The Role of the Primary Visual Cortex in Perceptual Suppression of Salient Visual Stimuli

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The role of primary visual cortex (area V1) in subjective perception has intrigued students of vision for decades. Specifically, the extent to which the activity of different types of cells (monocular versus binocular) and electrophysiological signals (i.e., local field potentials versus spiking activity) reflect perception is still debated. To address these questions we recorded from area V1 of the macaque using tetrodes during the paradigm of binocular flash suppression, where incongruent images presented dichoptically compete for perceptual dominance. We found that the activity of a minority (20%) of neurons reflect the perceived visual stimulus and these cells exhibited perceptual modulations substantially weaker compared with their sensory modulation induced by congruent stimuli. Importantly, perceptual modulations were found equally often for monocular and binocular cells, demonstrating that perceptual competition in V1 involves mechanisms across both types of neurons. The power of the local field potential (LFP) also showed moderate perceptual modulations with similar percentages of sites showing significant effects across frequency bands (18–22%). The possibility remains that perception may be strongly reflected in more elaborate aspects of activity in V1 circuits (e.g., specific neuronal subtypes) or perceptual states might have a modulatory role on more intricate aspects of V1 firing patterns (e.g., synchronization), not necessarily altering the firing rates of single cells or the LFP power dramatically.

Introduction

The use of visual stimuli that induce bistable perception has been established as a classical paradigm to identify the neural circuits subserving subjective perception (Attenave, 1971; Rock et al., 1994; Logothetis, 1999). A celebrated example of such a perceptual phenomenon is binocular rivalry (BR), involving alternations of visual perception between two different images presented dichoptically at corresponding retinal locations (DuTour, 1760; Wheatstone, 1838; Breese, 1899, 1909).

The primary visual cortex (V1) was implicated as an important candidate for the site of perceptual suppression during BR based on numerous psychophysical studies (Abadi, 1976; Cogan, 1987; Blake, 1989; Blake et al., 2006). In particular, competition between monocular channels offered a straightforward mechanism for the suppression of one of the two stimuli (Lehky, 1988). However, neurophysiological results in monkeys did not corroborate this hypothesis, but instead provided evidence for competition primarily between neurons in areas beyond V1 and specifically areas V4, V5/MT and IT (Logothetis and Schall, 1989; Leopold and Logothetis, 1996; Steinberg and Logothetis, 1997). Moreover, a set of intriguing human psychophysical results conjectured that BR may involve competition between alternative higher-level stimulus perceptual interpretations (Diaz-Caneja, 1928; Kovács et al., 1996; Logothetis et al., 1996) similar to other bistable stimuli (e.g., necker cube) that do not involve interocular competition (Blake and Logothetis, 2002). Yet, subsequent studies using functional magnetic resonance imaging (fMRI) in humans, provided evidence that activity in V1 is robustly modulated by the subjective percept supporting the ocular competition hypothesis (Polonsky et al., 2000; Tong and Engel, 2001). These results engendered an apparent controversy between human fMRI and monkey electrophysiological recordings. Given the relationship between the BOLD signal and the LFP (Logothetis et al., 2001; Goense and Logothetis, 2008), one could speculate that the robust perceptual modulations reported in human fMRI studies may also be reflected in LFP signals. To this end, recent studies using the paradigm of generalized flash suppression (GFS) implicated that low-frequency LFPs show stronger modulations with perception compared with single-unit activity and high-frequency LFP (Wilke et al., 2006; Maier et al., 2008). Importantly though, GFS does not involve interocular competition like BR.

Here we undertook a study to characterize in detail and compare the extent to which different electrophysiological signals (spiking activity and various LFP frequency bands) are modulated by perception under conditions of interocular competition. We also tested directly the conjecture that monocular neurons in...
by intravenous injections of fentanyl (0.003 mg/kg), trapanal (5 mg/kg) and lysthenol (3 mg/kg). During surgery, the animals received balanced anesthesia consisting of isoflurane 1.3%. The surgical procedures are described in detail previously (Logothetis et al., 2002). All recordings were conducted with tetrodes attached to microdrives that could be manually adjusted independently. For the chronic recordings, neural activity was recorded using a custom-built array of tetrodes (Tolias et al., 2007). The distance between nearby tetrodes was 200 μm. For the nonchronic recordings, one to four (in most sessions) manually adjustable microdrives (Crist Instrument Co.) were inserted into a custom-built grid and activity was recorded using tetrodes.

Multiunit and single-unit activity was sampled at 32 kHz, digitized (12 bits), and stored using the Cheetah data acquisition system (Neuralynx). LFP signals were recorded by filtering the raw voltage signal using analog bandpass filtering (high-pass set at 1 Hz and low-pass set at 475 Hz) and digitized at 2 kHz (12 bits). Multiunit activity was defined as the events that exceeded a predefined threshold (25 μV) of the filtered, digitized signal (analog filtering high-pass set at 600 Hz and low-pass set at 6 kHz and digitized at 32 kHz, 12 bits). Single units were isolated using a custom-built offline clustering system working on features extracted from the recorded waveforms (Tolias et al., 2007). No preselection functional criteria were applied for the neurons. Details of single-unit isolation methods have been described previously (Tolias et al., 2007).

The animals were implanted with a scleral search coil (Robinson, 1963; Judge et al., 1980) and their eye movements were monitored on-line. Data were also collected for off-line analysis using both the QNX-based data acquisition system at 200 Hz and the Cheetah data acquisition system at 2000 Hz.

