Efficient Coding Theory Predicts a Tilt Aftereffect from Viewing Untilted Patterns

Highlights
- There are separately adaptable binocular summation and differencing channels
- The brain enhances efficiency by adjusting the sensitivities of these channels
- Adaptation of these channels using unoriented patterns can determine perceived tilt
- This adaptation effect was found to be stronger in men than women

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In Brief
May and Zhaoping show that the brain contains binocular summation and differencing channels and enhances coding efficiency by adjusting the sensitivities of these channels. Surprisingly, perceived tilt can be manipulated by desensitizing these channels through exposure to visual patterns that are untilted or have no orientation signal at all.
Efficient Coding Theory Predicts a Tilt Aftereffect from Viewing Untilted Patterns

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SUMMARY

The brain is bombarded with a continuous stream of sensory information, but biological limitations on the data-transmission rate require this information to be encoded very efficiently [1]. Li and Atick [2] proposed that the two eyes’ signals are coded efficiently in the brain using mutually decorrelated binocular summation and differencing channels; when a channel is strongly stimulated by the visual input, such that sensory noise is negligible, the channel should undergo temporary desensitization (known as adaptation). To date, the evidence for this theory has been limited [3, 4], and the binocular differencing channel is missing from many models of binocular integration [5–10]. Li and Atick’s theory makes the remarkable prediction that perceived direction of tilt (clockwise or counterclockwise) of a test pattern can be controlled by pre-exposing observers to visual adaptation of the summation and difference signals, which selectively desensitized the summation channel. In anticorrelated adaptation, each eye received the same image. This produced a zero summation signal, and a strong summation signal, which selectively desensitized the summation channel. In anticorrelated adaptation, each eye received the photographic negative of the other eye’s image. This produced a zero summation signal, and a strong difference signal, which selectively desensitized the differencing channel.

In experiment 1, the adaptation images were non-oriented random patterns (Figure 2A). The procedure is illustrated in Figure 3. On some blocks of trials, the test pattern components were tilted ±3.58° from vertical (as shown in Figure 1; we refer to these patterns as “vertical plaids”); on other blocks, the test pattern components were tilted ±3.58° from horizontal (henceforth, “horizontal plaids”). We recorded the proportion of trials on which each participant reported a tilt direction (clockwise or counterclockwise of vertical or horizontal) in the same direction as the summation signal (which itself was randomly chosen to be clockwise or counterclockwise on each trial). Because the tilt direction of the summation signal was random and unpredictable from the adaptation pattern, any response bias in either direction would push performance (vertical axis in Figure 2A) toward 50%, so any measured effect of adaptation must reflect a genuine perceptual bias, not a response bias.

Participants found the tilt judgment difficult and were often unsure of their response. This is not surprising because the summation and difference signals provide conflicting information about the tilt of our test patterns, so neither tilt direction would be well supported by the pattern of neuronal activity; participants had to choose the more likely of two weakly supported hypotheses. For this reason, we do not provide a demonstration of the effect.

The results are plotted in Figure 4A. A 2 x 2 repeated-measures ANOVA ([15], section 13.6) showed highly significant main effects of adaptation condition \(F(1, 34) = 167, p = 1.12 \times 10^{-14}\) and orientation of the test pattern (vertical or horizontal plaid) \(F(1, 34) = 51.6, p = 2.60 \times 10^{-8}\), with no significant interaction \(F(1, 34) = 0.727, p = 0.400\).
For vertical plaid test patterns, the results were exactly as predicted. With anticorrelated adaptation, participants reported tilt in the same direction as the summation signal on 37.1% of trials (significantly below chance: \(t(34) = 6.04, p = 7.73 \times 10^{-10}\)), i.e., they tended to report tilt in the same direction as the difference signal. For horizontal plaid test patterns, the adaptation had a similar effect, but overall, perception was biased toward the summation signal, so that only the score for anticorrelated adaptation differed significantly from chance (\(t(34) = 15.0, p = 1.54 \times 10^{-16}\)).

