# Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry

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**During binocular rivalry, two incompatible monocular images compete for perceptual dominance, with one pattern temporarily suppressed from conscious awareness. We measured fMRI signals in early visual cortex while subjects viewed rival dichoptic images of two different contrasts; the contrast difference served as a 'tag' for the neuronal representations of the two monocular images. Activity in primary visual cortex (V1) increased when subjects perceived the higher contrast pattern and decreased when subjects perceived the lower contrast pattern. These fluctuations in V1 activity during rivalry were about 55% as large as those evoked by alternately presenting the two monocular images without rivalry. The rivalry-related fluctuations in V1 activity were roughly equal to those observed in other visual areas (V2, V3, V3a and V4v). These results challenge the view that the neuronal mechanisms responsible for binocular rivalry occur primarily in later visual areas.**



When dissimilar images are shown to the two eyes, one experiences binocular rivalry: one eye's view dominates for several seconds, only to be replaced in conscious awareness by the other eye's view. What makes rivalry remarkable is the dissociation between a constant physical stimulation and fluctuating perceptual experience. Because of this dissociation, binocular rivalry presents an opportunity for studying visual awareness.

Several computational models posit a special role for primary visual cortex (V1) in triggering the perceptual alternations during binocular rivalry[1–4]. The published data concerning the role of V1 in binocular rivalry are, however, inconclusive. Results from a series of electrophysiology experiments on awake, behaving monkeys suggest that the neuronal mechanisms governing binocular rivalry take place primarily in later visual areas[5–9]. These experiments measured the percentage of neurons in each of several visual areas that modulated their firing rates with the monkeys' perceptual alternations during binocular rivalry. This number increased progressively across a hierarchy of cortical visual areas: approximately 20% in early cortical visual areas (V1/V2), approximately 40% in intermediate cortical visual areas (MT and V4), and approximately 90% in later cortical areas (IT). The results from the different areas were, however, obtained with different stimuli and thus may not be directly comparable. In addition, some V1 neurons exhibited strong firing rate modulations during binocular rivalry (for example, Fig. 23 from ref. 7 and Allman, personal communication); there are several reasons to believe that the results, as reported, may have underestimated the possible role of V1 in rivalry (Discussion). Single-cell electrophysiological recordings in anesthetized cats, although initially interpreted as evidence in support of a special role for V1 in rivalry[10,11], have since been reinterpreted as supporting the opposite conclusion[12]. Further studies in awake cats found that although the synchronous activity of a population of V1 neurons correlated with perception during rivalry, the mean firing rates of individual neurons did not fluctuate during rivalry[13,14]. However, those studies were done on animals with induced strabismus and, therefore, abnormal binocular vision.

Neuronal correlates of rivalry have been measured in humans using visual-evoked potentials (VEP; for example, ref. 15) and magnetoencephalography (MEG)[16,17]. These studies reported strong fluctuations in the VEP and MEG signals using sensors placed over posterior (occipital) areas, but it was not possible to pinpoint the precise visual area(s) from which those signals arose. Another VEP study inferred the involvement of V1 in rivalry based on the early component of the VEP signals[18], but the inference about spatial localization from the timing of VEPs is uncertain. Functional magnetic resonance imaging (fMRI) studies have demonstrated a correlation between fluctuations in perception during rivalry and activity in several areas of the human brain[19–21]. However, these studies could not assess the potential involvement of V1 in rivalry because the rival images they used were not designed to evoke differential levels of activity in V1.

We used fMRI to measure fluctuations in cortical activity that correlated with the perceptual alternations during binocular rivalry. We measured V1 activity while subjects viewed a pair of rival grating patterns presented to the two eyes, one higher in contrast than the other. From earlier work, we know that fMRI responses in V1 increase monotonically with stimulus contrast (for example, ref. 22), hence the magnitude of the fMRI signal can serve as a 'tag' for the V1 representations of the two monocular gratings. We found that fMRI responses in V1 fluctuate strongly with the perceptual alternations between the higher and lower contrasts.

