Continuous flash suppression reduces negative afterimages

Naotsugu Tsuchiya & Christof Koch

Illusions that produce perceptual suppression despite constant retinal input are used to manipulate visual consciousness. Here we report on a powerful variant of existing techniques, continuous flash suppression. Distinct images flashed successively at ~10 Hz into one eye reliably suppress an image presented to the other eye. The duration of perceptual suppression is at least ten times greater than that produced by binocular rivalry. Using this tool we show that the strength of the negative afterimage of an adaptor was reduced by half when it was perceptually suppressed by input from the other eye. The more completely the adaptor was suppressed, the more strongly the afterimage intensity was reduced. Paradoxically, trial-to-trial visibility of the adaptor did not correlate with the degree of reduction. Our results imply that formation of afterimages involves neuronal structures that access input from both eyes but that do not correspond directly to the neuronal correlates of perceptual awareness.

The question of the neuronal correlates of conscious perception has seen renewed interest over the last decade¹. One powerful tool in this area is illusions that give rise to effects that are measurable, yet are not, or are only occasionally, consciously seen^{2–5}. In backward masking⁶, inattentional blindness⁷, motion-induced blindness⁸, binocular rivalry^{9–16} and flash suppression^{11,17–19}, an image is presented to one or both eyes of the observer yet is not seen.

Binocular rivalry is a popular method to determine if a visual aftereffect occurs before or after the neuronal site for the suppression of rivalry^{2,20–23}. In binocular rivalry, two different images are shown to the two eyes, and the subject's percept alternates between one and the other image²⁴. The strength of the aftereffect when the adaptor is presented to one eye and is plainly visible throughout the adaptation period is compared with the aftereffect when the adaptor is suppressed by the input to the other eye.

However, the duration and timing of perceptual suppression are difficult to control because of the stochastic nature of rivalry. Flash suppression^{11,17–19} provides better control over the timing of suppression, but at the price of shorter periods of suppression, too brief to produce strong aftereffects. Furthermore, flash suppression requires a pre-adapting period, preventing complete unawareness of the adaptor. Here we combine aspects of both binocular rivalry and flash suppression into a potent procedure we term continuous flash suppression (CFS). We continuously flash different images rapidly into one eye while the input to the corresponding location in the other eye remains the same (see demonstration at http://www.klab.caltech.edu/~naotsu/ CFSdemo.html). Most observers do not see the image in one eye even though it is present for a long time, sometimes for several minutes.

We used CFS to examine the neuronal site for negative afterimages. These are vivid percepts that demonstrate the tenuous link between physical stimuli and their associated subjective percepts. A variety of evidence supports their origin among neurons in the retina^{25–31} or lateral geniculate nucleus (LGN)³². In particular, negative afterimages do not transfer across eyes, nor is their strength reduced by suppression of the inducing image by pressure blinding^{20,33} (but see ref. 29). Neither binocular rivalry²⁰ nor motion-induced blindness (MIB)⁵ reduces either the duration or the strength of afterimages. All of these observations suggest that afterimages are retinal phenomena.

However, both binocular rivalry and MIB suppress the adaptor only intermittently. By using CFS, we asked what happens when the adapting stimulus is completely suppressed from awareness. We found that when an adaptor was reliably suppressed by CFS, the intensity of the negative afterimage of the adaptor was reduced by half. Our results imply that formation of afterimages involves neuronal structures that access input from both eyes but that do not correspond directly to the neuronal correlates of perceptual awareness.

RESULTS

Prolonged invisibility by continuous flash suppression

We first compared the initial duration of stimulus suppression in CFS and binocular rivalry without pre-exposure to the suppressed image. While a constant, gray image was presented to one eye, CFS stimuli composed of different Mondrians were presented at the corresponding location in the other eye (**Fig. 1**). Each Mondrian was replaced by a different pattern every 100 ms. Seventeen naive subjects pressed a button as soon as any part of the gray figure became visible. The mean initial suppression time in 16 trials was 4.3 s for binocular rivalry and 56.0 s for CFS (13 times longer than for binocular rivalry; paired t-test, t-score = 4.81, d.f. = 16, P < 0.001). In 40 out of 272 CFS trials, no part of the gray image was seen at all for the full 3-min trial. As we treated those

Computation and Neural Systems Program, California Institute of Technology, M/s 139-74, 1200 East California Boulevard, Pasadena, California 91125, USA. Correspondence should be addressed to N.T. (naotsu@klab.caltech.edu).

