Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry

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When the two eyes view dissimilar images, we experience binocular rivalry, in which one eye's view dominates for several seconds and is then replaced by that of the other eye[1,2]. What causes these perceptual changes in the absence of any change in the stimulus? We showed previously that some neurons in monkey cortical area MT show changes in activity during motion rivalry that reflect the perceived direction of motion[3]. To determine whether perception-related modulation of activity occurs in other visual cortical areas, we recorded from individual neurons in V1, V2 and V4 while monkeys reported the perceived orientation of rival gratings of two orthogonal orientations. Many cells, particularly in V4, showed patterns of activity that correlated with the perceptual dominance and suppression of one stimulus. The majority were orientation-selective and could be driven equally well from either eye. It has been previously suggested that binocular rivalry involves reciprocal inhibition between monocular neurons within V1 (for example, see ref. 4), but our results do not support this view; rather, we propose that binocular rivalry arises through interactions between binocular neurons at several levels in the visual pathways, and that similar mechanisms may underlie other multistable perceptual states that occur when viewing ambiguous images.

Two monkeys (*Macada mulatta*) were trained to fixate on a light spot and to report their perceived orientation of a grating stimulus by pressing levers. Once they had learned to respond rapidly and accurately to orientation changes, periods of rivalrous stimulation (4–12 seconds) were randomly intermixed with periods of congruent stimulation in observation periods of up to 25 seconds.

It was important to ensure that the monkeys were reporting their perceptions reliably rather than pressing levers at random, and we confirmed this in three ways. First, we introduced two types of catch trials in which the orientation of one grating was smoothly replaced after a lever response to yield a coherent binocular stimulus. In some cases the orientation was the same as that indicated by the monkey's last report, and the monkey was expected not to respond, and in other cases the orthogonal grating was faded in, and the monkey was expected to respond immediately to the change. Performance in both the non-rivalrous periods and the catch trials was consistently above 95%. As a second test, we compared the distribution of the durations of rivalry phases with parallel data from human subjects. As average phase durations depend on stimulus parameters that were adjusted for each recording session (such as contrast, size and spatial frequency; see below)[5], phase durations were normalized to the mean for that session. Figure 1*a* shows the distributions obtained from monkeys and humans, together with the γ-density functions typically used to describe such distributions. The similarity between the two distributions argues against the possibility of random reporting. As a final control, we varied the contrast for each eye independently. Increasing the stimulus contrast in one eye is known to decrease the time for which that stimulus remains suppressed, while minimally affecting the time for which it remains dominant[5]. Again, a similar relationship between stimulus contrast and eye dominance was seen in monkeys and humans (Fig. 1*b*). Such consistency is very unlikely to arise by chance.

Having established that monkeys were reporting their perceptions accurately, we recorded from individual neurons in the foveal V1/V2 (which cannot be clearly distinguished without histology) and in V4, while monkeys reported the orientations of congruent or rivalrous stimuli. Many cells in both V1/V2 and V4 respond best to gratings of a specific orientation, and they also vary in the extent to which they are driven by one or both eyes. Because cell responses during rivalry can best be studied by presenting the neurons with their optimal and non-optimal stimuli simultaneously, we were interested first to accurately determine each neuron's orientation preference. Moreover, as it has been suggested that binocular rivalry is a manifestation of reciprocal inhibition between the two monocular inputs[4], we were also interested in examining the ocular dominance of each cell. We therefore characterized the receptive field properties of each neuron under non-rivalry conditions, during passive fixation, before testing its response during rivalry. Each neuron was then tested with rivalrous stimulation, with its optimal orientation presented to one eye at random while the orthogonal orientation was presented to the other eye. In total, we characterized 101 neurons from two monkeys (three hemispheres). Figures 1–4 show data from one monkey; Fig. 5 shows pooled data from both monkeys.

Figure 2 shows observation periods for a single V4 neuron with a foveal receptive field, which was binocular and tuned for a right-tilting 45° orientation. The figure shows the spike trains, spike density functions, eye position, and reports of perceived grating orientation (the latter indicated by the red/green bar, in which each colour change represents a lever press). Note that the firing rate is elevated before the monkey reports perceiving the cell's preferred orientation, and often remains high for about the same time as the dominance phase of that orientation. This occurs regardless of whether the preferred orientation is presented to the right or the left eye.

