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Neuronal Activity Related to Motion Perception in the Middle Temporal (MT) Visual Area of the Macaque

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The middle temporal (MT) visual area of primates, including humans, has been shown to play an essential role in analyzing visual motion. We have been interested in how the neuronal activity in this area is related to the perceptual processing that occurs during binocular motion rivalry. Single units were recorded while monkeys (*Macaca mulatta*) discriminated the direction of motion of an ambiguous stimulus that could be seen moving in opposite directions. We found that the direction of pursuit eye movements corresponded to the behaviorally reported, perceived direction during motion rivalry even though the gain of pursuit was reduced and the latency was increased. A variety of responses were observed in the directionally specific neurons of MT, revealing a diversity of processing occurring in this area. Certain neurons responded only when their optimal stimulus was present in the dominant eye during rivalry; that is, their activity reflected the monkeys' perceptual decision about the direction of motion. Other neurons responded only when the optimal stimulus was present in the suppressed eye during binocular rivalry; these neurons may provide the inhibitory signal mediating the suppression phase of binocular rivalry. The activity of the remaining neurons was not related to rivalry dominance or suppression. Some of these cells were active during rivalry and others were not. We think that this difference reflects the diversity in the circuitry underlying the directional specificity of the different neuron classes in MT. These results provide new information about both the functional properties of the cells in area MT and the mechanisms underlying motion perception during binocular rivalry.

Introduction

If one could see directly the image of the world as it impinges on the retina, before any of the sophisticated processing provided by the visual system, one would be amazed at how little one could make sense of or recognize. The ease

and quality of normal human vision belies and yet is a result of a number of very complicated processes. A fundamental goal of visual neuroscience is to understand how the processes which result in an accurate and meaningful internal representation of the visual world are instantiated in the structure and function of the visual system. Ultimately, this comes down to the question: what is the physiological basis of the procedure generating a perceptual attribute from the sensory data representing a property of a visual stimulus?

Neurophysiological work over three decades, initiated by the pioneering work of David Hubel and Torsten Wiesel,[1] has shown that specific features of a visual stimulus are required to evoke neuronal responses at different stations of the visual pathway. Neurons in the visual cortex of higher mammals respond only to specific properties of a visual stimulus located in their receptive field, their window to the world, and neurons with similar properties are grouped together in a topographic map of the visual field.[2] Furthermore, there are several visual maps located in segregated cortical regions, the cells of which show a pronounced functional specialization, meaning that they can specifically respond to the form or the color or the motion of an object.[3]

Developing techniques for recording single-unit activity in alert, behaving animals now provides the opportunity to relate neuronal activity not just to physical stimulus characteristics but also to the on-going perceptual processes. The sensory capacities of nonhuman primates can be determined in as precise and reliable a fashion as those of humans by training them, through operant conditioning, to report what they see under an interesting variety of conditions.[4] Similarly, monkeys can be trained to report their percepts, although some challenging problems in both the training and the testing will become evident. Thus, while the animal is performing a particular task, one can record the activity of nerve cells and study their relation to the reported sensations and percepts.

One way to distinguish neuronal activity related to a perceptual process rather than to a passive sensory input is to expose the visual system to stimuli that allow more than one percept; that is, when the visual cues provided constrain the interpretation to one description of the scene, perception is unique and stable. However, when the sensory data are insufficient for just one interpretation, rival possibilities can be entertained and perception becomes ambiguous, switching between two or more alternatives. In this study we took advantage of the unstable percept that ensues when the two eyes are shown different stimuli, a phenomenon known as binocular rivalry.[5] When both eyes see roughly the same stimulus, as is usually the case, then the binocular visual system derives a single image through a process know as binocular fusion (Figure 1a,e). However, when the right eye sees, for example, horizontal and the left, vertical contours, the process of fusion might predict that one would perceive a composite image such as a plaid or a checker board (Figure 1b). What actually happens is that if the stimuli are large, one

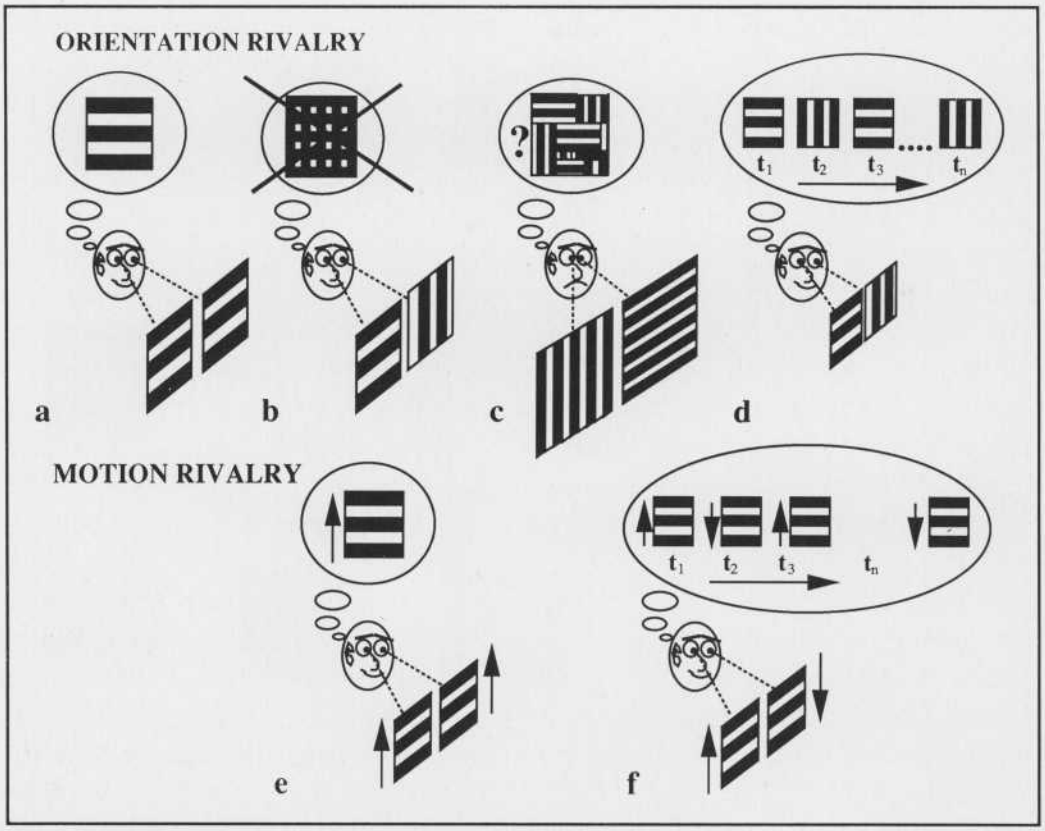


Figure 1. Illustration of the phenomenology of binocular rivalry.

perceives a field broken into horizontal and vertical patches (Figure 1c), and if the stimuli are smaller, one's perception alternates between the horizontal and the vertical grating (Figure 1d). Similarly an alternation in the perception of the direction of motion is observed when gratings moving in opposite directions are presented to each eye (Figure 1f). In the broadest sense, dissimilar monocular stimuli presented to corresponding retinal areas cannot be fused by the cyclopean visual system; the visual system reacts to this highly conflicting situation by temporarily suppressing one eye's view such that perception alternates between the stimulus seen by the right eye alone and that seen by the left eye.

Binocular rivalry is not simply a whimsical laboratory construct. During natural vision both binocular fusion and binocular rivalry occur continuously even though the latter goes unnoticed. By definition, all objects in space that do not fall on corresponding points of our retina cast disparate images in the two eyes. The geometry of binocular space presents the visual system with a tremendous amount of conflicting information; recall that Panum's fusional area occupies a small fraction of binocular space. Consequently, binocular suppression must be the protagonist in the processes establishing unambiguous and clear binocular vision.