**Table 1. Stimulus conditions and perceptual dominance.**

| Subject | Stimulus | Contrast (percent) | Mean luminance (cd/m$^2$) | Spatial frequency (c/deg) | Temporal frequency (Hz) | Speed (deg/s) | Mean dominance (s) | Predominance (percent) |
|---|---|---|---|---|---|---|---|---|
| AH | contrast | 13 | 3.39 | 0.5 | 1.5 | – | 3.3 | 36 |
| | reversing | 50 | 4.07 | 0.5 | 1.5 | | 4.0 | 41 |
| AP | contrast | 10 | 3.23 | 0.5 | 1.5 | – | 2.6 | 32 |
| | reversing | 40 | 3.81 | 0.5 | 1.5 | | 4.1 | 49 |
| AP | moving | 10 | 3.23 | 0.4 | – | 2.5 | 2.2 | 33 |
| | | 40 | 3.81 | 0.4 | | 1.5 | 2.7 | 39 |
| RB | moving | 8 | 3.43 | 0.55 | – | 3 | 5.7 | 37 |
| | | 32 | 3.28 | 0.4 | | 1.5 | 6.8 | 53 |

Predominance is the percentage of time that the subject reported perceiving each of the two stimuli. Note that the percentages of predominance of the two images do not add up to 100%; subjects perceived a mixture of images during the remainder of the time.

## RESULTS

### Rivalry experiment

Stimuli were sinusoidal gratings, either moving or contrast-reversing, appearing within an annular region centered around a foveal fixation mark. The two monocular images (**Fig. 1a**) were of different orientations, colors and contrasts in the two eyes (non-dominant eye, vertical, red, lower contrast; dominant eye, horizontal, green, higher contrast). The orientation difference was the essential feature for inducing rivalry, without which the two images would fuse. The gratings changed over time (moving and contrast-reversing) to maintain a uniform level of light adaptation. The moving gratings alternated direction every two seconds to eliminate motion aftereffects. When viewing rival stimuli, one sometimes perceives piecemeal dominance, a dynamic patchwork with parts of one stimulus visible in some subregions and parts of the other visible in the remaining subregions. The color difference between the two images, along with the narrow annulus and relatively low mean luminances, all helped to minimize the periods of piecemeal dominance[23,24].

We chose the higher and lower contrast levels separately for each subject (**Table 1**), based on psychophysical pilot data, to maximize the difference between the two contrasts (and hence, the associated fMRI signals) while maintaining sufficiently long and stable periods of dominance. The other stimulus parameters (for example, mean luminance in each eye, spatial frequencies and speeds of the moving gratings) were chosen in an attempt to equate the predominance of the higher- and lower-contrasts (**Table 1**).

While in the scanner, subjects pressed one button to indicate when they perceived the higher-contrast green grating, and a second button to indicate when they perceived the lower-contrast red grating. Subjects were instructed to press a third button when less than 75% of the stimulus annulus corresponded to a homogeneous percept of either the higher- or lower-contrast, during transitions between the two percepts or during piecemeal dominance.