The difference between horizontal and vertical test patterns is consistent with the fact that, in natural viewing, horizontal disparities are much larger and more useful for depth perception than vertical disparities. Information about horizontal disparities is carried by the vertical differentiating channel, so it is important to maintain a strong response in this channel. Zhaoping [1, 16] noted that perception through decoding (or inference) often employs “analysis by synthesis,” whereby the high-level interpretation is validated by synthesizing from it the would-be low-level signals and then comparing the synthesized signals with the actual low-level signals [17]. A Bayesian prior for high interocular correlation at horizontal orientations makes the synthesized signal stronger in the summation channel, so an inferred tilt consistent with the summation signal (rather than the difference signal) is more likely to be validated, causing the perceptual bias toward the summation signal for horizontal test stimuli. This bias is weaker for vertically oriented patterns because the expected binocular correlation is much lower due to the horizontal disparity between the eyes [2]. This would explain why the data for vertical plaid test stimuli are almost perfectly symmetrical about chance level. The horizontal-vertical anisotropy in binocular correlation also leads efficient coding theory to predict a corresponding physiological anisotropy: V1 neurons should be more likely binocular if they prefer horizontal rather than vertical orientations, consistent with physiological data in cat V1 [1, 2].

For each participant, we calculated the (signed) size of the effect of adaptation by subtracting the score (% of trials reporting tilt in the summation direction) from correlated adaptation from the score for anticorrelated adaptation and then averaging these differences across test pattern orientation. After running 10 participants (5 male, 5 female), we were surprised to find that each male participant showed a much stronger effect of adaptation than each female participant (male mean effect size 45.7; female mean effect size 11.9; \(p\) (two-tailed) = 0.00794, Wilcoxon rank sum test). To confirm this gender difference as a planned comparison, we ran a further 25 subjects (12 male, 13 female) and again found a significant, but weaker, gender difference (male mean effect size 33.1; female mean effect size 25.5; \(p\) (two-tailed) = 0.0362, Wilcoxon rank sum test). Within the whole group of 35 subjects, the gender difference was highly significant (male mean effect size 36.8; female mean effect size 21.7; \(p\) (two-tailed) = 0.000439, Wilcoxon rank sum test). The male and female sets of participants did not differ significantly in age or amount of psychophysical experience (measured by asking all the participants to estimate how many hours they had spent in their lives doing visual psychophysical tasks).

In experiment 2, the test plaids and procedure were identical to experiment 1, but the adaptation images were horizontal or vertical random patterns (Figure 2B). The results (Figure 4B) showed a similar pattern to experiment 1. A 2 \(\times\) 2 repeated-measures ANOVA ([18], section 14.9) showed significant main effects of adaptation condition (\(F(1, 15) = 105, p = 3.73 \times 10^{-7}\)), test plaid...
Importantly, there was a significant interaction between adaptation condition (correlated/anticorrelated) and relative orientation of test and adaptor (adaptor parallel or orthogonal to test), reflecting a reduced effect of adaptation when the test and adaptor were orthogonal \((F(1, 15) = 25.0, p = 1.59 \times 10^{-4})\). There was also a significant interaction between test plaid orientation and relative orientation of test and adaptor, which reflected the fact that the test plaid orientation had more effect when the adaptor was perpendicular \((F(1, 15) = 14.4, p = 0.00179)\). Neither of the other interactions approached significance.

For each participant in experiment 2, we calculated the size of the adaptation effect as for experiment 1, averaging across test plaid orientation but giving separate scores for the different relative orientation conditions (adaptor parallel or orthogonal to test plaid). The effect size was significantly above zero whatever the relative orientation of the adaptation and test stimuli but was significantly larger (about twice as large) when they had the same orientation. For each participant in experiment 2, we also found the mean effect size across all combinations of test and adaptor orientation. This score was significantly correlated with the subject’s effect size in experiment 1 (Spearman’s \(r = 0.585, p \text{ (two-tailed)} = 0.0193\)).