The successive phases of domi-

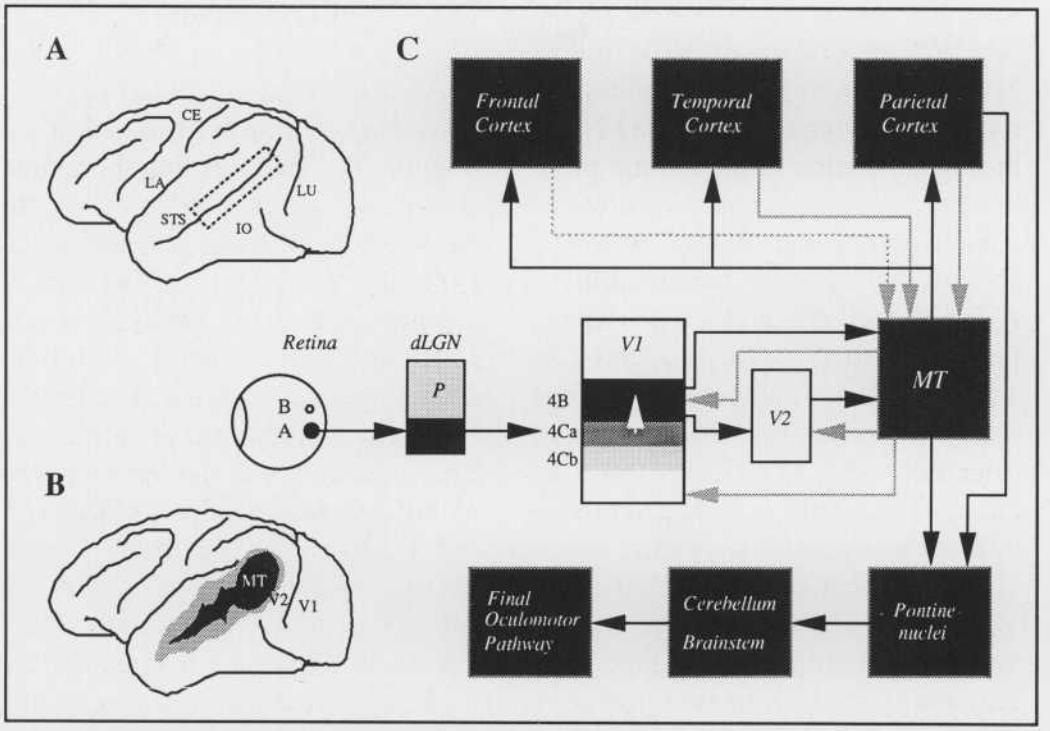


Figure 2. A. Side view of macaque monkey brain. The superior temporal sulcus is demarcated by the rectangle. **B.** Side view of brain with superior temporal sulcus opened to expose MT. **C.** Motion processing pathway. The "motion processing" pathway originates in the A/P-alpha broad-band retinal ganglion cells which project to the magnocellular layers of the dLGN. These relay cells in turn project to layer 4c-alpha of striate cortex which provides afferents to layer 4B. While the neurons in 4c-alpha are orientation selective, the cells in layer 4B are direction selective. Layer 4B projects to disparity but not direction selective cells in V2 which in turn projects to MT, which is itself comprised almost entirely of direction-specific cells. The neurons in 4B also send a direct projection to area MT. Area MT sends projections to higher cortical areas in frontal, temporal, and parietal cortices. All of the cortical projections are reciprocal (indicated by the dashed lighter lines). MT also provides major afferents to the pontine nuclei which project to cerebellar regions involved in gaze control.

nance and suppression are salient features of the process of binocular rivalry, and they are considered the characteristic dependent variables of this phenomenon. Myerson, Miezin, and Allman[6] have shown that rhesus monkeys experience binocular rivalry just like humans do. These authors have shown that there is a great similarity in the distribution of the perceptual alternation frequency and the phase duration during binocular rivalry of human and monkey. The same investigators have also shown that when rivalry is induced by gratings moving in opposite directions for the two eyes, the alternation rate increases with the velocity of the gratings. The remarkable similarity in these measures of binocular rivalry in the two species indicates that the underlying mechanisms which result in the alternating perceptions during rivalry probably do not differ between man and monkey.

Our goal was to study the role of the middle temporal (MT) area, an ex-

trastriate visual area located in the superior temporal sulcus (STS) (Figure 2A,B), in the perception of motion using rivalrous moving stimuli. Area MT is a prominent station in the motion processing channel of the visual pathway.[7] Anatomically, the motion pathway (Figure 2C) begins in the broad-band, A/P-alpha retinal ganglion cells which, through the magnocellular layers of the dorsal lateral geniculate nucleus (dLGN), project via the monocular, orientation-specific cells of layer 4c-alpha to the binocular direction-specific cells of layer 4B of striate cortex (V1). The neurons of 4B send direct afferents to the cytochrome oxidase labeled thick stripes of the second visual area, V2 which in turn project to MT. Layer 4B also sends a direct projection to MT. MT is the source of a divergent projection to higher cortical areas in temporal, parietal and frontal cortices. Furthermore, MT and the neighboring middle superior temporal visual area (MST) form the basic sensory input to the oculomotor pursuit system; these areas project to the pontine nuclei that relay cortical signals to the cerebellum which controls the initiation and maintenance of pursuit eye movements.[8] Functionally, area MT has been shown to play an important role in analyzing visual motion. This is based on the results of single unit recordings in nonhuman primates,[9] which demonstrate that cells in MT and MST are selective for the direction and speed of a moving stimulus, and on lesion studies in monkeys[10] and humans,[11] which show that loss of these regions of the STS results in severe deficits in visual motion tasks.

Experimental Methods

Three rhesus monkeys were trained in a motion discrimination task (Figure 3). Two drifting horizontal gratings were generated by computer on a video monitor using a raster display system and were presented independently to the two eyes through a stereoscopic viewer. Vertically drifting gratings were used exclusively to prevent any vergence eye movements. The monkey's eye movements were monitored using a scleral search coil, and the experiment was under computer control. A trial began with the appearance of a central fixation spot. After the monkey fixated it, drifting gratings were presented for a specified period and then replaced by two spots on the left and right of the fixation spot. If the monkey perceived upward motion during the grating presentation, he was required to saccade to the right spot; a saccade to the left spot was required following downward movement.

As mentioned previously there are some challenging problems with perceptual experiments using nonhuman primates. In a sensory experiment using unambiguous stimuli, the experimenter can uniquely specify the correct response required for reinforcement. In a perceptual experiment using ambiguous stimuli like the rivalrous stimuli used in this experiment, there is no correct response defined by external criteria. Accordingly, we started the training procedure with only non-rivalrous stimuli and gradually introduced rivalry trials. In rivalry trials, however, the monkey had to be rewarded for whichever choice he made. Being less

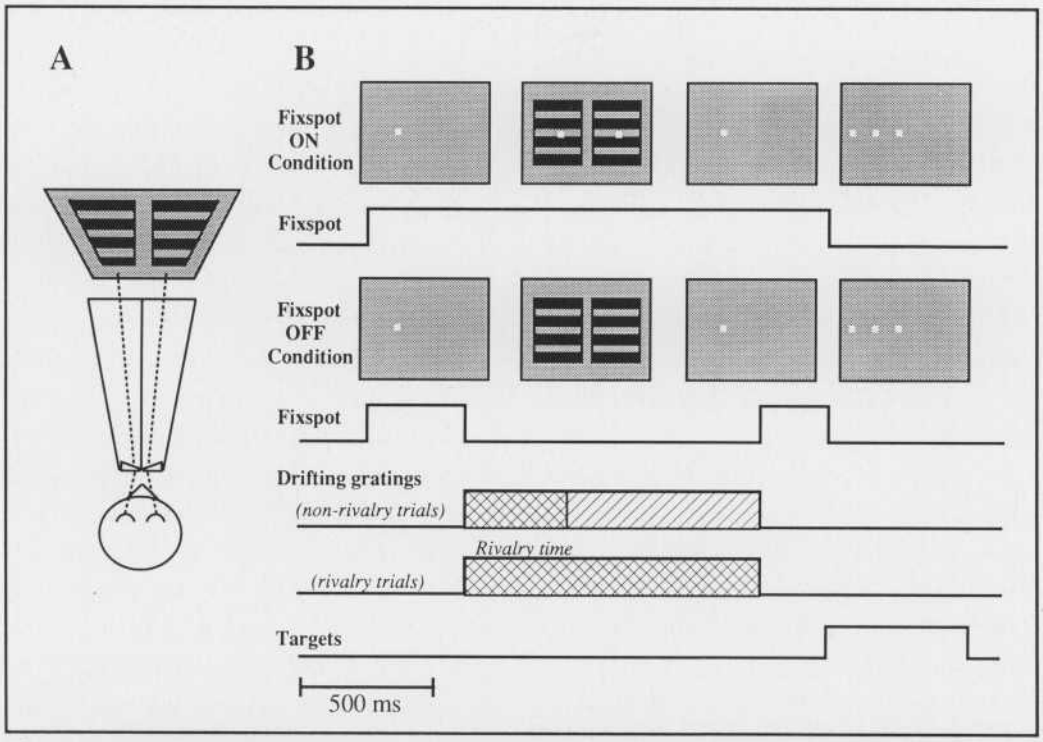


Figure 3. A. Two gratings were presented independently to the two eyes through a stereoscopic viewer. **B.** Binocular rivalry motion discrimination task. A trial began with the appearance of a central fixation spot. After the monkey fixated it for 200msec to 300msec, drifting gratings were presented for 400msec to 1500msec. The gratings were replaced by two spots on the left and right of the fixation spot. If the monkey perceived upward motion, he was required to saccade to the right spot; a saccade to the left spot was required following downward movement. In half of the trials the gratings drifted in the same direction, and in the other half, they were rivalrous. In the rivalrous trials the monkeys were rewarded for either response. In half of the trials the fixation spot was removed when the gratings appeared to allow pursuit eye movements, and in the other half it remained visible to suppress pursuit. The various trial types were pseudo-randomly interleaved. The gratings were sufficiently small to allow one of the eyes to be dominant and the other suppressed.