To analyse further the neural activity associated with a perceptual change in the absence of a stimulus change, we constructed peristimulus time histograms (PSTHs) aligned to the animal's reports. Figure 3*a* shows data for the cell shown in Fig. 2. The activity from periods when the direction of gaze was outside the target was excluded from the analysis. The left panel shows reported transitions to the preferred orientation (green to red in Fig. 2); the right panel shows transitions to the suppression of this orientation. Note the increase in activity before the monkey reports perceiving the cell's optimal orientation, and the decrease before the report of the orthogonal orientation. Similar patterns of activity were seen in V1/V2 neurons (Fig. 4), but another type of behaviour was also seen in V4, in which some neurons discharged in association with the perceptual suppression (rather than activation) of the orientation that was preferred in non-rivalrous stimulation (Fig. 3*b*).

A quantitative analysis of all the responses revealed several classes of cells that differ in their responses to congruent and rivalrous stimuli (Fig. 5). About one third of the neurons studied were found to modulate their activity during rivalry in accordance with the monkey's report, whereas the rest were either inhibited throughout the rivalrous period or remained unaffected, spiking at the same rate under monocular, binocular or rivalrous conditions. In V1/V2, 6/33 neurons examined showed modulation, of which three were orientation-selective during congruent stimulation, whereas the other three showed no statistically significant preference for either orientation. In V4, 26/68 cells were modulating; twelve of these fired best when their preferred orientation was perceived, six fired when their preferred orientation was suppressed, and the remaining eight showed no preferred orientation during congruent stimulation. All but one of the cells showing response modulation during rivalry were binocular.

In a previous study on binocular motion rivalry[3], we showed that some neurons in MT respond when their preferred stimulus is perceived, some respond when it is suppressed, and others are relatively untuned during coherent stimulation but show enhanced selectivity in response to rivalrous stimuli. In addition,

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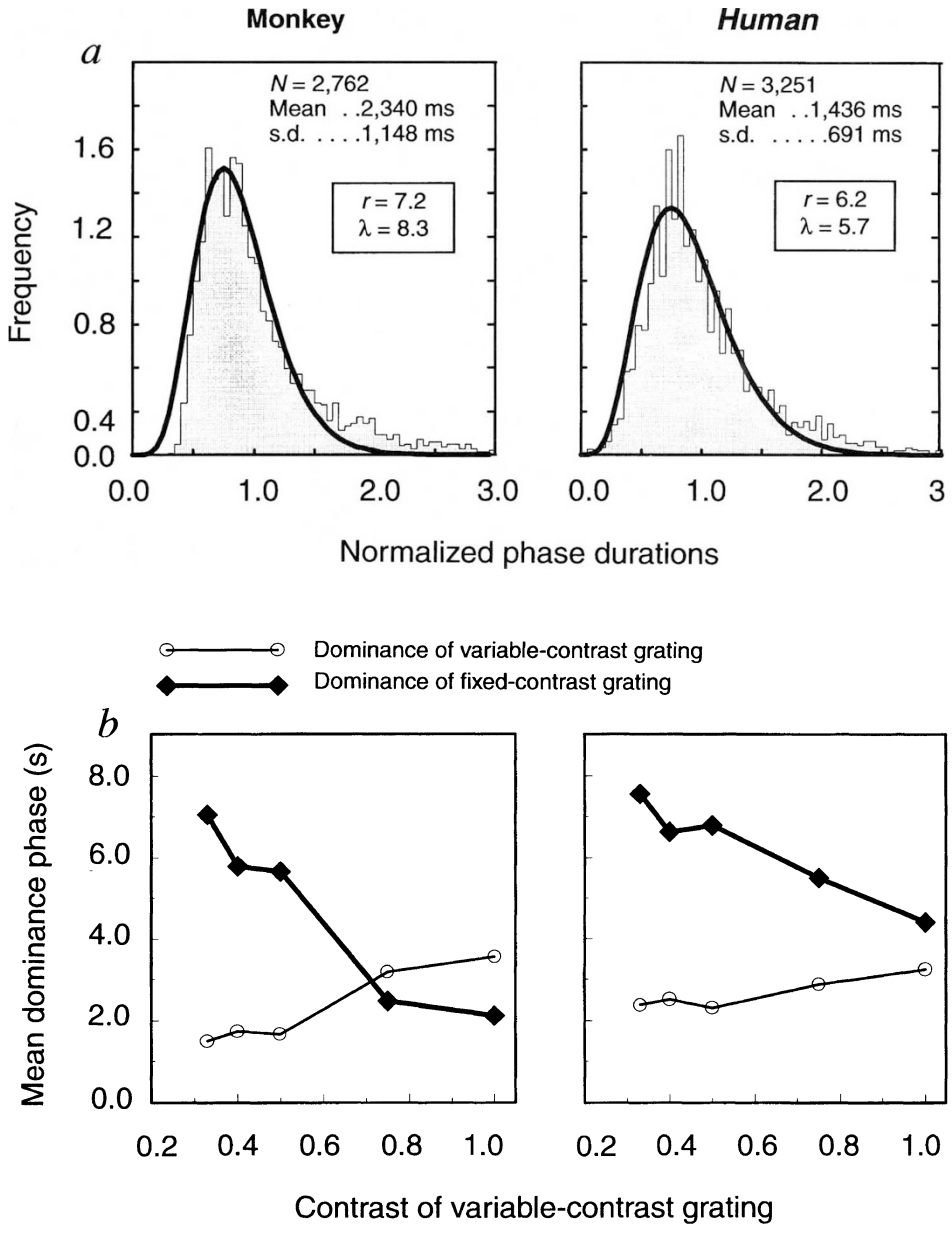


