unchanged (Barlow, Macleod, & van Meeteren, 1976), or worsen (Clifford, Wyatt, Arnold, Smith, & Wenderoth, 2001) following adaptation (for a review, see Clifford, 2002). In the present experiments, positive TAEs indicated that, following adaptation, there was a bias in orientation judgments away from the true orientation, while an increase in sigma indicated that orientation discrimination worsened. This reduction in discriminability occurred irrespective of adapting or testing stimulus type or saliency.

The direction of adaptation effects on orientation discrimination may depend on whether the testing stimulus was near, far from, or orthogonal to the testing stimulus (Clifford et al., 2001; Dragoi, Sharma, Miller, & Sur, 2002; Regan & Beverley, 1985). In Clifford et al. (2001), participants adapted to oriented gratings that were either vertical or tilted by 7.5°, 15°, or 90° and subsequently asked to make a two-alternative forced-choice (2AFC) orientation discrimination judgments about two grating (which was more clockwise) tilted by a small amount away from the vertical. Orientation discrimination thresholds were impaired relative to a no-adaptation comparison for adapting stimuli tilted by 7–15°, but were improved if adapting stimuli had similar orientation as the testing stimuli or if the adapting and the testing stimuli were orthogonal. Although it should be noted that the elevated orientation discrimination thresholds post-adaptation for the 15° adapting stimulus reached statistical significance only for two experienced observers, and, although the trend was in the correct direction, the improvement in threshold was not significant when the experiment was repeated with ten naïve observers. In the current experiments, the adapting stimuli were always tilted 15° away from the vertical and the testing stimuli were within 3° of the vertical, falling within the range where one would expect orientation discrimination to be impaired. Although we did not measure orientation discrimination directly with a 2AFC task, increased orientation uncertainty following adaptation is consistent with these results.

Clifford et al. (2001) proposed a model in which adaptation decreases the signal-to-noise ratio of neurons tuned to orientations similar to the adapting stimulus and increases the orientation bandwidth of neurons tuned to other orientations. Neurons in macaque V1 have been found to demonstrate these tuning properties, including increases in tuning bandwidth at nearby orientations following adaptation, even for brief adaptation periods (Dragoi et al., 2002). Physiologically, these changes may occur due to recurrent connections both within local V1 circuits and across cortical areas (Felsen et al., 2002; Westrick, Heeger, & Landy, 2016). The fact that similar relationships between pre- and post-adaptation orientation uncertainty were observed for all contour types in the present study, including illusory contours, supports the idea that feedback from higher-level cortical areas where such contours may be represented may be involved in tilt adaptation. If higher-level areas are involved in contour representations, then this may also account for the difference between visible (RC and IC) and less clearly visible (RT, PT, and PT2) contours. When the adapting and testing stimuli were the same (within-stimulus adaptation), TAE and orientation uncertainty were correlated only when the stimulus was visible. Perhaps visible contours have both low- and high-level representations, which are both adapted, resulting in subsequently larger TAEs. In contrast, less clearly visible stimuli may be represented at higher levels, but there is little representation and therefore, adaptation at low levels, resulting in weaker adaptation effects. This could also explain why TAE was hard to estimate for such contours, in addition to idiosyncratic differences between participants: greater orientation uncertainty corresponds to shallower psychometric functions, and for such functions estimates of the midpoint may not be accurate. Therefore, cases where no correlations were found between pre-sigma and TAE should be taken with caution, perhaps requiring more sensitive methods for estimating TAE in future research.

TAE and orientation uncertainty were also considered for cross-adaptation conditions. A TAE was found for all adaptor-test pairs, except for IC-RC. Paradiso et al. (1989) found the same cross-adaptation asymmetry. However, other studies have previously found either no asymmetry (Smith & Over, 1975) or a great degree of variability in TAE magnitude across participants and cross-adaptation effects (Berkley et al., 1994). One explanation for this difference may be idiosyncrasies in the adapting stimulus design: Smith and Over (1975) used real contours parallel to the orientation of the adapting and test orientations to induce illusory contours. These may have strengthened the adaptation effects and reduced any asymmetries (see Paradiso et al. (1989) for a discussion). Berkley et al. (1994) only presented individual participant data because of the large variability in TAE magnitude across adaptor-test pairs. However, visual inspection of their Fig. 2 also suggests an asymmetry in average TAE between RC-IC and IC-RC (labeled in that figure as LU-IL and IL-LU, respectively). One possible reason for asymmetrical effects could be due to differences in the contour saliency of the adapting and testing stimuli (Berkley et al., 1994).