motivated about the experiment than we were, the monkeys quickly learned that they could pay no attention to the stimuli whatsoever and always go one direction to get a reward. We were consequently forced to keep the monkeys honest; this was accomplished in three ways. First, we could adjust the contrast of the gratings in the two eyes and reward the monkey according to the direction of motion of the higher contrast grating. This forced him to attend to the rivalrous gratings and make a real decision. Second, following the methods of Myerson *et al.*,[6] we started every trial with rivalrous gratings and in half of the trials switched to non-rivalrous. This effectively taught the monkeys that a period of ambiguity would be followed by resolution. In rivalry trials we hoped the monkey would provide the resolution. Finally,

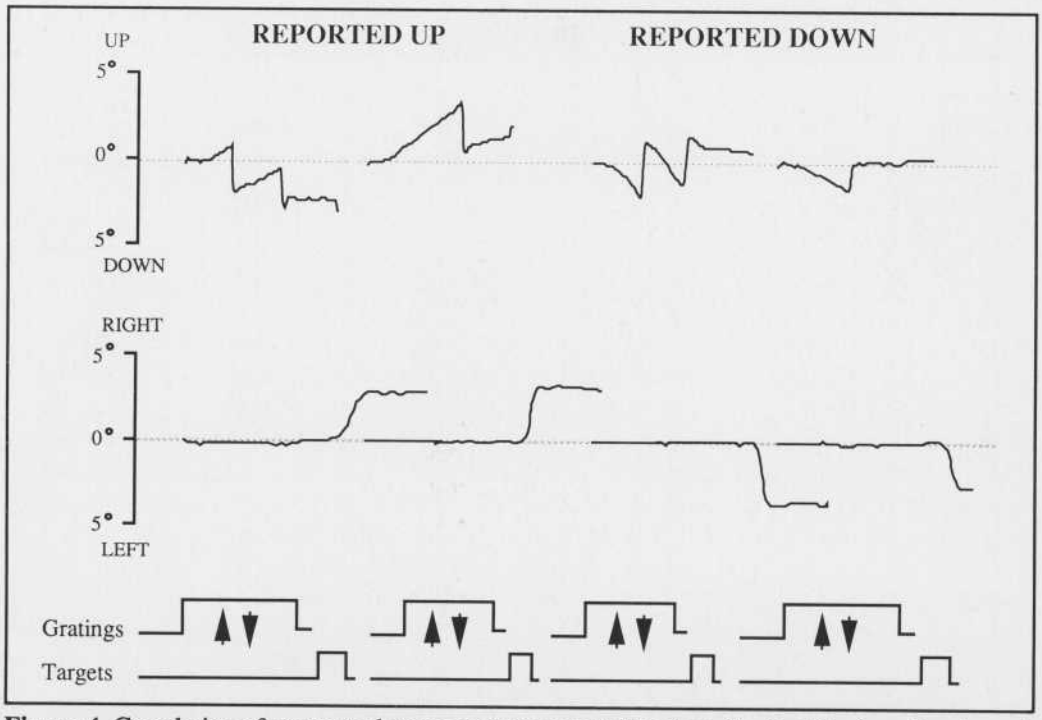


Figure 4. Correlation of perceptual response and pursuit direction. Vertical (top) and horizontal (bottom) eye movement traces are shown for rivalry trials in which monkeys reported upward (left) and downward (right) motion. The monkey pursued up on the trials in which his behavioral response, indicated by the rightward saccade, was up. The converse was observed for trials in which the monkey perceived downward motion.

the reason we chose to use motion rivalry in the first place was because the eye-movement response to the moving gratings provided an objective measure of the animals' perception.[12, 13]

Pursuit During Binocular Motion Rivalry

Enoksson[12] and Fox and colleagues[13] have demonstrated that the direction of the slow phase of optokinetic nystagmus elicited during binocular motion rivalry corresponds to the perceived direction of motion. In agreement with this work, we found a significant correlation between the behaviorally reported direction of motion and the direction of pursuit (Figure 4). Table 1 presents the correspondence between direction of pursuit and reported direction of motion for the three monkeys. Overall, in 93 percent of the trials in which pursuit could be measured, the direction of pursuit was the same as the perceptual choice, and in the remaining trials the behavioral response was opposite the direction of pursuit. In 10 percent of the rivalry trials no pursuit could be measured even though the monkey made a perceptual decision. In rivalry trials in which the monkeys reported downward motion no particular pursuit was observed more commonly, but this

Table 1

Behavioral Response	Pursuit	Monkeys *Walter*	*Vinnie*	*Lily*
up	up	97%	95%	90%
	down	3%	5%	10%
	none	10%	5%	9%
down	up	12%	8%	6%
	down	88%	92%	94%
	none	18%	11%	8%

Table 1. Correlation of pursuit direction and behavioral response. The percent of trials of the type indicated by the behavioral response and pursuit direction is given for each monkey. This analysis only represents rivalry trials in which the fixation spot was absent, allowing pursuit.

may be a consequence of the observation that the gain of downward pursuit was less than that for upward pursuit.

The distribution of pursuit gain during rivalrous and non-rivalrous grating presentation is illustrated in Figure 5. It is clear that the gain of pursuit during rivalry is less than that during non-rivalry; the average gain of pursuit for all monkeys during non-rivalry was 0.92, and during rivalry was 0.50. Further evidence that the pursuit system is compromised during rivalry is presented in Figure 6 which shows the latency of pursuit for the three monkeys. The latency of pursuit during rivalry is longer than the latency in non-rivalry; the average latency of pursuit for all monkeys during non-rivalry was 185msec, and during rivalry was 294msec.

The latency of pursuit during rivalry has not been investigated before,[12,13] but in general the longer latency that we observed is in agreement with the results of Fox and Check[14] and Blake and Boothroyd,[15] who showed that manual reaction times are elevated during rivalry suppression. Also, despite the complete dominance of one of the eyes during rivalry, the gain of the pursuit of the phenomenally coherent moving grating is cut in half. This result indicates that a signal derived from the suppressed eye is still impacting on the oculomotor pursuit system.

Single-Unit Activity Recorded During Binocular Motion Rivalry

Single-unit recordings were performed in two monkeys using standard procedures. A total of 66 neurons were recorded in the STS of both monkeys; seven of the units had receptive fields which did not include the fovea and were therefore not used in this analysis. The remaining units exhibited directional specificity; their receptive fields

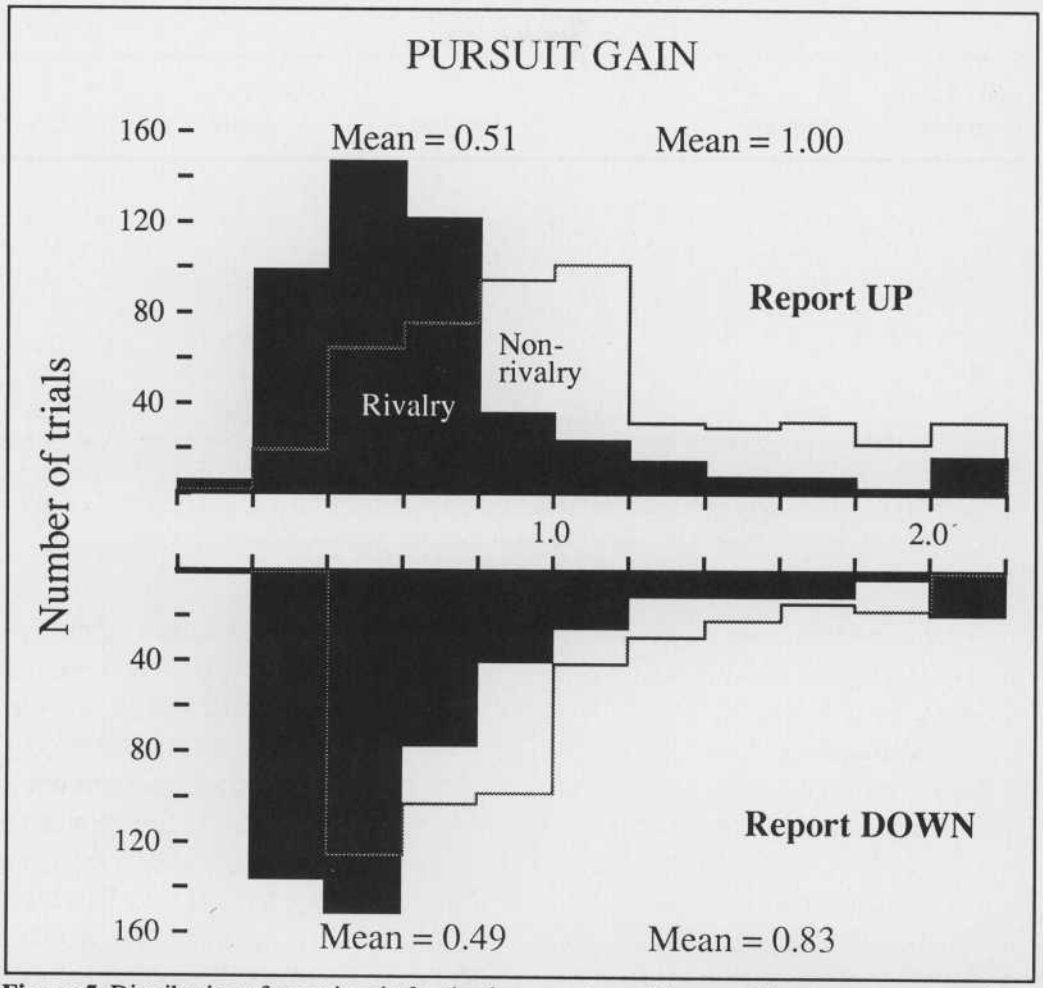


Figure 5. Distribution of pursuit gain for the three monkeys. The open histogram represents data collected during non-rivalry trials, and the solid histogram represents data collected during rivalry trials. The top histograms represent trials in which the monkeys reported upward motion, and the bottom histograms represent trials in which the monkeys reported downward motion. The mean gain for non-rivalry and rivalry trials are displayed above each histogram. The gain of the pursuit during rivalry was significantly less than normal.

included the fovea and their size was comparable to the eccentricity of their receptive-field centers. According to these receptive-field properties, we believe these units were in MT.

