

A Quantitative Measure for Short-term Cortical Plasticity in Human Vision

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The human visual system is normally very good at determining the relative positions of objects in space, but under certain conditions contextual influences can cause significant errors in this process. We studied spatial localization around an artificial scotoma, a small mask that occludes part of the visual field while a dynamic pattern is shown over a surrounding region, and found that the ability to determine the position of short line segments was strongly biased toward the interior of the scotoma. We attribute this “shift” or misassignment of position to receptive field (RF) expansions within the artificial scotoma as seen in recent physiological studies. Furthermore, our findings show that this shift begins within 1 sec of stimulus presentation, suggesting that RFs are constantly altered by their local context and that these dynamics are a part of normal vision.

[Key words: cortical plasticity, visual cortex, visual perception, spatial localization, receptive field expansion, contextual influences, horizontal connections]

Hyperacuity tasks have demonstrated that under normal conditions the spatial precision of the human visual system can be finer than the diameter of a single retinal photoreceptor (Westheimer, 1975). Under certain circumstances, however, the system becomes perturbed and changes in normal localization are seen. For example, the apparent alignment of two features is disturbed when a new neighboring feature is introduced (Badcock and Westheimer, 1985; Burbeck and Hadden, 1993). Similar biases also occur for other spatial attributes such as orientation and depth (Westheimer et al., 1976; Westheimer, 1986, 1990). These observations at the perceptual level have their counterpart in findings from the recording of cortical neurons, where the response of a single cell is influenced by stimuli lying outside the cell's receptive field (RF) (Nelson and Frost, 1978, 1985; Allman et al., 1985; Tanaka et al., 1986; Orban et al., 1987; Von der Heydt and Peterhans, 1989; Gilbert and Wiesel, 1990). Recently, a fivefold increase in RF area has been reported when the surround of an RF is stimulated but the RF itself is not (Pettet and Gilbert, 1992). RFs within the unstimulated

area, which we term an artificial scotoma, expand, while cells outside of this region remain unaffected.

We wondered what effects this differential expansion would have on normal visual perception—specifically, on the perception of the position of objects located around the scotoma. Our results indicated that the artificial scotoma causes stimuli to be pulled toward its center, changing the location of an object from where it appears before the scotoma is introduced. After establishing this shift on several observers, we examined various spatial and temporal characteristics of the effect.

Materials and Methods

The stimuli used in the course of the experiment were presented on a monitor whose viewing area subtended $14^\circ \times 18.5^\circ$ of arc at the observation distance of 114 cm, refreshed at a rate of 60 Hz. This display was controlled by a Sergeant Pepper #9 graphics board and a PC-compatible 486 computer. Observers had 20/20 vision, with refractive correction if necessary, and no error feedback was provided. Stimuli were white of average photopic intensity, seen with high contrast on the screen with 1.4 cd/m^2 background luminance. Observation was binocular with normal pupils and free head (It has been found that hyperacuity measurements of the kind reported here are not improved significantly when a head rest is used.)

To produce an artificial scotoma, the screen was filled with dynamic random dots (5% coverage, 30 Hz refresh rate) that were blanked out in a $2.4^\circ \times 2.4^\circ$ square. To obviate brightness cues, the area of the scotoma was given a luminance above background approximately 1/20 of that of the screen areas that were given random dots. The random dot stimuli were white and were created with a screen brightness that had a luminance of 40 cd/m^2 . The test lines that were used as hyperacuity pattern elements had a luminance of 72 cd/m^2 . Measurements were made with a three-line bisection task: the observer had to indicate whether the middle one of three short horizontal bars appeared nearer to the top or the bottom one.

There was always a large dot on the screen on which the observer was instructed to maintain fixation. Its distance from the hyperacuity test pattern could be adjusted to allow examination of various eccentric regions of the retina. The main data were obtained at an eccentricity of 6° to the left of the fixation point.