**Visual stimulation and behavioral paradigm.** Visual stimuli were displayed using a dedicated graphics workstation (TDZ 2000; Intergraph Systems) running an OpenGL-based stimulation program. Stimuli were presented dichoptically by using a custom-made stereotype with two LCD monitors at both sides running at a resolution of 1280 × 1024 and a refresh rate of 60 Hz. The behavioral aspects of the experiment were controlled using the QNX real-time operating system (QNX Software Systems Ltd).

At the beginning of each session, the mirror stereoscope was positioned in front of the monkeys’ head and two circular apertures were aligned with the animal’s eyes. These apertures served to limit the visual field to the central 15° of visual angle and prevented nasal viewing of the opposite display. In succession, we calibrated the monkeys’ eye movements using a fixation-saccade task. To ensure that the two displays were correctly aligned in front of the two eyes we used the following procedure. First we calibrated the left eye alone while the right eye display was kept blank. The animal had to fixate briefly on a central fixation spot (1°) and then perform a saccade to a second fixation spot on the periphery randomly in eight different directions (Δθ = 45°). After successful acquisition of the presented saccadic locations, the amplitude of the saccades was increased until the monkey failed, in this way mapping exactly the visible portion of the monitor. When the first eye was fully calibrated we switched to an iterative procedure between the two eyes: first the central fixation spot was presented briefly to the left eye. After the monkey acquired fixation, it was switched off and switched on in the right eye. If the monkey could not fuse (i.e., directly overlay the two stimuli) he performed a saccade to a new location. The monitoring system estimated the amplitude of his saccade by calculating the difference between the two fixations and moved the location of the right eye fixation in the opposite direction for the following trial. Usually after a few trials of calibration (typically four to five) the monkeys were able to fixate the target continuously (although it was switched between the eyes) and we concluded that they could correctly overlay (fuse) the two displays. The fixation-saccade procedure was then performed for the right eye alone with all the targets displaced according to the offset values registered in the previous eye-switching procedure. Finally, we checked the calibration with both displays on. The full calibration described above was performed additionally at the end of the experiments and sometimes between the sessions to ascertain that the two displays remained correctly aligned. During calibration, the monkey received a drop of juice at end of each trial.
A experimenter could evaluate the gross location of the receptive fields and were put through a sound amplifier (Grass Technologies) so that the key kept fixating the central target. The multiunit responses of the cells position, size and orientation could be changed manually while the monkeys were presented parafoveally while the monkey fixated a central target for 2–3 s. These gratings were presented binocularly and their movements were presented parafoveally while the monkey fixated a central target for 300 ms and then a circular sinusoidal grating stimulus was presented parafoveally for 1 s in one of the two eyes. In succession, a grating with orthogonal orientation to the initially presented one was shown in a corresponding location in the opposite eye while the first grating remained on the display for another second. During this binocular presentation period, the newly appearing grating is invariably perceived while the simultaneously presented grating in the opposite eye is extinguished from perception.

After eye calibration and alignment of the displays, a coarse receptive field mapping was performed to position the stimulus for the experiments. Oriented gratings (similar to the ones used in the BFS experiments) were presented parafoveally while the monkey fixated a central target for 2–3 s. These gratings were presented binocularly and their position, size and orientation could be changed manually while the monkey kept fixating the central target. The multiunit responses of the cells were put through a sound amplifier (Grass Technologies) so that the experimenter could evaluate the gross location of the receptive fields and the orientation preferences of the multiunit responses. The pair of orthogonal orientations exhibiting maximal differential multiunit responses was then selected to be used in the BFS experiments. We will further refer to these two orthogonal orientations as $\theta$ and $\theta_{\text{orth}}$. In a subset of experiments for which more than one tetrode was used, the stimulus optimization was typically performed separately for each site.

To study the relationship between neural activity and perception, we used the paradigm of BFS. In this case, two rivalrous patterns are presented dichoptically and asynchronously to the two eyes. Under these conditions, the latter pattern dominates perceptually over the first, provided the two differ sufficiently in their structure (Wolf, 1984). Several studies have shown that BFS is intimately related to BR at the psychophysical level. Specifically, the results of several parametric manipulations of BFS suggested a common mechanism between BR and BFS. Moreover, forward masking or simple light adaptation are not thought to underlie the perceptual suppression during BFS (Wolfe, 1984; Blake et al., 1990; Baldwin et al., 1996; Kreiman and Koch, 1999; Kreiman, 2001; Kreiman and Koch, 2002; Kreiman et al., 2007). A recent study (Tsuchiya et al., 2006) compared the depth of suppression for BR and BFS by using a probe detection task and found that BFS induces a transient increase of suppression up to 300 ms after the flash but then suppression becomes at the same level as in the case of BR (to avoid this transient effects of BFS in our study we excluded the first 500 ms after the flash). Based on this evidence, the authors argue that the two paradigms are based on the same mechanism of perceptual suppression. Similarly, a computational modeling study (Nichols and Wilson, 2009) demonstrated that the differences between the techniques can be attributed to the sustained versus transient stimulation rather than a difference in the mechanism of perceptual suppression. Therefore, BFS is thought to involve a temporary burst of inhibition at the onset of the flash that might be critical for the perceptual switch (Macknik and Livingstone, 1998; Macknik et al., 2000) but it is certain that BR prevails after a short delay and the subjects experience spontaneous alternations.