FIG. 1 Temporal dynamics of binocular rivalry (BR) in monkeys and humans. *a*, The frequency histograms show the distribution of relative phase durations, that is, phase durations expressed as a fraction of the mean phase duration. The smooth, thick, black lines illustrate the approximation of the data with a γ function $f(x) = \lambda^r/\Gamma(r)x^{r-1}\exp(-\lambda x)$, where $\Gamma(r) = (r-1)!$. The parameters of the theoretical distribution describing the monkey's data were not significantly different ($\bar{r} = 5.57$, $\sigma_r = 3.83$, $t_r = 0.41$, and $\bar{\lambda} = 6.02$, $\sigma_\lambda = 4.55$, $t_\lambda = 0.48$; two-tailed *t*-test) from those obtained in human experiments in this and other laboratories[5,10,11]. *b*, Effects of variation of stimulus strength on the mean dominance phase. Fixed contrast was set to 1.0. On the abscissa is plotted the varied contrast of the stimulus in one eye, and on the ordinate the mean dominance duration of that eye (circles) and of the eye receiving the grating with the fixed contrast (diamonds). All data were collected from the same animal used to study the cell responses illustrated in Figs 2–4. Frequency histograms were built from the rivalry reports during the physiology sessions. The effects of stimulus strength, which require varying the stimulus contrast, were studied during dedicated psychophysical sessions.