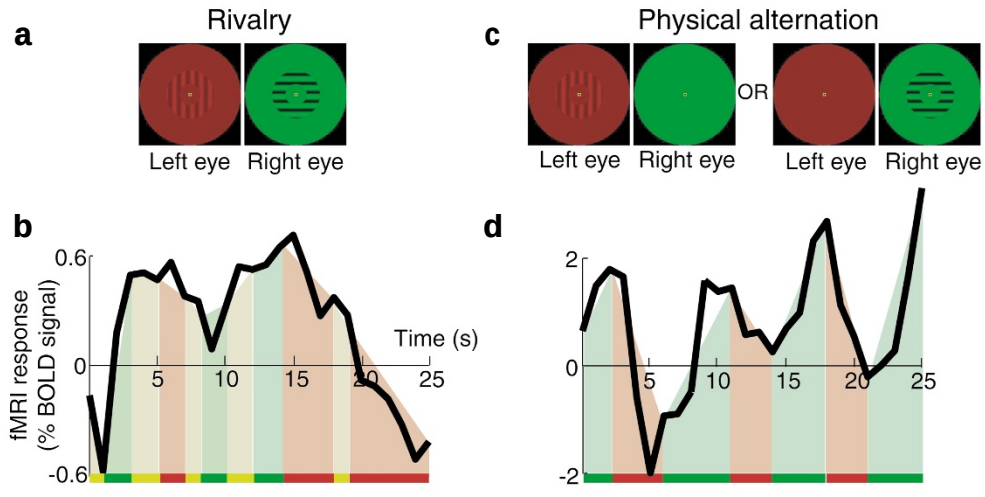


**Fig. 1.** Experimental design. Stimuli were sinusoidal gratings (**Table 1**), either moving (alternating direction of motion every 2 seconds, asynchronously in the two eyes) or contrast-reversing (90° out of phase in the two eyes), and restricted to a peripheral annulus (2.4–5.4°) of the visual field. (**a**) Rivalry experiments. Stimuli were presented continuously to both eyes throughout each fMRI scan. Non-dominant eye: lower contrast, vertical, red-black grating. Dominant eye: higher contrast, horizontal, green-black grating. Some readers can 'free-fuse' the boundary contours of the two images to experience rivalry between the gratings. (**b**) V1 activity and subject's percept, excerpted from one rivalry scan. Red and green bars indicate, respectively, periods of dominance by the red and green monocular images. Yellow bars indicate periods during which the percept was ambiguous or inhomogeneous. The perceptual time course has been delayed relative to the fMRI signal to compensate for the hemodynamic delay. (**c**) Physical alternation experiments. Stimuli alternated between two dichoptic displays, each with a grating presented to one eye and a uniform field presented to the other eye. Contrasts, colors and mean luminances were the same as in the rivalry experiments. (**d**) V1 activity and subject's percept, excerpted from one physical alternation scan (same format as in **b**).

The time course of the fMRI signal recorded in V1 correlated strongly with the subjects' reported percepts. V1 activity tended to increase when subjects reported seeing the higher contrast green grating, and the activity tended to decrease when they reported seeing the lower-contrast red grating (**Fig. 1b**). We averaged the time courses of the fMRI signals following each transition to the higher contrast percept and, separately, the time courses following each transition to the lower contrast percept. V1 responded differentially following the perceptual alternations during binocular rivalry (**Fig. 2a**). These differences were statistically significant ($p < 0.05$, one-tailed $t$-test) for at least 5 of the 8 data points in each panel of Fig. 2a.

### Physical alternation experiment

Just how large are these fluctuations in the fMRI signal during rivalry? For comparison, we did a separate series of scans measuring V1 activity while the stimuli physically alternated between the two monocular gratings (**Fig. 1c**). The duration of each stimulus presentation was determined by randomly sampling from the distribution of durations reported (via the subject's button presses) during the rivalry scans. To maintain attention and engage the same motor responses, subjects again pressed buttons to indicate which grating was visible. Because only one monocular grating was displayed at a time, it was always visible, and there was no rivalry. As expected based on previous reports (for example, ref. 22), V1 activity followed the stimulus alternations, increasing when the higher-contrast grating was present and decreasing when the lower-contrast grating was present (**Figs. 1d** and **2b**).

### Rivalry versus physical alternation in V1

To quantitatively compare V1 activity under these two physically different but perceptually similar conditions, we fitted the data with a model (**Fig. 2**, solid curves). The model (Methods) was used to estimate two parameters, separately for each of the rivalry and physical alternation data sets: first, the state amplitude (**Fig. 3a**), that is, the difference between the response levels for the two (high- and low-contrast) perceptual states, and second, the transition amplitude (**Fig. 3b**), the amplitude of the transient responses during transitions. The model fits were very good (**Fig. 2**); even though there were only two free parameters for each panel of the figure, the model accounted for 80–98% of the variance in the data. With this model, the state amplitudes evoked in V1 during rivalry were 45–83% as large as those evoked during physical alternation (**Table 2**).

To ensure that our conclusions did not depend critically on the assumptions of the model, we did a complementary analysis, fitting (weighted least-squares) a pair of lines passing through the origin to the rivalry and physical alternation data, separately for each panel of Fig. 2. This analysis (**Table 3**) produced similar state amplitudes to the model fits (**Table 2**).

### Transitions

Previous fMRI studies show that activity in several human cortical areas reflects transitions between percepts rather than the percepts themselves[20,21]. Our measurements also reveal these transition responses, superimposed with the fluctuations in activity between the two (high and low contrast) states. The transition amplitudes in V1 (**Fig. 3b**) were statistically significant for physical alternation ($p < 0.05$; one-tailed $t$-test), but not for rivalry ($p = 0.15$, one-tailed $t$-test). Even so, the transition amplitudes in V1 during physical alternation were not significantly larger than during rivalry ($p = 0.10$; one-tailed paired $t$-test).