When the IC stimulus was the testing stimulus, orientation uncertainty increased after adaptation, irrespective of the type of adapting stimulus, consistent with the within-stimulus adaptation results. Importantly, when linear regressions were fitted to the data, the slopes of the regression lines were inversely related to the clarity of the adapting stimulus. That is, the weaker the saliency of the adapting stimulus, as measuring by contour clarity ratings, the greater the increase in orientation uncertainty following adaptation. One possible reason why this may occur is that for an adapting stimulus whose orientation is uncertain, more orientation tuned units are responding and adapting. This then results in a broader range of responses after adaptation. The relationship between adapting stimulus orientation uncertainty and TAE is less clear, however. In the RC-IC condition, for example, pre-adaptation sigma is positively correlated with TAE. On the one hand, this is at odds with Bockisch (1999), who would predict that TAE should decrease with increasing adapting stimulus uncertainty. On the other hand, when the test stimulus is an illusory contour and therefore has lower salience than the adapting stimulus, then it should lead to a larger TAE. These, then, act as competing factors and the relationship between TAE magnitude and stimulus salience may be more complicated than previously thought. Indeed, Bockisch acknowledges that even when stimulus saliency is matched between adapting and testing stimuli, asymmetries can still arise. One possible source of such asymmetries may be the visibility of the contours.

In summary, we report three new findings. First, a relationship between pre- and post-adaptation uncertainty and TAE magnitude.

Second, a positive correlation between pre-adaptation uncertainty and post-adaptation. Taken together, these results suggest adaptation induces both shifts and widening of orientation tuning functions. Finally, we found that adaptation could occur in displays in which the adapting contour's visibility was greatly reduced or completely abolished suggesting that these effects may occur at processing stages beyond early visual cortex. Among these results, we believe that the most significant is the increase of orientation uncertainty after adaptation.

References

Abbonizio, G., Langley, K., & Clifford, C. W. G. (1998). Adaptation improves contrast discrimination. *Investigative Ophthalmology and Visual Science, 39*, S409.

Barlow, H. B., Macleod, D. I. A., & van Meeteren, A. (1976). Adaptation to gratings: No compensatory advantage found. *Vision Research, 16*, 1043–1045.

Berkley, M. A., Debruyn, B., & Orban, G. (1994). Illusory, motion, and luminance-defined contours interact in the human visual system. *Vision Research, 34*(2), 209–216.

Bockisch, C. J. (1999). Orientation discrimination and tilt aftereffects with luminance and illusory contours. *Vision Research, 39*, 765–776.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*, 433–436. https://doi.org/10.1163/156856897X00357.

Clifford, C. W. G. (2002). Perceptual adaptation: Motion parallels orientation. *Trends in Cognitive Sciences, 6*(3), 136–143.

Clifford, C. W. G., Wyatt, A. M., Arnold, D. H., Smith, S. T., & Wenderoth, P. (2001). Orthogonal adaptation improves orientation discrimination. *Vision Research, 41*, 151–159.

Cruickshank, A. G., & Schofield, A. J. (2005). Transfer of tilt-aftereffects between second-order cues. *Spatial Vision, 18*(4), 379–397.

Dragoi, V., Sharma, J., Miller, E. K., & Sur, M. (2002). Dynamics of neuronal sensitivity in visual cortex and local feature discrimination. *Nature Neuroscience, 5*(9), 883–891.

Felsen, G., Shen, Y. S., Yao, H., Spor, G., Li, C., & Dan, Y. (2002). Dynamic modification of cortical orientation tuning mediated by recurrent connections. *Neuron, 36*(5), 945–954.

Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. *Perception, 20*(5), 186–196.

Greenlee, M. W., & Heitger, F. (1988). The functional role of contrast adaptation. *Vision Research, 28*, 791–797.

Hawley, S. J., & Keeble, D. R. (2006). Tilt aftereffect for texture edges is larger than in matches subjective edges, but both are strong adaptors of luminance edges. *Journal of Vision, 6*, 37–52.

