

Current Biology

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 patterns that are untilted or even have no orientation signal. Here, we confirm this prediction. Each test pattern consisted of different images presented to the two eyes such that the binocular summation and difference signals were tilted in opposite directions, to give ambiguous information about tilt; by selectively desensitizing one or other of the binocular channels using untilted or non-oriented binocular adaptation patterns, we controlled the perceived tilt of the test pattern. Our results provide compelling evidence that the brain contains binocular summation and differencing channels that adapt to the prevailing binocular statistics.

RESULTS AND DISCUSSION

Figure 1 shows an example of our test patterns. Each eye receives a “plaid” pattern, the sum of two sine wave gratings, S_+ and S_- . In this example, S_+ is tilted clockwise from vertical, and S_- is tilted counterclockwise. The left and right eyes' patterns are given by $S_L = (S_+ + S_-)/2$ and $S_R = (S_+ - S_-)/2$, respectively. When the two eyes' signals are added together, the S_- component cancels out, leaving just the S_+ component; when one eye's signal is subtracted from the other, the S_+ component cancels out, leaving just the S_- component. Thus, the summation and difference signals each consist of a single

sine wave component, one tilted clockwise, and the other tilted counterclockwise, giving ambiguous information about tilt. Selective adaptation (desensitization) of the summation channel should make the observer more likely to perceive the test pattern as being tilted in the same direction as the difference signal, whereas selective adaptation of the differencing channel should make the observer more likely to perceive the test pattern as being tilted in the same direction as the summation signal.

Adaptation was achieved by prolonged viewing of sequences of binocular images. There were two adaptation conditions: correlated and anticorrelated. In correlated adaptation, each eye received the same image. This produced a zero difference 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 $\pm 3.58^\circ$ from vertical (as shown in Figure 1; we refer to these patterns as “vertical plaids”); on other blocks, the test pattern components were tilted $\pm 3.58^\circ$ 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 2×2 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 ($F(1, 34) = 0.727, p = 0.400$).



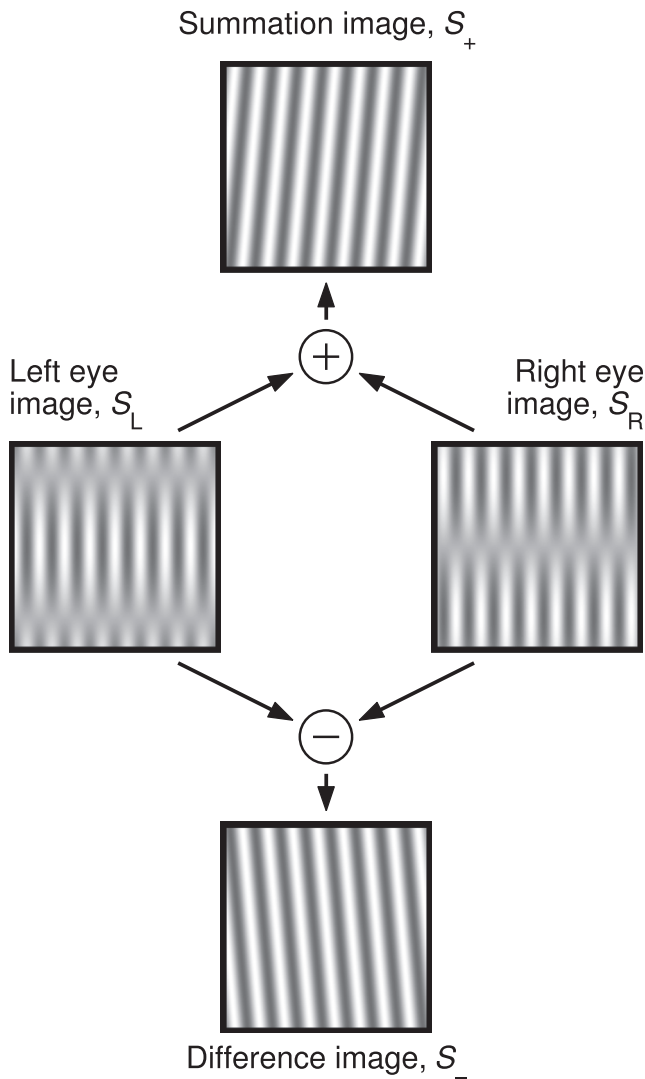


Figure 1. The “Vertical Plaid” Test Pattern and the Results of Processing It with the Summation and Differencing Channels in Li and Atick’s Theory

The summation (S_+) and difference (S_-) images are sine wave gratings tilted $\pm 3.58^\circ$ from vertical. Each sine wave grating is formed by modulating the luminance sinusoidally along a single direction (with spatial frequency 1/16 cycles per pixel, i.e., 1.37 cycles per degree of visual angle). In the example shown, the left and right eyes’ images are given by $S_L = (S_+ + S_-)/2$ and $S_R = (S_+ - S_-)/2$, respectively. These “plaid” patterns were presented to each eye at a Michelson contrast of 0.3, surrounded by a black, square border (inner width 128 pixels, thickness 4 pixels). The “horizontal plaid” test stimulus was made in the same way, except with components tilted $\pm 3.58^\circ$ from horizontal. This test stimulus was devised by Zhaoping [11] and is the space-time plot of the Shadlen-Carney dichoptic motion stimulus [12–14] that we used in our earlier study [4].