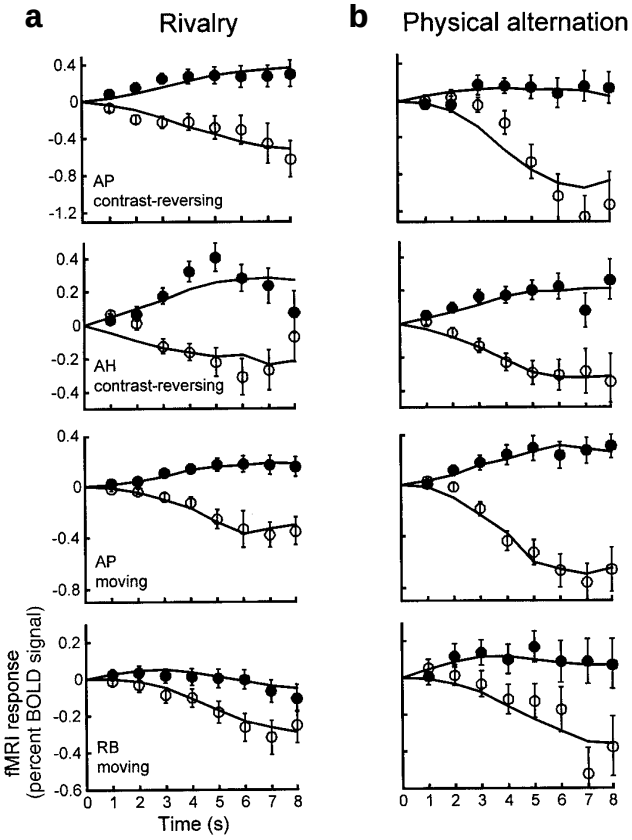


**Fig. 2.** V1 activity correlates with the percept. (**a**) Rivalry experiments. V1 activity averaged separately for epochs during which the subjects reported seeing the lower (open circles) and the higher (filled circles) contrasts. Error bars represent one standard error of the mean. (**b**) Physical alternation experiments. V1 activity evoked by physical alternation of the two monocular gratings (same format as in **a**). Solid curves represent the model fits (Methods).

### Extrastriate visual cortex

The data were analyzed separately in secondary cortical visual areas V2, V3, V4v and V3a, but because of the slice selection, we did not have complete data sets in all visual areas for all subjects (**Fig. 3**; **Tables 2** and **3**). The response fluctuations during rivalry, when expressed as a percentage of the fluctuations during physical alternation, were roughly equal in V1 and extrastriate visual areas (**Tables 2** and **3**). In particular, we did not observe a systematic increase in rivalry related activity in the later visual areas, as one might have predicted based on single-neuron electrophysiological data[6,7] (but see below for a re-analysis of the single-neuron data).

## Discussion

We found that V1 activity was coupled with the perceptual alternations during binocular rivalry. The amplitude of the fluctuations in V1 activity during rivalry was 45–83% of the amplitude evoked during physical stimulus alternation. Moreover, the fluctuations in V1 activity were roughly equal to those observed in nearby visual areas (V2, V3, V4v and V3a). These results could mean that neuronal events underlying rivalry are initiated in V1 and then propagated to later areas, or that those neuronal events

**Table 2. Rivalry versus physical alternation (model fits).**

| Subject | Stimulus | V1 | V2 | V3 | V4v | V3a |
|---|---|---|---|---|---|---|
| AH | contrast reversing | 83 | 57 | 93 | 62 | 28 |
| AP | contrast reversing | 45 | 37 | 19 | – | – |
| AP | moving | 47 | 45 | – | – | – |
| RB | moving | 48 | 30 | 26 | 39 | – |
| Group average | | 56 | 42 | 46 | 51 | 28 |

The amplitude of fluctuation in cortical activity during rivalry as a percentage of that during physical stimulus alternation.

are initiated at later stages of processing and then propagated via feedback to V1. It is also possible that both processes occur. Specifically, local interactions among V1 neurons may trigger the perceptual alternations during rivalry, whereas interactions in later visual areas may reinforce the neuronal representations of coherent percepts, just as they do during normal vision (see page 1812 of ref. 9 for a similar proposal). This proposal includes both early- and late-stage contributions to rivalry, thereby reconciling the perceptual data previously interpreted as supporting one or the other[25–29]. In any case, the neuronal events underlying rivalry are likely to be evident in the firing rates of V1 neurons, not just in synchronization of V1 activity as has been proposed[4,13,14].