The tilt aftereffect is a well-known visual aftereffect in which prolonged viewing of a tilted pattern (the adaptor) makes an untitled test pattern appear tilted. In all previous demonstrations of the tilt aftereffect, the adaptor has had a strong orientation signal, with a clearly visible tilt. In experiment 1, we demonstrated, for the first time, a tilt aftereffect using adaptors that have no orientation signal—the adaptation pattern was isotropic, bounded by a circular border. In experiment 2, we obtained similar results with adaptation stimuli that were strongly oriented, but not tilted. These results are not explained by any current model of orientation perception but are readily predicted by Li and Atick’s theory of efficient coding of dichoptic inputs.

Our finding of a tilt aftereffect with untitled adaptors is the spatial equivalent of our previous work in which we demonstrated a motion aftereffect with static adaptors [4]. This is because motion can be expressed as tilt in space-time; the test images in our current experiments are the space-time plots of the test stimuli in our previous work, with one important difference: in our previous study, the test stimuli carried a weak monocular signal that had the same motion direction as that in the difference signal, so the results were consistent with a model that contains monocular channels and an adaptable summation channel, but no differencing channel. In our current study, the monocular signals in the test patterns were not biased in either tilt direction, so monocular channels could not have mediated orientation \((F(1, 15) = 28.4, p = 8.37 \times 10^{-5})\), and relative orientation of test plaid and adaptor pattern \((F(1, 15) = 8.37, p = 0.0112)\).

**Figure 2. Examples of the Adaptation Patterns**

(A) Experiment 1. The patterns were isotropic Gaussian low-pass filtered noise (SD in Fourier space was equal to the spatial frequency of the sine wave components of the test plaid, 1/16 cycles per pixel), surrounded by a black, circular border (inner diameter 256 pixels, thickness 4 pixels).

(B) Experiment 2. The patterns were Gaussian low-pass filtered noise (SD 1/16 cycles per pixel) that varied along only one dimension of the image, surrounded by a black, square border (inner width 256 pixels, thickness 4 pixels).
perception. Our current data therefore provide stronger evidence for the existence of the binocular differencing channel.

Although a binocular differencing channel is missing from many published models of binocular integration [5–10], there is accumulating evidence that such channels exist in human vision [3, 4, 24–30]. Separately adaptable binocular summation and differencing channels provide an elegant means for the visual system to achieve optimally efficient transmission of binocular information [1–4].

At the physiological level, the signals from the summation and differencing channels are multiplexed so that each V1 neuron receives a weighted sum of the signals in these two channels [1, 2]. This gives a variety of V1 neurons tuned to a range of different disparities; the tuned excitatory and inhibitory neurons [31, 32]...
are examples in which neurons receive dominant inputs from summation and differing channels, respectively, so that they are excited or suppressed, respectively, by inputs of zero disparity. Being sensitive to binocular disparities, the differing channel also carries information critical for stereopsis, but at this early stage of processing, the physiological responses do not correspond to the conscious perception of stereopsis [33, 34]; depth and segmentation from binocular disparity are more likely to be computed in V2 [35]. It has been suggested that the responses of V1 neurons may serve to guide vergence eye movements [33, 36, 37] and carry out preliminary computations such as the detection of false matches in stereo correspondence [38]. Our work highlights a role of V1 neurons in efficient coding. Li and Atick [2] presented a physiologically plausible way of achieving efficient binocular coding as soon as the signals from the two eyes converge in V1. Our study gives strong support to this theory, with the novel finding that, as predicted by the theory, perceived orientation can be manipulated by adaptation effects that are not orientation specific. With the recent surge in ownership of 3D televisions and the continued popularity of 3D movies in cinemas and 3D video games, it is becoming increasingly important to understand the effects of unnatural binocular viewing. Our study shows that the human visual system adapts to unnatural binocular stimulation in a way that is consistent with efficient coding theory.