METHODS. The monkeys underwent an aseptic surgery, using isoflurane anaesthesia (1.2%–1.5%), for the placement of the head restraint post and the scleral search eye coil. Throughout the surgical procedure, the heart rate, blood pressure and respiration were monitored constantly and recorded every 15 min. Body temperature was kept at 37 °C. Postoperatively, the monkeys were administered an opioid analgesic (buprenorphine hydrochloride 0.02 mg kg^{-1}; IM) every 6 h for 2 d, and tylenol (10 mg kg^{-1}) and antibiotics (tribissen, 30 mg kg^{-1} for 3–5 days. At the end of the training period, another sterile surgical operation was performed to implant a chamber for the electrophysiological recordings. The visual stimuli were generated with an image processing system (MV200 Datacube, Inc.), and were presented on a display monitor (BARCO CDID 7651) placed 97 cm away from the animal. Stereoscopic presentations were accomplished using a liquid crystal polarizer (Tektronix SGS 610), which allowed alternate transmission of images with circularly opposite polarization at the rate of 120 frames s^{-1} (60 frames s^{-1} for each eye). Humans and monkeys wore glasses that allowed the passage of only every other image to each eye. The monkeys were trained to discriminate the orientation of the grating stimulus. Initially, they were rewarded for each correct response. When they consistently attained better than 95% accuracy, the training continued by reinforcing them only at the end of each observation period; however, feedback as to the correctness of the response was always given by aborting the observation period each time the monkey broke fixation or responded incorrectly. Once they had learned the orientation discrimination task, periods of rivalrous stimulation were randomly intermixed with periods of congruent stimulation. Standard techniques were used for recording from single units[12]. The receptive field (RF) of each isolated neuron was first plotted with a computer controlled bar stimulus. The width and height of the optimally oriented bar were used to determine the orientation, spatial frequency and size of a test-grating. Quantitative tests of each neuron's specificity for orientation, disparity and ocular dominance were then conducted while the monkey performed a fixation task. The average RF size of the V1/V2 and the V4 neurons was found to be 0.52 ± 0.16 and 0.66 ± 0.14 degrees respectively. The average position, in terms of azimuth and elevation, of the RF's centre was (−0.01, 0.10) degrees for V1/V2, and (0.02, −0.02) degrees for V4. The size of the stimuli, which were centred in the receptive field, was kept as small as possible (usually about 0.7 to 1.2 degrees) to minimize piecemeal rivalry; that is, the perception of a mosaic-like collage consisting of different portions of each eye's stimulus-pattern. Decreasing stimulus size increases the exclusive visibility of a stimulus, and therefore optimizes the conditions for studying correlations between cell and monkey responses. Following the quantitative tests, each neuron was tested during the orientation discrimination task with congruent and rivalrous stimuli. The relationship between eye and preferred orientation was pseudorandomized across rivalrous observation periods, so that in each session an equal number of preferred and non-preferred orientations were presented to each eye. Cells were collected from the foveal representation of the areas V1 and V2. As no histology is yet available, the cells in the two early areas are referred to as V1/V2 neurons. However, based on our preliminary topographical mapping, and on ocular dominance preferences in single penetrations, about half of the tested V1/V2 cells are most likely in striate cortex and the other half in area V2. On the basis of stereotaxic coordinates, RF size and position, and RF properties, most neurons on the prelunate gyrus or the anterior bank of the lunate were in V4.

many neurons continue to respond to their preferred stimulus regardless of the perceptual state. The present study shows that a similar range of response patterns exists in V4 and V1/V2, although areas V1/V2 did not have neurons responding during the suppression of their preferred stimulus. As the duration of dominance and suppression can vary independently as the stimulus strength is changed, it is tempting to speculate that the neurons firing during dominance mediate the perception of one stimulus, whereas those firing during suppression underlie the phenomenal suppression of the other. Interestingly, a number of modulating neurons were influenced by the perceptual requirements of the task. Thus some cells were tuned for orientation (this work) or direction[3] during the discrimination task but showed no preference during the fixation task, whereas others were tuned during rivalrous but not congruent stimulation. Such cells may be mediating the effects of selective attention on perception. It remains a puzzle, however, why the discharges of the large number of neurons that continue to fire during suppression is not sufficient to mediate perception. It will be of great interest to determine whether the different response properties are in any way correlated with the anatomical location and connectivity patterns. Preliminary results suggest that many of the modulating neurons in MT are located in deep cortical layers (N.K.L., unpublished results).

It has been proposed that the phenomenal suppression during binocular rivalry is the result of a blockade of monocular information triggered by reciprocal inhibition between monocular neurons in striate cortex[4]. Such a blockade would result in the removal of the representation of the suppressed stimulus at all subsequent sites in the visual pathway. Our results do not support