It is not surprising that physical alternation evoked larger fluctuations of V1 activity than did rivalry. The responses of only a subpopulation of V1 neurons seem to correlate with perceptual fluctuations during rivalry, whereas physical alternation modulates the responses of virtually all V1 neurons. In addition, a number of psychophysical observations suggest that the physical removal of a stimulus is not the same as the phenomenal suppression of that stimulus. First, visual sensitivity is depressed only a fraction of a log-unit during suppression phases of rivalry[30–32], suggesting that suppression, unlike physical removal, does not involve the wholesale elimination of evoked neuronal activity. Second, suppressed stimuli can induce adaptation, giving rise to visual aftereffects, including the motion aftereffect[33–37]. Third, a suppressed stimulus can affect motion perception, that is, even though there is no percept of the suppressed pattern, there remains a percept of its motion[38,39]. (Indeed, subjects in our moving gratings experiments reported experiencing this phenomenon.) Finally, subjects in our experiments were instructed to report piecemeal dominance when less than 75% of the stimulus was homogeneous; hence bits of both stimuli were sometimes visible during epochs that our analysis treated as fully homogeneous.

Although attention can strongly influence fMRI measurements of V1 activity (for example, ref. 40), there is evidence that our measurements were not dominated by differential attention to the lower and higher contrasts. Subjects reported that the rival percepts were equally engaging. Furthermore, the stimuli were chosen to roughly equate predominance (**Table 1**).

Our results are comparable to previous MEG studies of human cortical activity during rivalry[16], which found that the modulation of the MEG signals evoked during rivalry is 50–85% as large as that evoked during physical stimulus alternation, comparable to the range we observed across subjects and across visual areas (**Table 2**). The specific subset of MEG channels showing such modulation, which varied from subject to subject, included occipital channels but was not restricted to them.

How do we reconcile our findings with single-neuron recordings from awake monkeys[6,7]? The electrophysiological data were originally reported as the percentage of neurons that exhibited statistically significant modulations of activity during rivalry. For example, only approximately 20% of V1 neurons exhibited a statistically significant activity modulation during rivalry. However, the fMRI signal depends not only on the number of active neurons, but also on their firing rates. To obtain a more direct comparison between the fMRI measurements and the single-neuron data, we reanalyzed the single-neuron data to compute the average firing rate modulations during rivalry and physical alternation (Methods). In V1, the average firing rate modulation during rivalry was thus found to be 33% as large as that evoked by physically alternating between the two stimulus patterns. The results in V2 and V4 were 23% and 27%, respectively. In our fMRI experiments, we obtained 56%, 42% and 51% in V1, V2 and V4v, respectively (**Table 2**, bottom row). These percentages were nearly twice as large in the fMRI data than in the single-neuron data, in all three visual areas. However, the single-neuron and fMRI results are consistent in one respect: the effects in V1 were roughly equal to those in V2 and V4.

In reanalyzing the single-neuron data, we averaged across all of the neurons from each visual area. This was appropriate for

**Table 3. Rivalry versus physical alternation (line fits).**

| Subject | Stimulus | V1 | V2 | V3 | V4v | V3a percent |
|---|---|---|---|---|---|---|
| AH | contrast reversing | 85 | 61 | 106 | 42 | 40 |
| AP | contrast reversing | 72 | 67 | 30 | – | – |
| AP | moving | 53 | 47 | – | – | – |
| RB | moving | 51 | 32 | 27 | 40 | – |
| Group average | | 65 | 52 | 54 | 41 | 40 |

The amplitude of fluctuation in cortical activity during rivalry as a percentage of that during physical stimulus alternation.