Neurons not related to rivalry dominance and suppression. Different populations of neurons could be distinguished by comparing their modulation during non-rivalrous and rivalrous grating presentation. For example, the activity of most of the neurons during rivalry did not vary according to the direction of motion the monkeys reported (Figure 7). This cell preferred upward motion during non-rivalrous trials and discharged equally in rivalrous trials regardless of the monkeys

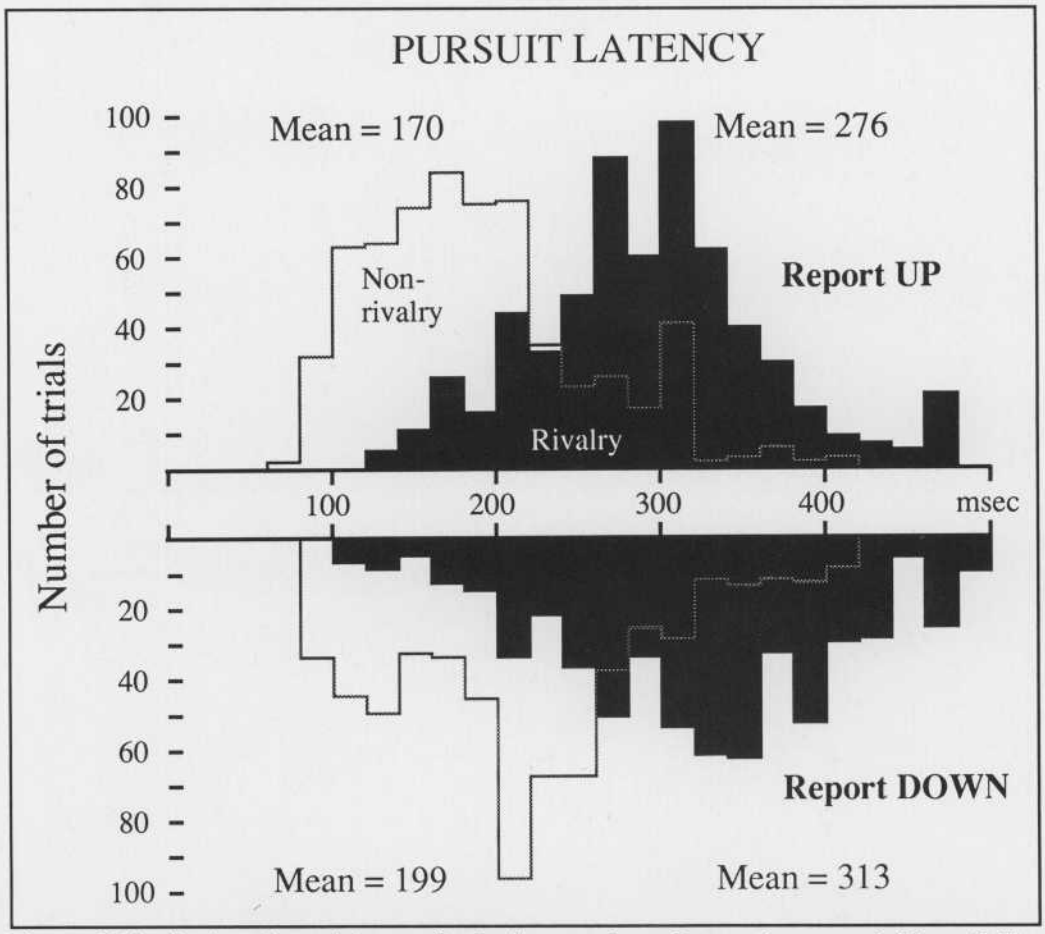


Figure 6. Distribution of pursuit latency for the three monkeys. Conventions are as in Figure 5. The latency of pursuit during rivalry was significantly longer than normal.

perceptual choice. Other units were recorded which were equally active in rivalry trials in which the monkey chose up or down, but their activity when compared to non-rivalrous trials was attenuated (Figure 8).

Figure 9 shows a unit that exhibited an entirely different pattern of modulation. This unit responded slightly better for up than for down in non-rivalrous trials. During rivalry trials this cell responded preferentially when up was presented to the left and down to the right eye. When this cell was stimulated by gratings presented to each eye independently, we found that it preferred up in the left eye and down in the right eye; in other words, this cell appeared to have opposite preferred directions in the two eyes. Such cells have been observed in area 18 of the cat,[16] as well as striate cortex[17] and area MT of macaque monkey.[18]

Neurons with opposite preferred directions in the two eyes have been believed to play a role in signaling motion in depth, but these units are only appropriate if they prefer horizontal motion. In contrast, cells preferring vertically opposed directions have been consid-

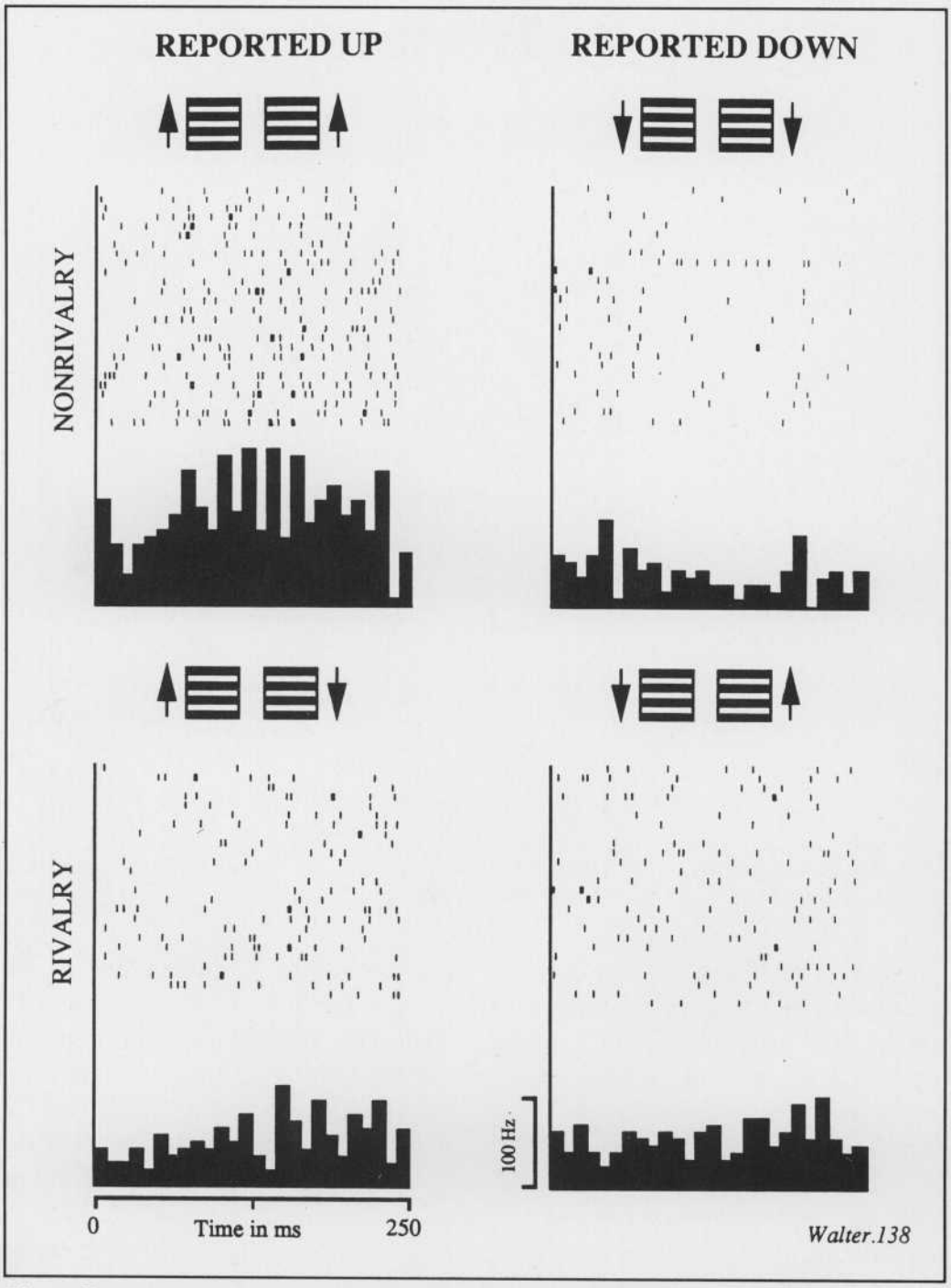


Figure 7. Response of a single unit recorded in MT to non-rivalrous (top) and rivalrous (bottom) motion when the monkey reported perceiving upward (left) and downward (right) motion. Single-unit activity is represented by a raster in which each mark signifies one action potential and by a histogram of the firing rate. The raster and histogram are aligned on the onset of the non-rivalrous or rivalrous motion. This neuron preferred upward motion when presented with non-rivalrous gratings. During rivalry the activity of this cell did not vary with the monkey's perceptual choice even though it was approximately as active as during non-rivalry.