Published online 3 July 2005; doi:10.1038/nn1500

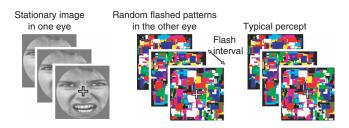


Figure 1 Continuous flash suppression. A stationary gray stimulus was presented in one eye (left) while different, colored Mondrian patterns were flashed in the other eye (center) every 100 ms. Subjects fixated the central cross and pressed a button to report when the gray figure started to become visible. Initial suppression duration in CFS was more than ten times longer than in binocular rivalry, using the same stimulus but with a stationary Mondrian pattern.

trials' suppression time as 180 s, we underestimated the true duration of the initial period during which the adaptor remains invisible.

Pilot experiments on afterimage reduction

We next examined if CFS interferes with the formation of negative afterimages. These experiments were partly motivated by the observation that only a single subject in one out of 40 trials reported a negative afterimage of the gray figure. We did not expect this, given that the image was present for 3 min on the retina.

In a second experiment, we presented two isoluminant Gabor patches in one eye to the left and right of fixation for 5 s (**Fig. 2**, left). At the same time, suppressing CFS stimuli were continuously flashed only to one side of the other eye (**Fig. 2**, center). CFS in one eye effectively renders the Gabor patch at the corresponding location in the other eye invisible (**Fig. 2**, right).

Sixteen naive subjects verbally described their percepts after a 5-s adaptation in two trials (**Supplementary Table 1** online). Subjects usually reported that the adaptor suppressed by CFS produced a weaker afterimage (87% in the two-trial experiment and 83% in the 30-trial experiment). No subjects reported seeing an afterimage of the Mondrians. This consistency was notable, given the known variability in the strength of afterimages across trials, subjects and hemifields^{5,27,34}. Under the retinal origin hypothesis, input from the other eye should not influence afterimage formation. As adaptation at the retina is the same for both visible and suppressed locations, the weakened afterimage must be due to interference from sites at or beyond binocular convergence.

Ruling out nonspecific effects of the flashes

Although no subjects reported seeing afterimages of the ever-changing Mondrians, such dynamic and luminance-equated patterns could have created afterimages²⁹. Though their contrast may have been too low to perceive, they may nevertheless have interfered with the afterimage from the Gabor adaptor³⁵. In a third experiment, we tested for this possibility. We compared the subjective ratings of the afterimage intensity from three intermittently presented adaptors (2 s 'on' and 2 s 'off' for 30 s, Fig. 3). One eye was stimulated by three separate Gabor patches while the other eye was stimulated at two of these three locations with Mondrians in such a way that this pattern synchronously coincided for 2 s with one of the Gabor patches but was asynchronously delayed by 2 s from the other Gabor pattern. A third location was never suppressed by Mondrians but received a Gabor patch intermittently for 2 s and served as a control for the strength of the afterimage

(pegged at a subjective rating of 10). Any putative afterimage of the Mondrian would interfere with the afterimage of the Gabor in both synchronous and asynchronous CFS locations. If CFS had to be presented simultaneously with the adaptors to weaken afterimage amplitude, the afterimages should be equally strong for the control and the asynchronous CFS locations and should be weaker for the synchronous CFS location.

Each of six naive subjects performed 20 trials, rating the subjective intensity of the afterimages induced by the synchronously and asynchronously suppressed Gabor adaptors relative to the control, which received a rating of 10 (**Fig. 3**, bottom). The mean afterimage rating from the asynchronous CFS location was 11.1 ± 1.13 (s.e.m.), which was not significantly different from 10 (two-tailed *t*-test, P > 0.35, *t*-score = 0.98, d.f. = 5). The mean rating from the synchronous CFS location was 5.85 ± 1.63 , a reduction of 47% (one-tailed paired *t*-test on the rating between synchronous and asynchronous, P < 0.02). We conclude that the Mondrians themselves did not reduce the afterimage, and that coincidence of the adaptor with CFS was key to reduction of the afterimage.

Reliable suppression reduces afterimage intensity

Why does CFS reduce the intensity of the afterimage, whereas previous studies have shown that perceptual suppression does not influence the duration or the intensity of the afterimage using binocular rivalry²⁰ or MIB⁵? One notable difference is that CFS suppressed adaptors more consistently and completely than either of the other techniques; most

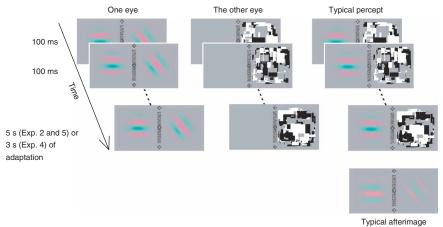


Figure 2 CFS suppresses a Gabor patch and reduces its afterimage. Left: two isoluminant Gabor patches, at 30% contrast and 0.6 cpd spatial frequency, were presented to the left and right of fixation in one eye for 5 s. Center: different Mondrian patterns that changed every 100 ms were projected in one-half of the visual field (here, the right side) of the other eye. Right: typically, subjects saw a Gabor on one side and flickering Mondrians on the other, not perceiving the Gabor on the right. In experiment 2, subjects verbally described their percepts at the end of the adaptation period ('What do you see?'). In experiment 4, subjects reported which afterimage was stronger and whether they saw the suppressed adaptor during a 3-s adaptation in a two-alternative forced choice. In experiment 5, subjects pressed and held a key whenever the suppressed adaptor was visible during the 5-s adaptation period and then reported which afterimage was stronger.