We used the following experimental paradigm in our experiment: after the monkey acquired fixation on a colored square target (0.2°) for 300 ms, static, sine-wave grating stimuli were presented dichoptically to the two eyes. Typically the size of the gratings was 1–2° in diameter, the spatial frequency 3–5 cycles per degree and the contrast 70%. During BFS, a grating stimulus was displayed for 1 s monocularly to the left or the right eye followed by the onset of a second orthogonal grating (“the flash”) to the corresponding location in the other eye for another second without removal of the first grating resulting in a binocular incongruent condition (Fig. 1). The 1 s initial monocular presentation reliably biases the perception toward the second grating flashed during the binocular presentation. At the end of each successful trial, a drop of apple juice was delivered to the animal as a reward. For the physical alternation condition, the trials started in the same way with a 300 ms fixation and a monocular presentation of a grating stimulus for 1 s. Then, similar to the BFS trials, a second orthogonal grating was presented in the second eye but the first grating was removed upon presentation of the second (Fig.

Figure 1. Illustration of the binocular flash suppression (BFS) behavioral paradigm. A. An example of two conditions for which the subject experiences different percepts (a horizontal or a vertical grating) although the exact same stimuli are shown in the two displays during the binocular period of presentation. In each condition, the subjects had to initially fixate a small red target at the center of the display for 300 ms and then a circular sinusoidal grating stimulus was presented parafoveally for 1 s in one of the two eyes. In succession, a grating with orthogonal orientation to the initially presented one was shown in a corresponding location in the opposite eye while the first grating remained on the display for another second. During this binocular presentation period, the newly appearing grating is invariably perceived while the simultaneously presented grating in the opposite eye is extinguished from perception. B. Battery of conditions used in our experiments. Note that in different sessions we have used different pairs of orthogonal orientations, not only horizontal and vertical as depicted here. The pair of conditions described above in A are depicted here in the diagrams 1–2. They compose one of two stimulus configurations that allow comparison of the exact same stimuli (which lead to different percepts) during the binocular presentation period. In the second configuration (diagrams 3–4), identical stimuli are presented with reversed eye of presentation. Each BFS condition (1–4) can also be compared with a “control” physical alternation condition (5–8), which demonstrates an identical perceptual experience without binocular conflict. In these conditions, the first grating is simply removed on presentation of the second. In each diagram, the leftward pair of displays represents the monocular period and the rightward the binocular. The green dots denote the grating that was perceived during the binocular period.

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Importantly, this resulted in no binocular incongruence but to a simple successive presentation of the two orthogonal orientation gratings in opposite eyes. These conditions mimic the perceptual experiences of the subjects during BFS without introducing binocular conflict and therefore are termed “physical alternation.” During presentation of the stimuli, the monkey had to keep fixating within a circular window with a radius of 0.5° from the center of the colored fixation target; failure to do so resulted in abortion of the trials and no juice reward.

After the end of all recording sessions, one of the animals (D98) was trained to directly report its perception during the presentation of the stimuli by holding one of two levers. The left lever corresponded to the perception of one orientation (135°) while the right lever to the perception of the orthogonal (45°). During training, the animal was solely presented with physical alternation trials (i.e., without incongruence) and the two orthogonal orientations were switched at intervals drawn from a gamma distribution given by the following:

$$f(x; \lambda, r) = \frac{x^{r-1} e^{-\lambda x}}{\Gamma(r)} \lambda^r,$$

with parameters $\lambda = 8.3$ and $r = 7.2$ that were identical with the ones calculated for monkeys reporting binocular rivalry (Leopold and Logothetis, 2001).
Trials started with the presentation of a fixation target for 300 ms after which one of the stimuli (pseudorandomly selected) was presented parafoveally. At the onset of the stimulus and after every stimulus switch, the animal was expected to press the correct lever within a maximum response time of 1 s or else the trial was considered incorrect and aborted. After pressing the correct lever, the animal had to keep holding the lever either up to the next stimulus switch (for which it was required to change its response) or until the end of the trial which was signified with the removal of the stimulus. If the animal responded correctly and kept his gaze within a window of ±0.5° around the fixation target for the whole interval, the trial was considered correct and the animal received a small amount of apple juice as a reward. Correct trials ended after a minimum prespecified time (typically 4 s) was crossed by the last stimulation interval, which was not interrupted until its completion (stimulation intervals were drawn from a gamma distribution as above). This resulted in trials of variable durations (depending on the duration of the last alternation period) and variable number of alternation periods. Typically, trials lasted 4–6 s and the animal had to report two to five stimulus switches. Importantly, in this stimulation scheme stimulus switches were unpredictable to the animal. When the animal reached a performance level of >95% correct responses, we gradually started presenting it to a small percentage (<25%) of incongruent stimulation trials randomly interleaved with the physical alternation trials. The incongruent stimulation trials started with a monocular presentation of one of the orthogonal gratings for 1 s after which the second orientation grating was switched on in the opposite eye without removal of the first grating. Note that this presentation is identical to the BFS presentation we have used during the recording sessions. During those sessions, the stimulus presentation lasted for 2 s (1 s monocular and 1 s binocular). For these experiments, the binocular stimulus presentation was extended to longer periods (as much as the minimum time of the physical alternation trials—typically 4 s) in contrast to the 1 s used for the BFS recordings. This was intentionally designed to allow the animal to respond to potential spontaneous perceptual reversals following the induced reversals, which we expected to happen shortly after the “flash” of the second stimulus. During the binocular stimulus presentation, the animal was allowed to press any of the two levers and to change its response from one to the other lever an arbitrary number of times. Similar to the physical alternation trials, we required that it did so within a maximum interval of 1 s, or else the trial was considered incorrect and aborted. If the animal followed the above criteria for the whole duration of the stimulation interval we considered the trial as correct and the animal was rewarded with a small amount of juice as in the physical alternation trials.

