

Synchronization of oscillatory responses in visual cortex correlates with perception in interocular rivalry

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ABSTRACT In subjects suffering from early onset strabismus, signals conveyed by the two eyes are not perceived simultaneously but in alternation. We exploited this phenomenon of interocular suppression to investigate the neuronal correlate of binocular rivalry in primary visual cortex of awake strabismic cats. Monocularly presented stimuli that were readily perceived by the animal evoked synchronized discharges with an oscillatory patterning in the γ -frequency range. Upon dichoptic stimulation, neurons responding to the stimulus that continued to be perceived increased the synchronicity and the regularity of their oscillatory patterning while the reverse was true for neurons responding to the stimulus that was no longer perceived. These differential changes were not associated with modifications of discharge rate, suggesting that at early stages of visual processing the degree of synchronicity rather than the amplitude of responses determines which signals are perceived and control behavioral responses.

A basic operation in sensory processing consists of perceptual grouping, requiring dynamic selection and binding of subsets of simultaneous neuronal responses for further joint processing (1, 2). A particularly interesting and representative case of dynamic response selection is interocular rivalry (3). When the images in the two eyes are incongruent and cannot be fused into a coherent percept, only signals from one of the two eyes are selected and perceived, whereas those from the other eye are suppressed (4, 5). In subjects suffering from early onset strabismus, interocular rivalry is permanently experienced irrespective of the congruency of the images in the two eyes (6). If a pattern is presented to one eye only, it is readily perceived. However, when a second but different pattern is presented to the other eye, two solutions are possible: (i) Either the first pattern continues to be perceived and the second pattern is suppressed, or (ii) the first pattern is suppressed and the second is perceived. In strabismic subjects the outcome of this competition is often biased toward one eye, because in most cases one eye becomes dominant. Because stimulation conditions in one eye remain unchanged during transition from monocular to dichoptic stimulation, the phenomenon of interocular rivalry can be exploited to investigate whether and how neuronal responses to a physically unchanged stimulus are modified through central selection. Here we examine how responses in primary visual cortex change with the introduction of a rivalrous stimulus (i) when they are selected and continue to support perception and (ii) when they are suppressed and pass from supporting perception to being no longer perceivable.

Previous studies have examined the hypothesis that response selection in interocular rivalry is achieved by a modulation of firing rate. Data obtained under general anesthesia from the

visual cortex of normal and strabismic cats seem to be compatible with this assumption (7) (see *Discussion*). Responses evoked from one eye were reduced when another, nonfusible stimulus was presented to the other eye. However, recordings from early visual areas (V1, V2, V4, MT) of awake monkeys experiencing binocular rivalry were less conclusive (8, 9). The fraction of neurons that decreased their firing rates upon suppression of the eye to which they responded was about the same as the fraction of cells that increased their discharge rate and altogether response amplitudes changed in <50% of the neurons when eye dominance switched. A clear and positive correlation between firing rate and perception was found only in inferotemporal cortex (10). Here we investigate the hypothesis that response selection in early visual areas might be achieved by a modulation of the synchronicity rather than the rate of discharges, synchronously discharging cells being more effective than asynchronously responding cells in driving neurons at subsequent processing stages (11–13).

MATERIALS AND METHODS

Behavioral Assessment of Rivalry. In this study, we used three cats in which convergent strabismus had been induced at the age of 3 weeks under ketamine/xylazine anesthesia by transecting the tendon of the lateral rectus muscle of the right eye. At the age of 3–4 years, a head fixation bolt was attached to the skull with dental acrylic and titanic screws and Ag/AgCl-electrodes were implanted subcutaneously lateral to each eye and above and below the left eye to record horizontal and vertical eye movements, respectively. All experimental procedures were in accordance with the German Law for the Protection of Experimental Animals and conformed with National Institutes of Health and Society for Neuroscience (U.S.) regulations. Optokinetic nystagmus (OKN) was used to assess under which stimulation condition the cats perceived the signals from either the right or the left eye, because this oculomotor response correlates with perception. Under rivalry conditions, animals as well as human subjects perceive only the stimulus that also controls OKN (14–16). For visual stimulation, square wave gratings covering $50 \times 60^\circ$ of the visual field were presented on two 21-inch computer screens at a frame rate of 100 Hz and a resolution of 1024×768 pixels. Monocular presentation of the two gratings was assured by placing one mirror in front of each eye. Appropriate shaping of the mirrors and additional occluders assured that the stimuli were only visible through the mirrors. The gratings had a spatial frequency of 0.1 cycles per degree, a velocity of $8^\circ/\text{sec}$ and moved continuously in temporo-nasal direction for both eyes. Monocular and dichoptic stimuli with different contrast ratios

Abbreviations: EOG, electrooculogram; OKN, optokinetic nystagmus; MUA, multiunit activity; PSTH, peri stimulus time histogram; CCH, cross-correlation histogram; RMA, relative modulation amplitude; LFP, local field potential; STA, spike-triggered average; SFC, spike-field coherence.