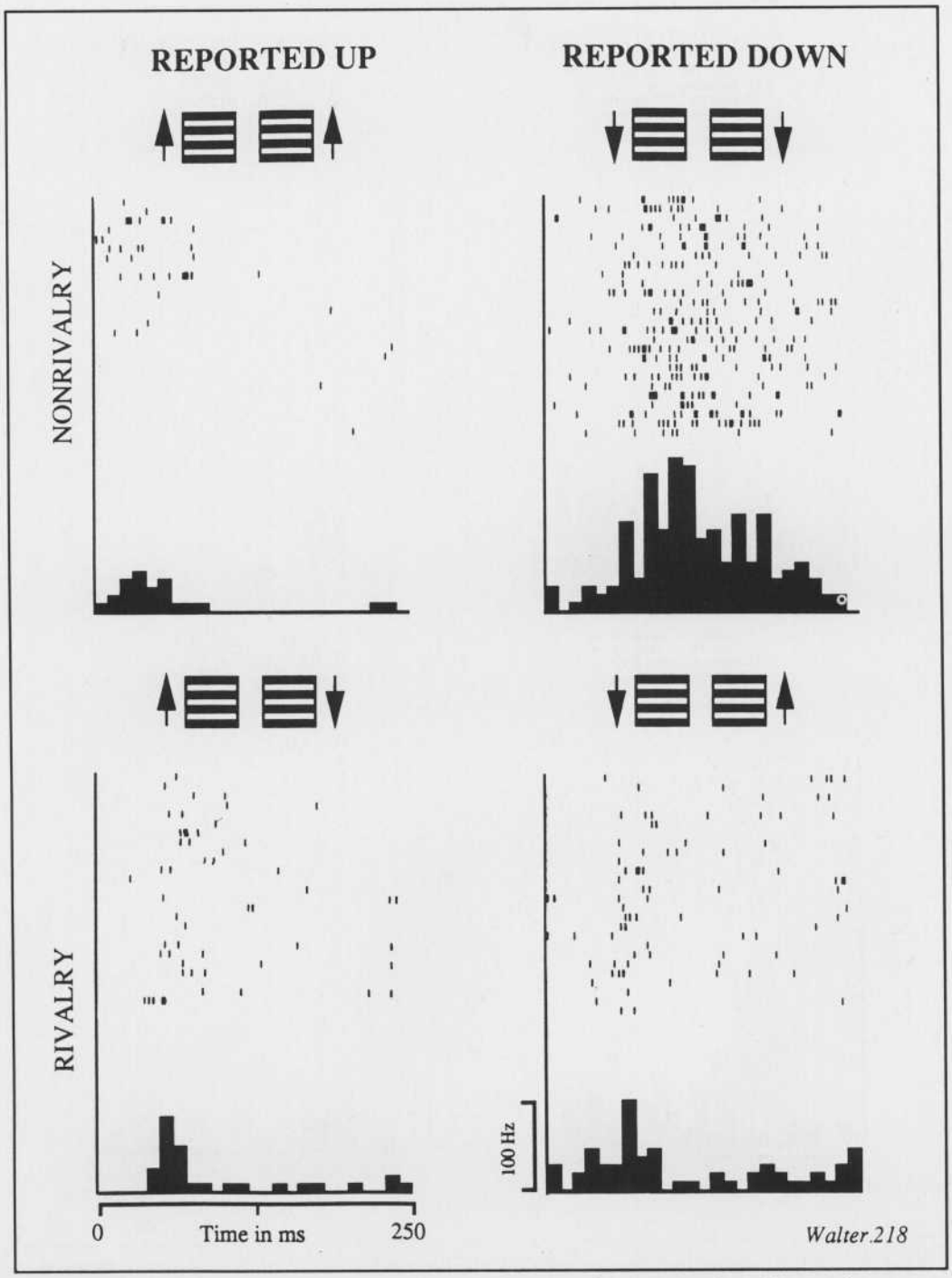


Figure 8. Response of a unit suppressed during rivalrous grating presentation. Conventions are as in Figure 7.

ered mistaken developmental by-products. We would like to point out, however, that there are real world stimuli for such cells. Rotations of the head in the frontal plane cause all stimuli outside of Panum's fusional area to drift in

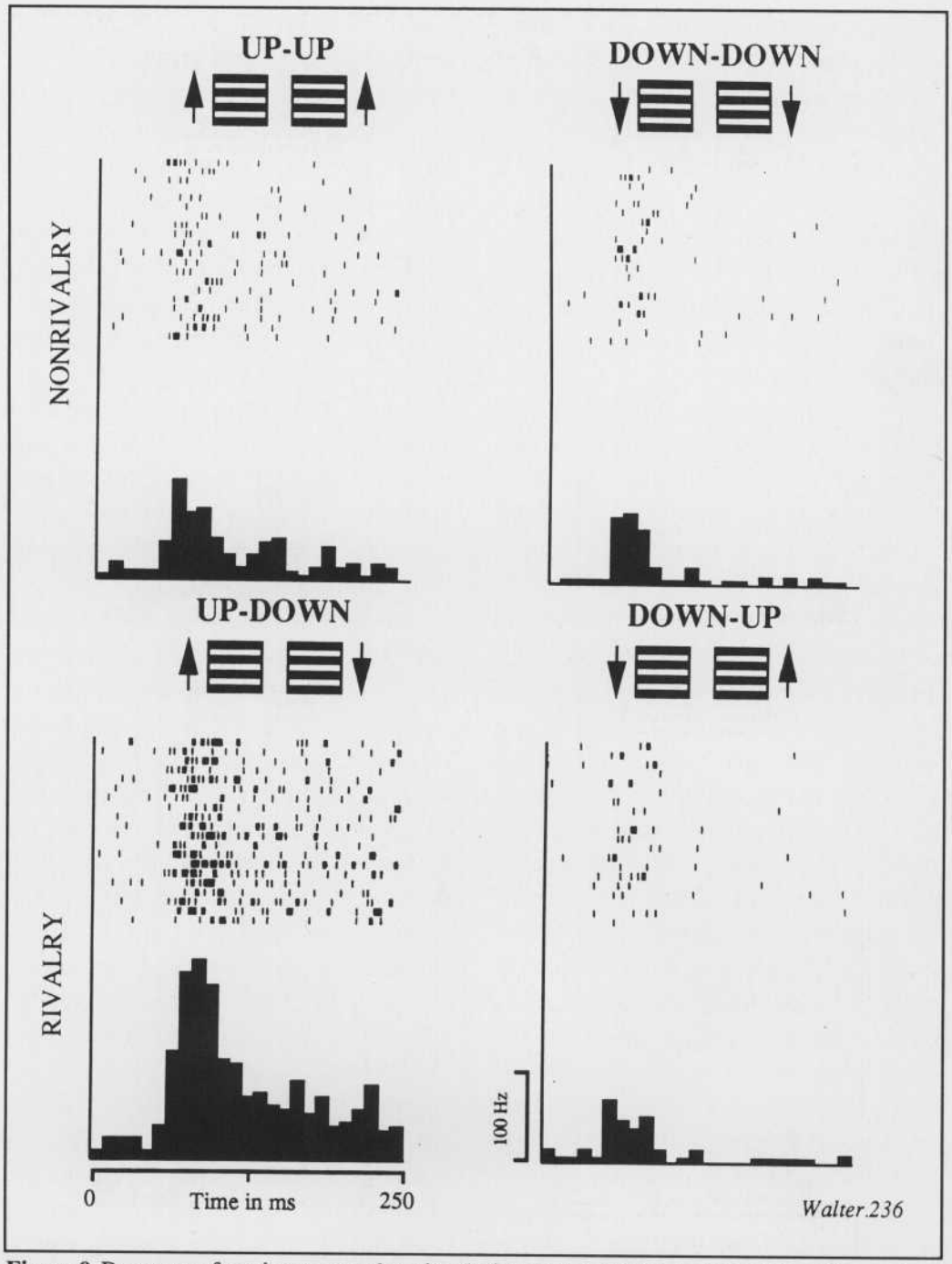


Figure 9. Response of a unit to opposed motion during rivalrous grating presentation. Conventions are slightly different from those in Figure 7. Instead of being sorted according to the monkey's behavioral response, the activity represents that collected during the specific stimulus conditions illustrated by the labeled gratings and arrows. This unit responds preferentially when upward motion is presented to the left eye and downward to the right eye.

vertically opposite directions on the retina of each eye. It is common experience, however, that during drifts of the retinal image produced by volun-

tary movements, our surroundings appear stationary. We believe that the neurons we and others have found with opposed direction preferences can signal this self-initiated and undesired retinal motion; in this case the image drift caused by the rotation of the head. This signal could be useful for those perceptual centers capable of comparing a corollary discharge signal with its corresponding input.