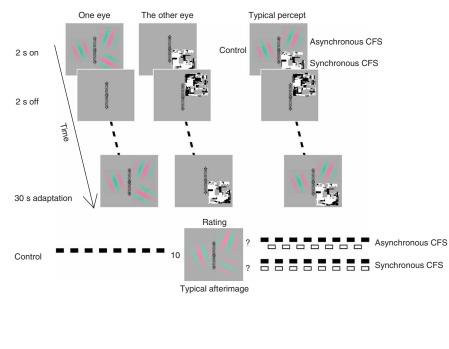


Figure 3 Mondrian flashes themselves do not reduce the afterimage of the Gabor. Left: three adaptors were presented to the left, upper right and lower right of fixation during 2-s 'on' periods and were removed during 2-s 'off' periods. The contrast of the adaptors was 50%. The position of the adaptors and Mondrians was balanced between top and bottom and between left and right across 20 trials (five trials for each configuration). Center: Mondrian flashes were presented synchronously with the adaptors during 2-s 'on' periods at the lower right and asynchronously during 2-s 'off' periods at the upper right. Right: during 2-s 'on' periods, subjects perceived two adaptors and a stream of Mondrians at the lower right, whereas during 2-s 'off' periods they saw only a stream of asynchronous Mondrians at the upper right. Bottom: after 30 s of adaptation, subjects rated the intensity of the afterimage relative to that at the left visible location (control), which was pegged at 10. Next to the expected afterimage, the time course of adaptors and Mondrians is shown for each location. Filled squares indicate the eight 2-s 'adaptor-on' periods, and open squares denote the 2-s 'CFS-on' periods.

subjects did not see the suppressed stimuli at all throughout the adaptation period.

In a fourth experiment, we tested the extent to which complete invisibility is necessary to weaken afterimage strength. We measured the reduction in the afterimage while manipulating the reliability of suppression of the Gabor patches by changing the stimulus properties of both adaptors and Mondrians. In preliminary experiments, we found that complete suppression occurred less frequently as the spatial frequency of adaptors was increased. Furthermore, as the contrast of adaptors increased, the suppression became less reliable, whereas increasing the contrast of Mondrians resulted in more reliable suppression. We used five different spatial frequencies for the adaptors and three combinations of adaptor and Mondrian contrast to manipulate the reliability of suppression. With the same setup as in Figure 2 (except for a 3-s adaptation period), subjects indicated which side had the stronger afterimage and whether they saw the Gabor adaptor at the

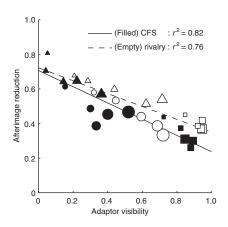
Figure 4 Relationship between afterimage reduction and the reliability of suppression. We used two different dichoptic suppression protocols: CFS (as in Fig. 3, except that the adaptation period was shortened to 3 s) and binocular rivalry with moving stimuli. Subjects reported which of the afterimages was stronger and whether or not they saw the suppressed Gabor patch during adaptation. To modulate the reliability of suppression, three combinations of contrasts for adaptors and Mondrians were used: 30% and 100% (triangles), 100% and 100% (circles) or 100% and 5% (squares). The Gabor had one of five different spatial frequencies. Subjects compared the intensity of the afterimage from two adaptors with the same contrast and spatial frequency. Increasing symbol size represents increasing spatial frequency of the adaptors: 0.60 through 0.84, 1.2, 1.7, to 2.5 cpd. In total, 30 different experimental conditions were evaluated. Filled symbols represent data obtained from CFS and open symbols, data from binocular rivalry. Each data point represents the average across five subjects. The y-axis is the proportion of trials in which the afterimage from the suppressed adaptor was weaker than the afterimage from the plainly visible Gabor patch, representing the degree of afterimage reduction. The x-axis is the fraction of trials during which any part of the adaptor was visible, representing the reliability of complete suppression in a statistical sense. The data clearly show that for both CFS and binocular rivalry, the less frequently the adapting stimulus is seen, the weaker its associated afterimage.