Statistical and data analysis. Custom programs written in Matlab (MathWorks) were used for data analysis. Statistical significance of sensory and perceptual modulations was assessed by using a nonparametric Wilcoxon rank sum test (also referred to as the Mann–Whitney U test) that performs a two sided test of the null hypothesis that the data of two conditions are independent samples from identical continuous distributions with equal medians, against the alternative that they do not have equal medians. Since for every neuron or recording site we presented two different configurations of the stimuli according to the eye of presentation, we tested each configuration independently and then we corrected for multiple comparisons using a Bonferroni correction. We considered a neuron/site to show significant sensory/perceptual modulations when at least one of the pairs of conditions tested achieved a significance level \( p \) (Bonferroni corrected) smaller than the critical significance level \( \alpha \) (\( \alpha = 0.05 \)). For all of our comparisons, we excluded the first 500 ms of the responses to avoid effects biased to the initial transients. As a result, we usually used the last 500 ms of each condition that effectively reflected the sustained part of the responses.

The preference/modulation index was computed using \( d' \) that is related to the discriminability of the two conditions and is defined as follows:

\[
d' = \frac{\mu_A - \mu_B}{\sigma}
\]

Here \( \mu_A \) and \( \mu_B \) denote the mean responses to the two conditions being compared and \( \sigma = \sqrt{\frac{\sigma_1^2 + \sigma_2^2}{2}} \) is the pooled variance of the two response distributions. For our purpose, \( d' \) indices were calculated either for pairs of monocularly presented orientation gratings (referred to as sensory or physical preference \( d' \)), or under the dichoptic presentation of two incongruent orthogonal gratings each perceived at a time (referred to as perceptual preference \( d' \)). Ocularity preference was calculated by comparing the monocular responses of the preferred orientation across the two eyes. We have always used right eye as condition A therefore responses were positive for right-eye selective sites and negative for left eye selective sites. The orientation preference for each cell was defined as the \( d' \) value between the two orthogonal orientations presented to the preferred eye. Similarly, perceptual modulation was defined as the \( d' \) value between the binocular incongruent conditions with the same stimuli and different percepts (Fig. 1).

The percentages of perceptual modulations in different classes of neurons were compared by using a \( \chi^2 \) test for homogeneity (also referred to as contingency table analysis) by using the following formula:

\[
\chi^2 = \sum \sum \frac{(f_{ij} - \hat{f}_{ij})^2}{\hat{f}_{ij}}
\]

In this formula, \( f_{ij} \) refers to the frequency expected in a row \( i \) column \( j \) if the null hypothesis (i.e., that the percentage is independent of class) is true. We analyzed the modulations across ocularity and orientation pref-
Perceptual Suppression in V1

The sensory preference (time window 500–1000 ms) was calculated for all visually responsive neurons, with a corresponding perceptual preference calculated because of orientation or ocularity preference, or a combination of both. A corresponding sensory preference (between orthogonal gratings in opposite eyes) can be because of orientation or ocularity preference, or a combination of both. A corresponding perceptual preference was calculated using a $d'$ index during the binocular presentation of the two gratings (time window 1500–2000 ms). Positive values indicate that the response of the neuron was greater during presentation/perception of the orthogonal orientation $\theta_{\text{ori}}$. Red filled circles correspond to the neurons that showed significant perceptual modulations (Wilcoxon rank sum test, $\alpha = 0.05$) in at least one of the two configurations. A Pearson correlation coefficient was calculated for the whole population of visually responsive (VR) cells as well as for the subset of perceptually modulating cells (PM) and are presented with their $p$ values at the upper left part of the plot in black and red, respectively. The inset at the lower right presents a bar plot of the mean absolute $d'$ versus $d'$ values at the upper left part of the plot in black and red, respectively. The inset at the lower right presents a bar plot of the mean absolute $d'$ versus $d'$ values at the upper left part of the plot in black and red, respectively. The inset at the lower right presents a bar plot of the mean absolute $d'$ versus $d'$ values at the upper left part of the plot in black and red, respectively.

Eye movement analysis. We first calculated the time series of eye-velocities by differentiation of the position signals. Then, the horizontal and vertical angular velocities were independently thresholded at seven times their median-based SD to detect putative microsaccades events. An event was classified as a microsaccade if the following additional criteria were satisfied: (1) it had a minimum duration of 8 ms, (2) it had an amplitude between 1 and 60 min of a degree, and (3) it had a maximum peak-velocity of 110° per second (Engbert and Kliegl, 2003). These parameters provided a fairly accurate detection of microsaccades according to visual inspection of the results (see for example supplemental Fig. 1A,B, available at www.jneurosci.org as supplemental material). In addition, the extracted microsaccades satisfied the main-sequence criterion and showed high correlation of amplitude and velocities (supplemental Fig. 1D, available at www.jneurosci.org as supplemental material). Fixation locations were extracted as the mean positions between saccades (supplemental Fig. 1A–C, available at www.jneurosci.org as supplemental material) and the microsaccade directions were calculated from the initial and final positions of the eye during a microsaccade event. Finally, we used the onset time of microsaccades to calculate microsaccadic rates over time. Statistical analysis was performed on a dataset by dataset basis and compared the distributions of the extracted eye-movement parameters (fixation locations, microsaccade amplitudes, microsaccade directions and microsaccade rates) under the same conditions and times as for the electrophysiological signals. A Wilcoxon-rank sum test ($\alpha = 0.05$) was used to compare the distributions of fixation locations, microsaccade amplitudes and microsaccade rates. A circular analog of the Kruskal–Wallis test and specifically the circ_cmtest function of the CircStat Matlab toolbox (Berens, 2009) was used for microsaccade directions.