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(Fig. 1) were pseudorandomly interleaved and presented for 60 sec per trial. Between stimulus presentations the animals were regularly aroused with noise. Eye dominance ratios were determined from the relative time OKN was controlled by the right or the left eye according to the formula $[t(\text{left}) - t(\text{right})]/[t(\text{left}) + t(\text{right})]$.

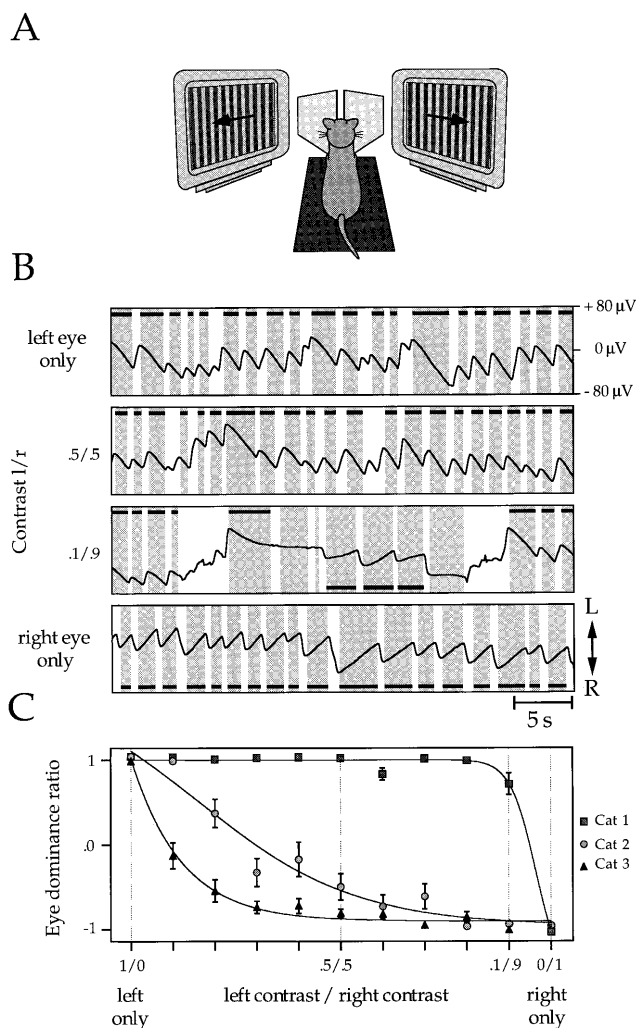


FIG. 1. Eye dominance assessed from OKN responses. (A) Cats were placed on a recording table and their head fixed by means of an implanted bolt (see *Materials and Methods*). In front of the head two mirrors were mounted such that each eye was viewing a separate monitor. (B) Recordings of horizontal OKN from cat 1 evoked by dichoptic presentation of gratings moving in opposite directions for four different contrast conditions. Phases devoid of saccades are underlaid with gray if they exceed 500 msec and those classified as smooth phases of OKN are marked with black bars whose position indicates which eye controls OKN (Top, left eye; Bottom, right eye). When only one grating is presented to either the left or the right eye, OKN is unidirectional, smooth phases of OKN reflecting the movement direction of the grating. If both eyes are stimulated with gratings of equal contrast ($l = 0.5, r = 0.5$), OKN is entirely dominated by the left eye. OKN is controlled by the two eyes in alternation only when contrast ratios are very asymmetric ($l = 0.1, r = 0.9$) indicating a pronounced dominance of the left eye. (C) Eye dominance ratios (see *Materials and Methods*) expressed as the fraction of time during which OKN was dominated by the left eye stimulus (ordinate) as a function of the contrast ratio (abscissa) between dichoptically presented gratings for all three cats. The curves correspond to significantly fitted sigmoidal functions. In two cats the deviated eye was dominant and in one cat the nondeviated eye. At equal contrast of the two gratings, eye dominance ratios are for cat 1, 0.96; cat 2, -0.53; and cat 3, -0.85. Bars = SEM. Dashed vertical lines are drawn at the contrast ratios shown in B.

