Neural Mechanisms of Perceptual Organization

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Pictures that spontaneously change in appearance, such as depth or figure-ground reversals, have always been thought of as powerful tools for understanding the nature of the perceptual system. The cause of the perceptual multistability that is experienced when viewing such figures most likely lies in the brain's physical organization; an organization that imposes several constraints on the processing of visual information. Why is it that our visual system fails to lock onto one aspect of an ambiguous figure? What accounts for the spontaneous changes of interpretation? What are the neural events that underlie such changes? Are there neurons in the visual pathways the activity of which reflects the visual awareness of the stimulus? In my paper I describe some combined psychophysical and physiological experiments that were motivated by these questions. In specific, we report on experiments in which neural activity in early visual cortex and in the inferior temporal cortex of monkeys was studied, while the animals experienced binocular rivalry. Our results provide us with new evidence not only on the neural mechanisms of binocular rivalry (one example of multistable perception), but also on the neural processes underlying image segmentation and perceptual grouping.

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1. Sensation and Perception

Research over many years has shown that perception is not simply determined by the patterns of neural activity in the eye's retina. The brain allows experience and expectation to play an important role in organizing sensory information, so that we do not "see" the data, but rather we use them to draw inferences as to what lies before us. Figure 1 illustrates this point clearly. The lines in 1a might at first appear as a set of nonsense lines, just as the patches in 1b might seem like splotches of meaningless ink. However, prior experience with these figures, or the mention of "a woman and a wash bucket", or a "dog in the yard", can dramatically alter one's perception of the very same pictures. Similarly, figure 1c can be seen as an either an Indian or as an Eskimo with his back turned to the viewer, figure 1d has two possible perspectives, and 1e - the celebrated "faces-and-vase" figure-ground reversal introduced by the Danish psychologist Edgar Rubin in 1915 - can be perceived as either a goblet or a pair of faces. The perceptual changes occurring when viewing ambiguous figures have been shown to occur even when these figures are stabilized in the retina and thus even under conditions that the retinal stimulus remains entirely unchanged. Finally, in figure 1f, the absence of visual stimulation appears to serve as input to our perception, as we see a white "filled" circle of high contrast in the middle and a concentric ring around it. Clearly our brain sees more than our eyes. The latter receives patterns of energy that are converted into patterns of neural excitation, while the former seldom sees such patterns. Instead the brain sees objects. Of obvious importance is the question: How does the brain derive

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Not only do we not know how the inputs of a “face-selective” neuron in the inferior temporal cortex are organized, and thus how such a neuron comes to acquire such an amazing configural selectivity, but we do not even know how the responses of such selective cells relate to perceptual experience. Do such cells mediate the recognition of an object? Do they represent the stage at which information is routed to the motor planning or motor areas? It is a notable fact that many of these neurons respond vigorously when presented a specific stimulus even when the animal is anesthetized. Do they then really relate to conscious perception? Which cells code for this “hedgepodge” of visual primitives and which relate directly to our knowledge of familiar objects?

Visual stimuli such as the ambiguous figures shown in Figure 1 are excellent tools for addressing such questions. Normally, when we look steadily at a picture of a real object, the information received by the retina remains largely constant, as does the perception of the object, presumably because the richness of information derived by integrating a large number of visual cues establishes an unambiguous, single interpretation of a scene. In such cases neural responses that may underlie the perception of a stimulus are confounded with the sensory responses to the stimulus or parts thereof. When the visual cues provided, however, do not suffice for a single interpretation, then rival possibilities can be entertained and perception becomes ambiguous, swiftly switching between two or more alternatives without concomitant changes in the message received from the eye. Classical examples of figures eliciting different perceptions are the figure-ground and depth reversals shown in figures 1d and 1e. The question of interest is: Would a cell, which responds selectively to, say, the profile of a face, discharge action potentials only when the faces in figure 1e are perceived, despite the fact that the pattern that can be interpreted as face is always available to the visual system? Addressing directly this question in invasive, laboratory animal experiments is extremely difficult for two reasons. First, the subject, presumably a monkey, must learn to report subtle configural changes for one of the handful of known multistable stimuli. Second, individual neurons must be isolated that specifically respond to this stimulus, with the hope that

descriptions of definite objects out of the hedgepodge of visual elements provided through the sensory organs?