Local field potential analysis. The power spectral density (PSD) of the raw LFP signals was estimated using the multitaper method (Thomson, 1982). This method uses linear or nonlinear combinations of modified periodograms to estimate the PSD. These periodograms are computed using a sequence of orthogonal tapers (windows in the frequency domain) specified from the discrete prolate spheroidal sequences. We used an adaptive nonlinear combination of seven tapers with a time-bandwidth product (NW = 4) of four for each 500 ms data segment. This resulted in spectra with independent frequency bins with a bandwidth of 8 Hz. Average spectrograms were calculated by moving 500 ms windows with 90% overlap.

The LFP power over time was calculated by bandpass filtering the raw signal in different frequency bands. Digital filters were constructed via the Parks-McClellan optimal equiripple FIR filter design with an attenuation factor of 60 dB/Hz outside the cutoff frequencies.
Results

Perceptual modulations of single-unit activity

We recorded neuronal activity from 582 single units from three hemispheres of two awake, behaving monkeys (M. mulatta). Ninety percent (n = 523) of these cells were visually responsive (280/303 for D98 and 243/279 for F03). Activity was recorded during binocular flash suppression (BFS), a behavioral paradigm that ensures robust perceptual suppression of a monocular stimulus upon presentation of a second stimulus to the other eye after a delay (Wolfe, 1984; Sheinberg and Logothetis, 1997; Maier et al., 2007). The stimuli were positioned so that they covered the classical receptive fields of the neurons (see Materials and Methods for details).

From a total of 523 visually responsive cells, 371 (71%) showed significant sensory tuning, which we also refer to as physiological preference (Wilcoxon rank-sum test, $\alpha = 0.05$). A substantially smaller number of cells [104 neurons (20%)] exhibited significant perceptual modulation (i.e., responses modulated with subjective perception, Table 1). Moreover, only a couple of cells (three to four in each monkey) exploited perceptual modulations comparable to their physical preference (see for example Fig. 2A, D). Instead, most of the perceptually modulated cells showed substantially weaker perceptual modulations compared with their sensory preference during physical alternation (Fig. 2B, C, E, F).

Specifically, the magnitude of the average perceptual modulation across these neurons was only 27% [D98: 26%, F03: 29%] compared with the sensory preferences of these cells. Across the population of all cells showing significant physical preference (see method for details) the average magnitude of the perceptual modulation was 15% [D98: 16%, F03: 14%] (Fig. 3). The magnitude of the perceptual effect was also substantially smaller as measured by the absolute value of $d'$ indices [perceptual $d'$: 0.41 ± 0.02 (SEM), sensory $d'$: 1.48 ± 0.09 (SEM)] (Fig. 4A, inset).

We also found that the sensory and perceptual $d'$ indices were significantly positively correlated (Fig. 4A, red dots; Pearson $r = 0.62, p = 1.87 \times 10^{-23}$) demonstrating that the strength of the perceptual effect depends on the strength of sensory tuning to the stimuli. Accordingly, the great majority of perceptually modulating cells (84/104) show modulations in the same direction as their physical preference. This is in contrast to other areas like V4 and V5/MT where it was previously shown that half of the perceptually modulated cells showed higher activity during the perception of their non-preferred stimuli (Logothetis and Schall, 1989; Leopold and Logothetis, 1996). In our study, a very small number of cells ($n = 10$) showed significant perceptual modulations (Wilcoxon rank-sum test, $\alpha = 0.05$) without showing significant preference in the physical alternation conditions. The rest of the perceptually modulating cells ($n = 94$) showed significant preference during both physical and perceptual alternations (see Table 1).

Monocular and orientation preference

We found both monocular and binocular feature-selective cells to be modulated with perception. In addition, neurons that exhibited stronger orientation or ocularity tuning were more likely to show statistically significant perceptual modulations (Fig. 5). We calculated an orientation and an ocularity preference index for each cell, based on their responses to the two orthogonal gratings presented monocularly to each eye (see Materials and Details).
with orientation (Fig. 5A). Next, we tested whether the distribution of perceptually modulated cells over these two parameters was different from the distribution of all visually responsive cells. We used a Gessaman partitioning scheme to split the data into four blocks containing approximately equal numbers of cells and performed a $\chi^2$ test of homogeneity for these different subpopulations. This type of analysis (Fig. 5B), revealed a significant difference ($\chi^2$ test of homogeneity, $p = 8.8 \times 10^{-5}$) between the percentage of perceptually modulated cells with weak physical tuning (partition near the origin, 8/131 cells) versus all the other three subpopulations that showed stronger physical tuning either in orientation (27/131 cells), ocularity (25/131 cells), or both (44/130 cells). The comparison between the latter three classes did not show a significant difference ($\chi^2$ test of homogeneity, $p = 0.07$) but the percentage of cells showing strong physical tuning to both orientation and ocularity (44/130 cells) showed a trend to be higher. Gessaman partitioning across orientation alone (see marginal distribution in Fig. 5B, ordinate) revealed a gradual increase in the percentages of significantly modulating neurons ($\chi^2$ test of homogeneity, $p = 0.007$) with increasing orientation preference. Similarly, Gessaman partitioning across ocularity (see marginal distribution in Fig. 5B, abscissa) revealed significant gradual increases across ocularity preference ($\chi^2$ test of homogeneity, $p = 1.1 \times 10^{-5}$).

