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Ensemble cortical responses to rival visual stimuli: Effect of monocular transient

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ABSTRACT

Binocular rivalry is a fascinating perceptual phenomenon that has been characterized extensively at the psychophysical level. However, the underlying neural mechanism remains poorly understood. In particular, the role of the early visual pathway remains controversial. In this study, we used voltage-sensitive dye imaging to measure the spatiotemporal activity patterns in cat area 18 evoked by dichoptic orthogonal grating stimuli. We found that after several seconds of monocular stimulation with an oriented grating, an orthogonal stimulus to the other eye evoked a reversal of the cortical response pattern, which may contribute to flash suppression in perception. Furthermore, after several seconds of rival binocular stimulation with unequal contrasts, transient increase in the contrast of the weak stimulus evoked a long-lasting cortical response. This transient-triggered response could contribute to the perceptual switch during binocular rivalry. Together, these results point to a significant contribution of early visual cortex to transient-triggered switch in perceptual dominance.

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In binocular rivalry, only one image is perceived when the two eyes view conflicting images, and perception alternates stochastically between the two images [1,2]. For example, when two gratings at orthogonal orientations are presented to the two eyes, each grating is perceived in turn, but a plaid consisting of both gratings is rarely perceived. This powerful perceptual phenomenon has been known for several centuries [3]. Since the perceptual switch can occur without any change in the visual input, it provides a unique opportunity for studying the neural correlate of perception and awareness.

Although binocular rivalry has been characterized extensively in psychophysical experiments, its underlying neural mechanism remains unclear. A key question is which brain regions play the primary role in determining the perceptual state. Human fMRI studies demonstrated strong correlations between V1 activity and the perceptual fluctuations of the observer [4–7], suggesting an important role of the early visual pathway. However, single-unit recordings from non-human primates strongly supported the roles of higher-order brain areas: while very few V1 neurons exhibited firing patterns that are correlated with the perceptual dominance, the activity of most neurons in the inferior temporal cortex corresponded to perception [8,9]. A major difficulty in resolving the discrepancy between these studies resides in the differences in both the nature of the recorded signal (blood-oxygen level vs. spike rate) and the spatial scale of the measurement (several mm^3 of brain tissue vs. single neurons). To assess the role of a given brain area in binocular rivalry, it is important to measure the electrical activity of large neuronal populations.

In this study, we used voltage-sensitive-dye (VSD) imaging to measure the spatiotemporal activity patterns in cat visual cortex evoked by binocular stimuli. In particular, we focused on the effect of abrupt visual stimuli. Abrupt stimuli are known to be effective in triggering perceptual switches [10–14]. Human fMRI studies have also shown that stimulus transients can reliably trigger activity switches in V1 [4] independent of attention or conscious perception [15], making them well suited for studies in anesthetized animals. In a series of VSD imaging experiments, we found that monocular transients exert long-lasting impact on cortical responses, which may contribute to transient-triggered perceptual switches in binocular rivalry.

Materials and methods

Animal preparation. Adult cats (1.9–3.1 kg) were initially anesthetized with ketamine hydrochloride (30 mg/kg, i.m.) and maintained with urethane (15 mg/kg/hr, i.v., supplemented as needed). Lidocaine was injected before all incisions. Tracheostomy was made before the cat was moved to a stereotaxic frame (NARISHIGE). To minimize brain movement, suspension of lumbar vertebrae and pneumothorax were performed. Craniotomy (4 × 5 mm^2) was made over area 18, and the underlying dura re-

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moved. Pupils were dilated (1% atropine sulfate) and nictitating membranes retracted (5% neosynephrine). The cat was paralyzed with Gallamine Triethiodide (10 mg/kg/hr, i.v.) and artificially ventilated. End-expiratory CO_2 was maintained at 4–5%, core body temperature at 38–38.5 °C, and ECG and EEG were monitored continuously. Eyes were refracted, fitted with contact lenses, and focused on the monitors. The animal use protocol was approved by Animal Use Committee of Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences. A total of 8 cats were used.

Visual stimulation. Visual stimuli were created with a PC containing a graphics card (NVIDIA Ti 4600, frame rate: 100 Hz). Stimuli for the two eyes were displayed on two CRT monitors (mean luminance: 30 cd/m^2) and projected to the two eyes by a Wheatstone stereoscope. Full-field (36 × 28°) horizontal and vertical drifting square-wave gratings (spatial frequency: 0.15 cycles/°, temporal frequency: 3 Hz) were used.

