



Cortical Oscillatory Responses do not Affect Visual Segmentation

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We tested the hypothesis that synchronization of oscillatory responses between populations of visually driven neurons could be the basis for visual segmentation and perceptual grouping. We reasoned that oscillations in response induced by flickering visual targets should have an effect on visual performance in these tasks. We therefore measured the psychophysical performance of human subjects in a texture segregation task (Expt I) and in a perceptual grouping task (Expt II). In both experiments, the elements composing the stimuli were flickered and presented in a variety of flicker conditions. These experimental conditions were designed to either interfere with naturally occurring synchronization of oscillations, or to induce synchronization and bias a subject's perceptual judgment. Performance in these tasks was neither helped nor hindered by the temporal pattern of flicker. These results suggest that physiologically observed oscillatory responses are unrelated to the processes underlying visual segmentation and perceptual grouping.

Cortical oscillations Visual segmentation Flicker

INTRODUCTION

Visual cortical neurons sometimes produce oscillatory responses to visual stimuli: their activity is modulated at a frequency in the range of 20–60 Hz in the cat (Eckhorn, Bauer, Jordan, Brosh, Kruse, Munk & Reitboeck, 1988; Gray & Singer, 1989; Gray, Engel, König & Singer, 1990) and slightly higher in the monkey (Eckhorn, Frien, Bauer & Woelbern, 1994). Oscillatory activity is less frequently observed in individual neurons than in multi-unit activity (Eckhorn *et al.*, 1994), and seems to be less prevalent in monkeys than in cats (Young, Tanaka & Yamane, 1992; Bair, Koch, Newsome & Britten, 1994). Multiple-electrode recordings reveal that when two separated neurons give oscillatory responses, the degree to which their oscillatory activity is synchronized can depend on the particulars of the visual stimulus (Gray, König, Engel & Singer, 1989; Kreiter & Singer, 1994; König, Engel, Roelfsema & Singer, 1994). The synchronized oscillatory activity of visual cortical neurons has intrigued those who study perceptual grouping and segmentation. It has been postulated that this kind of

temporal synchronization could underlie the processes by which objects separated in the visual field are combined by the visual system to form perceptual groups (von der Malsburg, 1983; von der Malsburg & Singer, 1988; Singer, 1991; Kreiter & Singer, 1994). This intriguing notion lacks direct experimental support, but has nonetheless proved to have wide appeal. We have attempted to test this idea by exploring the effect of *visually* induced synchronization on perceptual grouping.

Cortical neurons respond to stimulus flicker with a rhythmic, phase-locked discharge (Hubel & Wiesel, 1959; Bullier, Nowak & Munk, 1994), and many cells respond to temporal modulation at frequencies in the “oscillation” range [>20 Hz (Hawken, Shapley & Grosf, 1991; Levitt, Kiper & Movshon, 1994)]. We have observed responses of this kind in monkey V1 neurons to flickering grating and bar targets (unpublished observations). Moreover, many cells of the complex class respond to flicker with a discharge at twice the stimulus frequency (Movshon, Thompson & Tolhurst, 1978). The firing elicited by flicker is similar to the synchronous oscillatory activity of cortical neurons which is said to underlie perceptual grouping phenomena. Even though the sources of the oscillatory firing patterns may be different, we reasoned that they should be *indistinguishable* for subsequent stages of processing. We exploited this presumed similarity to measure the effect of synchronization and desynchronization of the stimulus components in a texture segmentation task (Expt I) and a perceptual grouping task (Expt II). If oscillatory

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responses are important for perceptual grouping, a visually-induced modification of the relationships among cells' firing patterns should affect subject's perceptual judgments.

We have briefly presented some of these results elsewhere (Kiper & Gegenfurtner, 1991).