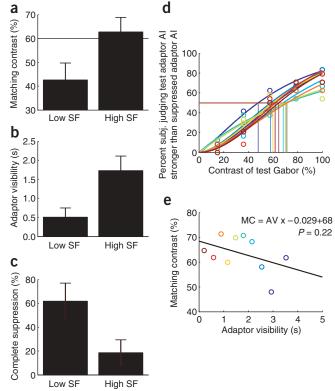
CFS location during adaptation. We also used binocular rivalry to suppress the inducing image for comparison with the efficiency of CFS methods. The results (**Fig. 4**) are unambiguous: the less the Gabor patch was visible during adaptation, the weaker the associated afterimage (for CFS, $r^2 = 0.82$, $P < 1 \times 10^{-5}$; for binocular rivalry, $r^2 = 0.76$, $P < 1 \times 10^{-4}$). If suppression was sufficiently reliable (in a statistical sense), the intensity of the afterimage was reduced.

Trial-by-trial visibility and afterimage intensity

CFS-induced suppression may reduce the afterimage either by eliminating the afterimage entirely on some fraction of trials or by lowering the afterimage intensity uniformly on all trials.

In a fifth experiment, we tried to distinguish between these hypotheses. We repeated three of the conditions from the fourth experiment more extensively to estimate the matching contrast. In the low–spatial frequency condition (**Fig. 4**, small filled triangle), the contrast of a test Gabor patch that matched the 60% contrast Gabor patch suppressed by CFS was 42.7% \pm 7.1% (n=5, t-score = 2.45, P < 0.05, one-tailed t-adaptor visibility duration was 0.51 ± 0.24 s during the 5-s adaptation period (**Fig. 5b**). Subjects did not report seeing any part of the Gabor in 61.8 \pm 15.2% of trials (**Fig. 5c**). In the high–spatial frequency





condition (**Fig. 4**, large filled triangle), the matching contrast was 62.8 \pm 6.1%; that is, there was no reduction of afterimage intensity (n=4, t-score = 0.46, P>0.6). The mean adaptor visibility duration was 1.73 \pm 0.38 s, and complete suppression occurred in 18.6 \pm 10.9% of trials.

To evaluate the effect of adaptor visibility, we sorted the 60 trials with the high-spatial frequency patches at each test contrast into ten bins according to the duration of the visibility of the adaptor. Figure 5d shows each data point averaged across four subjects and psychometric curves fitted for each of ten bins. Matching contrast was independent of adaptor visibility duration (Fig. 5e, $r^2 = 0.18$, P = 0.22). Although it did not reach significance, the slope is slightly negative $(-2.9\% \text{ s}^{-1})$, contrary to the prediction that only invisible trials contribute to afterimage reduction. We obtained similar results using low-spatial frequency Gabor patches and low-contrast Mondrians (n = 5; the matching contrast was $61.2 \pm 1.8\%$, the mean adaptor visible duration was 2.03 \pm 0.38 s and complete suppression occurred in 4.12 \pm 10.9% of trials). Again, we did not find any correlation between matching contrast and the adaptor visibility duration ($r^2 = 0.23$, P = 0.16; slope of the regression line was slightly negative: -3.2% s⁻¹). Dividing trials into two or three bins did not change the results.

For a given stimulus setting, trial-by-trial variability in the visibility of the adaptor did not change the intensity of the afterimage. This is consistent with previous studies of afterimages^{5,20} but was contrary to the suppression of high-level aftereffects^{21,23}. Since the statistical reliability of suppression is correlated with the reduction of the afterimage, the visibility of the adaptor seems only indirectly related to the percepts of the associated afterimage.

DISCUSSION

We have identified dichoptic visual stimuli that, for at least ten times longer than existing techniques, reliably suppress from conscious

Figure 5 Visibility and afterimage reduction. We repeated three conditions of the fourth experiment. Subjects reported the visibility of the suppressed Gabor by holding a key during the 5-s adaptation period and then compared the afterimage intensity. (a-c) We used low- (0.6 cpd, left) and high-spatial frequency (2.0 cpd, right) Gabor patches. (a) Matching contrast (estimated by the method of constant stimuli), showing a significant reduction of contrast in the low spatial frequency condition (error bars represent s.e.m.). (b) Mean duration that the adaptor was visible. (c) Proportion of trials where subjects did not see the adaptor at all. (d) We divided 60 trials at each test contrast for each subject into ten bins based on the adaptor visibility duration in the high spatial frequency condition (a-c, right). Six trials from each of four subjects were pooled to fit a Weibull function, which was used to estimate the matching contrast for which the afterimage (AI) induced by the test adaptor was stronger than the afterimage induced by a suppressed Gabor adaptor in 50% of trials (vertical lines in d). (e) The duration for which the adaptor was visible was weakly but negatively correlated (one-tailed t-test; P = 0.22) with the matching contrast. Different colors in **d** and **e** represent different durations of mean adaptor visibility.

perception salient figures presented to one eye. With CFS as a tool, vivid images can be rendered invisible for long periods with excellent control of timing. This suppression of a continuously presented stimulus at the fovea dissociates physical stimuli from their associated subjective percepts. CFS does not require pre-adaptation, a key aspect of flash suppression^{15,17,19,23}, to achieve reliable disappearance. This property makes CFS attractive for studies that require complete unawareness.