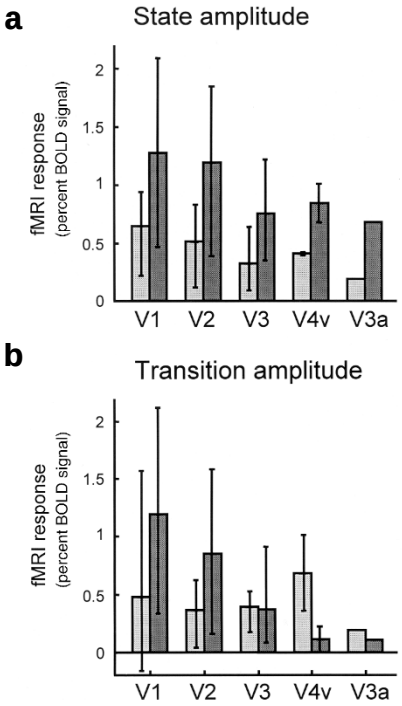


**Fig. 3.** Comparison of cortical activity during rivalry and physical alternation. (**a**) Differences between the response levels for the two (high- and low-contrast) states, averaged across subjects. (**b**) Transient responses during transitions, averaged across subjects. Light bars, rivalry. Dark bars, physical alternation. Error bars represent minimum and maximum range across subjects.

comparing fMRI responses with average firing rates, but overlooked the possibility that different neuronal subpopulations may have different roles during rivalry. Indeed, there seem to be separate subpopulations of neurons in monkey areas V4 and MT[5–7]. The responses of some neurons were correlated with the monkeys' reported percepts. The responses of other neurons were anti-correlated with the perceptual reports, responding more when the monkeys reported the non-preferred stimulus and responding less when the monkeys reported the preferred stimulus. Our fMRI measurements and our reanalysis of the single-neuron data averaged indiscriminately across these subpopulations, confounding the relative numbers of neurons in each category with their firing rates.

Given the differences between the two experimental protocols, the twofold discrepancy between the fMRI and single-neuron results can be reconciled in at least four ways. First, there may be a genuine species difference so that the effect we observed in human V1 is not as strong in monkey V1. Indeed, there are notable anatomical differences between human and monkey V1(ref. 41). Second, the interpretation of the fMRI data may be confounded given that the sequence of events from neuronal activity to fMRI response is only partially understood. For example, the fMRI signal might reflect not only neuronal firing rates but also subthreshold synaptic activity (for example, because of simultaneous excitation and inhibition, or because of cortico-cortical excitation from distant inputs) that would be invisible to the extracellular electrode. However, the available data suggest that the fMRI signal is roughly proportional to local average firing rates[22,42]. A third possible explanation for the discrepancy is that the single-neuron measurements might have underestimated the average V1 activity. The single-neuron data were collected from a relatively small sample of neurons (30 neurons in V1, 21 neurons in V2, 65 neurons in V4), whereas our fMRI measurements reflected the pooled responses of a very large number of neurons. In addition, small shifts in eye position, equal in size to the receptive fields, present a difficulty for the single-neuron experiments because the firing rates may vary substantially depending on the precise position of the stimulus within the receptive field. This is especially worrisome in the V1/V2 data that were recorded from neurons with foveal receptive fields. The receptive fields of foveal V1 neurons are typically a small fraction of a degree in diameter, smaller than the window used to control the monkeys' fixation. Small shifts in eye position do not present a difficulty in the fMRI experiments because they have a negligible effect on measurements of pooled neuronal activity. The fourth possible explanation for the discrepancy has to do with the transient, transition-related activity that we and others[20,21] have observed. We analyzed our data by segregating the transition-related responses from the state-related fluctuations in activity. The single-neuron data were analyzed within approximately one to two seconds of the transitions[6,7]. If monkeys, like humans, also showed considerable transient responses during transitions, then the single-neuron results, as analyzed, would have been confounded by these transients.

Our findings imply that in human vision, neuronal events critical for binocular rivalry are expressed as early as V1. More measurements will be required to fully reconcile the results from monkeys and humans. Ideally, one would like to replicate our human fMRI study in monkeys, and then record multi-neuron and single-neuron electrophysiological activity under the same stimulus conditions.