EXPERIMENT I

Methods

In the first experiment, our subjects performed a texture segmentation task in which they discriminated the orientation of a rectangular region containing line segments different in orientation from those in a surrounding region (Nothdurft, 1991). To induce various forms of oscillatory response, we flickered the individual texture elements at rates of 15–60 Hz, a range of frequencies to which primate cortical cells are known to be responsive (Foster, Gaska, Nagler & Pollen, 1985; Hawken *et al.*, 1991; Levitt *et al.*, 1994), and at which oscillatory responses have been observed. To modify the synchronization of these responses, we varied the temporal phase at which different elements in the display were flickered. Our stimulus was a briefly-presented (100 msec) 20×20 deg field containing elements whose positions were randomly jittered by up to 0.64 deg from a regular square array with 2 deg spacing. Within a centered rectangular patch subtending 9×13 deg, containing 24 elements, we made the orientation of the line segments different from those outside the patch. The subject's task on each trial was to indicate whether the rectangular patch was horizontally or vertically oriented; the absolute orientation of the line segments that defined the patch varied randomly from trial to trial. We varied the difference in orientation between the lines within and outside the rectangle, and measured the variation in performance that resulted. Each element was a short bright line segment subtending 54×5 min arc, having a luminance of 70 cd/m^2 ; the display background was dimly illuminated to a luminance of 5 cd/m^2 . We preferred this low illumination to a completely dark background to avoid problems with phosphor decay. We chose to use a stimulus duration that was long enough for there to be a sufficient number of frames to define the different temporal stimulus conditions, and brief enough to ensure that the subjects would base their responses on the effortless, salient "pop-out" of the target and not on a serial search for less salient elements (Nothdurft, 1991). Preliminary experiments showed that subjects' performance improved until it reached a plateau at around 100 msec, as illustrated by one subject's results in Fig. 1. We therefore chose a duration of 100 msec for our experimental observations.

Stimuli were presented on a Mitsubishi HL6605 monitor, driven by a Truevision Vista graphics controller at a frame rate of 120 Hz. A stimulus duration of 100 msec corresponded to exactly 12 frames of display. We used four different stimulus conditions. In the *no flicker* condition, all texture elements were presented on

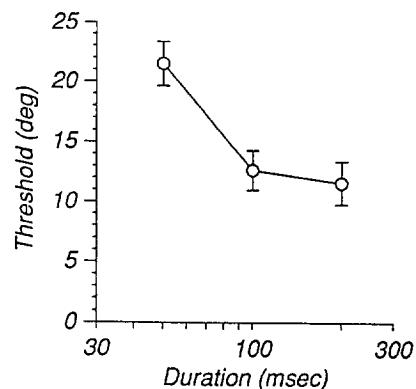


FIGURE 1. Performance for observer DK as a function of stimulus duration in the *random* condition. Psychometric functions like those shown in Fig. 3(A) were used to measure orientation difference thresholds for durations of 50, 100, and 200 msec.

every frame. In the *synchronized* condition, all texture elements were presented every n th frame, where the value of n was varied to change flicker frequency. In the *synchronized region* condition, the texture elements were also presented every n th frame, but those in the rectangular region to be discriminated were presented one or more frames out of phase with those in the surrounding region. In the *random* condition, the texture elements were each presented every n th frame, but the phase relationships among the elements were entirely random. The frame sequences for the three flicker conditions are diagrammed in Fig. 2, which shows the display conditions for a particular value of n , here 3, yielding a flicker rate of 40 Hz. For a flicker rate of 30 Hz, the sequence would have contained 4 frames and been repeated 3 times. The time-averaged luminance of the stimulus elements was adjusted to be identical across all conditions.

It should be noted that because the line elements were drawn on a raster display, there was a timing difference across the display, with the topmost elements in each frame drawn roughly 5 msec before the bottommost elements. The maximum timing difference between an element in the central rectangle and one outside it was, however, always less than 3 msec.

We collected choice data for a range of orientation differences, and compiled psychometric functions from which we defined threshold as the orientation difference supporting 75% correct performance.

Results

Figure 3(A) shows example psychometric functions for two subjects in the first experiment for the different flicker conditions described above. It is evident that variations in the relative phase of the texture elements did not alter the subjects' performance. Figure 3(B) plots the threshold orientation difference values for a range of flicker frequencies and phases. These thresholds agree well with those found by Nothdurft (1991) under similar conditions.

Synchronizing or desynchronizing the elements comprising the region to be discriminated had no discernible