EXPERIMENTAL PROCEDURES

The visual stimuli are described in Figures 1 and 2 and the Supplemental Experimental Procedures. The stimuli were presented on a Sony Trinitron CRT monitor with a refresh rate of 100 Hz, driven by a ViSaGe stimulus generator (Cambridge Research Systems), which produced images with a grayscale resolution of 14 bits per pixel. The mean luminance was 54 cd/m^2. The images were viewed through a mirror stereoscope (described previously [39]) with an effective viewing distance of 50 cm, giving 2.73 arcmin of visual angle per pixel. The research was conducted in accordance with the Declaration of Helsinki. Informed consent was obtained from all observers, and approval of the study was obtained from the UCL Research Ethics Committee. Experiment 1 used 17 male and 18 female participants, aged between 22 and 52, with corrected-to-normal vision, and binocular vision confirmed using a random-dot stereogram. All were naive about the purpose of the experiment except for one male participant, the author K.A.M. Experiment 2 used a subset of the participants from experiment 1 (8 male, 8 female). The procedure is outlined in Figure 3 and described in full in the Supplemental Experimental Procedures.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.04.037.

AUTHOR CONTRIBUTIONS

Conceptualization, L.Z. and K.A.M.; Methodology, K.A.M. and L.Z.; Software, K.A.M.; Formal Analysis, K.A.M.; Investigation, K.A.M.; Resources, L.Z.; Writing – Original Draft, K.A.M.; Writing – Review & Editing, K.A.M. and L.Z.; Visualization, K.A.M.; Supervision, L.Z.; Project Administration, K.A.M.; Funding Acquisition, L.Z.

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Supplemental Information

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Supplemental Experimental Procedures

**Test Stimuli.** Here we describe the horizontal test plaids. Vertical test plaids were generated in the same way, and then rotated counterclockwise by 90°. The stimulus images are expressed in terms of the contrast signal, c(x, y), at each point in space (x, y). The stimulus luminance, L(x, y), is obtained from the contrast as follows:

\[ L(x, y) = L_0[1 + c(x, y)], \]

where \( L_0 \) is the background luminance, 54 cd/m². The contrast images \( c(x, y) \) presented to the two eyes are given by

\[
S_1 = \alpha \cos Y \cos X
\]

\[
S_2 = \alpha \sin Y \sin X
\]

where \( \alpha \) is the stimulus Michelson contrast (always 0.3), and \( X \) and \( Y \) are given by

\[
X = 2 \pi f x \sin \theta + \phi_x
\]

\[
Y = 2 \pi f y \cos \theta + \phi_y
\]

Equations (2) and (3) show that our binocular stimulus is the spatial equivalent of Shadlen and Carney’s dichoptic motion stimulus [S1] that we used in our earlier study [S2].

The test stimuli were windowed by a square envelope with size 128×128 pixels, and surrounded by a black, square border 4 pixels wide. The purpose of the square border was to aid fixation and present horizontal and vertical references against which the observer could compare the perceived orientation of the test stimulus. The border came on with the test stimulus, and remained on until the observer had responded. In earlier pilot work, we found that, if the temporal offset of the border coincided with that of the test stimulus, it tended to mask the test stimulus, making the test stimulus difficult to see.

**Adaptation stimuli.** In Experiment 1, the adaptation stimuli were isotropic Gaussian low-pass filtered noise (see Figure 2A). Noise images with size 256×256 pixels were created in the Fourier domain with an amplitude that was a Gaussian function of spatial frequency with standard deviation given by the spatial frequency, \( f \), of the summation and difference images. Each Fourier component was given a random phase value subject to the constraint that equal-frequency components on opposite sides of the origin of Fourier space had phase values with the same magnitude but opposite sign; this complex-conjugate relationship was necessary for generating noise images without imaginary components. The zero-frequency component had an amplitude of zero. We then applied an inverse Fourier transform to generate the spatial noise pattern. The pattern was used as the contrast signal \( c(x, y) \) of the noise pattern, and it was scaled in amplitude so that the magnitude of the largest-magnitude pixel was 0.95. For correlated adaptation, each eye received the same noise image; for anticorrelated adaptation, the
contrast was reversed between the eyes by multiplying each pixel in one eye’s image by $-1$. Each eye’s pattern was then windowed with a sharp, circular envelope (diameter 256 pixels), and surrounded by a black ring 4 pixels wide. Both the circular envelope and the black ring were anti-aliased by sampling their values from sine edges with half-period equal to 1 pixel. The purpose of the circular envelope and ring was to make the stimuli as non-oriented as possible. A small black fixation cross on an opaque white disk of diameter 8 pixels was inserted into the centre of each adaptation image. The contrast signal was then converted to a luminance signal according to Equation (1), and gamma-corrected for accurate presentation on the CRT monitor.