VSD imaging. Voltage-sensitive dye RH1691 was dissolved in aCSF (1.2 mg/ml) and topically applied to the cortex for 3–5 h. The cortex was then washed with aCSF for 0.5 h and covered with a sealed chamber filled with silicon oil. Fluorescence signals were collected with a CCD camera (Quantix 0206, Roper Scientific Inc., 383 × 288 pixels, 22 μm/pixel) mounted on a macroscope (LIGHT02, Optical Imaging Inc; magnification 1.6). Light from an LED source (1 W; center wavelength, 630 nm) was filtered by a 630 ± 20 nm filter and reflected down onto the cortex by a 650 nm dichroic mirror. Signals were filtered with a 665 nm long-pass filter. Images were acquired with custom-written software at 20 or 40 ms/frame. In each trial (4–7 s, synchronized with artificial ventilator), VSD signals were collected for 320 ms before stimulus onset to obtain $F_0(x,y)$. To measure the orientation template, recording was made for 500–1000 ms under binocular stimulation. Recording trials with different stimulus configurations (e.g., RVLH and RHLV, Fig. 1B) were interleaved at a random sequence, with 25 s between consecutive trials.

Data analysis. All analyses were performed in Matlab. We calculated $\Delta F/F$ as $(F(x,y,t) - F_0(x,y))/F_0(x,y)$, where $F(x,y,t)$ represents the fluorescence signal at location x, y and time t, and F_0 represents the spatial pattern averaged over the 320 ms before stimulus onset. We then applied a 2D spatial filter (boxcar, 275 × 275 μm) to the image in each frame. To reduce the noise due to heart beat and respiration, we performed principal component analysis (PCA) on the images collected in each recording trial. We found that the few principal components (PCs) with the largest eigenvalues generally corresponded to blood vessel patterns, indicating that they reflected heartbeat and respiratory noise. Thus, we subtracted the top 5–8 PCs from each image before further analysis. For each experiment, data from 3 to 20 trials were averaged.

Results

We used VSD imaging to measure the spatiotemporal activity patterns in area 18 of anesthetized adult cat (Materials and methods). To measure the orientation map, drifting gratings at the same orientation and spatiotemporal frequency were presented to both eyes. The "horizontal template" was computed as the time-averaged response to the horizontal grating minus that to the vertical grating (Fig. 1A), which was used as a spatial template for analyzing the cortical responses to other binocular stimuli.

Cortical responses during flash suppression

In the first set of experiments, we measured the cortical responses to stimuli known to induce flash suppression, in which perception of a monocular stimulus is suppressed by flash of a different stimulus to the other eye [11]. As illustrated in Fig. 1B, the vertical