Research, initiated by the pioneering work of David Hubel and Torsten Wiesel, has shown that the visual cortex has all the machinery requisite for the formation of neural descriptions of objects. Neurons are topographically organized, show high selectivity for distinct stimulus attributes, and possess a receptive field complexity that increases in successively higher visual cortical areas. Cells in the retina and the dorsal lateral geniculate nucleus – a small thalamic structure that receives direct input from the retina and relays it to the primary visual cortex – respond to light spots; neurons in primary visual cortex respond selectively to the orientation or motion direction of line-segments; and cells in the inferior temporal cortex – a large area in the temporal lobe – may respond selectively to very complex patterns, including animate objects such as faces or body parts.

Loosely speaking, retinal processing is optimized for the detection of intensity and wavelength contrast, while early cortical areas extract fundamental stimulus descriptors, such as orientation and curvature, spatial frequencies and stimulus velocities. Higher visual areas in both the parietal and temporal lobes process information about the spatial relationships and the identity of visual objects. Yet, despite the plethora of data on the properties of individual neurons, we know very little about how their responses contribute to unified percepts, and how these percepts lead to semantic knowledge of objects.
Psychophysical “switch” paradigm. The stimulus consisted of a pair of sinusoidal gratings of 20% contrast and 2.5 cycles per degree spatial frequency, and which were orthogonally oriented in the two eyes. The stimuli were flickered on and off at 18 Hz, and exchanged between the eyes each 333 msec. Despite the constantly reversing stimulus, perception was dominated by prolonged periods of leftward and rightward unitary dominance, with intervening periods of mixed rivalry. Subjects viewed the stimulus for two minute periods and held down buttons on a computer mouse to indicate leftward, rightward or mixed perceptual dominance.

alternate perceptual configurations differentially activate the cell.

Fortunately, perceptual bistability can also be elicited by simply presenting a conflict to the two eyes, where the monocular images differ substantially in their spatial organization, color, or direction of motion. Rarely if ever will nonmatching stimuli be binocularly fused into a stable coherent stimulus. Instead each monocular pattern takes its turn at perceptual dominance, only to be overtaken by its competitor after a number of seconds. This phenomenon, known as binocular rivalry, was first noted over two centuries ago (DuTour, 1760) and its phenomenology has been studied extensively over the past three decades in the field of binocular vision (for a review see Blake, 1989)). Psychophysical experiments initially suggested a peripheral inhibitory mechanism for rivalry, specifically involving competition between the two monocular pathways. Rivalry has therefore been generally considered a form of interocular, rather than perceptual, competition. In other words, perception of a stimulus was thought to amount to “dominance” of the eye viewing this stimulus. Yet, we have recently shown that the notion of “eye dominance” fails to account for the long periods of perceptual dominance of a stimulus presented alternately to one eye and then to the other (Logothetis et al., 1996).

2. Binocular Rivalry: Interocular or Interstimulus Competition?

Human observers were presented incongruent stimuli via a mirror stereoscope – a device permitting dichoptic stimulation of each eye under normal vergence conditions – and were asked to report periods of sustained dominance of a left or right tilted grating pattern by pressing and holding the left and right computer-mouse buttons respectively. Our experimental paradigm is outlined in Figure 2. As in many other experiments on binocular rivalry, the visual stimuli consisted of square patches of sinusoidal gratings that were orthogonally oriented in the two eyes. However, in contrast to all other experiments, the two monocular stimuli in our paradigm were exchanged between eyes every third of a second, resulting in periodic orientation reversals of each monocular view. In addition, the gratings were flickered on and off at a frequency of
18 times in a second in order to minimize the perception of transients caused by the physical exchanges. What would one expect to see under these stimulation conditions? Traditional wisdom would predict that perception will be dominated by a grating regularly switching orientations, as would be seen if the subject closed one eye. In contrast, if the perceptual rivalry were some form of competition between the central representations of the stimuli, one would expect slow alternations in perceived orientation that are uncorrelated with the physical exchange of the monocular stimuli. In our experiments, observers reported indeed seeing prolonged periods of unitary dominance of each orientation, lasting up to several seconds.