Cortical Recordings. Teflon-coated platinum iridium wires (28–34 wires, 25 μm diameter) were chronically implanted in areas 17 and 18 (17). All surgical procedures in the adult cat were performed under $\text{N}_2\text{O}/\text{O}_2$ anesthesia supplemented by 1% halothane. For the analysis of multiunit activity (MUA) the signal from the intracortical wire electrodes was amplified, band-pass filtered in the range of 1–3 kHz (3 dB per octave) and fed into a Schmitt trigger with a threshold that exceeded the noise level by at least a factor of two. Responses were elicited by moving gratings with the same parameters as those used for OKN measurements, except that now their orientation was changed in steps of 45° to obtain joint responses from as many pairs of recording sites as possible, and direction of motion was reversed every 1.5 sec to prevent eye movements (see below). These stimulus sets were presented either monocularly or dichoptically. Individual trials lasted for 9 sec (stimulus onset after 3 sec), and a particular stimulation condition was repeated at least 40 times and interleaved in a pseudorandom sequence with other conditions. Visual responses were considered significant if they exceeded the ongoing activity by a factor of 1.5. Stimuli were presented for only 6 sec, to enhance the perceptual asymmetry between the eyes. Behavioral testing had revealed that the dominant eye virtually always initiated OKN and that perceptual switches occurred only after tens of seconds. The same holds for human subjects. Even if asymmetries in eye dominance are minute, it is almost always the dominant eye that initiates nystagmus after stimulus onset (14).

The effects of binocular rivalry were assessed by comparing the responses of cells connected to the same eye under monocular and dichoptic stimulation conditions. For all responses, auto- and cross-correlation histograms (CCHs) were computed and quantified according to a standard procedure described previously (18) that involved the fitting of a damped cosine wave (Gabor function) to the correlogram. The function had to account for at least 15% of the data variance and the z scores of significant peaks had to be >2 . The strength of synchronization and the regularity of oscillations were quantified by calculating the relative modulation amplitude (RMA) for the central and the first satellite peak, respectively. RMA (as a percentage) was defined as the amplitude of the respective peak (measured from the offset caused by accidental coincidences) divided by the offset (and multiplied by a factor of 100). Pairs of recording sites were included in the cross-correlation analysis of MUA responses if both responded jointly to a grating of a particular orientation. Because the measured orientation preferences were distributed rather evenly in our sample of recording sites, the pooled correlation data comprise responses to all possible orientations and drift directions. To avoid contamination of the correlograms by transient responses to stimulus onset, we selected for data analysis either the response epoch between the first and second or the second and third reversal of stimulus motion (Fig. 2), depending on where the product of the firing rates was larger. However, results were essentially the same for the respective other response epoch.

Eye Movement Controls. Electrooculogram (EOG) recordings were routinely performed during the electrophysiological measurements to control for the absence of eye movements. As we had no reliable control over the cat's fixation behavior, we could not calibrate the EOG recordings in visual angle. However, EOG recording conditions were the same during behavioral testing and electrophysiological measurements. Because the EOG signals were strongly modulated in the first condition and flat in the second, we are confident that eye movements were absent during data acquisition. There are several reasons why eye movements were not evoked during electrophysiological measurements. (i) Even in normal cats and under optimal conditions for the induction of OKN, eye movements are readily abolished by the movement