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 65.2% of trials, which is significantly above the chance level of 50% ($t(34) = 6.91$, $p = 5.89 \times 10^{-8}$). With correlated adaptation, participants reported tilt in the same direction as the summation

signal on 37.1% of trials (significantly below chance: $t(34) = 6.04$, $p = 7.73 \times 10^{-7}$), 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 differencing 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) for 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 $2 \times 2 \times 2$ repeated-measures ANOVA ([18], section 14.9) showed significant main effects of adaptation condition ($F(1, 15) = 105$, $p = 3.73 \times 10^{-8}$), test plaid

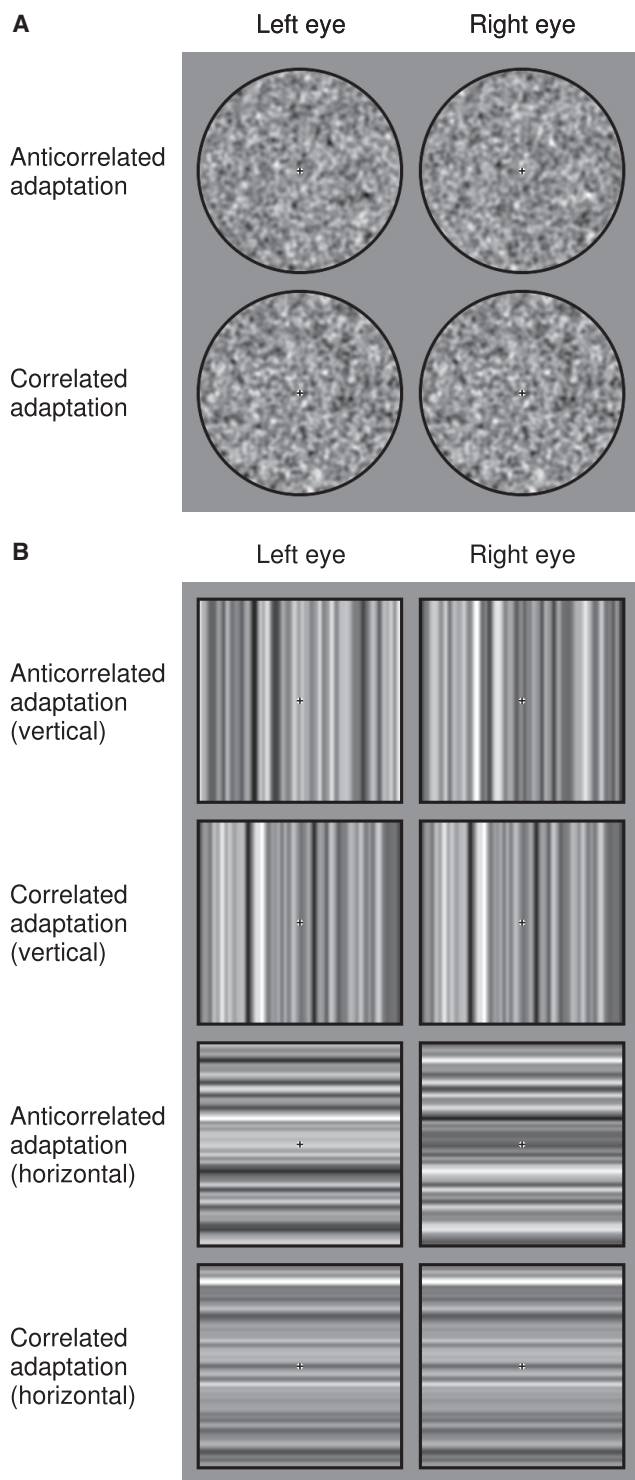


Figure 2. Examples of the Adaptation Patterns

(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).

orientation ($F(1, 15) = 28.4, p = 8.37 \times 10^{-5}$), and relative orientation of test plaid and adaptor pattern ($F(1, 15) = 8.37, p = 0.0112$). 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 (see Figure 4C). Thus, although the effect of adaptation was reduced when the test and adaptor were orthogonal, it was still quite substantial. This finding mirrors our previous finding of weak orientation selectivity in adaptation of the binocular channels [4] and adds strength to our proposal that the binocular differencing channel is at least partly mediated by neurons with non-oriented receptive fields that have opposite polarity in the two eyes [2, 4]. Such neurons had been reported previously [19, 20], but their role was unknown.

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 $\rho = 0.585, p$ (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 untilted test pattern appear tilted [21–23]. 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 [2].