Recently, human fMRI experiments have shown that BOLD activity from V1 voxels can predict the eye-of-presentation of the perceived stimulus but not its color (Haynes and Rees, 2005). Similarly, we tested whether the strength of perceptual modulations in V1 correlate with the physical orientation preference or the ocularity of the cells recorded. We tested this hypothesis by calculating the correlation coefficients between the amplitude of the perceptual modulations and the physical tuning to orientation and ocularity. We found that perceptual modulations were significantly correlated both with orientation (Fig. 5C; Pearson $r = 0.31$, $p = 8.04 \times 10^{-25}$) and ocularity (Fig. 5D; Pearson $r = 0.27$, $p = 2.54 \times 10^{-19}$) preferences of all visually responsive cells. The respective correlation for orientation preference in the population of perceptually modulating cells was (Fig. 5C, red dots; Pearson $r = 0.47$, $p = 4.26 \times 10^{-13}$) and for ocularity (Fig. 5D, red dots; Pearson $r = 0.40$, $p = 1.33 \times 10^{-9}$).

**Modulations of the local field potentials**

Local field potential signals were acquired from 381 sites recorded from the two monkeys. A typical example of the raw LFP data recorded from a single site is presented in Figure 6, in which an increase in oscillatory activity in the gamma frequency range with a short delay after stimulus onset is evident. In addition, the magnitude of the gamma-band oscillations is significantly different for the two orthogonal monocular gratings (see Fig. 6 for details), indicative of orientation tuning of the gamma-band oscillations (Frien et al., 2000; Berens et al., 2008a,b). In contrast, during the dichoptic presentation representing differences only in the perception of the two stimuli, there was no obvious differ-

**Figure 6.** LFP modulations in an example recording site. In A and B, we present a sample of 20 single-trial LFP-traces from two same-stimulus different-percept conditions (see Fig. 1). The stimulus sequence is depicted by the diagrams on the top of each panel with the green dots depicting the perceived stimulus during the binocular presentation. C, Power spectra estimates for the two conditions during the monocular stimulus presentation. The power spectra were estimated at a time window between 500 and 1000 ms (light blue shading) to avoid effects caused by the initial transient response to visual stimulation. A clear increase in gamma-frequencies (30–100 Hz) and a concurrent decrease in lower LFP frequencies (<20 Hz) with respect to the spectrum during fixation baseline (black dashed line) can be observed for both conditions. In addition, a clear physical preference for the horizontal grating in the right eye (gray spectrum) versus the vertical grating in the left eye (red spectrum) is noted, especially in the gamma-frequencies. D, Similar estimation of spectra performed for the binocular period for which both gratings were present in the two conditions but only one was readily perceived (horizontal grating in the right eye for A condition or vertical grating in the left eye for B condition). Here, the preference for the horizontal grating in the right eye is clearly smaller (red dashed line spectrum versus gray dashed line spectrum). E, Time course of LFP modulation in the gamma-frequency range. The LFP traces were bandpass filtered between 30 and 90 Hz and the average power of the signal is plotted over time. During the monocular presentation there is clear sensory preference to the horizontal grating in the right eye (gray trace) in comparison with the vertical grating in the left eye (light red trace). During the binocular period (1000–2000 ms), the power shows strong selectivity when the horizontal grating is perceived versus when the vertical is perceived only during the initial 300 ms, after which there is only a very weak difference between the traces of the two conditions. F, Similar to E, but the LFP traces were bandpass filtered between 4 and 20 Hz. Here both the sensory (0–1000 ms) and perceptual (1000–2000 ms) preferences are weak.
enone the raw LFP signals. The same was evident in the power spectral estimates of the LFPs (Fig. 6C,D) and in the band-passed averages in different frequency bands (Fig. 6E,F).

For each LFP site, we estimated the power spectral densities using the Thomson multitaper method (see Materials and Methods) and compared the modulations of different bands for the physical alternation and BFS conditions. The results for two frequency bands are presented in Table 1. We found that 18% of the visually responsive sites in the gamma frequency band (30–90 Hz) and 22% of the visually responsive sites in the frequency band 4–20 Hz modulated with perception. These values were not significantly different between the two frequency bands and the percentage of perceptually modulated single units ($\chi^2$ test of homogeneity, $p = 0.5$).

We quantified the population mean of LFP modulations by using the difference of the average spectrograms of the preferred and non-preferred orientations (see Materials and Methods). The average power change under the flash suppression conditions was 0.4 dB (Fig. 7B) compared with 2.1 dB under physical alternation conditions (Fig. 7A). We also analyzed perceptual modulations across different frequency bands of the LFP. The average perceptual modulation in the gamma frequency band was weak compared with the modulation during physical alternation (Fig. 7C,D). On average, the perceptual modulation (during the last 500 ms) was 23% of the modulation of the physical alternation conditions (Fig. 7E,F). The average perceptual modulations of the lower frequency band (4–20 Hz) were also very weak (Fig. 7G,H) with an amplitude of ~8% of the modulation during physical alternation (Fig. 7I,J). The magnitude of the perceptual effect in both frequency bands was also very small as measured by using the $d'$ indices of each LFP site (Fig. 8). Notably, the gamma frequency band showed substantially higher sensory preferences compared with the low frequencies (Fig. 8A,B).

### Behavioral responses
We analyzed the behavioral responses of one animal from a total of 43 sessions [corresponding to 17,230 physical alternation trials and 4025 (24.4%)] binocular flash suppression/binocular rivalry (BFS/BR) trials] while the animal reported its perception. All

**Figure 7.** Population averages of the LFP signals for all sites showing physical preferences. Before averaging, conditions were sorted to preferred (P) and nonpreferred (N) according to the responses during the monocular period of presentation. A, The average differences in the spectrograms (frequencies <100 Hz) between the preferred and nonpreferred orientations during physical alternation. B, The average differences in spectrograms for the same sites under the flash suppression conditions. C, D, G, H, Time-domain bandpass filtered averages for the physical alternation and flash suppression conditions for two different frequency bands: the gamma band (30–90 Hz) (C, D), which showed the highest physical preferences ($n = 275$), and the lower frequencies (4–20 Hz) (G, H), which showed weaker preferences ($n = 149$). The sequence of presentation of preferred and nonpreferred is depicted in the diagrams in the upper part of C and D (the black dots denote the perceived stimulus). E, F, I, J, Average modulations expressed as differences between preferred and nonpreferred stimuli and shown as a percentage of the maximum modulations during the monocular presentation (0–1000 ms) for the same two frequency bands: 30–90 Hz (E, F) and 4–20 Hz (I, J). The dotted lines in F and J are copies of the physical alternation in E and I and are presented to provide a means of direct comparison between the flash suppression and the physical alternation modulations.