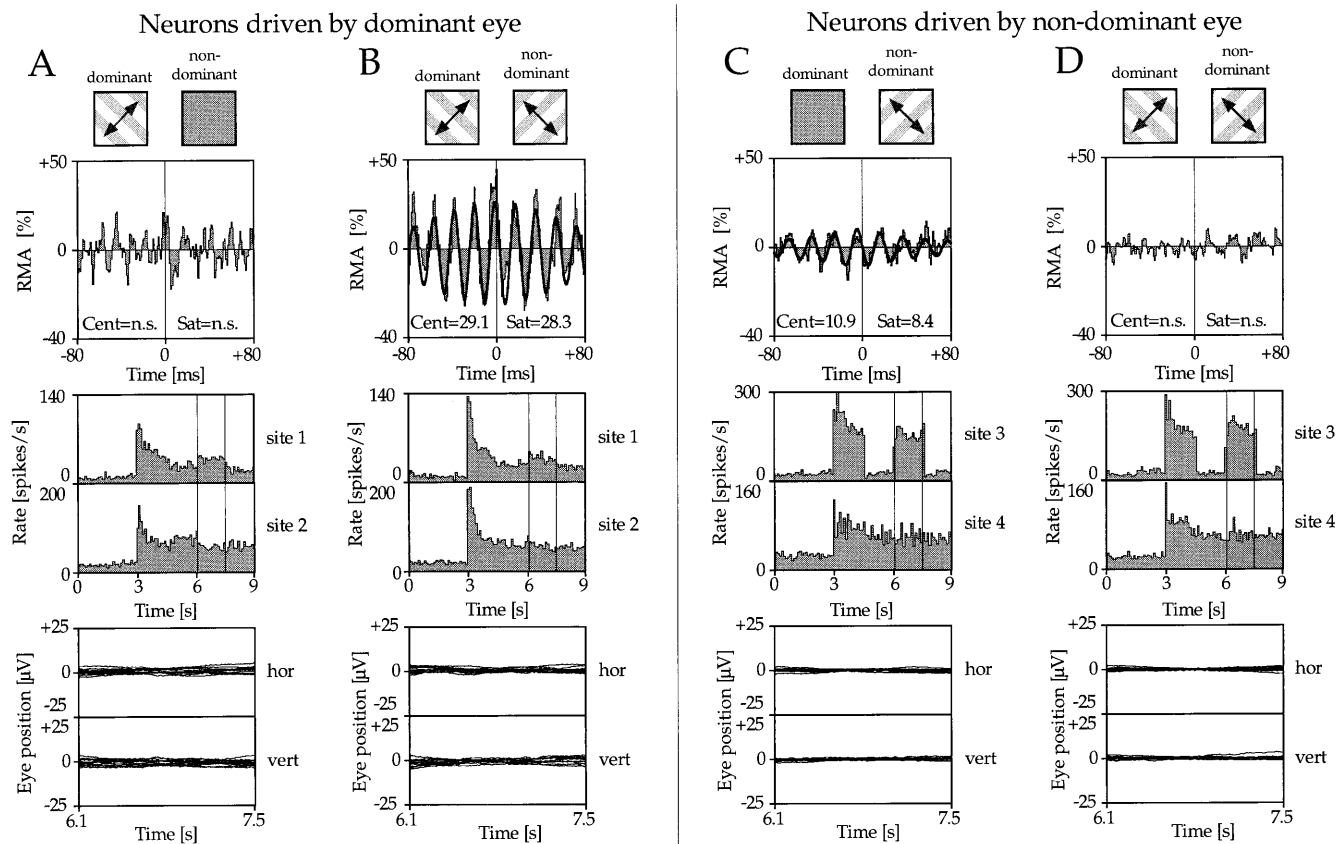


FIG. 2. Normalized CCH and peri stimulus time histograms (PSTH) for two pairs of recording sites connected to the dominant (*A* and *B*) and nondominant eye (*C* and *D*), respectively, under monocular (*A* and *C*) and dichoptic (*B* and *D*) stimulation conditions. (*A*) CCH and the corresponding PSTHs for a pair of recording sites connected to the dominant eye under monocular stimulation conditions. Insets above the correlation histograms indicate stimulation conditions. Cent and Sat, RMA (in %) of the center peak (Cent) and first satellite peak (Sat) in the CCHs; n.s., CCH modulation was not significant (see *Materials and Methods*). Vertical lines in the PSTHs indicate the response epoch between the second and third reversal of stimulus motion, for which the CCH was calculated (see *Materials and Methods*). *Bottom*, superimposed single trial EOG recordings of horizontal and vertical (lower traces) eye position obtained during the measurement window indicated in the PSTHs. (*B*) Responses from the same recording sites as in *A* under dichoptic stimulation conditions. Note that synchrony and oscillatory patterning are enhanced without significant alteration of discharge rates. (*C* and *D*) CCHs and PSTHs for a pair of recording sites connected to the nondominant eye under monocular (*C*) and dichoptic stimulation conditions (*D*). Note the decrease of synchronization and oscillatory modulation in *D* and the lack of changes in discharge rate. Note also that eye movements were absent under all stimulation conditions.

direction of the inducing stimulus at intervals similar to those used in this study (19). (*ii*) The gain of OKN is reduced in strabismic animals (20). (*iii*) Stimuli were most often suboptimal for OKN induction because their drift direction was only occasionally in the temporo-nasal direction (21). To rule out any potentially confounding influence of small residual eye movements we made two tests: (*i*) We restricted analysis to recording epochs that were completely devoid of any residual eye movements. This reduced the number of entries in the cross-correlograms and consequently the number of significant fits but otherwise the results remained the same. (*ii*) We compared the frequency of occurrence, the direction, and the amplitude of residual eye movements for monocular and dichoptic stimulation conditions. No significant difference was found. Because our interpretations rest on a comparison between responses obtained under monocular and dichoptic stimulation conditions, all data are included in the statistics.