CFS extends the total duration for which Mondrians are perceived by prolonging their period of dominance without shortening their period of suppression (**Supplementary Note** online). In binocular rivalry, strong stimuli shorten each period of suppression of the strong stimuli, with little effect on their period of dominance^{24,36,37} (but see ref. 38). Thus, CFS is not simply a stronger version of binocular rivalry. This observation is compatible with the hypothesis that CFS involves a repetitive flash suppression component, in addition to binocular suppression. Indeed, we present a simple model (**Supplementary Note**) that combines aspects of flash suppression and binocular rivalry and describes the measured periods of CFS dominance and suppression in a quantitative manner.

We applied CFS to ascertain the extent to which dichoptic inhibition interferes with the formation of negative afterimages. Though it is widely believed that afterimages originate among retinal neurons^{20,25–31,33}, some experiments imply that cortical processing can modulate^{39–42} or possibly even create^{34,43} negative afterimages. Our results are consistent with these latter studies, and notably, they imply that such cortical components may be necessary for the formation of afterimages. Dichoptic inhibition that underlies the afterimage reduction has been found as early as the LGN⁴⁴.

The possibility that latent afterimages from the Mondrians interfered with the afterimage of the Gabor pattern was ruled out by the third experiment. Asynchronously presented Mondrian patterns did not reduce the intensity of the afterimage, whereas synchronously presented Mondrians reduced it by about 50%. This suggests that the peculiarity of CFS (that is, continuously present transient signals) is not sufficient for the reduction of the afterimage. Rather, the adaptor has to be suppressed strongly by stimuli presented simultaneously to the other eye.

We found that the degree of afterimage reduction correlated with how reliably adaptors are suppressed. This relationship exists for both binocular rivalry and CFS (**Fig. 4**), implying that the inconsistency between our results and previous studies²⁰ arises from the strong suppression induced by CFS. Although cortical neurons may adapt under partial suppression, they seem to adapt less under reliable

suppression. In an analogy with lesion studies, partial suppression techniques can be compared with 'unilateral lesions' and CFS with 'bilateral lesions'; often, bilateral, but not unilateral, lesions result in behavioral deficits. Partial suppression by binocular rivalry and MIB may leave sufficient residual activity to produce full-blown adaptation and an afterimage.

Furthermore, in this study, we replicated previous findings from our laboratory⁵ that afterimage intensity was not influenced by trial-by-

Furthermore, in this study, we replicated previous findings from our laboratory⁵ that afterimage intensity was not influenced by trial-by-trial variability in adaptor visibility, indicating the cortical component for the afterimage is only indirectly related to neuronal correlates of awareness.

Can we explain our results by the total lack of attention to the adaptor owing to complete suppression? Attending to adaptors during adaptation weakens the afterimage^{41,42}. If one assumes that lack of attention to an object is equivalent to not being aware of it⁴⁵, one would expect that both would cause the same effects on the afterimage. However, lack of attention enhances afterimages, while complete invisibility reduces afterimages. These results support the view that attention and awareness involve different mechanisms^{1,46}.

A reduction of 50% in the strength of the afterimage when the inducing image is present on the retina but not seen by the observer seems to be at odds with the fact that afterimages do not transfer across eyes; when the subject closes the adapted eye, no afterimage is seen. It is known that the binocular components of afterimages have access to the direction of gaze⁴⁰. Likewise, these mechanisms may have access to the overall brightness from the eye and, if it is closed, may reduce or even eliminate afterimages, resulting in no transfer of afterimages. The involvement of a cortical suppression mechanism is supported by patients with cortical lesions who report abnormally long afterimages that transfer across eyes^{47,48}. This may reflect the disruption of cortical mechanisms for afterimage reduction. If normal observers open both eyes during the test period, the inter ocular transfer effect, albeit weak, can be measured psychophysically in detection or discrimination procedures⁴⁹.

In summary, dichoptic suppression by means of CFS significantly reduces the strength of the negative afterimage. This reduction was correlated with the reliability of suppression of the adaptors, but not with trial-by-trial visibility. One implication of our finding is that failure of interocular transfer and failure of reduction of afterimage intensity by partial suppression does not imply that structures that have access to information from both eyes, such as visual cortex, are not involved in the formation of negative afterimages.