The mean dominance duration exceeded two seconds, spanning seven physical changes of the gratings. Subjects reported that they rarely if ever saw a grating rapidly changing its orientation at the exchange frequency, as "eye dominance" would predict, and which could easily be observed by closing one eye. In order to compare rivalry during the "switch" paradigm with conventional rivalry, the statistics of the alternation phases were evaluated. First, successive dominance phases were shown to be independent both by autocorrelation analysis and the Lathrop test for sequential dependence (Lathrop, 1966) in agreement with conventional rivalry (Fox & Herrmann, 1967). Second, the distribution of these durations (Figure 3c, pooled for 3 subjects) was found to closely resemble those obtained during conventional rivalry for a human (Figure 3a) and a monkey (Figure 3b), both of which match those previously reported in the literature (Fox & Herrmann, 1967; Leopold et al., 1995; Leopold & Logothetis, 1995; Leopold & Logothetis, 1996; Logothetis & Leopold, 1995; Walker, 1975).

Finally, the effects of the strength of one stimulus on the mean dominance and suppression of each were examined. The contrast of one of the orientations was systematically varied while the other was held constant. Again, the pattern during "switch" rivalry (Figure 3f, average of 3 subjects) resembles those from a human (Figure 3d) and a monkey (Figure 3e) during conventional rivalry. In all cases the contrast of one orientation primarily affects the mean dominance time of the other orientation. Note that in the "switch" condition each eye sequentially sees both the fixed- and variable-contrast stimuli, and it is therefore the strength of the competing stimuli rather than the strength in the two eyes that governs this effect. The results of this analysis show that the dynamics of the rivalry experienced when monocular stimuli are continually swapped between the eyes is indistinguishable from conventional binocular rivalry.

Our finding clearly suggests that the perceptual alternations experienced during binocular rivalry involve perturbations of the same neural machinery involved in other bistable perceptual phenomena, such as monocular rivalry (Campbell & Howell, 1972) and ambiguous figures, which incidently show similar dynamics to binocular rivalry (Borsellino et al., 1972). Thus dichoptic stimulation, in which arbitrary combinations of conflicting stimuli can be brought into competition for dominance, can be an excellent tool for the physiological study of perceptual organization and visual awareness in experimental animals.

3. Cell Responses in Early Visual Cortex to Ambiguous Stimuli

To examine the neural responses in primary visual cortex and the early extrastriate visual areas (of visual areas surrounding and receiving input from primary visual cortex) we trained monkeys to report the perceived orientation of a stimulus under congruent and dichoptic stimulation conditions (Leopold & Logothetis, 1996). During the initial shaping and training phase, each monkey was shown monocular grating patterns on a computer monitor and taught to press one of two levers according to whether the tilt of the grating was left or right of vertical. The animal eventually learned to respond to several successive orientation changes, receiving a juice reward only at the end of each observation period (Figure 4). Once near-perfect performance was achieved, training was continued with stimuli that mimicked the stochastic changes of stimulus appearance during binocular rivalry. Simulating perception during rivalry with composed, mixed nonrivalrous stimuli allowed the monkey to grow accustomed to the "feel" of rivalry while still affording us full control over the animal's behavior, as incorrect responses would abort the observation period. Gradually, periods of real binocular
rivalry were introduced into the emulation, where the orientations in the right and left eyes were perpendicular. During those periods the monkeys continued to respond to orientation reversals, but now these changes were purely subjective as the physical stimuli remained unaltered, and hence feedback for inappropriate responses was impossible. The accuracy of response during these periods was, however, indirectly probed by introducing catch trials, in which the orientation of one of the gratings was smoothly replaced after a lever response to yield a coherent binocular stimulus. The monkey was expected to respond either immediately or not at all depending on whether the catch trial orientation was perpendicular to or the same as that indicated by the previous response, a test in which each monkey consistently performed above 95%.