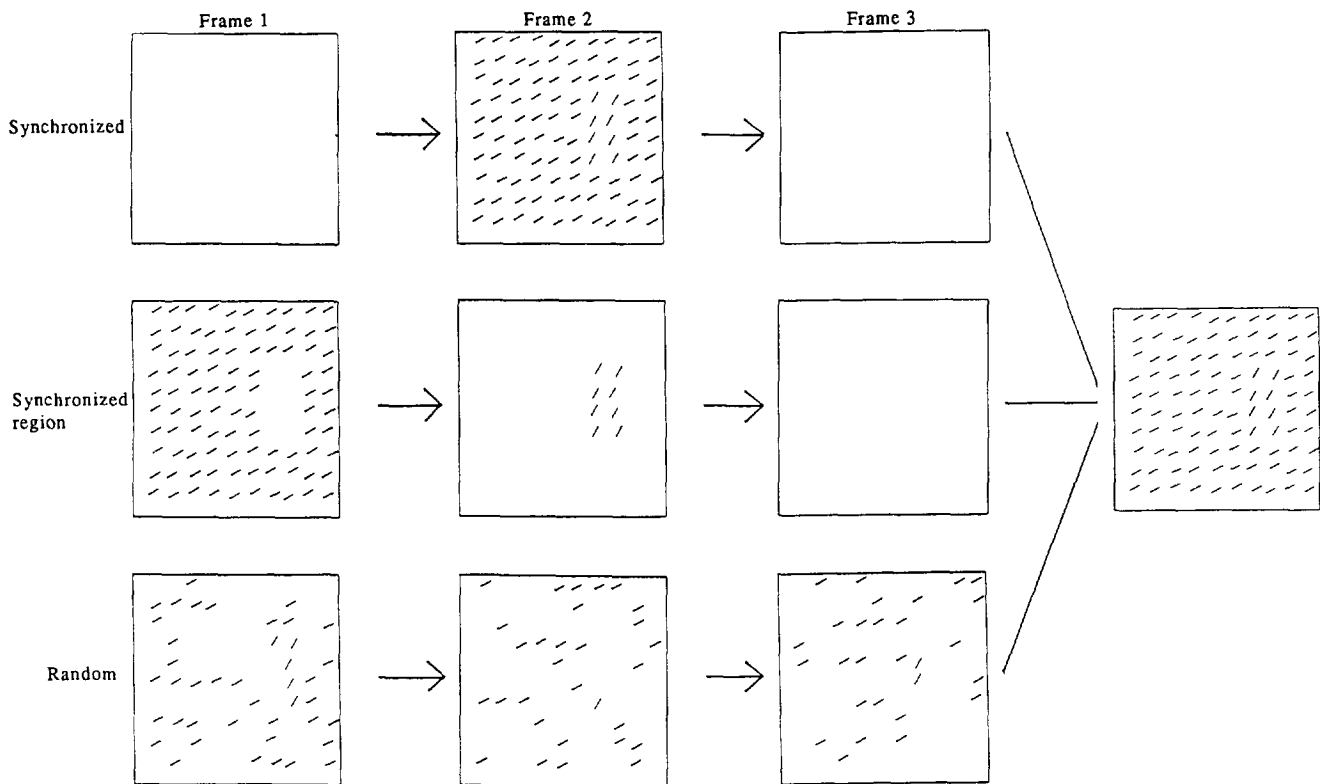


FIGURE 2. A diagram illustrating the three display phase conditions used in the experiment. The rightmost square shows the overall stimulus configuration. The subjects' task was to identify the orientation of the rectangular region containing lines of different orientation (here vertical). Each row represents a succession of three frames of the stimulus. In the first experimental condition (top row, the *synchronized* condition), all elements were presented at the same time. In the second condition (middle row, *synchronized region* condition), all the elements in the rectangular region were presented together, in phase, while the elements of the surround were also presented together, 120 deg out of phase. In the final condition (bottom row, *random* condition), the phase relationship among the elements was random. We also explored a *no flicker* condition, not shown, in which all elements were presented on each frame. The fundamental frame rate of the display was 120 Hz, and the rate of element flicker was varied from 15 to 60 Hz by suitable replication of frames. The particular case illustrated corresponds to a flicker rate of 40 Hz.

effect on subjects' ability to perform the segmentation task. Neither the frequency nor the relative phase of the texture elements influenced subjects' performance. Indeed, it is quite striking that even at relatively low frequencies (15 or 20 Hz), when the flicker of the lines was quite vivid, subjects were wholly unable to use a relative phase difference between the target region and the surround to support visual segmentation.

EXPERIMENT II

Methods

We also explored the effect of synchronized flicker on a perceptual grouping task, using the display shown in Fig. 4, a variant of Attneave's field of triangles (Attneave, 1968). The display was of the same size and luminance as that used in the line segmentation task. This field of equilateral triangles is typically perceived as a group all of whose members "point" in the same direction. The display is multistable, in that the pointing direction spontaneously shifts among the three possible choices. We reasoned that synchronizing the flicker of two of the three limbs of each triangle might bias the perceptual organization of the display so that the pointing direction

would be biased to that bisecting the synchronized features. The subject's task was simply to indicate the direction in which the triangles seemed to point. We ran the experiment on seven observers, with flicker rates of 30–60 Hz.

Results

The results are shown in Table 1. No observer showed any reliable tendency to choose the pointing direction specified by the phase-locked flicker. In only three of 21 experimental conditions were the results significantly different from chance [$P < 0.05$, based on the 95% confidence interval for the binomial distribution (Clopper & Pearson, 1943)], and there was no trend in these data. We also used random-phase flicker to see if this manipulation might disrupt the strong tendency of the figures in the display to group according to perceived direction; no such trend was detectable.