Spike-Triggered Average (STA). For analysis of local field potentials (LFP) the signal from the recording electrodes was band-pass filtered between 1–100 Hz. For calculation of STAs, LFPs were averaged within a window of ± 128 msec centered on each trigger spike (22). Response epochs were selected for analysis as described above, choosing the epoch with the higher number of trigger events. Results were essentially identical for other epochs. To obtain a measure of synchronization between spikes and field potential that is independent of the power

spectrum of the local field potential, we calculated the spike-field coherence (SFC). This allowed us to distinguish between changes in synchronization and changes in the regularity of oscillatory patterning, the latter enhancing the power of the field potential in the respective frequency band. For each of the LFP segments used for the computation of STAs, we calculated the power spectrum and by averaging these spectra, obtained the spike-triggered power spectrum. The SFC was then computed as the ratio of the power spectrum of the STA over the spike-triggered power spectrum. The raw power spectra of the STAs showed even stronger effects than the SFCs indicating that changes in the LFP power were in the same direction as the changes in synchronicity between MUA and LFP.

Averages of 64 LFP traces triggered with the vertical refresh signal of the monitor or with the line trigger showed no sign of externally locked modulation.

RESULTS

The Rivalry Paradigm. To find out which of the two eyes would win in interocular rivalry when both eyes are stimulated with incongruent gratings of equal contrast, we investigated three strabismic cats by behavioral assessment. To this end, we measured OKN during dichoptic stimulation with gratings moving in counterphase (see *Materials and Methods*). Eye

dominance was asymmetric in all animals, as is typical for strabismic subjects: At equal contrast, the stimulus presented to one eye (the dominant eye) controlled OKN for a significantly larger fraction of time than the stimulus seen by the other (nondominant) eye (Fig. 1). The eye that controls OKN is always also the eye that wins in rivalry, which allowed us to predict with great reliability which of the two eyes supports perception when both eyes see different stimuli. Two of the cats were also tested for visual acuity in a modified Mitchell jumping stand (23) and were found to have similar acuity in both eyes [values in cycles per degree (with 95% confidence interval) are for cat 1: 1.93 (1.56–2.72) for the nondeviated and 1.82 (1.56–2.29) for the deviated eye, cat 2: 3.4 (2.41–5.23) for the nondeviated and 2.49 (1.91–3.7) for the deviated eye]. Thus, strabismus has led to a marked asymmetry in ocular dominance but not to amblyopia (for comparison see ref. 23). After completion of the behavioral testing, cats were prepared for chronic recording. Up to 34 microelectrodes were implanted into areas 17 and 18 to permit measurement of MUA while the cats were exposed to alternating monocular and dichoptic stimulation (see *Materials and Methods*). As characteristic for strabismic animals, neurons at all recording sites were monocular and responded predominantly either to the right or the left eye (24). At 24 sites, the amplitude ratio of responses evoked from the two eyes was 23.3 ± 1.2 (mean \pm SEM) and at 13 sites, responses were strictly monocular. To study rivalry dependent changes of neuronal responses, we first presented a single moving grating to one eye only and computed peri stimulus time histograms as well as auto- and cross-correlation functions between responses that were recorded simultaneously from sites that responded to this eye. Subsequently, the rivalry condition was introduced by presenting an orthogonal grating of equal contrast to the other eye. Recording from cells driven by the dominant eye allowed us to assess how responses change for stimuli that are perceived with monocular stimulation and continue to be perceived under rivalry conditions; accordingly, recording from cells responding to the nondominant eye permitted assessment of changes in responses that support perception under monocular stimulation but are excluded from perception in the rivalry condition. During these measurements, the cats had to be prevented from engaging in OKN because this would have introduced asymmetries in retinal slip and, hence, uncontrollable interocular differences in stimulation conditions. To prevent the development of OKN, the movement direction of the gratings was reversed every 1.5 sec (see *Materials and Methods*). We always presented gratings of equal contrast to the two eyes because this allowed us to (i) compare responses evoked by monocular stimulation of the dominant and nondominant eye, (ii) to predict with certainty which of the two eyes was going to be selected or suppressed with dichoptic stimulation (Fig. 1, see also *Materials and Methods*), and (iii) to mimic the natural viewing conditions of a strabismic animal.