## Methods

The experiments were undertaken with the written consent of each subject, and in compliance with the safety guidelines for MR research, as approved by the Stanford University Panel on Human Subjects in Medical Research. The stimulus conditions for each subject were selected during pilot sessions so that the two contrasts were sufficiently different (about a factor of 4, with the higher contrast presented to the dominant eye), and that during rivalry the two stimuli had sufficiently long dominance periods (maximum dominance durations longer than eight seconds) and roughly equal predominance. This proved to be impossible for several subjects, particularly if they had a strongly dominant eye, so they were excluded from the study. The remaining subjects each participated in multiple MR scanning sessions: one session to obtain a standard, high-resolution anatomical scan, one session to functionally define the retinotopic visual areas including V1, one session to locate the subregion of each visual area that corresponded to the stimulus annulus, and several sessions to measure fMRI responses during rivalry and physical alternation.

The stimuli were presented on a flat-panel display (NEC multisynch LCD 2000, Itasca, Illinois) positioned just beyond the end of the scanner bed. The display was viewed through binoculars. A pair of angled mirrors, attached to the binoculars, enabled the subject to see the LCD display. The two monocular images were displayed on the left and right halves of the LCD display, a septum was placed near the subjects' knees, and the mirrors were adjusted so that the subject could see only one image in each eye. A bite bar was used to stabilize subjects' heads.

MR imaging was done on a standard clinical GE (Milwaukee, Wisconsin) 1.5 T Signa scanner with a custom-designed dual surface coil. The fMRI scans were done using a T2*-sensitive, gradient recalled echo, spiral pulse sequence[43]. For the experiments with contrast-reversing gratings, eight adjacent slices were selected, with the most ventral slice positioned along the boundary between the occipital lobe and the cerebellum (TR, 1 second;

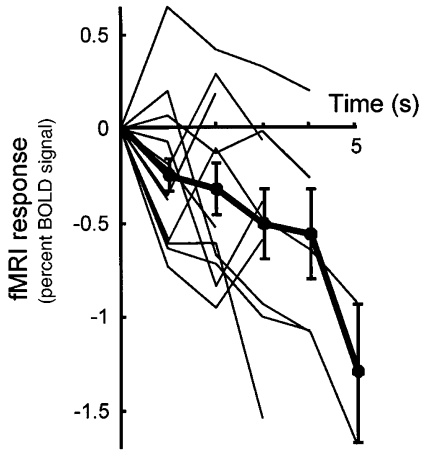


**Fig. 4.** Example of averaging across individual dominance epochs. Thin curves, fMRI signal (averaged within V1) during individual epochs of dominance by the lower-contrast stimulus. The response at the beginning of each epoch was subtracted from the time course of the signal during the rest of the epoch. Thick curve and data points, average of the individual epochs. Error bars, standard error of the mean. The average was computed over a greater number of repeated measures at short durations than at longer durations, which is reflected in the increasing size of the error bars over time.

1 interleave; TE, 40 ms; FA, 76°; inplane resolution, 3.2 × 3.2 mm; slice thickness, 4 mm). For the moving gratings, the eight slices were selected roughly orthogonal to the calcarine sulcus (TR, 0.5 seconds; 2 interleaves; TE, 40 ms; FA, 55°; inplane resolution, 3.2 × 3.2 mm; slice thickness, 4 mm).

A set of structural images was acquired during each scanning session, using a T1-weighted spin echo pulse sequence (TR, 500 ms; TE, 15 ms; FA, 90°), in the same slices and at the same resolution as the functional images. These inplane anatomical images were aligned to the high-resolution anatomical scan of each subject's brain using custom software[44], so that the functional data (across multiple scanning sessions) from a given subject were co-registered.

The fMRI data were analyzed as follows. First, the initial eight seconds of data from each scan were discarded to minimize effects of magnetic saturation and visual adaptation. Second, any residual head movements during each scan were corrected for, using custom software[44]. Third, the time-series at each voxel was divided by its mean intensity to convert the data from units of image intensity to units of fractional signal change, and to compensate for distance from the surface coil. Fourth, high-pass filtering was done to compensate for the slow signal drift in the fMRI signals[45]. Fifth, the resulting time-series were averaged over the set of voxels corresponding to the stimulus representation within V1 (and likewise for the other visual areas). Sixth, the signals were shifted in time by 1 second relative to the subjects' button presses, which, when combined with the 500–1000 ms reaction time, compensated for the hemodynamic delay. Seventh, signals were averaged following each transition to the higher-contrast percept and, separately, following each transition to the lower-contrast percept (**Fig. 4**).