METHODS

Subjects were recruited from the California Institute of Technology campus and gave informed written consent. Experiments were approved by the Institutional Review Board (Committee for the Protection of Human Subjects) of the California Institute of Technology. They had normal or corrected eyesight and normal stereo vision. Subjects observed the display through a set of mirrors. The distance between the eyes and the display was 92 cm. To stabilize fixation, a headrest and chinrest were used. We used Matlab 6.5 under Windows 98, Matlab 5.2.1 under Mac OS and the Psychophysics Toolbox⁵⁰. The Mondrian images consisted of randomly generated squares of random colors (experiment 1) or white, black and gray squares (the other experiments) superimposed onto each other. Twenty distinct Mondrians were generated before each session.

Experiment 1. Seventeen naive subjects participated. They were instructed to hit a space bar when any part of a gray image became visible and to describe it verbally to the experimenter. The time to key press was taken as the duration of initial suppression. One of four types of gray images was used in each trial: a 45° left-tilted Gabor patch of 30% contrast, a 45° right-tilted Gabor patch of 60% contrast, an angry face and a blurred angry face. Spatial frequency and s.d. of the Gabor patches were 0.5 cpd and 1° , respectively. Each type of image

appeared once in a block of four trials. In total, four blocks of 16 trials were run. The images were presented at the fovea and extended $6 \times 6^{\circ}$.

Experiment 2. Sixteen naive subjects participated. Isoluminant Gabor patches (spatial frequency, 0.6 cpd; s.d., 0.83°) were used as afterimage inducers. The green level was equated with pink (CIE [x, y] = [0.389,0.205]; luminance 18.7 cd/mm²) using a flicker minimization for each subject. The average green level was [x, y] = [0.201,0.278]. The contrast of the isoluminant Gabor patch was defined as the contrast modulation of the red or the green intensity,

$$Contrast = \frac{\max(red, green) - \min(red, green)}{\max(red, green) + \min(red, green)}$$

Peaks of the red intensity coincided with troughs of the green. The luminance for black and white was 0.028 and 67.6 cd/mm², respectively. Three crosses on a rectangle with random texture $(0.48^{\circ} \times 4.8^{\circ})$ stabilized binocular fusion. Subjects fixated the middle cross. Each of two Gabor patches of 30% contrast was presented within an imaginary $4.8^{\circ} \times 4.8^{\circ}$ square, with the center of the square 2.6° away from the fixation (Fig. 2, left). The phase and orientation of the adaptor were randomized for each trial. The Mondrians flashed at 10 Hz were presented in the corresponding square (Fig. 2, center). After 5 s of adaptation, the adaptors and Mondrians were replaced with a uniform gray background to induce negative afterimages, and subjects described their percepts (Supplementary Table).

Experiment 3. Six naive subjects performed 20 trials. Three 50% contrast Gabor adaptors were presented spaced apart (**Fig. 3**). One visible control adaptor was placed to the left (or right) of fixation $(3.6^{\circ}$ square, with its center location 2° from fixation); two other adaptors were placed at the top or bottom right (or left) from the fixation $(3.6^{\circ}$ square, 1.8° above or below fixation). Three adaptors appeared simultaneously for 2 s and were turned off for 2 s, repeating for seven cycles and ending with a 2-s 'on' period. After 30 s of adaptation, subjects rated the intensity of the afterimage on a linear scale relative to the control, which was pegged at 10. If no afterimage was visible, the rating was 0. A rating of 5 (or 20) was given when the intensity was half (or twice) as strong as the afterimage from the control adaptor.

Experiment 4. Four naive subjects and the first author participated. Subjects compared the intensity of afterimages produced by a pair of adaptors with the same contrast and spatial frequency. Different spatial frequencies (0.60, 0.84, 1.2, 1.7 and 2.5 cpd) and two types of dichoptic suppression (CFS and binocular rivalry) were randomly interleaved within a block. The contrast of adaptors and Mondrians was constant in one block of 100 trials. Each subject completed at least 30 trials for each combination of the suppression protocol, the spatial frequency of adaptors, and contrasts of adaptors and Mondrians (30% versus 100%, 100% versus 100%, 100% versus 5%). We created motion binocular rivalry stimuli by sliding the right and left half of the texture at $0.71^{\circ} \, \text{s}^{-1}$ to converge at the midline (see demonstration at http://www.klab. caltech.edu/~naotsu/CFSdemo.html). The motion binocular rivalry stimulus was randomly created before each trial.