Our finding of a tilt aftereffect with untilted 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

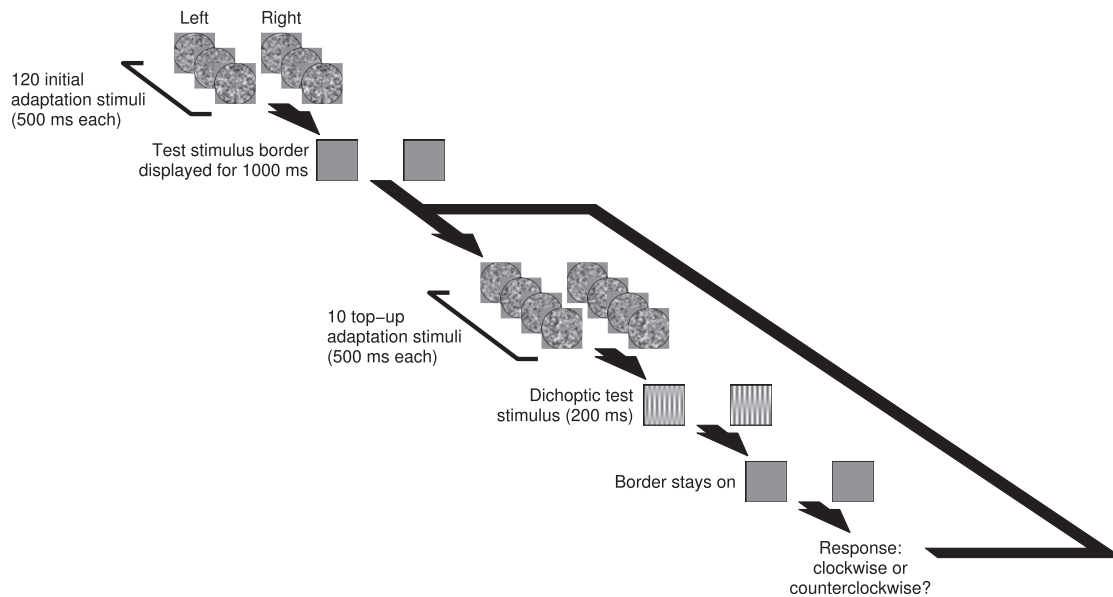


Figure 3. Procedure

The adaptation stimuli illustrated here are from experiment 1 (Figure 2A). Experiment 2 used the noise patterns illustrated in Figure 2B.

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]

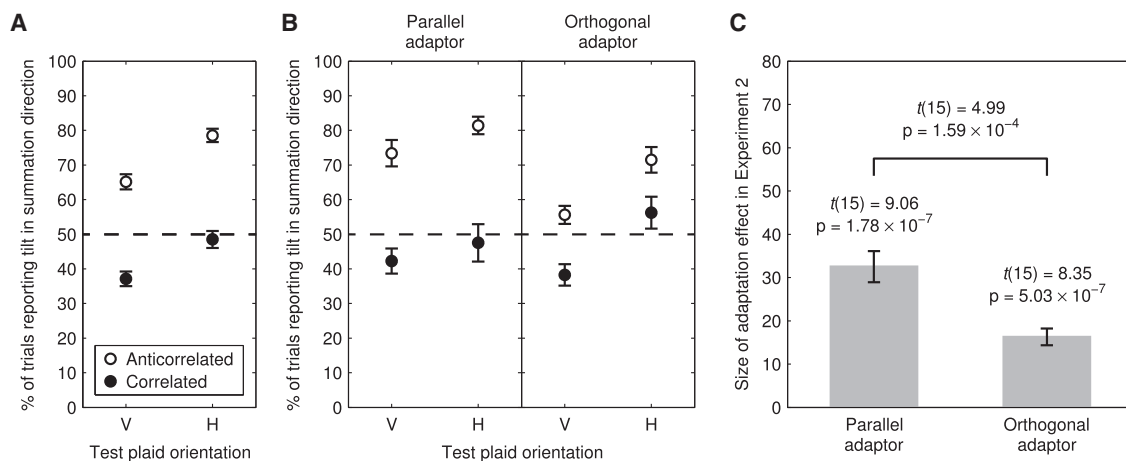


Figure 4. Results

(A) Perceived tilt in experiment 1. Symbols plot the mean scores (% of trials reporting tilt in the summation direction) across the participants for the different conditions. Open symbols represent anticorrelated adaptation conditions, and filled symbols represent correlated adaptation. The position along the horizontal axis represents vertical (V) or horizontal (H) test plaid orientation.

(B) Perceived tilt in experiment 2, plotted as in (A).

(C) Effect sizes (score in anticorrelated adaptation minus score in correlated adaptation) in experiment 2. The left and right bars, respectively, show the mean effect sizes across participants in the left and right panels of (B). The p and t values above each bar indicate the results of a two-tailed one-sample t test against a hypothesized mean of zero. The p and t values straddling the two bars indicate the results of a two-tailed repeated-measures t test comparing the effect sizes in the two conditions.

All error bars indicate ± 1 SEM.

are examples in which neurons receive dominant inputs from summation and differencing channels, respectively, so that they are excited or suppressed, respectively, by inputs of zero disparity. Being sensitive to binocular disparities, the differencing 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/m². 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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