In addition, two psychophysical controls were employed to show that the monkey was faithfully reporting his perception during rivalry. First, the distribution of dominance phase durations were compared to those obtained from humans under identical stimulus conditions. The normalized distribution of monkey's phases (Figure 3b) resembled that obtained from a human observer (Figure 3a), and both were representative of those described previously for both monkeys and humans (Myerson et al., 1981; Walker, 1975). Even stronger evidence as to the reliability of the monkeys' reports came from the study of the effects of interocular contrast differences...
The monkey fixated a small spot and maintained fixation as a series of nonrivalrous (monocular or binocular) and rivalrous grating patterns were presented. The animal signaled perceptual transitions between the two orientations by pressing one of two levers (R or L) mounted on the primate chair. During the rivalry period the perceived transitions were not accompanied by changes in the physical stimulus. Incorrect responses for a nonrivalry trial, or failure to maintain accurate fixation (within a 0.8 degree window) resulted in abortion of the 15-25 second observation period, and the monkey would forfeit his juice reward.

on the mean phase-duration. During rivalrous stimulation, increasing the stimulus strength in one eye increases the visibility of that stimulus, not by increasing its mean dominance phase, but by decreasing the mean period for which this stimulus remains suppressed (Fox & Rasche, 1969; Levelt, 1965). The data obtained from the monkey (Figure 3e) show the same relationship between stimulus strength and eye dominance as do the human data in the present (Figure 3d) and other studies. No random tapping of the levers could possibly yield this type of consistency, nor is it likely that animals or humans systematically adjust their behavior for different interocular contrasts.

During the behavioral-testing sessions single neurons were isolated in the central representations of the fourth visual area (V4) as well as the border of striate cortex and V2 (V1/V2). As the monkey fixated a small point, each individual cell was evaluated for its orientation selectivity and binocularity using a computer-automated procedure. Specialized glasses worn by the animal produced complete isolation of the right and left monocular images. Rivalry stimuli were constructed based on the preferred attributes of the specific cell, where the preferred orientation was placed in one eye and the orthogonal orientation in the other, whereas nonrivalry stimuli consisted of either the preferred or nonpreferred orientation presented either monocularly or binocularly. During testing, a typical observation period consisted of several nonrivalry periods, each lasting 1–5 seconds, and a single rivalry period, lasting up to 15 seconds (Figure 4). The monkey responded to orientation changes during the nonrivalry periods and to perceived orientation changes during rivalry, while individual neurons in his brain were monitored using standard extracellular recording techniques (see (Leopold & Logothetis, 1996)). Of special interest were the rivalry periods, during which neurons exhibited a diversity of responses, and often modulated their activity according the monkey’s perceived stim-
Figure 5

Four examples of the various cell types encountered during rivalry. For each pair of plots, the shaded regions correspond to the activity of the cell during rivalry around the time of a perceptual transition. The lighter shading represents trials in which the monkey reported a transition to the cell’s preferred orientation, and the darker shading to the nonpreferred. The plots are centered around the animal’s lever responses (vertical lines) and the activity is shown before and after the response. (a) The most common class of modulating cell, which increased its firing shortly before the monkey reported seeing a transition to the cell’s preferred orientation and decreased before the nonpreferred orientation. (b) A cell whose elevation in activity was sustained as the monkey perceived the preferred orientation. (c) A cell which was representative of some cells in V4 that became more active when the monkey reported seeing the cell’s nonpreferred orientation. (d) A non-modulating cell, whose activity was not influenced by the monkey’s perceptual state.