Experiment 5. Four experienced (but naive to the hypothesis of this experiment) subjects and the first author participated. Subjects pressed a key to indicate if the suppressed Gabor became visible during a 5-s adaptation period and then reported on which side the afterimage was stronger. The spatial frequency of Gabor was either 0.6 or 2.0 cpd, and the contrast of Mondrian was either 100% or 2–4%.

In the low–spatial frequency and high–Mondrian contrast condition, the test contrast was adjusted either from 10% to 50% or from 15% to 100% in five linear steps, depending on the matching contrast for each subject. In one block of 50 trials (ten trials at each of five contrast levels), test contrasts were randomized. Each subject completed at least two blocks. In other conditions, the test contrast was adjusted from 15% to 100% in five linear steps, and six blocks were conducted.

To estimate the matching contrast for the test adaptor, we fitted a Weibull function to the data. For the correlation analysis, 60 trials at each test contrast were sorted according to the adaptor visibility duration: the six trials with the shortest visibility duration were categorized in the first bin, the six trials with the next shortest visibility duration in the second bin, and so on.

ACKNOWLEDGMENTS

We thank R. Kanai, C. Hofstoetter, D.A. Wu, F. Moradi, R. Van Rullen and S. Shimojo for discussion. This research was funded by grants from the US National Institute of Mental Health, the US National Science Foundation, the Keck Foundation and the Moore Foundation.

Note: Supplementary information is available on the Nature Neuroscience website.

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

Received 5 April; accepted 16 June 2005 Published online at http://www.nature.com/natureneuroscience/

- Koch, C. The Quest for Consciousness: A Neurobiological Approach (Roberts, Greenwood Village, Colorado, 2004).
- Blake, R. & Fox, R. Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature* 249, 488–490 (1974).
- He, S., Cavanagh, P. & Intriligator, J. Attentional resolution and the locus of visual awareness. *Nature* 383, 334–337 (1996).
- 4. Rajimehr, R. Unconscious orientation processing. Neuron 41, 663-673 (2004).
- Hofstoetter, C., Koch, C. & Kiper, D.C. Motion-induced blindness does not affect the formation of negative afterimages. *Conscious. Cogn.* 13, 691–708 (2004).
- Macknik, S.L. & Martinez-Conde, S. Dichoptic visual masking reveals that early binocular neurons exhibit weak interocular suppression: implications for binocular vision and visual awareness. *J. Cogn. Neurosci.* 16, 1049–1059 (2004).
- Rees, G., Russell, C., Frith, C.D. & Driver, J. Inattentional blindness versus inattentional amnesia for fixated but ignored words. Science 286, 2504–2507 (1999).
- Bonneh, Y.S., Cooperman, A. & Sagi, D. Motion-induced blindness in normal observers. Nature 411, 798–801 (2001).
- Logothetis, N.K. & Schall, J.D. Neuronal correlates of subjective visual perception. Science 245, 761–763 (1989).
- Leopold, D.A. & Logothetis, N.K. Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature* 379, 549–553 (1996).
- Sheinberg, D.L. & Logothetis, N.K. The role of temporal cortical areas in perceptual organization. *Proc. Natl. Acad. Sci. USA* 94, 3408–3413 (1997).
- Lumer, E.D., Friston, K.J. & Rees, G. Neural correlates of perceptual rivalry in the human brain. Science 280, 1930–1934 (1998).
- Tong, F., Nakayama, K., Vaughan, J.T. & Kanwisher, N. Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron* 21, 753–759 (1998).
- Polonsky, A., Blake, R., Braun, J. & Heeger, D.J. Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nat. Neurosci.* 3, 1153–1159 (2000).
- Pasley, B.N., Mayes, L.C. & Schultz, R.T. Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron* 42, 163–172 (2004).
- Williams, M.A., Morris, A.P., McGlone, F., Abbott, D.F. & Mattingley, J.B. Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. J. Neurosci. 24, 2898–2904 (2004).
- 17. Wolfe, J.M. Reversing ocular dominance and suppression in a single flash. *Vision Res.* **24**, 471–478 (1984).
- Kreiman, G., Fried, I. & Koch, C. Single-neuron correlates of subjective vision in the human medial temporal lobe. *Proc. Natl. Acad. Sci. USA* 99, 8378–8383 (2002).
- Wilke, M., Logothetis, N.K. & Leopold, D.A. Generalized flash suppression of salient visual targets. *Neuron* 39, 1043–1052 (2003).
- Lack, L.C. Selective Attention and the Control of Binocular Rivalry 117–169 (Mouton, The Hague, The Netherlands, 1978).