We fit the data using a variant of a model described previously[20]. The time course of the fMRI signal was assumed to be proportional to the underlying neuronal activity, averaged over time by convolution with the hemodynamic impulse response. The underlying neuronal activity was assumed to fluctuate between two states corresponding to the higher and lower contrasts. Periods of piecemeal dominance were modeled as being halfway between the higher- and lower-contrast states. In addition, the model allowed for transient responses during transitions, that is, time-locked to the subjects' button presses. The model thus had two parameters: a state amplitude and a transition amplitude. A nonlinear optimization algorithm was used to determine the choices of these parameters that gave the best fit (weighted least-squares) to the data, separately for the rivalry and physical alternation experiments (**Fig. 2**). We confirmed, by sampling the two-dimensional parameter space, that the optimization algorithm achieved the global minimum.

The hemodynamic impulse response was modeled as follows:

$$h(t) = \exp(-t/\tau_1)\sin(2\pi f_1 t) - a\exp(-t/\tau_2)\sin(2\pi f_2 t)$$

In this model, $t$ was time, and $h(t)$ was normalized to have unit area so that its step response would achieve the same steady state regardless of its parameter values. Two of the parameters ($\tau_2 = 7.4$ s, $f_2 = 0.12$ Hz) were set equal to the average best-fit values from previous measurements (D. Ress, B.T. Backus & D.J.H., *Soc. Neurosci. Abstr.*, in press). Because the hemodynamic impulse response can vary across subjects[46], the other three parameters ($a$, $\tau_1$, $f_1$) were chosen separately for each subject to fit the average time series from an independent set of measurements, which were also used to localize the cortical representations of the stimulus annulus (see below). The resulting parameters were in the following ranges: $a = 0.1$–$0.12$; $\tau_1 = 7.22$–$7.27$ s; $f_1 = 0.03$–$0.05$ Hz.

Area V1 within each hemisphere was identified as a large region (200–675 mm$^3$) of gray matter in and/or near the calcarine sulcus with a retinotopic map spanning a hemifield. Following well-established methods[47], the polar angle component of the retinotopic map was measured by recording fMRI responses to a stimulus rotating slowly (like the second hand of a clock) in the visual field. To visualize these retinotopy measurements, a high-resolution MRI of each subject's brain was computationally flattened using custom software[48,49]. To be conservative, we selected the region of V1 that represented the visual field within 60° on either side of the horizontal meridian, thereby staying away from the vertical meridian representation at the V1/V2 border. Because the fMRI data recorded during successive scanning sessions in a given subject were all co-registered, we could localize V1 across scanning sessions.

A further series of measurements were used to define the subregion of V1 that represented the stimulus annulus. Subjects held fixation while the display alternated every 18 seconds between a contrast-reversing, high-contrast, plaid pattern within the 2.4–5.4° radius annulus, surrounded by a uniform (luminance-matched) gray field, and its geometric complement, a contrast-reversing plaid pattern everywhere except the annulus. Data were averaged across five to eight repeated scans, each with six cycles of alternation. Voxels were included in the final V1 region only if they were strongly correlated ($r > 0.3$ and 0–9 s time lag for subjects AH and RB; $r > 0.5$ and 0–9 s time lag for subject AP) with the stimulus alternations. Visual areas V2, V3, V4v and V3a were identified and restricted analogously.

We reanalyzed the data from Fig. 38 of ref. 7 to estimate the average firing rate modulations from their sample of V1, V2 and V4 neurons. In that figure, each data point corresponds to a single neuron. The abscissa plots a firing rate modulation index during physical alternation, and the ordinate plots the equivalent modulation index during rivalry. The firing rate modulation index was defined as $(R_p - R_n)/(R_p + R_n)$, where $R_p$ is the response to the more preferred stimulus, and $R_n$ is the response to the less preferred stimulus. The average firing rate modulation index, averaged across all V1 neurons during rivalry, was 0.10, and the average modulation index during physical alternation was 0.31. We computed the ratio between these two numbers (0.33) and reported it as a percentage (Discussion). Analogous calculations were done for V2 and V4. Assuming that the denominators $(R_p + R_n)$ were roughly equal for rivalry and physical alternation, then this calculation would give an estimate of the firing rate modulation $(R_p - R_n)$ during rivalry as a percentage of the firing rate modulation during physical alternation, averaged across the neurons in each visual area.

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