The variation in activity of MT neurons under non-rivalrous and rivalrous grating presentation may also reveal differences in the circuitry mediating the directional specificity of these diverse populations of cells. Earlier work has demonstrated distinguishable populations of neurons in MT with different expressions of directional specificity.[19] Several lines of evidence indicate that intracortical inhibition plays a fundamental role in the generation and maintenance of directional specificity.[20] The fact that some cells are attenuated when their non-optimal stimulus is presented to one eye during rivalry while other cells are not indicates that the different populations participate in different ways in the cortical network. The directional specificity of those neurons which are not suppressed during rivalry would appear to have a more purely excitatory basis, perhaps derived from afferents from layer 4B of area V1. On the other hand, it is possible that the directional specificity of the other units is derived from processing within the STS. How the different populations of neurons observed in this experiment relate to classifications observed before has yet to be worked out.

Neurons related to dominance and suppression. We recorded other neurons whose activity appeared to be related to the perceptual choice the monkeys made when presented with rivalrous moving gratings. Figure 10 illustrates the responses of one neuron whose activity was correlated with the perceived direction of motion during rivalry. When the gratings presented to either eye were moving in the same direction, the response of the cell reflected its upward directional preference. However, when the gratings presented to either eye were moving in opposite directions during rivalry, then the cell discharged on those trials in which the monkey responded that he perceived up. In contrast, this unit did not discharge on trials in which the monkey responded that he perceived down even though the optimal upward moving stimulus was being presented to one eye. It is also evident that the differential activity was present as long as the gratings were presented. Thus, it appears that the activity of this neuron reflected the perceived and not the retinal stimulus motion. In other words, this neuron was specifically active when the optimal stimulus was present in the dominant eye during rivalry.

Since neuronal activity related to pursuit eye movements has been recorded in STS,[21] it might be that the modulation of a cell like this one is related not to the perception of motion but rather to the pursuit eye movements which are also correlated with the perceived direction of motion. There are, however, several arguments against this interpretation. First, during the trials in which the fixation spot remained vis-

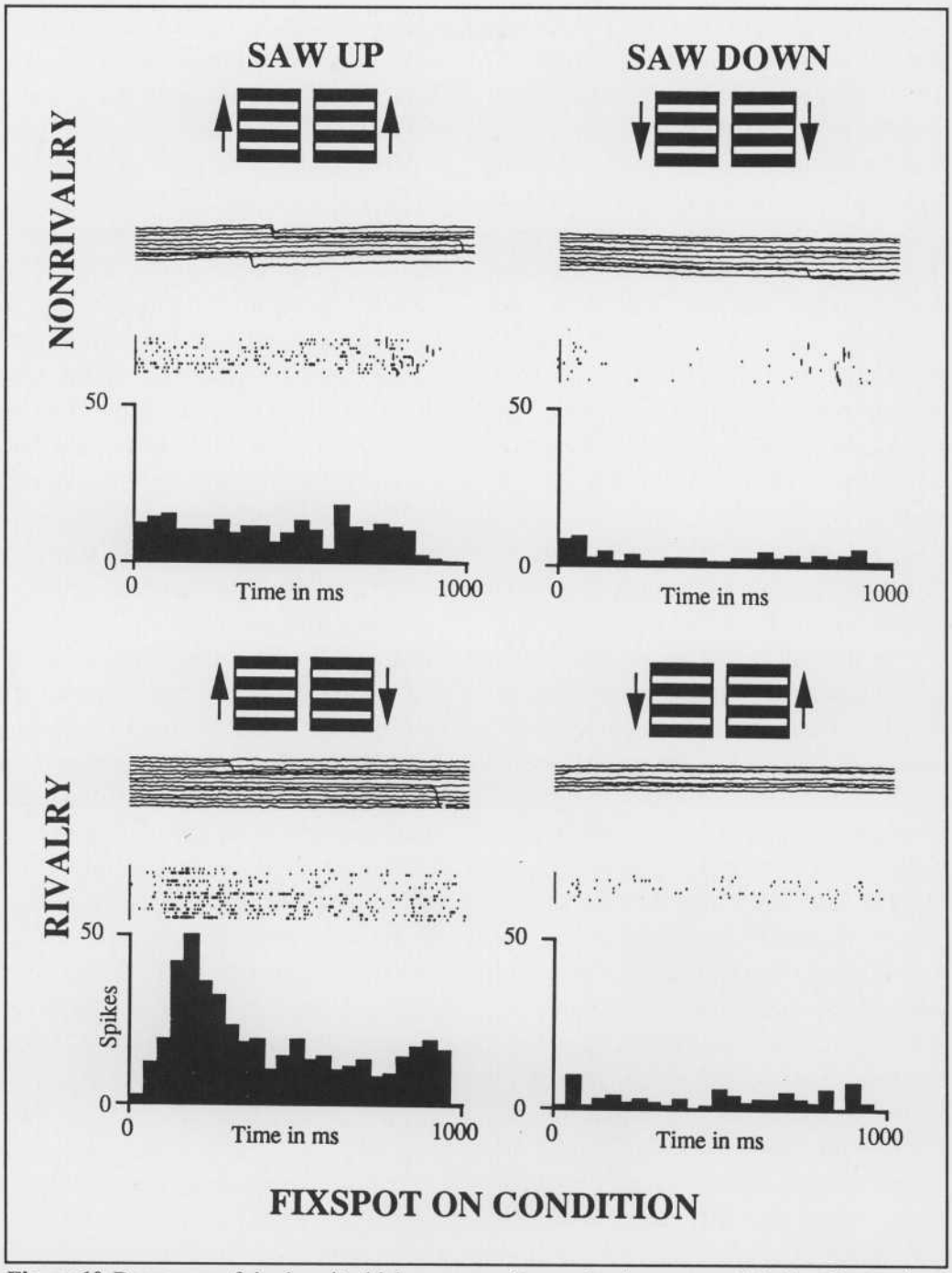


Figure 10. Responses of single unit which correspond to monkey's perceptual choice. Conventions are similar to those in Figure 7. Notice that a longer time is illustrated. Beneath the gratings, the vertical eye movement traces are shown for each trial. The fixation spot was visible, so pursuit was suppressed. The responses of the neuron during non-rivalrous grating presentation reflected the upward direction preference. During rivalry this neuron discharged significantly more when the direction of motion reported by the monkey corresponded to the preferred direction of the cell, that is, when the optimal stimulus was present in the dominant eye. Also notice that after an initial transient burst in response to rivalrous stimuli, the differential activity is evident for the duration of the presentation of the gratings.

ible, the monkey did not exhibit measurable pursuit eye movements (Figure 10), yet the pattern of neuronal response was the same as when the fixation spot was removed. Second, the differential neuronal modulation was evident within 80msec after grating presentation, well before pursuit was initiated. Finally, we analyzed whether the onset of neuronal activity was statistically correlated with the visual stimulus or with the pursuit eye movements. The neuronal response latency was compared to the stimulus and the pursuit onset.

The neuronal latencies were determined from spike-density functions which were derived from convolving the spike train with a Gaussian filter.[22] The onset of activation was defined as the time when the spike-density function deviated from the pre-stimulus baseline by three standard deviations. A statistical analysis of the correlations between the neuronal response latency, the pursuit latency and their difference was performed.[23] There was no correlation between the neuronal latency and the pursuit latency ($r = -0.07$); in contrast there was a strong correlation between the time period from neuronal response to the pursuit initiation and the pursuit latency ($r = 0.97$). In addition, the ratio of the variance of neuronal latency to the variance of the difference between neuronal and pursuit latency was large (15.6). This ratio, tested with the appropriate statistical estimator, has been shown to provide a highly reliable indicator of the relation of neuronal activity to sensory or motor processes.[23] These tests indicated that the neuronal activity was correlated with the presentation of the gratings and not the initiation of pursuit. Therefore, the differential neuronal activity of these units during rivalry reflected a perceptual and not an oculomotor process.

The activity of yet another MT unit is illustrated in Figure 11. This unit was different from that shown in Figure 10 in that it was more active in rivalry trials in which the monkey reported the direction of motion corresponding to the non-preferred direction of the cell. A more revealing way to describe this is that this unit discharged during rivalry trials when the optimal stimulus was present in the suppressed eye.

Quantitative analysis. A quantitative analysis of the modulation of each neuron during non-rivalry and rivalry trials was performed, the results of which are shown in Figure 12. Twenty-five percent (15/59) of the neurons were not significantly modulated under non-rivalrous or rivalrous conditions; the direction preferences of these cells were horizontal, so they were poorly driven by the vertically drifting gratings. Thirty-two percent (19/59) of the single units exhibited significantly different responses for the up versus down non-rivalrous gratings but their response during rivalry was independent of the perceptual choice of the monkeys. Some of these units discharged whenever their optimal stimulus was presented, and others were suppressed by the non-optimal stimulus. Twenty percent (12/59) of the recorded neurons were significantly modulated during rivalry but not during the non-rivalrous grating presentation; they are not shown on the plot.