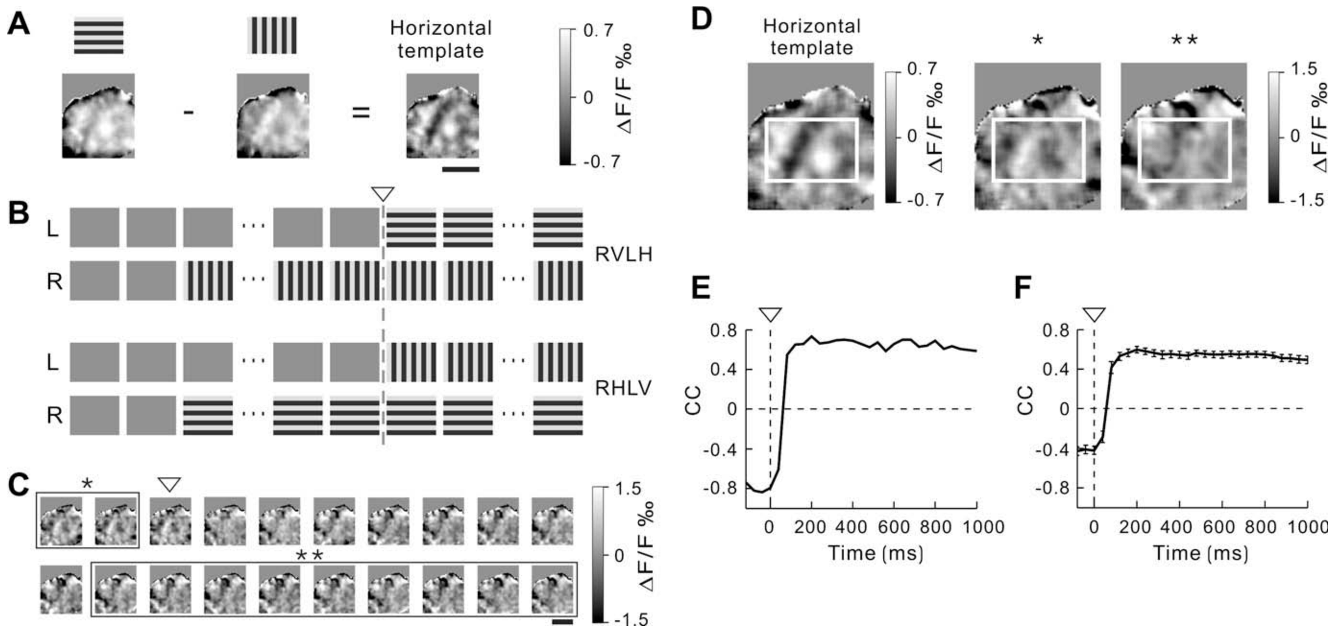

Fig. 1. Cortical responses to flash suppression stimuli. (A) Definition of horizontal template. Shown are time-averaged VSD responses to binocular presentations of horizontal (left) and vertical (middle) gratings, and the difference between them (right). Scale bar, 2 mm. Scale for $\Delta F/F$ is shown on the right. (B) Schematic illustration of visual stimuli for flash suppression. L/R, stimulus to left/right eye. Arrowhead, onset of second grating. (C) Difference response ($R_{\mathrm{RVLH}} - R_{\mathrm{RHLV}} + R_{\mathrm{LVRH}} - R_{\mathrm{LHRV}}$) averaged from 10 trials, shown in 60 ms intervals. Arrowhead, onset time of second grating. Responses within each box ($*$ and $**$) were averaged and shown in (D). (D) Spatial response patterns averaged from the period before ($*$) and 520–1060 ms after ($**$) onset of second stimulus. Horizontal template (left) is the same as in (A). White box delineates a cortical region to facilitate comparison between $*$, $**$, and horizontal template. (E) CC between each frame of the difference response and the horizontal template for the experiment shown in (C). Arrowhead and vertical dashed line indicate onset of second grating. (F) CC averaged from 37 experiments in 9 hemispheres. Error bars: ±sem.

grating was presented to the right eye for 2–5 s before the horizontal grating was presented to the left eye (referred to as "RVLH", upper panel), or the horizontal grating was presented to the right eye before the vertical grating was presented to the left eye ("RHLV", lower panel). Two other configurations ("LVRH" and "LHRV") were similarly defined. To determine the relative strengths of the cortical responses to the horizontal and vertical stimuli, we computed their difference as $R_{\mathrm{RVLH}} - \mathrm{R}_{\mathrm{RHLV}} + R_{\mathrm{LVRH}} - \mathrm{R}_{\mathrm{LHRV}}$ (R represents cortical response). As expected, this difference response was approximately the inverse of the horizontal template before onset of the second grating (Fig. 1C, before open arrowhead), since it reflected the monocular response to the vertical grating minus that to the horizontal grating. The onset of the second grating, however, triggered a reversal of the activity pattern over a period of $\sim$60 ms, and the difference response became similar to the horizontal template. The reversal of the map can also be seen clearly in the cortical responses averaged over the period before (∗) and 520–1060 ms after (∗∗) onset of the second grating (Fig. 1D).

To quantify the similarity between the difference response and the horizontal template, we computed the correlation coefficient (CC) between each frame of the response and the template. As shown in Fig. 1E, CC was negative during monocular stimulation, but rapidly switched to positive values after onset of the second grating. The population summary (Fig. 1F) exhibited a similar time course. Since at $t > 0$, the horizontal and vertical gratings were present at equal contrast, the resemblance of the difference response to the horizontal template indicates that prior monocular exposure to the vertical grating caused a strong bias of the cortical response toward the horizontal stimulus. Such an effect could contribute to flash suppression in visual perception [11].

Monocular transient embedded in constant binocular stimuli

Previous studies showed that when two orthogonal stimuli with unequal contrasts are presented to separate eyes, perception is often dominated by the stimulus with higher contrast [16]. However, a transient increase in the contrast of the weak stimulus can trigger a perceptual switch, and the latter stimulus is perceived even after its contrast returns to the initial low value [10,12,13]. Functional MRI studies in human subjects also showed that the transient contrast increase can trigger a change in V1 activity consistent with the perceptual switch [4,15]. We thus used VSD imaging to measure the cortical response to a monocular transient embedded in constant binocular stimuli with unequal contrasts.