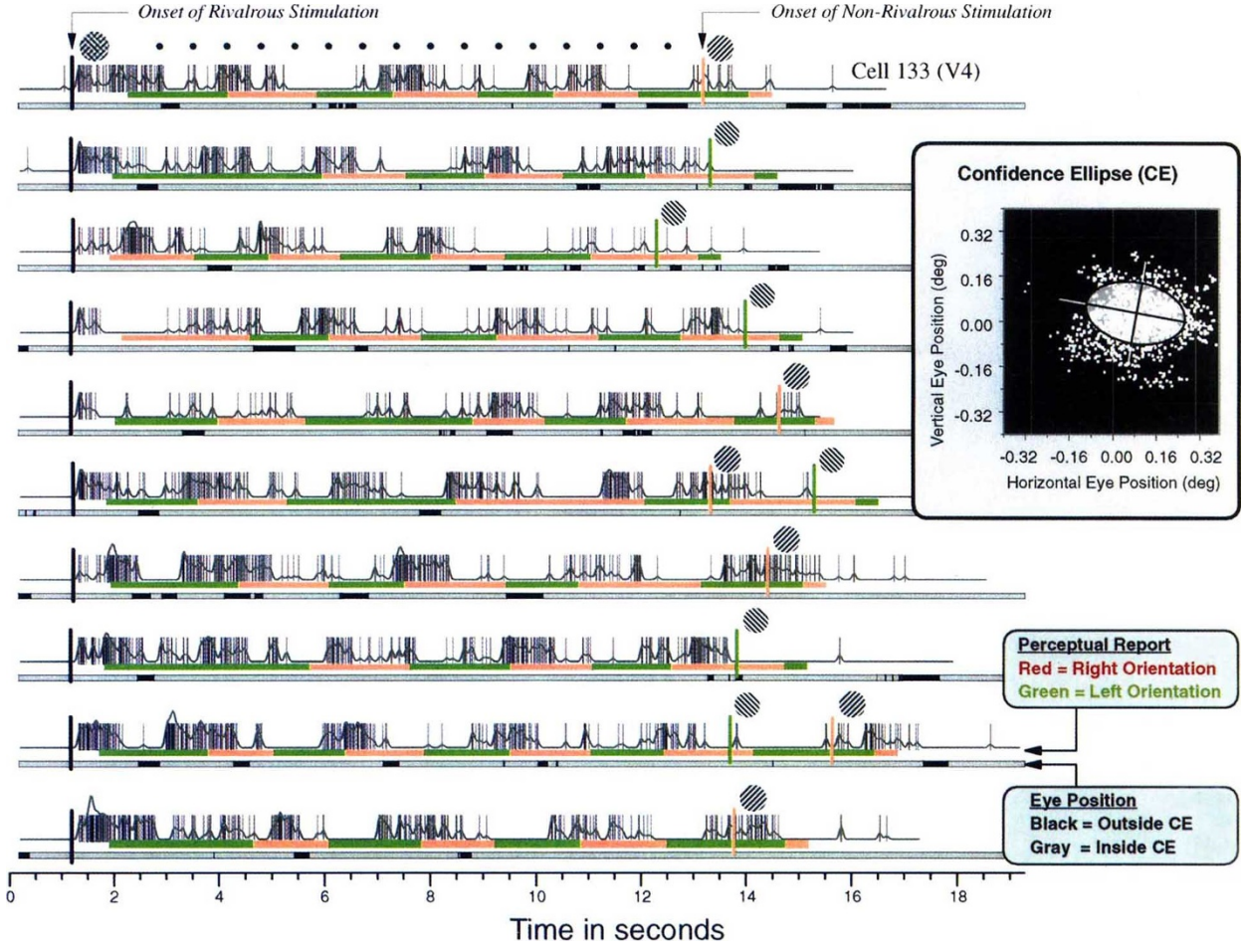
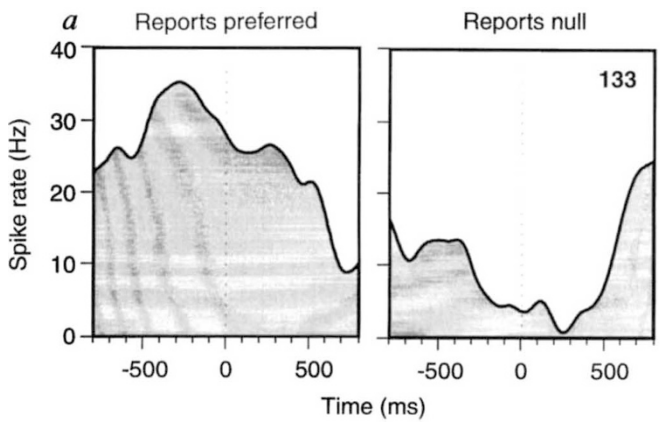