Analysis of Spike Correlations. The probability that two simultaneously recorded cells synchronize their responses depends on the configuration of the applied stimuli, on the distance between the recorded neurons and on the similarity of the feature preferences of the respective neurons (2). Because the chronic implantation technique provides a random sample of recording sites with an arbitrary distribution of the respective parameters, not all pairs of recording sites exhibited synchronized responses to monocularly presented gratings. Moreover, as shown previously for strabismic cats (23, 25), synchrony was never observed between recording sites responding to different eyes. Of the 99 examined pairs of recording sites, 77 were driven by the dominant and 22 by the nondominant eye, respectively. Twenty (26%) of the former and 9 (41%) of the latter exhibited synchronized responses with monocular stimulation. In most of the significant correlograms the peak was centered around zero delay, indicating

that synchronization had occurred with zero phase lag. For quantification of changes in synchrony, the average strength of synchronization was assessed from the RMA of the center peak of the CCHs (RMA in %, see *Materials and Methods*). Synchronization strength changed with the transition from monocular to dichoptic stimulation conditions and these changes were in opposite direction for cells driven by the dominant and nondominant eye, respectively. Upon introduction of the second, rivalrous stimulus, synchrony increased among responses evoked from the dominant eye and decreased among responses evoked through the nondominant eye (Fig. 2). Of the 20 pairs of recording sites activated through the dominant eye, all but two exhibited enhanced synchronization upon costimulation of the nondominant eye (Fig. 3A). The RMA of the center peak in the cross-correlograms increased by 55% [from 10.5 ± 1.3 (mean \pm SEM) to 16.3 ± 1.8 , $P < 0.0005$, paired t test]. In addition, 11 of the pairs that had shown no significant synchronization with monocular stimulation became synchronized upon coactivation of the nondominant eye (average RMA = 9.9 ± 1.0). Of the nine pairs exhibiting synchronized responses with monocular stimulation of the nondominant eye, six continued to exhibit synchronized responses upon co-stimulation of the dominant eye. In all six cases, however, RMA values decreased, on average, by 31% (from 6.3 ± 1.0 to 4.4 ± 0.8 , $P < 0.005$, paired t test). In the three remaining cases (average RMA = 5.5 ± 2.1) synchro-

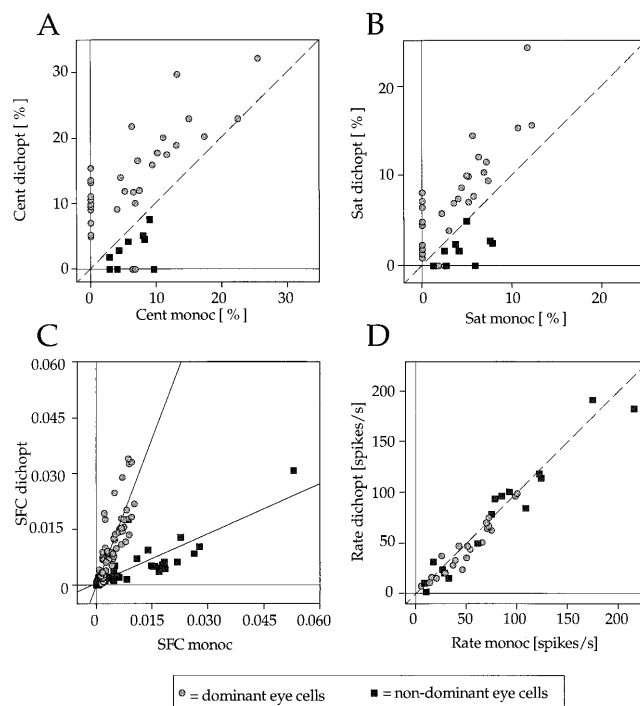


FIG. 3. (A) Scatter plot of RMA values of the center peak (Cent) of CCHs under monocular (abscissa) vs. dichoptic (ordinate) stimulation conditions for recording pairs connected to the dominant (circles) and nondominant (squares) eye. (B) Scatter plot of RMA values of the first satellite peaks (Sat) in CCHs. Same conventions as in A. (C) Scatter plot of SFCs (see *Materials and Methods*) between 39 and 63 Hz of STAs during monocular (abscissa) vs. dichoptic (ordinate) stimulation. Circles and squares refer to STAs computed for recording sites driven by the dominant and nondominant eye, respectively. Regression lines were calculated separately for STAs computed between responses evoked from the dominant and nondominant eye, respectively, and have slopes of 2.6 ($R^2 = 0.8$, $P < 0.0001$) and 0.4 ($R^2 = 0.7$, $P < 0.0001$), respectively. (D) Scatter plot of average firing rates (evoked minus ongoing activity) under monocular (abscissa) and dichoptic (ordinate) stimulation conditions. Circles and squares represent responses evoked from the dominant and nondominant eye, respectively.

nization dropped below our significance threshold upon dichoptic stimulation (Fig. 3A). The 13 pairs driven by the nondominant eye that did not show synchronization with monocular stimulation remained unsynchronized with dichoptic stimulation.