The stimulus sequence is illustrated in Fig. 2A. The horizontal and vertical gratings were presented to the two eyes at unequal contrasts (C_{high} and C_{low}). After 2–5 s, contrast of the weak stimulus was transiently elevated (for 200 ms) to 100% before it was returned to the original level (C_{low}). As shown in the example experiment in Fig. 2B (C_{high} = 70%, C_{low} = 10%, transient was presented 5 s after onset of the binocular stimuli), the initial cortical response was approximately the inverse of the horizontal template, but the transient elevation of C_{low} to 100% evoked a strong cortical response resembling the horizontal template. Interestingly, even after the contrast of this grating was returned to 10%, the response pattern continued to resemble the horizontal template (Fig. 2C, ∗∗), indicating a long-lasting dominance by the horizontal stimulus. As shown in Fig. 2D, the CC between each frame of the response and the horizontal template remains at a positive value throughout the recording period (up to 1 s after the transient).

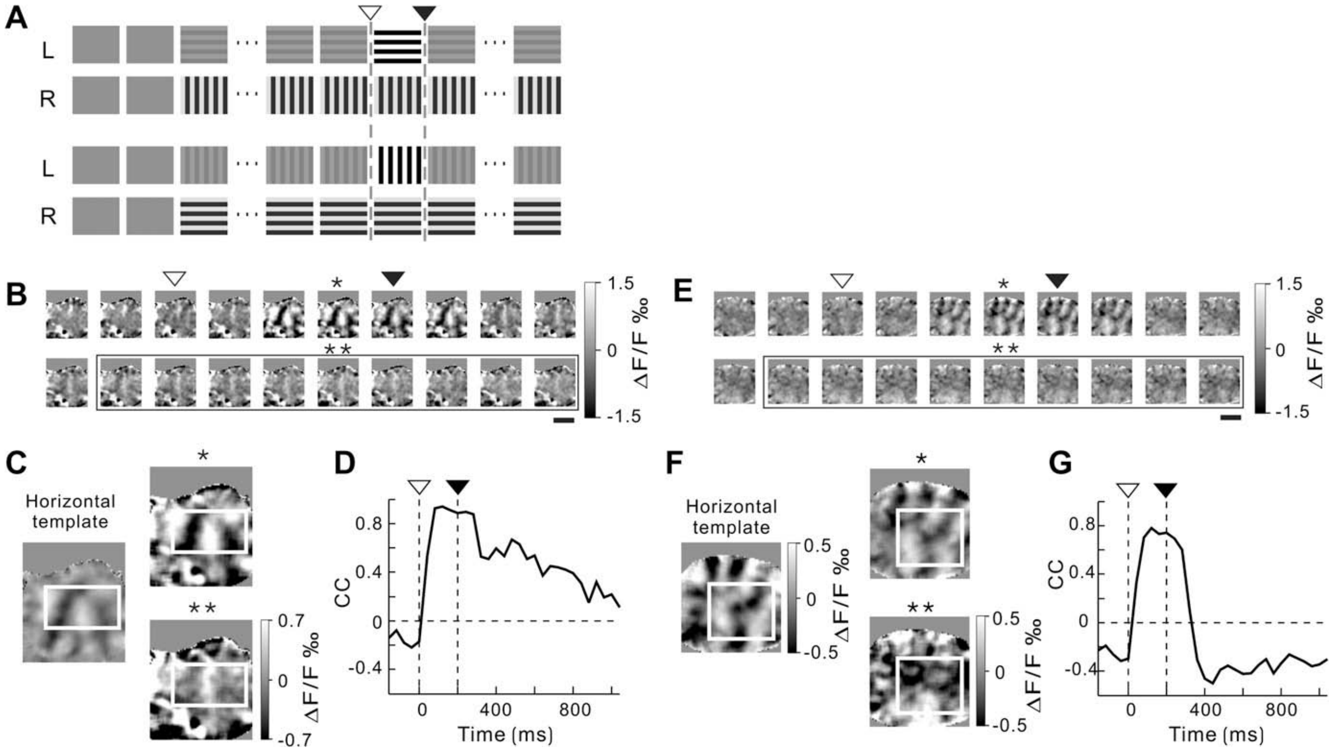

Fig. 2. Cortical responses to monocular transient embedded in constant binocular stimuli. (A) Schematic illustration of visual stimuli. Open/filled arrowheads: onset/offset of transient. (B) Example experiment in which the transient triggered a long-lasting reversal of cortical response pattern. Difference response was averaged from 10 trials, shown in 60 ms intervals. (C) Response pattern at peak of transient-evoked response (∗) and that averaged over 480–1020 ms after transient onset (∗∗, box in B). For horizontal template and ∗, the scale for $\Delta F/F$ is the same as (B). White box delineates a cortical region to facilitate comparison between ∗, ∗∗, and horizontal template. (D) CC between each frame of difference response and horizontal template for the experiment in (B). Only 2/8 experiments (in 1/4 hemispheres) showed such a long-lasting reversal. (E–G) Similar to (B–D), for an experiment in which monocular transient did not trigger a long-lasting reversal of response pattern. The difference response was averaged from 14 trials.