CONCLUSIONS

The results of our experiments were uniformly negative, in the sense that we could find no flicker manipulation that changed subjects' segmentation per-

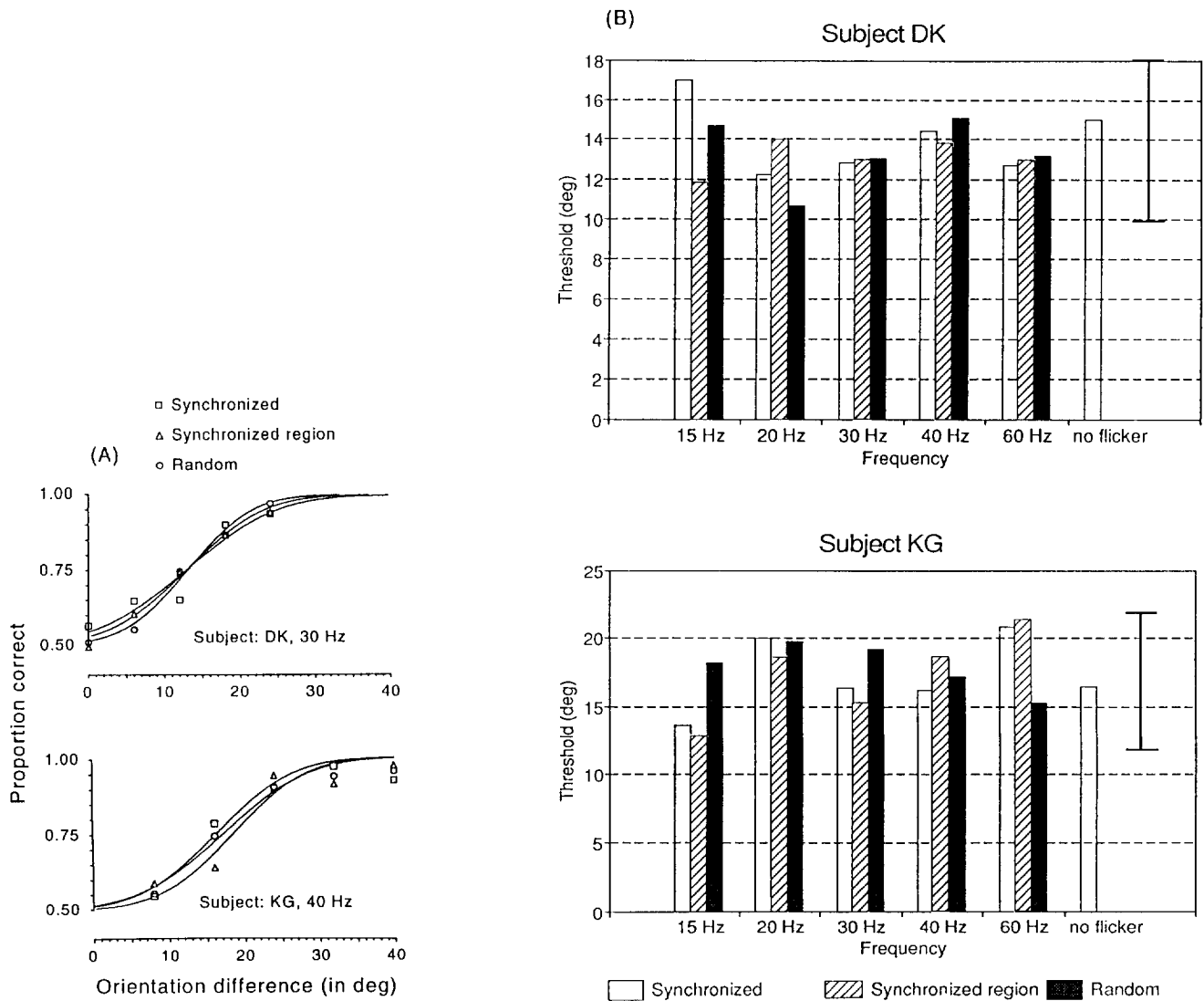


FIGURE 3. (A) Psychometric functions showing the performance of two observers on the rectangle-orientation-identification task (Expt 1). Proportion of correct responses is plotted as a function of the difference in orientation between the elements within the figure and those in the surround, and separate functions are plotted for the three phase conditions shown in Fig. 2. Psychometric functions like these were analyzed to determine orientation-difference thresholds (at 75% correct performance). (B) Orientation-difference thresholds for two observers at a variety of stimulus frequencies are shown, for the three different phase conditions. For comparison: thresholds are shown for the *no flicker* condition on the right. The error bars at the right of each panel show the average SE of the threshold estimates. Neither the frequency nor the phase of the flicker influenced thresholds.