Procedure 1. Each trial consisted of a 2 sec cycle. During the first 1.67 sec the observers saw the conditioning pattern (Fig. 1a), and this was followed for 0.33 sec by the hyperacuity test stimulus shown without background (Fig. 1b). The conditioning pattern in the scotoma and control conditions differed in only one respect: in the control condition the whole field was filled with random dots during the 1.67 sec it was exposed, while in the scotoma condition there was an area in the field within which the random dots were blanked out. During each presentation of the test stimulus the top and bottom bars of the three-bar test pattern remained 1.7° apart, while the center bar was positioned randomly in one of seven predetermined conditions, either centered between the top and bottom bars or moved by one, two, or three units of 3.4° above or below this point. The relative position of the test bar triad and the scotoma varied between trials, but the main data were taken when the middle bar in its centered position was just inside the lower edge of the scotoma. For each trial, the observer indicated whether the

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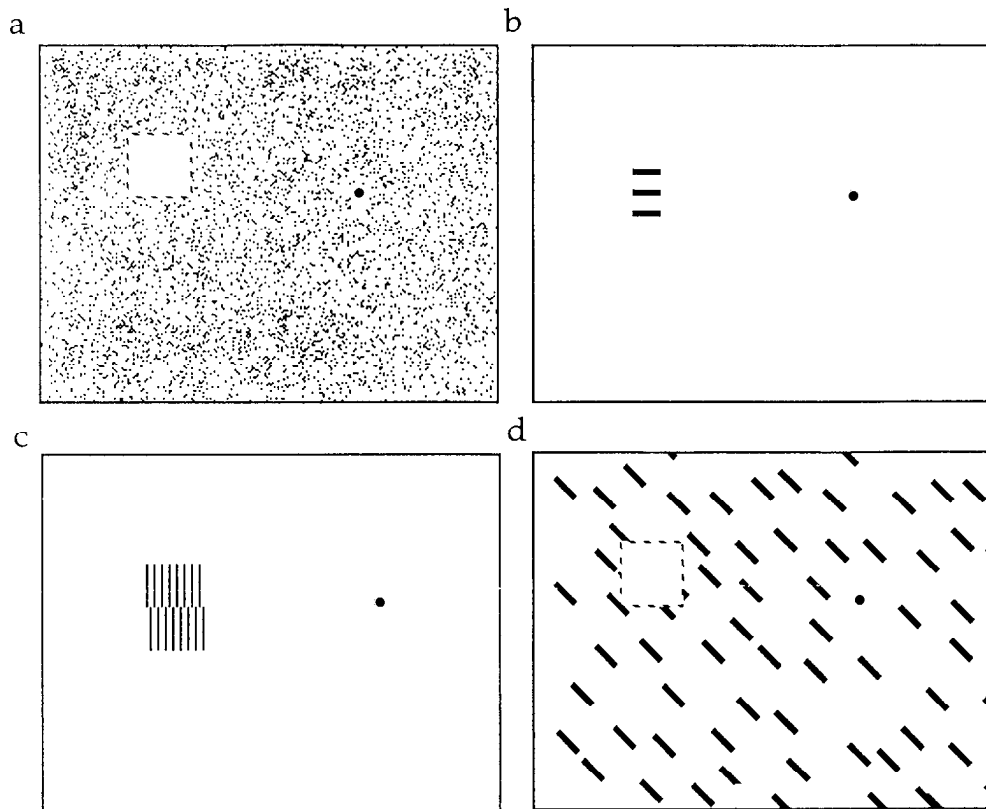


Figure 1. Diagrammatic representations of stimuli used during the experiment. Each stimulus contained a circular fixation point of diameter 0.25° to ensure that targets remained at the proper eccentricity. *a*, The random dot conditioning stimulus. The display consisted of a dynamic noise pattern of 20 separate frames of $3.4' \times 3.4'$ squares that filled 5% of the screen and played successively at 30 Hz. During experimental runs a scotoma was presented that occluded the random dot pattern and was not present in control runs. The test bars and conditioning stimulus were presented alternately. The middle bar of the test stimulus, when centered between the two end bars, lay at the inside edge of the scotoma. Like the test bars, the bottom of the scotoma was 6.0° to the left of the fixation point. *b*, The three-bar bisection task (or test stimulus). The three $0.1^\circ \times 0.7^\circ$ line segments were horizontally aligned 6.0° left of the fixation point when measured center to center. The top and bottom bars maintained a fixed separation, while the vertical position of the middle bar varied between trials. *c*, The virtual border stimulus. Two rows of eight evenly spaced lines were placed so that the top of the bottom row corresponded to the bottom of the top row. The bottom row was horizontally offset from the top row by half the distance between adjacent lines. The pattern was positioned so the artificial edge formed between the two rows corresponded to the bottom edge of the scotoma in the other two conditioning stimuli. *d*, The oriented bar conditioning stimulus. The 60 bars had the same dimensions as the line segments of the test stimulus and were placed at random positions on the screen. The bars were oriented in the same direction and moved back and forth in a direction orthogonal to their orientations by a distance of 5.75° every 1.3 sec. A scotoma was present only in experimental runs and had the same dimensions and placement as in the random dot conditioning stimulus. The scotoma masked only the portion of the bars that fell within its borders, making it appear to be in a separate plane from the rest of the stimulus.