FIG. 2 Single observation periods showing modulations in the firing rate of a V4 neuron as the monkey reports perceptual changes during continued viewing of the same stimulus. Each thin dark-grey vertical line signifies the occurrence of an action potential. Superimposed on the action potentials are spike density functions illustrating the probability of occurrence of a single spike within successive 5-ms periods. The horizontal green and red bars show the alternating phases of perceptual dominance of the left- and right-tilted grating. The black regions on the grey bar show periods in which the eye position was outside the confidence ellipse shown in the inset. This ellipse surrounds the region within which eye positions kept the stimulus within the central part of the neuron's receptive field. This region was computed as follows: mean eye position (X, Y) and spike rate R were first calculated over 35 small time windows (a 250-ms window that was shifted by 50 ms, beginning 1,000 ms before and ending 750 ms after each lever press) during non-rivalrous periods in which the neuron was stimulated with its preferred orientation. The average ($\bar{X}$, $\bar{Y}$) of the X, Y values for which $R > (\bar{R} + \sigma_R)$, was taken as the centre of the ellipse that represents the eye position that 'centres' the stimulus within the RF. The slope and length of the axes of the confidence ellipses correspond to the eigenvectors and eigenvalues of the distribution of the selected eye positions. Only rivalrous trials during which the eye position remained within the confidence ellipse were used to build the PSTHs shown in the next figures. Note that the firing rate of the neuron is elevated immediately before each report of perceiving the cell's preferred orientation, and remains high often for a time-period roughly corresponding to the following dominance phase of the preferred stimulus. In about half of the illustrated observation periods the left-tilted grating is presented to the left and the other half to the right eye.



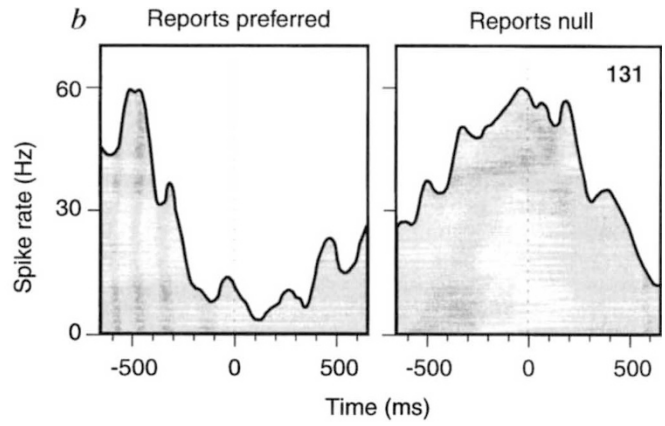


FIG. 3 Peristimulus time histograms for two V4 neurons during BR. The ordinate represents the spike rate and the abscissa the time before and after the monkey's report, depicted by a slashed line. The left and right plots show the activity of the cell for those trials in which the monkey reported the perceptual dominance of the neuron's preferred and non-preferred orientation respectively. Because the phase durations vary greatly within a session, averaging within any time window may often include cell responses from the previous or next report. Thus the selection of a time window—here [−650,650] ms—around the animal's response is arbitrary, usually based on the mean phase duration of the session. *a*, Mean response of the neuron shown in Fig. 2 before and during the report of phenomenal dominance and suppression of a right-tilted grating. *b*, An example of a neuron firing exclusively before and during the suppression of its preferred orientation. The neuron's response is reduced before the monkey reports seeing the cell's optimal orientation, and remains very low for more than 600–700 ms. In contrast, the response gradually increases before the monkey's report that the optimal orientation is suppressed, and remains high for a similar time period (600–700 ms).