We did not include a “no adaptation” condition. Even in a “no adaptation” condition, the observer is adapted to what has recently been seen; the question is whether or not adaptation has been explicitly controlled. If we had used no adaptation stimuli, then, at any time during a block of trials the recent visual input would have consisted of the repeating sequence of fixation cross (correlated) followed by the very brief test stimulus (uncorrelated apart from the surrounding border). Without a full, quantitative model of the spatial and temporal properties of the adaptation mechanism, we would not have known the adaptational state of the observer, so it would have been difficult to interpret the results of a “no adaptation” condition.

In Experiment 2, the adaptation stimuli were Gaussian low-pass filtered noise that varied along only one dimension, horizontal or vertical (see Figure 2b). Noise images with size 256×256 pixels were created in the space domain by adding together horizontal or vertical sine wave gratings with random phase, and with the amplitude given by a Gaussian function of spatial frequency with standard deviation equal to $f$, the spatial frequency of the summation and difference images. The noise image amplitude was scaled to 95% contrast. For anticorrelated adaptation conditions, a contrast-reversed version was made. Each eye’s image had a fixation cross as in Experiment 1, and the image was surrounded by a black, square border 4 pixels wide.

**Procedure.** Trials were grouped into blocks of 40, each lasting about 5 minutes. The sequence of events in each block of trials is illustrated in Figure 3. Each block began with 120 randomly generated adaptation stimuli, each presented for 500 ms. Then, the black, square border of the test stimulus (but not the test stimulus itself) appeared for 1000 ms to indicate that the first trial was about to start. Each trial began with a sequence of 10 top-up adaptation stimuli generated in the same way as the initial adaptation stimuli. The test stimulus was presented immediately after the last top-up adaptation stimulus, and lasted for 200 ms. On a random half of the trials, the summation tilt for the test stimulus was clockwise (as in Figure 1); on the other half, the summation tilt was counterclockwise. The participant had to indicate whether the test stimulus appeared tilted clockwise (right button press) or counterclockwise (left button press). We recorded the proportion of trials on which the subject reported a tilt direction corresponding to the summation signal. Within a block, the plaid test stimulus always had the same orientation (“vertical” or “horizontal”). The participant was informed before each block whether the test stimuli would be close to vertical or horizontal. In Experiment 2, the adaptation stimuli could be horizontal or vertical, giving four combinations of adaptor and test stimulus orientation. Each combination was tested in a different block, and the participant was informed of the combination before the block. For both experiments, there were five blocks for each combination of adaptation type (correlated or anticorrelated), test orientation and (in Experiment 2 only) adaptor orientation, giving 200 trials per condition for each participant.

In our experiments, any response bias towards clockwise or counterclockwise pushes performance towards chance performance, i.e. 50%. To understand this, consider what would happen if the observer always responded “counterclockwise” – they would report tilt in the summation direction on exactly half the trials; similarly, if the observer always responded “clockwise” they would report tilt in the summation direction on exactly half the trials. Therefore, due to our experimental design, any response bias in either direction would have worked in the opposite direction to the perceptual bias that we wanted to measure. This allowed us to disentangle response bias from perceptual bias to an extent that is not normally achievable in experiments on perceptual aftereffects. We can therefore be fully confident that the measured effect is a genuine perceptual bias and not a response bias.

**Supplemental References**

S1. Shadlen, M., and Carney, T. (1986). Mechanisms of human motion perception revealed by a new cyclopean illusion. Science 232, 95–97.

S2. May, K.A., Zhaoping, L., and Hibbard, P.B. (2012). Perceived direction of motion determined by adaptation to static binocular images. Curr. Biol. 22, 28–32.