middle bar appeared closer to the top or bottom end bars by making the appropriate choice on a keyboard, guessing if necessary. The three-bar test stimulus and the scotoma were never presented simultaneously because the border of the scotoma could be used as a reference in the decision making process.

Most data points shown here consisted of at least 300 trials each for the experimental and control components of the experiment, accumulated over a period of 2 or more days. During each session, both in the control and in the scotoma conditions, the observer was presented with 165 trials of which the first 15 were discarded to reduce differences from short-term learning effects between trials (Poggio et al., 1992). A psychometric function was fitted using the method of probits to the percentage of "up" responses in the seven positions of the middle bar. This allowed the identification of the mean of the data, that is, the point at which the middle bar appeared closer to the top and bottom bars an equal number of times. The values that we reported as shifts corresponded to the difference between the means of control and scotoma runs for a given set of parameters, with a positive value indicating the middle bar was perceived as being higher in experimental runs than in control runs. This analysis technique also yielded standard errors, which are presented here as the square root of the sums of squares of the individual standard errors of the means of the control and scotoma runs.

We performed several additional experiments to test various features of the shift, including one in which the scotoma was removed and its lower boundary replaced by a virtual border (Fig. 1*c*) and a second in which the random dot pattern was replaced by a series of oriented bars (Fig. 1*d*).

Procedure 2. In order to study the temporal nature of the shift and the relationship of the shift effect to perceptual filling-in, several changes were made to the original stimuli. The artificial scotoma was reduced to $1.5^\circ \times 1.5^\circ$, and the test bars of the three-bar bisection test stimulus were repositioned accordingly. The top bar was placed at a location corresponding to the center of the scotoma and separated from the bottom bar by 1.4° .

In the experiments exploring the temporal characteristics of the shift, we showed the following sequence of stimuli: a random dot pattern with a scotoma, the test stimulus, and a random dot pattern without a scotoma. The third pattern was intended to reverse the effects of the scotoma so that apparent shift in test bar position could be attributed to the single conditioning period immediately prior to the test. As a control, we presented the same three stimuli but interchanged the two random dot patterns. In this manner the control could be used to eliminate whatever remained of the shift effect between trials. The full-screen random dot pattern, that is, the pattern without the artificial scotoma, was presented for 4 sec, while the pattern that included the scotoma