Ismail, A. M. H., Solomon, J. A., Hansard, M., & Mareschal, I. (2016). A tilt after-effect for images of buildings: Evidence of selectivity for the orientation of everyday scenes. *Royal Society Open Science, 3*, 160551. https://doi.org/10.1098/rsos.160551.

Joung, W., & Latimer, C. R. (2003). Tilt aftereffects generated by symmetrical dot patterns with two or four axes of symmetry. *Spatial Vision, 16*(2), 155–182.

Joung, W., van der Zwan, R., & Latimer, C. R. (2000). Tilt aftereffects generated by bilaterally symmetrical patterns. *Spatial Vision, 13*(1), 107–128.

Kellman, P. J., & Shipley, T. F. (1991). A theory of visual interpolation in object perception. *Cognitive Psychology, 23*(2), 141–221.

Krekelberg, B., van Wezel, R. J., & Albright, T. D. (2006). Adaptation in macaque MT reduces perceived speed and improves speed discrimination. *Journal of Neurophysiology, 95*, 255–270.

Larsson, J., Landy, M. S., & Heeger, D. J. (2006). Orientation-selective adaptation to first- and second-order patterns in human visual cortex. *Journal of Neurophysiology, 95*, 862–881.

Maatanen, L. M., & Koenderink, J. J. (1991). Contrast adaptation and contrast gain control. *Experimental Brain Research, 87*, 205–212.

Otswald, D., Lam, J. M., Li, S., & Kourtzi, Z. (2008). Neural coding of global form in the human visual cortex. *Journal of Neurophysiology, 99*(5), 2456–2469.

Paradiso, M. A., Shimojo, S., & Nakayama, K. (1989). Subjective contours, tilt aftereffects, and visual cortical organization. *Vision Research, 29*(9), 1205–1213.

Pavan, A., Hocketstaller, J., Contillo, A., & Greenlee, M. W. (2016). Tilt aftereffect following adaption to translational Glass patterns. *Scientific Reports, 6*, 23567.

Pelli, D. G. (1997). The videotoolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*, 437–442. https://doi.org/10.1163/156856897X00366.

Poom, L. (2000). Inter-attribute tilt effects and orientation analysis in the visual brain. *Vision Research, 40*, 2711–2722.

Rainville, S. J. M., & Kingdom, F. A. A. (2000). The functional role of oriented spatial filters in the perception of mirror symmetry – psychophysics and modeling. *Vision Research, 40*, 2621–2644.

Regan, D., & Beverley, K. I. (1985). Post-adaptation orientation discrimination. *Journal of the Optical Society of America A, 2*, 147–155.

Ross, J., Speed, H. D., & Morgan, M. J. (1993). The effects of adaptation and masking on incremental thresholds for contrast. *Vision Research, 33*, 2051–2056.

Shipley, T. F., & Kellman, P. J. (1990). The role of discontinuities in the perception of subjective figures. *Perception & Psychophysics, 48*(3), 259–270.

Smith, M. A., Bair, W., & Movshon, J. A. (2002). Signals in Macaque striate cortical neurons that support the perception of Glass patterns. *The Journal of Neuroscience, 22*(18), 8334–8345.

Smith, A., & Over, R. (1975). Tilt aftereffects with subjective contours. *Nature, 257*, 581–582.

Smith, A., & Over, R. (1976). Color-selective tilt aftereffects with subjective contours. *Perception & Psychophysics, 20*(4), 305–308.

van der Zwan, R., Leo, E., Joung, W., Latimer, C., & Wenderoth, P. (1998). Evidence that both area V1 and extrastriate visual cortex contribute to symmetry perception. *Current Biology, 8*, 889–892.

van der Zwan, R., & Wenderoth, P. (1995). Mechanisms of purely subjective contour tilt aftereffects. *Vision Research, 35*(18), 2547–2557.

von der Heydt, R., Machuda, T., & Qiu, F. (2005). Border-ownership dependent tilt aftereffect. *Journal of the Optical Society of America A. Optics, Image Science, and Vision, 22*(10), 2222–2229.

Westrick, Z. M., Heeger, D. J., & Landy, M. S. (2016). Pattern adaptation and normalization reweighting. *Journal of Neuroscience, 36*(38), 9805–9816.

Wolfe, J. M. (1984). Short test flashes produce large tilt aftereffects. *Vision Research, 24*(2), 1959–1964.