- Wiesenfelder, H. & Blake, R. The neural site of binocular rivalry relative to the analysis of motion in the human visual system. *J. Neurosci.* 10, 3880–3888 (1990).
- 22. Blake, R. Psychoanatomical strategies for studying human visual perception. in *Early Vision and Beyond* (eds. Papathomas, T.V., Chubb, C., Gorea, A., & Kowler, E.) 17–25 (M.I.T. Press, Cambridge, Massachusetts, 1995).
- 23. Moradi, F., Koch, C. & Shimojo, S. Face adaptation depends on seeing the face. *Neuron* 45. 169–175 (2005).
- **45**, 169–175 (2005). 24. Blake, R. & Logothetis, N.K. Visual competition. *Nat. Rev. Neurosci.* **3**, 13–21 (2002).
- Alpern, M. & Barr, L. Durations of the after-images of brief light flashes and the theory of the Broca and Sulzer phenomenon. J. Opt. Soc. Am. 52, 219–221 (1962).
- 26. Brindley, G.S. Two new properties of foveal after-images and a photochemical hypothesis to explain them. *J. Physiol. (Lond.)* **164**, 168–179 (1962).
- Loomis, J.M. The photopigment bleaching hypothesis of complementary after-images: a psychophysical test. Vision Res. 12, 1587–1594 (1972).
- Loomis, J.M. Complementary afterimages and the unequal adapting effects of steady and flickering light. J. Opt. Soc. Am. 68, 411–416 (1978).
- Virsu, V. & Laurinen, P. Long-lasting afterimages caused by neural adaptation. Vision Res. 17, 853–860 (1977).
- 30. Sakitt, B. Psychophysical correlates of photoreceptor activity. *Vision Res.* **16**, 129–140 (1976).
- Wilson, H.R. A neural model of foveal light adaptation and afterimage formation. Vis. Neurosci. 14, 403–423 (1997).
- Kelly, D.H. & Martinez-Uriegas, E. Measurements of chromatic and achromatic afterimages. J. Opt. Soc. Am. A 10, 29–37 (1993).
- 33. Craik, K.J.W. Origin of visual after-images. Nature 145, 512 (1940).
- 34. Shimojo, S., Kamitani, Y. & Nishida, S. Afterimage of perceptually filled-in surface. *Science* **293**, 1677–1680 (2001).
- 35. Breese, B.B. On Inhibition. Psychol. Monogr. 3, 1-65 (1899).
- Levelt, W.J.M. On Binocular Rivalry (Institute for Perception RVO-TNO, Soesterberg, The Netherlands, 1965).
- Fox, R. & Rasche, F. Binocular rivalry and reciprocal inhibition. Percept. Psychophys. 5, 215–217 (1969).
- Bossink, C.J., Stalmeier, P.F. & De Weert, C.M. A test of Levelt's second proposition for binocular rivalry. Vision Res. 33, 1413–1419 (1993).
- 39. Anstis, S., Rogers, B. & Henry, J. Interactions between simultaneous contrast and coloured afterimages. *Vision Res.* **18**, 899–911 (1978).
- 40. Hayhoe, M.M. & Williams, D.R. Disappearance of afterimages at 'impossible' locations in space. *Perception* **13**, 455–459 (1984).
- Suzuki, S. & Grabowecky, M. Attention during adaptation weakens negative afterimages.
 J. Exp. Psychol. Hum. Percept. Perform. 29, 793–807 (2003).
- Lou, L. Effects of voluntary attention on structured afterimages. *Perception* 30, 1439– 1448 (2001).
- 43. Weiskrantz, L. An unusual case of after-imagery following fixation of an 'imaginary' visual pattern. *Q. J. Exp. Psychol.* **2**, 170–175 (1950).
- 44. Sengpiel, F., Blakemore, C. & Harrad, R. Interocular suppression in the primary visual cortex: a possible neural basis of binocular rivalry. *Vision Res.* **35**, 179–195 (1995).
- 45.0'Regan, J.K. & Noe, A. A sensorimotor account of vision and visual consciousness. *Behav. Brain Sci.* **24**, 939–73 (2001).
- 46. Lamme, V.A. Why visual attention and awareness are different. *Trends Cogn. Sci.* **7**, 12–18 (2003).
- Chan, D., Crutch, S.J. & Warrington, E.K. A disorder of colour perception associated with abnormal colour after-images: a defect of the primary visual cortex. *J. Neurol. Neurosurg. Psychiatry* 71, 515–517 (2001).
- 48. Weiskrantz, L. Prime-sight and blindsight. Conscious. Cogn. 11, 568-581 (2002).
- 49. Schiller, P.H. & Dolan, R.P. Visual aftereffects and the consequences of visual system lesions on their perception in the rhesus monkey. *Vis. Neurosci.* **11**, 643–665 (1994)
- 50. Brainard, D.H. The Psychophysics Toolbox. Spat. Vis. 10, 433-436 (1997).