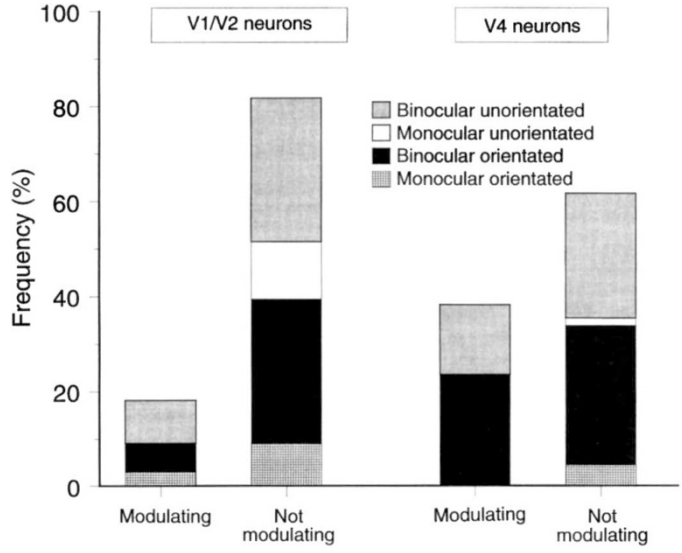


FIG. 5 Distribution of different cell properties within the population of response-modulating and non-modulating cells in the areas V1/V2 and V4. Cells were classified as monocular/binocular, oriented/unoriented and modulating/non-modulating (see text).

this view. First, almost all recorded monocular cells are unaffected by suppression. Second, the frequency of modulating cells is significantly higher in V4 (38%) and MT (43%; ref. 3) than it is in V1/V2 (18%) where the inputs from the two eyes are first combined. Third, the majority of cells in all areas continue to respond to their preferred stimulus even when it is perceptually suppressed; a fact that is consistent with a number of studies showing that suppression of an adapting stimulus during binocular rivalry does not curtail the strength of after-effects[6]. Thus, competition between monocular neurons is unlikely to explain rivalry; instead, we suspect that the rivalry is between alternative stimulus representations that are encoded in the activity of many neurons in different visual areas (among them V4 and MT) implicated in shape encoding or figure-ground segregation. This hypothesis is supported by a number of psychophysical observations. For example, rivalry can occur even when the conflicting patterns are presented to the same eye, ('monocular rivalry' or 'pattern rivalry')[7]. Also, when two pairs of rivalrous stimuli are presented together, the perceptions are more likely to change in synchrony if members of the two pairs form a coherent figure, even if the components of the figure are presented to opposite eyes[8].

Finally, the temporal dynamics of rivalry are similar to those experienced when viewing ambiguous figures, such as the Necker cube and other depth reversals[9]. It is therefore possible that a common neural mechanism underlies all these forms of multistable perception, and that understanding this mechanism will