Figure 5 illustrates four representative examples of the cell types encountered. For each cell, the left and right plots represent the activity averaged over numerous perceptual transitions to the preferred and null orientations, respectively. The activity is shown as a function of time, centered on the monkey’s lever responses (vertical lines). Roughly one in three neurons tested modulated its activity in accordance with the perceptual changes. These modulating cells were almost exclusively binocular, and had a higher preponderance in area V4 (38%) than V1/V2 (18%). The majority of modulating cells exhibited an increase in their firing rate a fraction of a second before the monkey reported perceiving the cell’s preferred orientation. Most often this elevation was temporary, declining again to the base rate after several hundred milliseconds (Figure 5a), although for some cells it was sustained significantly longer (Figure 5b). One class of neurons became most active when the nonpreferred stimulus was perceived, and the preferred stimulus was perceptually suppressed (Figure 5c). Finally, a large number of cells in all areas were generally uninfluenced by the animal’s perceptual state (Figure 5d).

4. Cell Responses in the Inferior Temporal Cortex

Neurons in the visual areas of the anterior temporal lobe of monkeys exhibit pattern-selective responses that are modulated by visual attention
Figure 6

Behavioral and physiological response of IT/STS cells during rivalry observation periods. Panel depicts a single observation period, taken from different monkeys, during which non-rivalrous and rivalrous stimuli were present. Whenever the monkeys perceived seeing the sunburst pattern, they pulled the left lever, and when they perceived the complex object (roller coaster in (a) monkey face in (b)) they pulled the right lever. During rivalrous stimulation, both stimuli were presented, but the monkeys’ percepts changed from seeing the sunburst pattern to seeing the effective stimulus. There is a clear correlation between the monkeys’ reported change of percept and the cells’ change in activity, even though the physical stimulus remain unchanged.

and are affected by the stimulus in memory, suggesting that these areas play an important role in the perception of visual patterns and the recognition of objects (Desimone & Duncan, 1995; Logothetis & Sheinberg, 1996). We have therefore examined the activity of neurons in these areas during binocular rivalry (Sheinberg & Logothetis, 1997). We have recorded from the inferior temporal cortex (IT) and from the lower bank of the superior temporal sulcus (STS). Because neurons in these areas respond better to complex patterns rather than oriented lines or gratings, the animal were taught to pull and hold the left lever whenever a sunburst-like pattern (left-object) was displayed, and to pull and hold the right lever upon presentation of other figures, including images of humans, monkeys, apes, wild animals, butterflies, reptiles, and various man-made objects (right-objects). Examples of such objects can be seen in the insets of Figure 6.

Figure 6 shows two observation periods during this task, taken from two different monkeys. The rivalry stimuli (gray regions) were created by presenting the effective stimulus to one eye and the ineffective stimulus (the sunburst) to the other. Each plot illustrates the stimulus configuration, the neuron’s activity, and the monkey’s reported percept throughout the entire observation period. In each case, the neuron discharged only before and during the periods in which the monkey reported seeing the effective stimulus. During rivalrous stimulation, the stimulus configuration remained constant, but significant changes in cell activity were accompanied by subsequent changes in the monkeys’ perceptual report. Of such selective neurons, 50 were tested during the object classification task under both non-rivalrous and rivalrous conditions.

To increase the instances of exclusive visibility of one stimulus, and to further ensure that the monkey’s report accurately reflected which stimulus he perceived at any given time, we also tested the psychophysical performance of the monkeys and the neural responses of STS and IT cells using the flash suppression paradigm (Wolfe, 1984). In this condition, one of the two
stimuli used to instigate rivalry is first viewed monocularly for 1-2 seconds. Following the monocular preview, rivalry is induced by presenting the second image to the contralateral eye. Under these conditions, human subjects invariably perceive only the newly presented image and the previewed stimulus is rendered invisible. Previous studies have shown that the suppression of the previewed stimulus is not due to forward masking or light adaptation (Wolfe, 1984) and that instead it shares much in common with the perceptual suppression experienced during binocular rivalry (Baldwin et al., 1996). In our experiments, the monkeys, just like the human subjects, consistently reported seeing the stimulus presented to the eye contralateral to the previewing eye during the flash suppression trials.