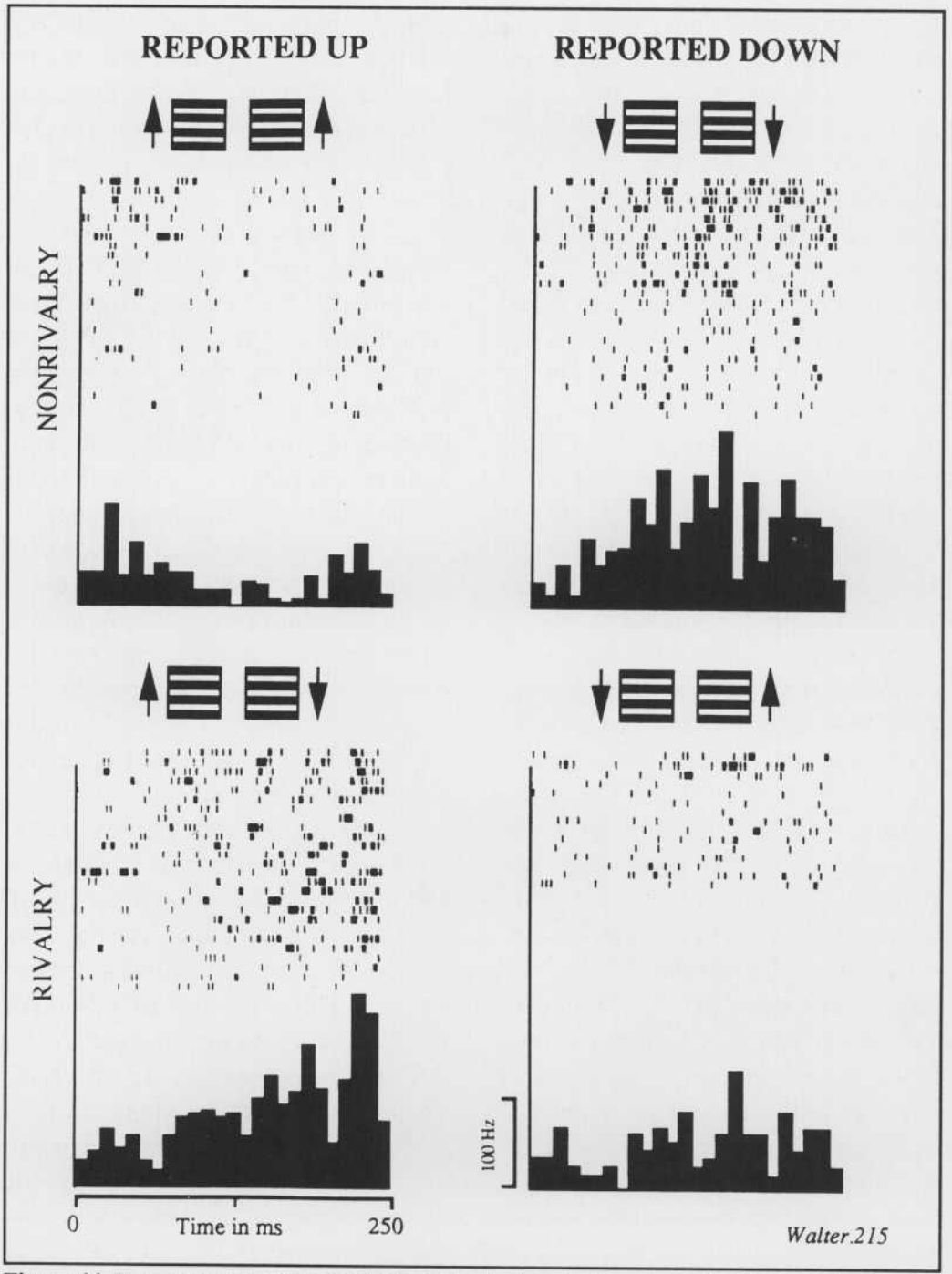
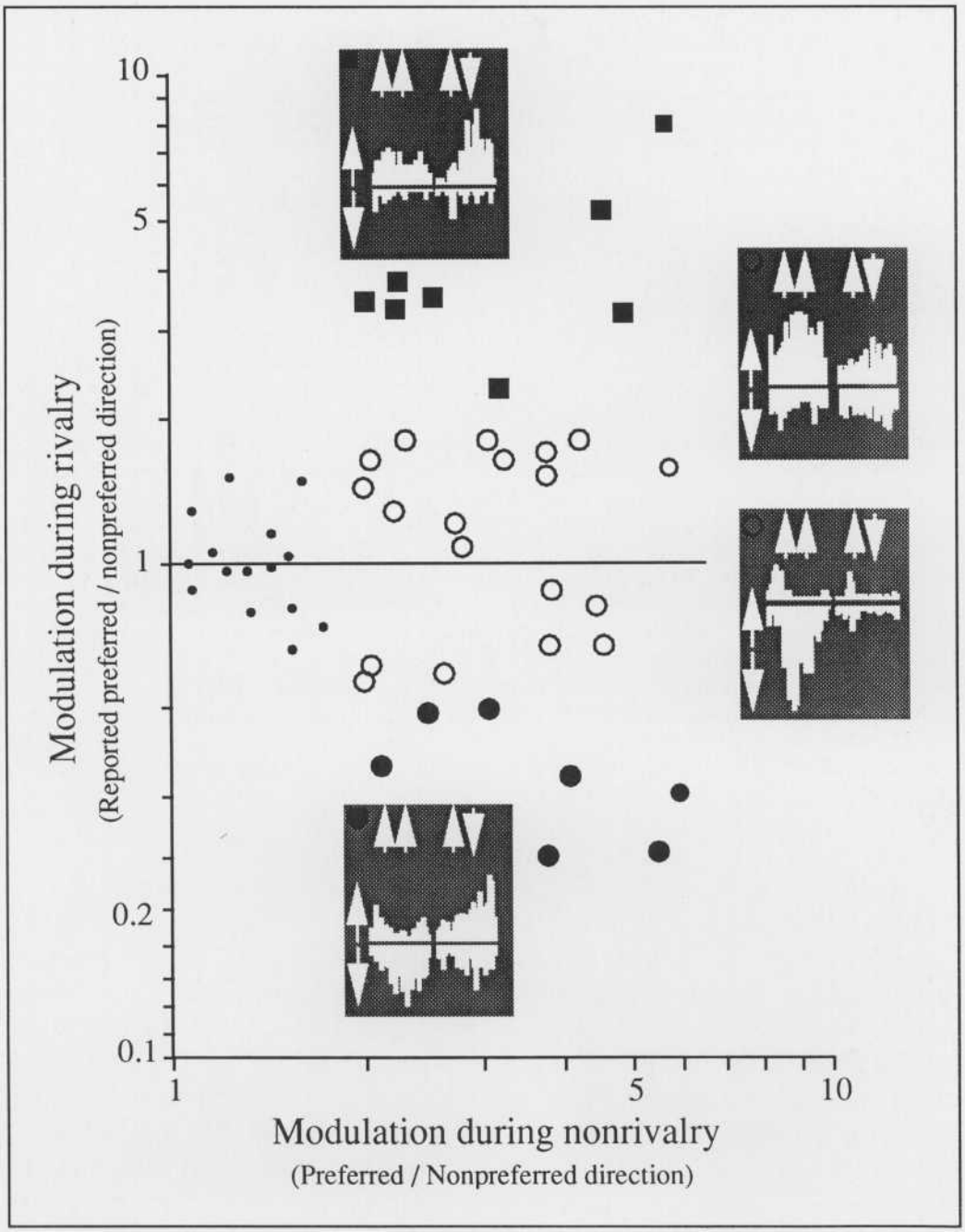


Figure 11. Response of a neuron which is active during rivalry suppression. Conventions are as in Figure 7. This neuron is distinguished by being more active in the rivalry trials in which the monkey reported the direction of motion opposite the preferred direction of the cell exhibited in non-rivalry or, to put it another way, when the optimal stimulus was present in the suppressed eye.

Finally, 22 percent (13/59) of the cells were modulated during rivalry in relation to the perceptual choice of the monkeys. Half of these units responded better during rivalry when the monkey's perceptual choice corresponded



to the preferred direction of the cell and the other half responded better when the preferred direction of motion was present in the suppressed eye.