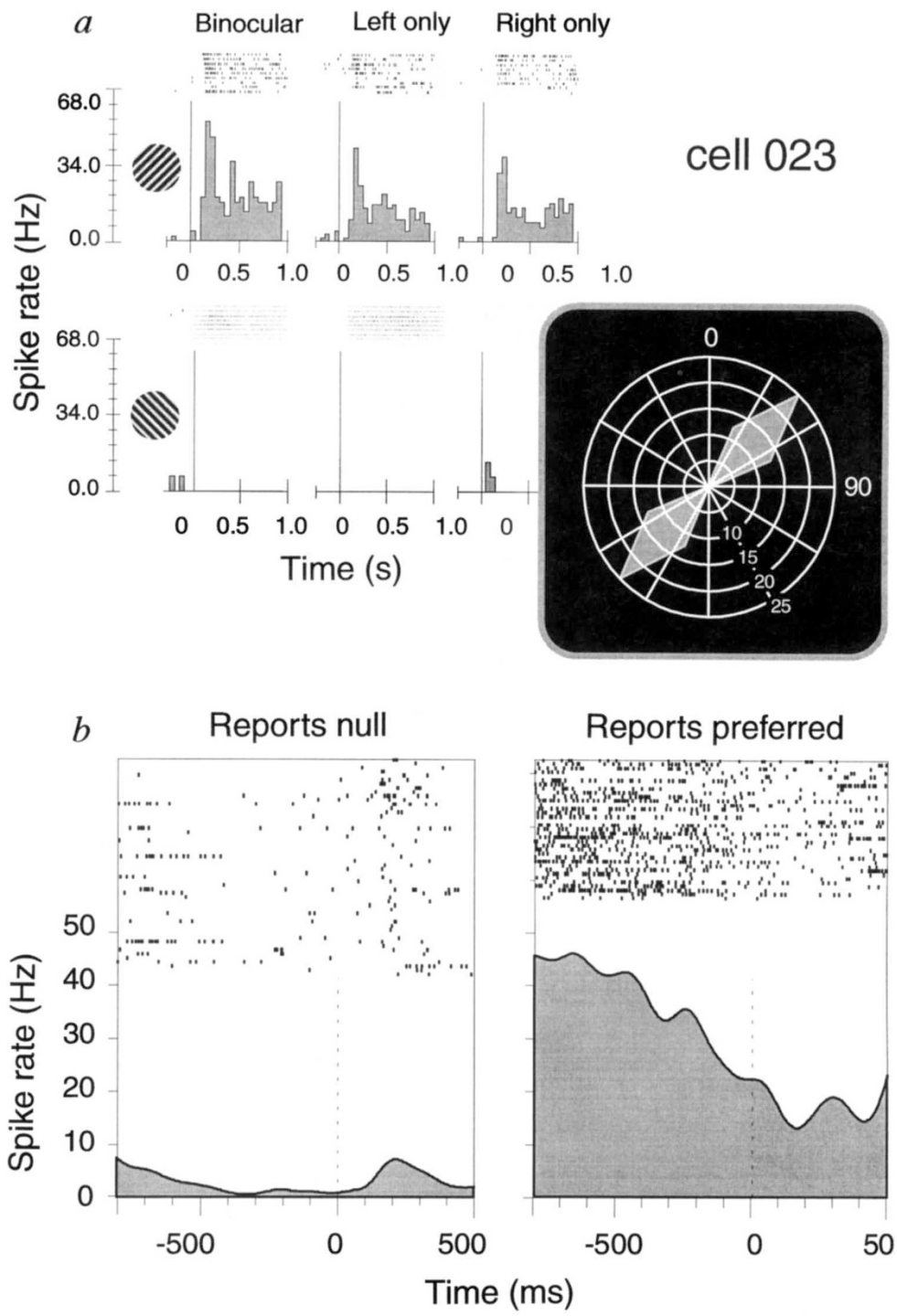


FIG. 4 Response of a V1/V2 neuron to rivalrous stimuli. *a*, PSTHs showing the cell's response to a grating of optimal (above) and of orthogonal-to-optimal (below) orientation, for binocular and monocular presentations. The polar-plot shows the neuron's orientation tuning. *b*, Rasters and PSTHs during rivalrous stimulation. Responses are averaged for a time window of [−800,500] ms around the monkey's response. Conventions as in Fig. 3.

lead to new insights regarding the neural basis of perceptual organization and of visual awareness. □

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1. Helmholtz, H. V. *Physiological Optics*, translated for Opt. Soc. Am. (1924) from *Handbuch der Physiologischen Optik* 3rd edn (Voss, Hamburg, 1909) (Dover, New York, 1962).
2. Breese, B. *Psychol. Rev.* **3,** 1–65 (1899).
3. Logothetis, N. & Schall, J. *Science* **245,** 761–763 (1989).
4. Blake, R. *Psychol. Rev.* **96,** 145–167 (1989).
5. Levelt, W. *On Binocular Rivalry* (Royal VanGorcum, Assen, 1965).
6. Blake, R. & Rox, R. *Nature* **249,** 488–490 (1974).
7. Campbell, F. & Howell, E. *J. Physiol., Lond.* **225,** 19P–21P (1972).
8. Whittle, P., Bloor, D. & Pocock, S. *Percept. Psychophys.* **4,** 183–188 (1968).
9. Borselino, A., De Marco, A., Allazetta, A., Rinesi, S. & Bartolini, B. *Kybernetik* **10,** 139–144 (1972).
10. Fox, R. & Herrmann, J. *Percept. Psychophys.* **2,** 432–436 (1967).
11. Walker, P. *Percept. Psychophys.* **18,** 467–473 (1975).
12. Logothetis, N., Pauls, J. & Poggio, T. *Curr. Biol.* **5,** 552–563 (1995).

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