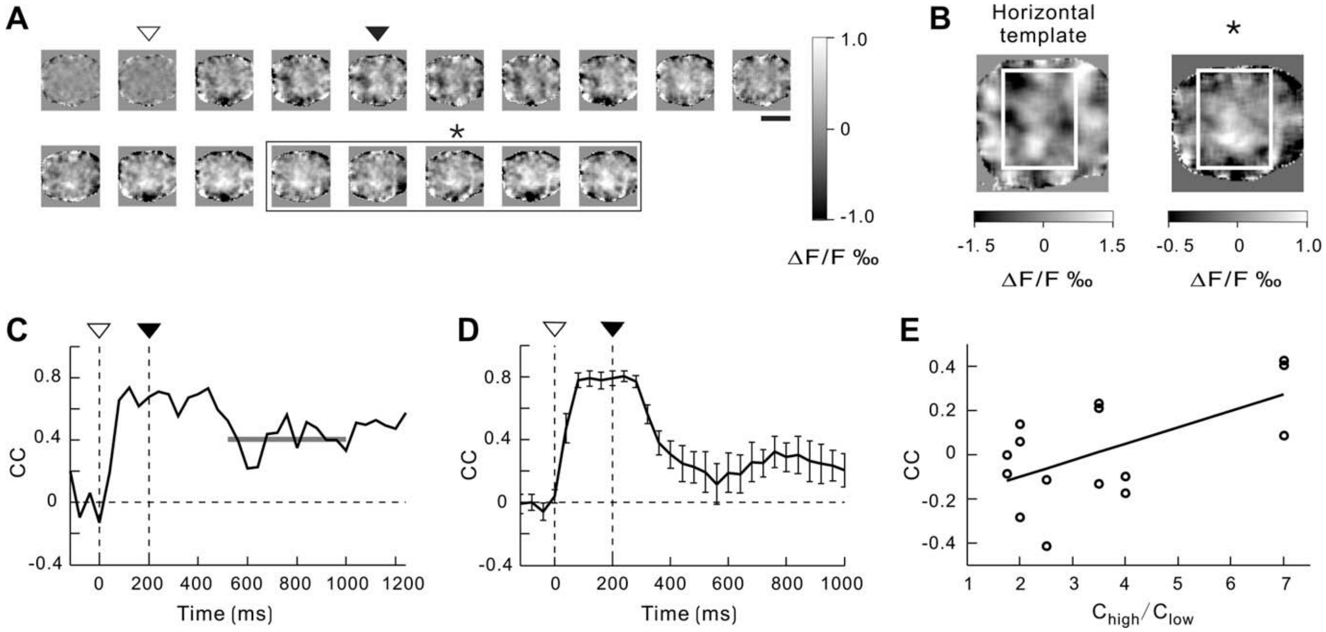

Fig. 3. Contribution of monocular transient to cortical response. (A) Example experiment using the stimuli in Fig. 2A. Difference response was averaged from 20 trials, shown in 80 ms intervals. Each frame of the response was subtracted by the mean response before transient onset. Open/filled arrowheads: transient onset/offset. (B) Horizontal template and response pattern averaged over 880–1280 ms after transient onset (∗, rectangular box in A). White box delineates a cortical region to facilitate comparison between ∗ and horizontal template. (C) CC between each frame in (A) and horizontal template. Horizontal gray line, mean CC 520–1000 ms after transient onset. (D) CC averaged from 7 experiments (in 3 hemispheres) with C_{high}/C_{low} = 3.5 to 7 and transient presented 2–3 s after onset of binocular stimuli. Error bars: ±sem. (E) Mean CC 520–1000 ms after transient onset (horizontal gray line in (C)) plotted against C_{high}/C_{low}. The correlation between mean CC and C_{high}/C_{low} was significant ($p < 0.02$).

However, such a long-lasting reversal of the cortical response was not triggered reliably by the high-contrast transient. As shown in another experiment in Fig. 2E, the transient evoked a brief response (~300 ms), but the activity pattern soon reverted back to the inverse of the horizontal template (Fig. 2F, ∗∗). This is reflected by the negative CC values following the positive peak (Fig. 2G). With C_{high} = 70%, C_{low} = 10% or 20%, and the transient presented 5 s after onset of the binocular stimuli, the transient evoked a long-lasting dominance by the horizontal stimulus (>1 s) in only 2/8 experiments.