To confirm that the animals responded only when a flashed stimulus was exclusively dominant, catch trials were introduced in which mixed stimuli were flashed, after which the monkey was required to release both levers. Performance for both animals was consistently above 95% for this task. The upper plots of Figure 7 show the cell responses for monocular presentations, and the lower plots of the same figure show the neuron’s activity at the end of the monocular preview (to the left of the dotted vertical line), and when perceptual dominance is exogenously reversed as the rival stimulus is presented to the other eye (to the right of dotted vertical line). The cell fires vigorously when the effective stimulus dominates perception and ceases firing entirely when the ineffective stimulus is made dominant. To better understand the differences between the temporal areas and the prefrontal areas, recordings were also performed in area V4 using the flash suppression paradigm [D. Leopold and N. Logothetis, unpublished observations]. V4 neurons were significantly less affected by the perceptual changes during flash suppression. Presenting the ineffective stimulus after priming with the effective one caused little or no suppression of the discharge of any of the cells; presenting the effective stimulus after priming with the other had an weak effect on a small percentage of V4 neurons. The activity of the vast majority of studied temporal cortex neurons was found to be contingent upon the perceptual dominance of an effective
visual stimulus. Neural representations in these cortical areas appear, therefore, to be very different from those in striate and early extrastriate cortex.

5. Neurons and Perception

The studies described above make a few new points regarding both binocular rivalry and perception in general. First, the physiological results - just like the psychophysical results described earlier - are incompatible with the hypothesis that phenomenal suppression during binocular rivalry results from a blockade of information emanating from either eye. Eye-specific inhibition would be almost certainly reflected by decreased activity of monocular neurons (Blake, 1989), yet most monocular cells remained entirely unaffected during rivalry suppression. Instead, the highest fraction of perception-related neurons were binocular and encountered in the extrastriate areas V4 (Leopold & Logothetis, 1996) and MT (Logothetis & Schall, 1989).

Second, it is interesting, though perhaps not surprising (given the responses obtained in the anesthetized preparation), that neural activity in visual cortex does not always predict awareness of a visual stimulus. While some neurons appear to modulate their activity in perfect correlation with the animal's changing perception, many others continue firing whether or not the stimulus is perceived. It will be of great interest to determine whether the different response properties of the response modulating neurons are in any way correlated with the anatomical location and connectivity patterns (Crick & Koch, 1995).

Finally, the data presented here suggest (in agreement with a number of studies on the physiology of visual attention; for a review see (Desimone & Duncan, 1995)) a prominent role of the extrastriate areas of the temporal stream in image segmentation and grouping. The early areas appear to have neurons that respond during perception but also during the suppression of the stimulus, and therefore appear to have the entire neural substrate of a system of reciprocal inhibition, explaining many of the characteristics of rivalry. They also have neurons, whose response depends on the task requirements, and whose activity is modulated by selective attention. Active inhibition, influences of attention, and selectivity of responses to complex two-dimensional patterns all strongly suggest an important role of early visual cortex in perceptual organization. In striking contrast with the early extrastriate areas, which show great variability in perception-related responses, in the inferior temporal cortex almost all neurons modulate their activity in synchrony with the monkey's perception when rivalry is initiated between faces or other complex images (Sheinberg & Logothetis, 1997). The response variability in areas V2, V3, V4 and MT may be the result of the feedforward and feedback cortical activity that underlies the processes of grouping and segmentation - processes that are probably perturbed when viewing ambiguous figures. The consistent correlation of cell activity with perceptual report in the areas of the temporal lobe may, on the other hand, represent a stage of processing beyond the resolution of perceptual ambiguities, where, neural activity reflects the integration of constructed visual percepts into those subsystems responsible for object recognition and visually guided action.

In the introductory section we asked: Which cells code for the "hodgepodge" of visual elements and which related directly to our knowledge of familiar objects? Obviously our experiments do not purport to answer this question, nor did we expect to understand perceptual organization in a few experiments or by only studying single cells and examining their average rate of firing. The study of dynamic interactions among neurons within and between areas (for review see Singer & Gray, 1995) will be of great importance for understanding image segmentation, as will also be the identification of different types of modulating neurons and their connectivity. Combination of such techniques in experiments with alert, trained animals using stimuli that instigate perceptual multistability may help us gain important insights into the neural processes that underlie the conscious perception of a visual stimulus.

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