formance or grouping preference. These results differ from those of Fahle (1993), who found that under his conditions, subjects could apparently use very small temporal offsets to perform reliably in a task very similar to ours. We are at a loss to explain this discrepancy; perhaps it is related to the longer presentation duration (1 sec) used in Fahle's experiments, which introduces the undesirable complication of scanning eye movements. Our results are in better agreement with those recently published by Fahle and Koch (1995). They used a stimulus made of two identical and partially overlapping Kanizsa triangles formed by illusory contours. In one of their experimental conditions, they studied the effects of temporal asynchrony in the presentation of the elements forming the illusory contours. They found a small effect for a display frequency of 5 Hz, but no effect for

TABLE 1. Results of seven observers for the triangle experiment (Fig. 4)

Subject	30 Hz	40 Hz	60 Hz
JS	0.40	0.47	0.33
AK	0.30	0.36	0.50
MG	0.33	0.33	0.33
RK	0.29	0.50	0.27
SF	0.27	0.57*	0.32
SO	0.68*	0.33	0.11*
CT	0.27	0.37	0.52

Proportion of trials when observers perceived the triangles from Fig. 4 as pointing in the direction the synchronized limbs were pointing to.

*Proportions significantly different from chance ($P < 0.05$). Only three out of 21 conditions gave significant biases. There was no systematic trend in the results.

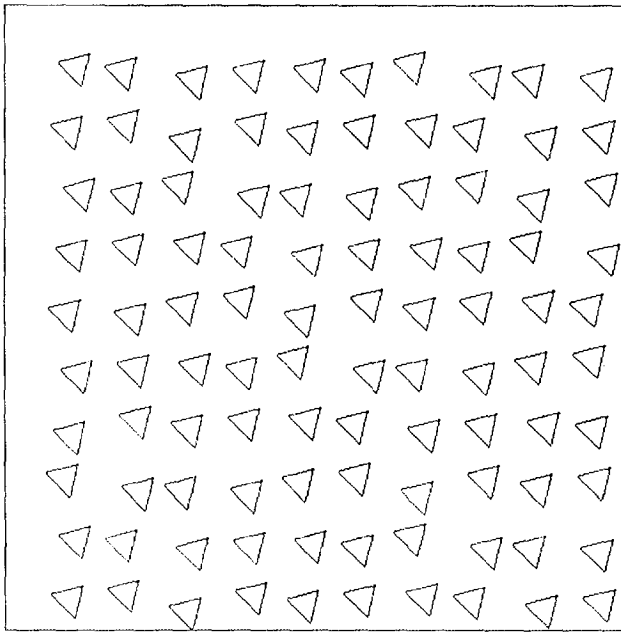


FIGURE 4. The display used to explore the effect of synchronized flicker on the grouping of the perceived "pointing" directions of Attneave's triangles. To examine the effect of synchronization on grouping, the same two of the three segments of each triangle were flickered synchronously.

frequencies between 10 and 75 Hz. In other words, for frequencies above 5 Hz, the subjects' perception of their stimulus was not affected by the temporal offsets in the presentation of the figure's elements. Fahle and Koch concluded that their results argue against the idea that the precise timing of external events induces temporally synchronized neuronal responses necessary for figural binding of spatial features. They noted however that their results do not rule out the possibility of an internal neural code based on the synchronicity of neuronal firing, independent of the temporal characteristics of the visual stimuli.

According to the theories of von der Malsburg (1983), Singer (1991) and others (Eckhorn *et al.*, 1988) the coherent oscillatory activity of cortical neurons responding to different elements of a single object carries the information that allows the object to be perceived as a whole. Our displays, which relied on the kind of grouping processes for which synchronized oscillatory activity ought to be well suited, were designed to induce oscillatory activity by visual flicker. Many cortical neurons give phase-locked modulated responses to flickering targets at rates in the range we used (Foster *et al.*, 1985; Hawken *et al.*, 1991) and by varying the phase relationships among the flickering elements we would certainly have altered the degree to which neurons signaling information about elements in the segmented region were giving coherent flicker responses. These visually induced oscillations should have interfered with those supporting visual segmentation in Expt I and should have induced a perceptual bias in the second experiment. The lack of any effect of this flicker or of its phase suggests that the temporal coherence of oscillatory

cortical responses may be unrelated to the processes that link perceptual features across a scene.

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