Although the transient did not consistently induce a long-lasting switch of the response pattern, it exerted a persistent impact on the cortical response. Since the binocular stimuli (vertical grating at C_{high} and horizontal grating at C_{low}) were identical before and after the 200 ms transient (Fig. 2A), the contribution of the transient to the cortical response can be isolated by subtracting the VSD signals prior to the transient. As shown in the example experiment in Fig. 3A (C_{high} = 70%, C_{low} = 10%, transient presented 3 s after binocular stimulus onset), although the signal became much weaker ~500 ms after the transient onset, a spatial pattern similar to the horizontal template was detectable throughout the stimulus sequence (Fig. 3B, ∗). Fig. 3C shows the time course of CC between the subtracted response and the horizontal template, which exhibited a strong peak induced by the transient, followed by a positive plateau lasting throughout the stimulus sequence (1200 ms after transient onset). The average result from 7 experiments (C_{high} = 70%, C_{low} = 10% or 20%, transient presented 2–3 s after binocular stimulus onset) showed a similar time course (Fig. 3D). When the ratio between C_{high} and C_{low} was varied over a range of values, we found that the long-lasting effect of the transient (measured by CC at 520–1000 ms after transient onset, gray horizontal line in Fig. 3C) was positively correlated with the C_{high}/C_{low} ratio (Fig. 3E, $p < 0.02$). This dependence on the contrast ratio suggests that the long-lasting effect of the transient depends on differential adaptation of the cortical neurons preferring the horizontal and vertical gratings.

Transient following monocular stimulation

While the long-lasting response to the transient (Fig. 3) was not always strong enough to override the unequal contrasts of the binocular stimuli to cause the reversal of the response pattern (Fig. 2E–G), the dependence of the effect on C_{high}/C_{low} (Fig. 3E) suggests that one way to strengthen the impact of the transient is to further reduce the cortical adaptation to the low-contrast stimulus prior to the transient. We thus modified the stimulus sequence shown in Fig. 2A by removing the low-contrast stimulus prior to the transient (Fig. 4A). As shown in Fig. 4B, the cortical response pattern was approximately the inverse of the horizontal template before onset of the transient stimulus. Onset of the second grating at 100% contrast (duration 200 ms) evoked a strong cortical response resembling the horizontal template. Importantly, even after the contrast of the second grating was reduced to 28% (filled arrowhead), the response continued to resemble the horizontal template, albeit at a reduced amplitude. The CC between the horizontal template and each frame of the response was negative before the onset of the horizontal grating, exhibited a strong positive peak between ~80 and 400 ms after transient onset, and remained at a lower positive value throughout the rest of the trial (Fig. 4C). The result averaged from 4 experiments (C_{high} = 70%, C_{low} = 28% or 40%, transient presented 4–5 s after monocular stimulus onset) showed a similar time course (Fig. 4D). Thus, eliminating the low-contrast stimulus prior to the transient significantly enhanced the impact of the transient, allowing it to trigger a long-lasting reversal of the cortical response pattern.

Discussion

In this study, we used VSD imaging to measure the spatiotemporal patterns of cortical activity evoked by binocular stimuli at orthogonal orientations. In particular, we have examined the effects of transient stimuli on triggering switches in the response