**Figure 8.** LFP perceptual modulations as a function of physical stimulus preference. A, Scatter plot of physical preference versus perceptual modulation of all LFP sites showing significant physical preference in the gamma frequency band ($n = 275$). A positive perceptual modulation index indicates that the response of the LFP site was greater during perception of the preferred grating. A negative perceptual modulation index indicates a higher response during perception of the nonpreferred grating. Dark symbols indicate the sites that showed significant perceptual modulations. B, The same as A for the 4–20 Hz frequency band ($n = 149$).
sessions were acquired after the animals’ performance stabilized over 95% correct responses to presentation of congruent stimuli.

To make sure that BFS worked behaviorally as expected, we analyzed the responses of the animal to both physical alternation and BFS/BR trials. First, we measured the response time and percentage of correct responses of the monkey to physical alternations of two orthogonal gratings (Fig. 9A, C). The monkey consistently reported the correct grating orientation in 96% of the trials with an average response time of 500 ± 3 ms (mean ± SEM). Then, we calculated the percentage of BFS trials that the monkey reported the new stimulus after the flash. The monkey reported perceiving the newly flashed stimulus in 97% of the trials (Fig. 9B), demonstrating that, under the stimulation conditions we have used, BFS works in almost all trials. The response time was slightly higher in comparison with physical alternations at 539 ± 6 ms (Fig. 9C). We kept the incongruent stimuli on the monitors for up to 5 s to record the time of spontaneous reversals after the flash. The monkey reported reversals with a mean time of 2057 ± 51 ms after the flash, which was longer than the 1000 ms recorded during the electrophysiological experiments (Fig. 9C). The minimum spontaneous reversal time was 1240 ms. The distribution of spontaneous reversals was fitted by a gamma distribution (Fig. 9C; \( r = 23.6 \) and \( \lambda = 10.9 \) Kolmogorov–Smirnov goodness-of-fit test, \( p = 0.001 \)).

BFS and neuronal adaptation

An inherent potential complication of the BFS paradigm is neuronal adaptation. In contrast to BR, the history of stimulation leading to the two alternative percepts is different. This can introduce differences in the level of adaptation in the neuronal populations encoding the competing stimuli. For example, it is expected that when the preferred stimulus of a neuron is presented first then its activity will be reduced further until the end of the trial compared with the case when the preferred stimulus is presented second. This is due to differences in the length of time for adaptation between these two conditions. Therefore, to appreciate the suppressive effect of the second stimulus on the first we should compare a neuron’s activity with a condition where the first stimulus is presented alone for the whole duration of the trial. To address this issue, we estimated the level of adaptation for the stimulus presented first across the whole duration of the trial by using an exponential decay function (Fig. 10). We find that the presence of the nonpreferred stimulus (presented second in this case) introduces additional suppression compared with the level of activity predicted by a simple adaptation mechanism (Fig. 10A). Moreover, when the presentation sequence is reversed (i.e., when the preferred appears second) the activity level is also suppressed in comparison with the presentation of the preferred stimulus alone (Fig. 10B).

These results demonstrate that a simple model of activity summation that takes into account adaptation, cannot explain the activity during the binocular incongruent stimulation. Instead, nonlinear interocular interactions are necessary to account for the suppression. Such nonlinear interactions were also present at the level of single neurons. Some cells demonstrated much more suppression than it would be predicted by adaptation (supplemental Fig. 3 D, F, K, available at www.jneurosci.org as supplemental material) while others exhibited a pronounced enhancement relative to the presentation of the preferred stimu-
lus alone (supplemental Fig. 3B, C, available at www.jneurosci.org as supplemental material) that also cannot be explained by adaptation. Importantly the direction of the modulation correlated with perception.

As we have shown above, a trivial model of adaptation cannot explain the responses of V1 neurons during BFS. Nevertheless, this does not exclude more complicated types of adaptation for example affecting only the neurons encoding the perceptually dominant stimulus. Indeed, some models of BR include neuronal adaptation (dependent on the stimulus that is being perceived) as a critical component (Tsuchiya et al., 2006; van Ee, 2009; Kang and Blake, 2010) therefore adaptation likely plays an important role even in studies of classical BR.

Eye movements

One possible confound that might account for the perceptual modulations we have found is a potential difference in the distribution of eye-movements between the two perceptual conditions. To control for this, we extracted various eye-movement parameters (fixation positions, microsaccade amplitudes, microsaccade directions and microsaccade rates) and compared their distributions between the two different perceptual conditions as we did for the electrophysiological signals (for details see Materials and Methods and supplemental Fig. 1, available at www.jneurosci.org as supplemental material). We did not find a significant difference between the distributions for any of these parameters (see supplemental Fig. 2, available at www.jneurosci.org as supplemental material).