Discussion

Psychophysical localization of rivalry suppression. Binocular rivalry,

Figure 12 (facing page). Scatter plot of the directional modulation with non-rivalrous and rivalrous stimulus presentation. The response of each neuron was defined as the number of spikes discharged up to 80msec after grating presentation in each trial. The abscissa represents the ratio of the average response of a cell in a block of non-rivalrous trials to gratings in its preferred direction divided by the average response to gratings in its non-preferred direction. The ordinate represents the modulation of the cell during rivalrous stimulus presentation. This modulation was defined as the ratio of the average response in trials in which the monkey reported seeing the direction of motion corresponding to the preferred direction of the cell divided by the average response in trials in which the monkey reported seeing the direction of motion opposite the preferred direction of the cell. Values greater than one indicate that the cell's response was greater when the perceptual choice corresponded to the preferred direction. Values less than one indicate the neuronal response was greater when the behavioral choice was opposite the preferred direction. This analysis does not reflect the overall level of activity of the cells but rather the ratio of activities for the two directions. Whether the directional modulation of a cell was significant was determined using a *t*-test. All of the cells in the plot were derived from the same sample, but different symbols have been used to illustrate the different types of modulation. Small spots represent cells which were not modulated during either the non-rivalrous or the rivalrous presentation of the gratings; these cells preferred horizontal motion. The open circles represent cells which exhibited significant directional modulation during the non-rivalrous presentation, but during rivalry their response was independent of the perceptual choice of the monkey. The solid squares and circles signify cells which exhibited significant modulation during both rivalrous and non-rivalrous stimulus presentation. Those cells which fall in the upper half of the plot (solid squares) responded more during rivalry when the monkeys' perceptual choice corresponded to the cell's preferred direction while those which fell in the lower half (solid circles) responded when the perceptual choice corresponded to the non-preferred direction. Post-stimulus spike histograms of examples of the three modulated cell classes are shown in the shaded insets; the type of symbol indicates the cell class. The two examples given for the open circle illustrate a cell that was active during rivalry (top) and another which was suppressed (bottom). The arrows at the top of each inset panel indicate the non-rivalrous and rivalrous trial types, and the arrows on the left indicate trials in which the monkey reported upward or downward motion.

while not noticed under natural viewing conditions, plays a fundamental role in cyclopean vision. The visual system derives accurate depth information from small disparities in spatial location, spatial frequency, orientation, direction of motion, in the image; however, larger disparities in these sensory cues cannot be fused. The visual system faces this situation every time objects in a scene are widely distributed in depth. Binocular suppression must necessarily be involved in resolving such a conflicting situation.

Psychoanatomical experiments, to use a term coined by Bela Julesz, have attempted to determine the mechanisms underlying binocular rivalry and the level(s) of the visual pathway at which suppression occurs. In sum, these experiments support the idea that suppression during rivalry is not an actual blindness of the suppressed eye; instead it appears to be an active inhibitory process at a relatively advanced stage of the visual system that prevents the suppressed stimulus from reaching the state of conscious awareness. There is considerable experimental evidence showing that rivalry suppression must occur at or beyond the initial stages of cortical visual processing.

One series of experiments concerns the effects of rivalry on afteref-

fects. Aftereffects are sensations which persist after prolonged exposure to a visual stimulus creating a measurable distortion in the perception of other figures. Typical aftereffects include threshold elevation,[24] spatial frequency shift,[25] motion aftereffect,[26] and tilt aftereffect.[27] Since these aftereffects are specific for the orientation and the spatial frequency of the stimulus, it is unlikely that they occur prior the neural stage at which feature selectivity like orientation or spatial frequency tuning emerges, and this stage is the primary visual cortex. An additional indication that aftereffects are due to cortical activity, and not, for instance, to a fatigue of the retinal or geniculate cells, is the fact that most of them show a considerable degree of interocular transfer. The interocular transfer occurs even after pressure blinding the adapted eye.[28]

The strength of an aftereffect for a given stimulus intensity is measured by its duration reported by the subject and increases with exposure. If the adapting stimulus is presented during rivalry, then the time of visibility is less than the time of exposure. This is because even though the visual system is continuously exposed to the adapting stimulus, the stimulus is not visible while the eye in which it is presented is suppressed. Now, if the adapting stimulus remains potent during this suppression phase, the strength of the aftereffect should grow to the level equivalent to that produced when the adapting stimulus is visible continuously. If, on the other hand suppression renders the adapting pattern ineffective, the strength of the aftereffect should be reduced to a level commensurate with the duration of phenomenal dominance. Several investigators[29] have shown that the strength of aftereffects is not reduced when the adapting stimulus is presented during rivalry. Moreover, binocular suppression does not interfere with the interocular transfer of aftereffects.[30] These results are consistent with two interpretations. First, the site of rivalry suppression follows the stage where the aftereffects occur and this stage is after the site at which the monocular signals combine to establish binocular vision. Alternatively, rivalry and aftereffects are processed in parallel without any convergence at the early stages.

Experiments in which an adapting stimulus is presented prior to rivalry can distinguish between these two alternatives. The duration of dominance of a stimulus during binocular rivalry is reduced if its intensity is physically reduced.[31] If adaptation precedes binocular rivalry, then stimuli to which the visual system was previously exposed should affect the dominance of this stimulus during binocular rivalry. In contrast, if aftereffects and rivalry are processed in parallel channels, there should not be any interaction. The results of such an experiment show that if the apparent contrast of a stimulus is reduced by prior adaption, then that stimulus is less dominant during rivalry.[32] Therefore, rivalry appears to be after the stage of adaptation.

The relationship between rivalry and stereopsis is an unsettled issue.[33] Some experiments indicate that rivalry and stereopsis can occur simultaneously.[34] This would indicate that the

components of the visual pathway participating in rivalry are independent of the components responsible for stereopsis and that rivalry and stereopsis are both continuously active. Other experiments suggest that fusion dominates over rivalry; that rivalry occurs only when stereoscopic fusion fails, meaning that stereopsis precedes rivalry in visual processing.[35]

Neurophysiological localization of rivalry suppression. Neuronal models for binocular rivalry have been proposed,[36] but there is scant neurophysiological data. The results of evoked potential studies are equivocal. Some investigators[37] find a reduction in the amplitude of the visual evoked potential during rivalry suppression, while others[38] find no change. Moreover, others[39] emphasize the contaminating effects of attention on the positive rivalry results.

Rivalrous stimuli have been used in recordings from the visual pathway in anesthetized cats. In the dorsal lateral geniculate nucleus a long latency but profound suppression is observed when the non-dominant eye is stimulated,[40] but such suppression is not observed in the primary visual cortex.[41] In these studies the non-dominant eye refers to that eye which provides little or no direct excitatory input to the cell.

Our experiment represents the first single-unit recordings in the visual pathway of alert, behaving primates experiencing binocular rivalry. We encountered a surprising diversity of neuronal responses; it will be interesting to learn how the cell classes revealed during binocular rivalry relate to the previously reported neuron groups[19] as well as to the patchy projections to and from MT.[7]

Neurons were encountered that discharged regardless of whether their optimal stimulus was in the suppressed or the dominant eye. These units provide unmasked information about their preferred direction whether this direction is perceived or not and might well be part of the channel mediating the motion aftereffects. It is possible that these are first order neurons in MT, receiving afferents that are themselves not inhibited during rivalry suppression. This conjecture implies that the neurons in layer 4B of V1 also are not compromised during binocular motion rivalry. Other neurons were suppressed during rivalry. If these particular neurons project to the dorsolateral pontine nuclei, then their reduced activity during rivalry may be the cause of the reduced pursuit gain during motion rivalry.

The neuron populations reviewed thus far appear to be more related to the sensory data provided by the physical stimulus. However, we observed a number of other units whose activity was clearly correlated with the behavioral response of the monkeys and thus, presumably, with their perceptual experience. Approximately half of these cells discharged only when the optimal stimulus was present in the suppressed eye, that is, when the grating corresponding to their preferred direction had to remain invisible in order for the visual system to resolve the conflicting retinal stimulation. The other half were specifically active only when the opti-

mal stimulus was present in the dominant eye, that is, when the monkeys reported seeing the direction of motion corresponding to the preferred direction of the cells. These neurons may be involved in the conscious perception of motion. It will be very instructive to ascertain where the signal from these two populations influence further visual processing. An alternative explanation, of course, is that MT is a target of higher areas that mediate the perceptual fluctuations of rivalry. If this is so, then the population of cells that show such perception-related modulation do so as a result of top-down, feedback processing.

Recent work by Newsome, Britten, and Movshon[42] reveals comparable properties of MT neurons. These investigators demonstrated that the directional resolution of single units in MT corresponds to the perceptual capacity of monkeys trained in a direction of motion discrimination task, and that when MT neurons are presented with stimuli that possess no net direction of motion, they fired more when the monkey reported that he perceived motion corresponding to the preferred direction of the cells.

In conclusion, our results indicate that MT contains elements necessary for a circuit that could mediate the periodic suppression and dominance of binocular motion rivalry. The experiment presented in this chapter is one initial step toward understanding the mechanisms which underlie the fluctuating perception during binocular rivalry. Such experiments address the fundamental issue of how the visual system can arrive at different descriptions of the same ambiguous scene. Since the visual stimuli are unvarying, any alternation in perception is a result of internal processes which are not themselves dictated by the physical stimuli. It will be interesting, using similar stimuli, to investigate such internal processes at the different stages of the visual pathway. We are hopeful that this approach will provide useful information about what the different stations of the visual pathway contribute to normal visual perception.

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