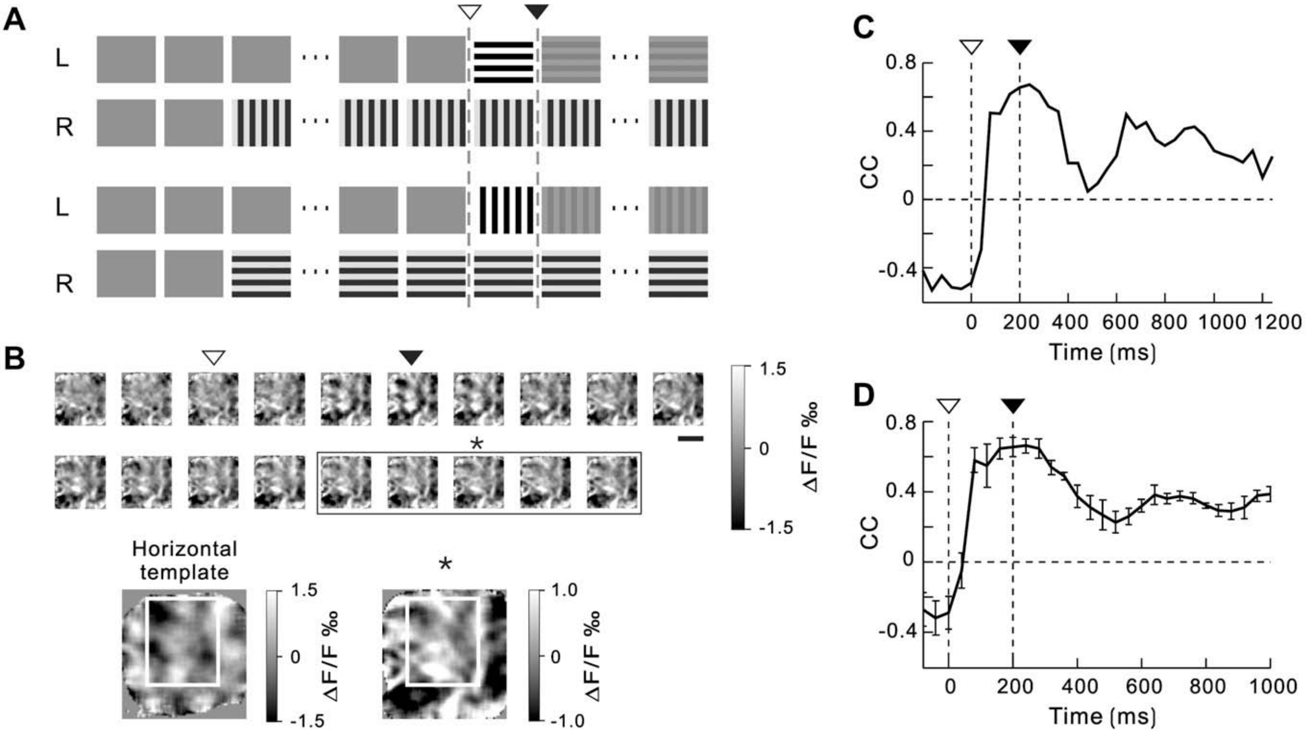

Fig. 4. Cortical responses to binocular stimuli following monocular adaptation. (A) Schematic illustration of visual stimuli. Open/filled arrowheads: transient onset/offset. (B) Example experiment (C_{high} = 70%, C_{low} = 28%, transient presented 4 s after onset of first stimulus). Difference response was averaged from 12 trials, shown in 80 ms intervals. Inset below, horizontal template and response pattern averaged over 880–1280 ms after transient onset. (C) CC between each frame of the difference response and horizontal template for the experiment in (B). (D) CC averaged from 4 experiments in 2 hemispheres. Error bars: ±sem.

pattern. In the first set of experiments, we measured the cortical responses to stimuli known to induce flash suppression [11]. We found that exposure to an oriented monocular stimulus for several seconds significantly biased the cortical response to its orthogonal stimulus when the two stimuli are presented at the same contrast (Fig. 1). This effect was highly robust, consistent with the fact that flash suppression is a very strong perceptual phenomenon. Mechanistically, the bias of the cortical response toward the second stimulus is likely to be mediated by pattern-specific adaptation [17], which selectively reduces the responses of the cortical neurons preferring the first stimulus. Such an adaptation effect may also explain the finding from a previous study, in which suppression of the neuronal response to a preferred monocular stimulus by a non-preferred stimulus presented to the other eye is effective only if the preferred stimulus is presented first [18,19].

In the second set of experiments, we tested the effect of a transient increase in the contrast of the weak input. We found that the impact of the transient on the cortical response persisted for >1 s (Fig. 3). Such a long-lasting impact may partly underlie the effectiveness of transients in triggering perceptual switches [4,10,12,13,15]. Psychophysical and fMRI studies indicate that the representations of the perceptually suppressed stimuli are not completely suppressed at the neuronal level [20–24]. Thus, we would expect significant cortical representation of the high-contrast stimulus even when perception is dominated by the low-contrast stimulus after the transient-triggered switch. The question is whether the transient could override the effect of unequal contrasts of the rival stimuli and cause a long-lasting reversal of the response pattern. In some cases, the reversal was indeed observed (Fig. 2B–D), which could directly support transient-triggered perceptual switch [4,13,15]. However, the reversal was not observed in other experiments (Fig. 2E–G), which may be partly attributable to the variability in the anesthesia state of individual animals. Another possibility is that the cortical activity measured by VSD imaging is biased, since both the staining and recording are restricted to the superficial layers, and the VSD signals represent a mixture of subthreshold and suprathreshold activity. Finally, resolution of the binocular conflict is likely to involve multiple stages of cortical processing [1,25,26]. The long-lasting effect of the transient may be progressively amplified in higher cortical areas. As shown in Fig. 4, reducing prior adaptation to the low-contrast stimulus can also enhance the effect of the transient and thereby allow consistent reversal of the cortical response pattern.