Discussion

Discovering which aspects of neural activity underlie our subjective percepts and not simply the sensory input impinging upon us has been a question that has fascinated scientists and philosophers for centuries. Specifically, the role that area V1 plays in perception has been a subject of debate (Crick and Koch, 1995; Pollen, 1995). Psychophysical, single-unit and more recently fMRI studies in primates have argued both for and against V1 activity robustly reflecting perception (Blake, 1989; Leopold and Logothetis, 1996; Logothetis et al., 1996; Polonsky et al., 2000; Tong and Engel, 2001). Here we have undertaken a comprehensive study to investi-
hierarchical levels of vision, and incorporating possible competition of both ocular and feature-selective channels. Furthermore, additional psychophysical and computational evidence supports the notion that indeed both competition between monocular channels and high-level stimulus interpretations are involved in perception during binocular competition (Dayan, 1998; Brascamp et al., 2007; Ikeda and Morotomi, 2007; Silver and Logothetis, 2007; Bhardwaj et al., 2008). However, electrophysiological evidence supporting this idea has been absent. Here we find that equal percentages of monocular and binocular cells are modulated with perception. In addition, the strength of the perceptual effect correlates with both the orientation and ocularity preferences of the neurons. These results provide the first direct electrophysiological support—at the level of the activity of single cells—for the idea that during BFS, competition does indeed involve mechanisms active across both monocular and binocular neurons. This finding is in agreement with human fMRI evidence for modulations in V1 according to the eye-of-origin of the perceived and suppressed stimuli that led those investigators to reinstate the hypothesis of ocular competition at the level of V1 (Tong and Engel, 2001; Haynes and Rees, 2005) and the lateral geniculate nucleus (Haynes et al., 2005; Wunderlich et al., 2005). Our findings however, illustrate that in addition to eye-of-origin signals, single cells in V1 contain at least equally strong signals for the perceived orientation of the stimulus. In addition, cells tuned to both orientation and ocularity showed a higher tendency to show perceptual modulations. These cells responded differentially for the two different stimulus configurations we have used depending whether the orientation eliciting the stronger response was presented in their preferred eye or the opposite. This further demonstrates that the competition does not happen exclusively for eye-of-origin or orientation signals.

Perceptual modulation of different frequency bands of the local field potential

In contrast to the electrophysiological studies in monkeys including ours (Leopold and Logothetis, 1996; Gail et al., 2004; Wilke et al., 2006), human fMRI studies have found strong effects of perceptual suppression in the activity of the primary visual cortex (Polonsky et al., 2000). Specifically, the BOLD signal during such perceptual alternations modulates almost as much when the stimuli are nonambiguously presented separately (physical modulation). The absence of large amplitude modulations in the spiking activity of single cells could potentially reside in a difference in the nature of the two signals (i.e., BOLD and spiking activity of single cells). The mod- est changes in V1 activity could reflect a modulatory input from higher visual cortices. Such a perception-related modulatory effect could be more pronounced in LFP signals that reflect somatodendritic integrative processes (Mitzdorf, 1987).

In the present study, we analyzed the effects of perceptual-transitions to the different bands of LFP to determine whether in- deed LFP signals would reflect perception more robustly. We did not find such evidence. LFP signals during the different perceptual states showed only small modulations compared with the modulations during physical alternation of the stimuli. Our result is partially consistent with a recent study that compared directly single-unit activity, LFP and BOLD activity in behaving-macauces using the generalized flash suppression (GFS) paradigm (Maier et al., 2008). They find different magnitudes of the effect for the electrophysiological and BOLD signals thus confirming the known discrepancy (human fMRI vs monkey electrophysiology) within the same species. However, in agreement with two previously contacted studies (Gail et al., 2004; Wilke et al., 2006), they find that low-frequency LFPs (<30 Hz) show a modulation ratio substantially larger than the single-unit activity. Moreover, a recent study (Wilke et al., 2009) has demonstrated that low-frequency LFPs in the visual thalamus are critically dependent on the active engagement of the subjects in the task. Specifically, they show that low-frequency LFPs show robust perceptual modulations only if the animals actively report their percepts during GFS. These modulations are eliminated when the animals passively fixate. Therefore, the absence of stronger low-frequency LFP modulations during passive-fixation-BFS we report in our study is entirely consistent with the hypothesis that low-frequency LFPs are reflecting feedback from higher visual areas, which is stronger when the subjects are actively engaged in the task. In addition, this hypothesis can potentially explain the modulations observed in human fMRI studies for which subjects actively reported their percepts. It remains to be shown if perceptual modulations observed in human fMRI can be significantly reduced or abolished when subjects only passively fixate during the presentation of the bistable stimuli. Alternatively, it is possible that differences in the experimental paradigms trigger distinct mechanisms involved in perceptual suppression introducing therefore additional differences in the results (e.g., a potential role of center surround mechanisms in the case of GFS).

Based on the ongoing disagreement between the BOLD results and these classical neurophysiological measures (spikes and power of the LFP in different frequency bands), it is possible that simply measuring the power of the LFP in different frequency bands is not sufficient to capture processes contributing to the modulations of the BOLD signal. Neural activity from multiple sources might be generating field potential changes with inverse signs that add to zero or show minimal changes when recorded using single-point measurements. An example could be spatially disorganized dipoles with minimal or no spatial summation. In addition, anatomy suggests that top-down influences reside mainly in the supragranular layers, pointing to a clear hypothesis for layer specificity.

More detailed studies of the microcircuit organization could reveal whether and how more intricate aspects of activity patterns in V1 may be more robustly related to the mechanisms of perceptual suppression. For instance, a particular subtype of neurons or specific interactions between cells could robustly encode the percept in V1. An important direction for future research is to dissect and understand in detail the microcircuit mechanisms involved in visual perception.

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