The center peaks in the CCHs were nearly always accompanied by additional side peaks indicating an oscillatory modulation of the synchronized neuronal responses in the γ -frequency range between 40 and 60 Hz (22, 26). The regularity of this oscillatory patterning is reflected by the amplitude of the side peaks and was therefore assessed from the RMA of this peak (Fig. 3B) (see *Materials and Methods*). In each pair of recording sites, the respective RMAs of the center and side peaks were closely correlated and upon introduction of the rivalry condition, the RMA values of the side peaks changed in the same direction as those of the center peaks (Fig. 3B). These changes in side peak RMA were again highly significant, both for the selected ($P < 0.0001$) and the suppressed eye ($P < 0.005$). This indicates that not only the synchronicity but also the regularity of the oscillatory patterning of the synchronous events increases for signals that continue to be perceived under rivalry conditions and decreases for responses that become suppressed.

Analysis of Spike-Field Coherence. Multiunit responses reflect only suprathreshold activity of cells in the immediate vicinity of the electrode tip. In contrast, LFPs that can be recorded from the same electrodes result from the average sub- and suprathreshold responses of neurons within a cortical volume of several 100 μm radius (27). Because only synchronous activity contributes effectively to LFPs, the amplitude and regularity of LFP fluctuations is a direct measure of response synchronization. Thus, changes of synchrony in large neuronal populations are reflected particularly well in correlation functions computed between MUA and LFP responses, i.e., STAs of LFPs. We calculated STAs for all possible combinations of recording sites connected to the same eye, both for monocular and dichoptic stimulation conditions (see *Materials and Methods*). Typically, STAs of monocularly evoked responses exhibited a strong oscillatory patterning in the frequency range of 40–60 Hz, indicating that unit discharges were tightly correlated with an oscillatory component of the LFP in the γ -frequency range (Fig. 4) (22). With dichoptic stimulation, the modulation amplitude of the STAs increased for pairs of recording sites connected to the dominant eye while it decreased for sites driven by the nondominant eye (Fig. 4). STAs were quantified by calculating the SFC, a measure that is independent of the firing rate at the MUA recording site and of the amount of power at the LFP recording site (see *Materials and Methods*). When stimulation conditions were switched from monocular to dichoptic, the SFC in the γ -frequency range increased by 141% ($n = 190$, $P < 0.0001$, paired t test) for recording sites driven by the selected eye and decreased by 44% ($n = 109$, $P < 0.0005$, paired t test) for sites driven by the suppressed eye (Fig. 3C).

Analysis of Spike Rates. In contrast to these highly significant changes in synchronicity and oscillatory patterning, no consistent changes were found during the transition from monocular to dichoptic viewing conditions for the discharge rates of the neurons (Fig. 3D). Both, neurons driven by the dominant and the nondominant eye tended to reduce their firing rates when the other eye was costimulated. Upon dichoptic stimulation, responses from the selected eye were reduced in 15 out of 21 recording sites (average reduction: 9.2%, $P < 0.02$, paired t test) and responses of the suppressed eye at 9 of 16 sites (average reduction: 3.2%, $P > 0.4$, paired t test). Thus, changes in firing rates did not distinguish between perceptual selection or suppression ($P > 0.5$, unpaired t test).