In summary, we have shown that abrupt visual stimuli can exert long-lasting impact on neuronal activity in the early visual pathway. These effects can strongly bias the competitive interaction between the stimuli presented to the two eyes that is known to be important in binocular rivalry. Although perceptual switches often occur spontaneously without externally imposed stimulus transients, some of these switches may in fact be triggered by the transients caused by involuntary eye movements [27]. Thus, characterization of cortical responses to transient visual stimuli is likely to be a key step in understanding the neural mechanisms underlying binocular rivalry.

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References

[1] F. Tong, M. Meng, R. Blake, Neural bases of binocular rivalry, Trends Cogn. Sci. 10 (2006) 502–511.
[2] G. Rees, G. Kreiman, C. Koch, Neural correlates of consciousness in humans, Nat. Rev. Neurosci. 3 (2002) 261–270.

[3] C. Wheatstone, On some remarkable and hitherto unobserved phenomena of binocular vision, Philos. Trans. R. Soc. Lond. 128 (1838) 371–394.
[4] S.H. Lee, R. Blake, D.J. Heeger, Traveling waves of activity in primary visual cortex during binocular rivalry, Nat. Neurosci. 8 (2005) 22–23.
[5] M. Meng, D.A. Remus, F. Tong, Filling-in of visual phantoms in the human brain, Nat. Neurosci. 8 (2005) 1248–1254.
[6] A. Polonsky, R. Blake, J. Braun, D.J. Heeger, Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry, Nat. Neurosci. 3 (2000) 1153–1159.
[7] F. Tong, S.A. Engel, Interocular rivalry revealed in the human cortical blind-spot representation, Nature 411 (2001) 195–199.
[8] D.A. Leopold, N.K. Logothetis, Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry, Nature 379 (1996) 549–553.
[9] D.L. Sheinberg, N.K. Logothetis, The role of temporal cortical areas in perceptual organization, Proc. Natl. Acad. Sci. USA 94 (1997) 3408–3413.
[10] R. Blake, D. Westendorf, R. Fox, Temporal perturbations of binocular rivalry, Percept. Psychophys. 48 (1990) 593–602.
[11] J.M. Wolfe, Reversing ocular dominance and suppression in a single flash, Vision Res. 24 (1984) 471–478.
[12] P. Walker, D.J. Powell, The sensitivity of binocular rivalry to changes in the nondominant stimulus, Vision Res. 19 (1979) 247–249.
[13] H.R. Wilson, R. Blake, S.H. Lee, Dynamics of travelling waves in visual perception, Nature 412 (2001) 907–910.
[14] R. Kanai, F. Moradi, S. Shimojo, F.A. Verstraten, Perceptual alternation induced by visual transients, Perception 34 (2005) 803–822.
[15] S.H. Lee, R. Blake, D.J. Heeger, Hierarchy of cortical responses underlying binocular rivalry, Nat. Neurosci. 10 (2007) 1048–1054.
[16] W.J. Levelt, Binocular brightness averaging and contour information, Br. J. Psychol. 56 (1965) 1–13.
[17] J.A. Movshon, P. Lennie, Pattern-selective adaptation in visual cortical neurones, Nature 278 (1979) 850–852.
[18] F. Sengpiel, C. Blakemore, Interocular control of neuronal responsiveness in cat visual cortex, Nature 368 (1994) 847–850.
[19] F. Sengpiel, C. Blakemore, R. Harrad, Interocular suppression in the primary visual cortex: a possible neural basis of binocular rivalry, Vision Res. 35 (1995) 179–195.
[20] J. Pearson, C.W. Clifford, Suppressed patterns alter vision during binocular rivalry, Curr. Biol. 15 (2005) 2142–2148.
[21] L.A. Gilroy, R. Blake, The interaction between binocular rivalry and negative afterimages, Curr. Biol. 15 (2005) 1740–1744.
[22] R. Blake, D. Tadin, K.V. Sobel, T.A. Raissian, S.C. Chong, Strength of early visual adaptation depends on visual awareness, Proc. Natl. Acad. Sci. USA 103 (2006) 4783–4788.
[23] N. Tsuchiya, C. Koch, Continuous flash suppression reduces negative afterimages, Nat. Neurosci. 8 (2005) 1096–1101.
[24] T.A. Carlson, S. He, Visible binocular beats from invisible monocular stimuli during binocular rivalry, Curr. Biol. 10 (2000) 1055–1058.
[25] H.R. Wilson, Computational evidence for a rivalry hierarchy in vision, Proc. Natl. Acad. Sci. USA 100 (2003) 14499–14503.
[26] A.W. Freeman, Multistage model for binocular rivalry, J. Neurophysiol. 94 (2005) 4412–4420.
[27] L.C. van Dam, R. van Ee, The role of saccades in exerting voluntary control in perceptual and binocular rivalry, Vision Res. 46 (2006) 787–799.