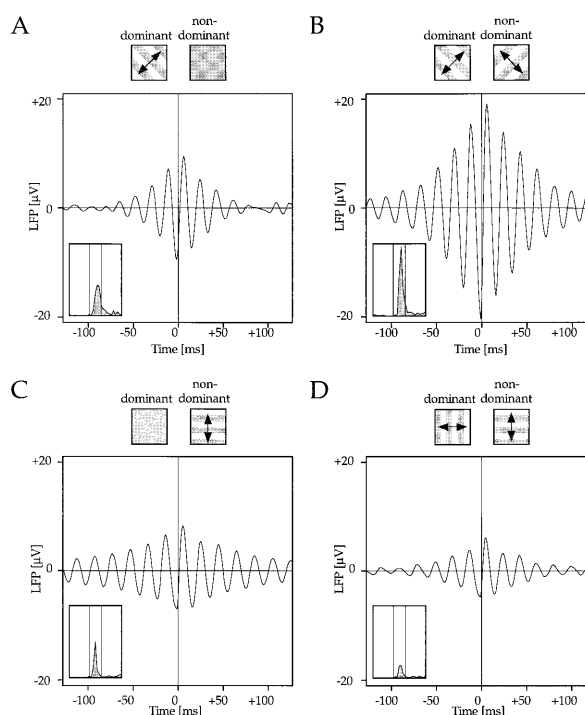


FIG. 4. STAs from pairs of recording sites driven by the dominant (A and B) and nondominant (C and D) eye, respectively for monocular (A and C) and dichoptic (B and D) stimulation conditions. Insets: Plot of SFC (see *Materials and Methods*) (ordinate, ranging from 0 to 0.1) as a function of frequency (abscissa, frequencies ranging from 0 to 102 Hz, binwidth 3.9 Hz). Vertical lines in the insets are at 39 and 63 Hz.

DISCUSSION

For the interpretation of the present results it is crucial to be confident that the dominant eye actually supported perception during rivalry. The marked asymmetry in ocular dominance, the short duration of stimulus presentation (see *Materials and Methods*) and the consistent changes in synchronicity suggest that the dominant eye was selected during rivalry. Still it cannot be excluded that there were brief episodes during which the nondominant eye took over. However, if this occurred, it would have attenuated the observed differences in synchronization behavior and hence would strengthen rather than weaken our conclusions. It appears thus, as if in areas 17 and 18 of awake, strabismic cats, dynamic selection and suppression of sensory signals are associated with modifications of the synchrony rather than the rate of neuronal discharges. In combination with the behavioral data this suggests that at an early level of visual processing, it is the degree of synchronicity rather than the amplitude of responses that determines which of the input signals will be processed further and then support perception and oculomotor responses.

Single unit recordings in awake monkeys trained to report their subjective perception in a rivalry situation revealed that a small percentage of neurons in primary visual cortex change their discharge rate as a function of the perceptual state of their preferred stimulus (9). However, discharge rates could either increase or decrease when the preferred stimulus was perceptually dominant. If such unsystematic changes had occurred in our experiments, they would probably have gone undetected because of the multiunit recordings. Moreover, the examined monkeys had normal vision and, as suggested by a recent psychophysical study (28), have probably experienced figural rivalry rather than interocular rivalry. In strabismic subjects, conditions are different, because of experience-dependent modifications of cortical circuitry that leads to a functional segregation of neurons driven by the two eyes (24,

29). In this case, competition is independent of figural congruence and occurs between the processing streams of the two eyes.

Single unit studies in area 17 of anesthetized cats (7) showed that the firing rate of neurons decreases when a second, nonfusible stimulus is presented to the other eye and this inhibition has been interpreted as a correlate of interocular suppression. Our results differ from those obtained under anesthesia. They show that the reduction in firing rate associated with rivalry is only very weak in the awake animal and merely reflects the presence of a rivalrous stimulus rather than the outcome of rivalry. According to the present results, the relevant variable appears to be the synchronicity of responses. Only those stimuli seem to control behavior and to be perceived, that give rise to well synchronized responses in a sufficient number of neurons. Under monocular viewing conditions, this is the case for stimuli presented to either eye but with dichoptic stimulation, only responses to the pattern that continues to be perceived stay well synchronized. Interestingly, the synchronicity of responses that remained perceivable did even increase when the rivalry condition was introduced, suggesting the action of a mechanism that enhances the salience of the selected responses. One possibility is that both the increase in synchronicity of the selected and the reduced synchronicity of the suppressed signals are due to local competition among the populations of neurons responding to the right and left eye, respectively, but it is also conceivable that attention-related top-down processes contribute to the selection of input signals by controlling their synchronicity. The possibility that attentional mechanisms act not only by modulating the rate but also the synchronicity of responses is supported by the evidence that neuronal synchronization increases during states characterized by arousal (30, 31) and focused attention (32) (for review see ref. 2).

In conclusion, the present results suggest that dynamic selection of a subset of simultaneously available responses may be achieved not only by modulating the discharge rates of the selected and suppressed responses, as has been shown at higher levels of processing (33, 34), but also by modifying their synchronicity. Selecting from a population of equally vigorous responses a subset for further processing is functionally equivalent with perceptual grouping. Thus, the present results also support the hypothesis that response synchronization could serve as a mechanism for perceptual grouping and binding. Changes in synchronicity at early stages of processing are bound to result in changes of discharge rate at later stages. Thus, the rate changes observed with perceptual rivalry (8–10) and selective attention (33, 34) in higher cortical areas could be secondary to modifications of neuronal synchronization at lower levels of processing.

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