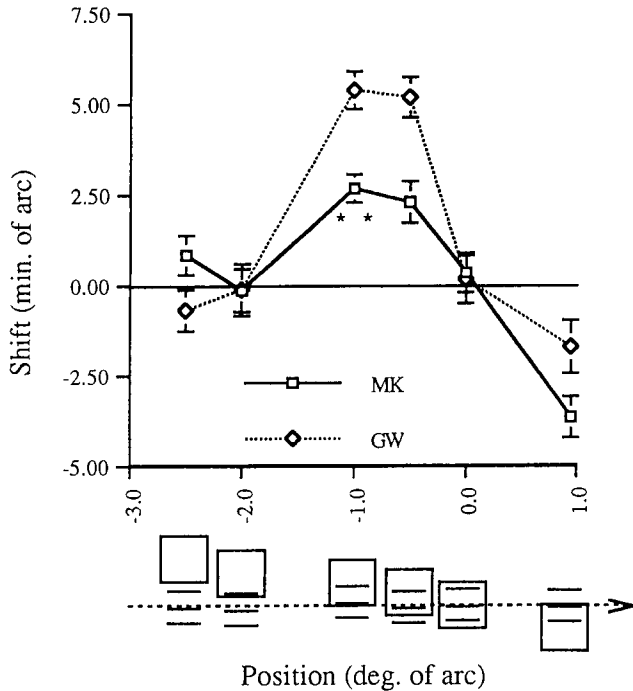


Figure 2. The effect of moving the test bars relative to the scotoma. To ensure that the bars remained at the same eccentricity (6.0°), the scotoma was placed at different vertical positions and the test bars remained stationary. The actual positions of the bars in relation to the scotoma are shown at the *bottom*. Positive shifts indicate that the center bar of the bisection task was perceived as being higher in experimental runs than in the corresponding controls. The *point marked with two asterisks* was taken under identical conditions as the marked data point in Figure 3.

was tested at various temporal durations. In one of these conditions, the next stimulus was not presented until the artificial scotoma had completely "filled in" (see Results) and was no longer visible.

Results

The primary experiment was designed to show whether the enlargement of RFs within an artificial scotoma would manifest itself as an alteration of feature localization. The artificial scotoma caused bars located near the edge of the scotoma to appear shifted toward the center of the scotoma. The effect was maximal when the triad of lines was centered near the edge of the scotoma, as shown in Figure 2. In this figure, the shift effect is shown for triad positions outside of the scotoma, bordering the edge of the scotoma, and inside the scotoma, obtained at a 6° eccentricity for two of the authors. Fragmentary data obtained on three other observers were in close agreement (C.G. $5.82' \pm 0.64$, J.J. $4.77' \pm 0.72$, E.L. $5.01' \pm 0.89$, under conditions identical to the marked data point). As expected, the largest shift or misassignment of position occurred when one of the outer bars was located firmly inside and the other well outside the artificial scotoma and the middle bar straddled either edge. When all three bars were entirely within or outside the scotoma, there was no shift.

The dependence of the shift on RF size and cortical magnification were studied by testing the effect at different eccentricities (Fig. 3). As is evident by the graph, center shift increased as a function of eccentricity, although more quickly for subject M.K. than for G.W.

In addition to our shift effect, we discovered a completely separate phenomenon, a long-term improvement in the hyper-

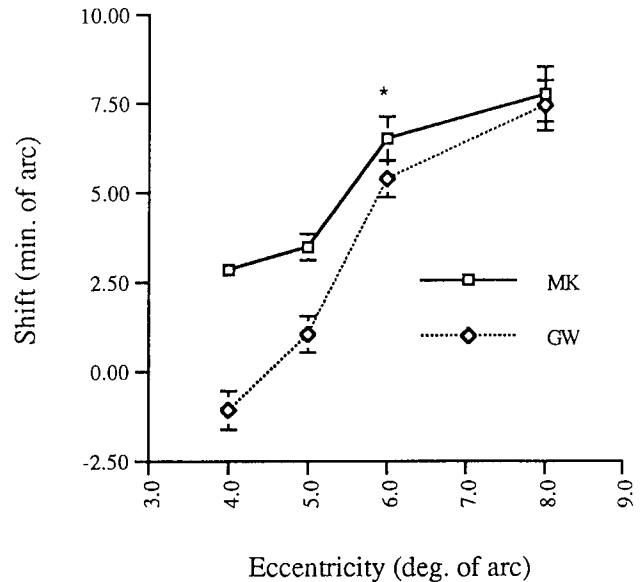


Figure 3. The shift effect at varying eccentricities. The experiment was performed by moving the fixation point to different horizontal separations from the scotoma. The *marked data point* represents data taken under identical conditions as the marked data point in Figure 2. Differences between the shift values for these two points are explained in the Figure 4 caption and the Discussion.

acuity task. This improvement develops over several weeks and is not to be confused with our shift, which occurs on the time scale of seconds. Differences in shift values for observer M.K. between the data in Figure 2 and Figure 3 (the latter were obtained first) can probably be explained by this change. The large number of trials performed by this observer gradually resulted in increased accuracy of his positional judgments in the control condition, while the mean of the scotoma condition remained almost stationary. Since the shift is measured as a difference in means between the control and scotoma conditions, the changing value of the control condition caused a corresponding decline in the shift (Fig. 4). Nonetheless, a strong shift was still observed even after tens of thousands of individual trials.

In the fovea the location of features can be influenced by the presence of adjoining ones (Badcock and Westheimer, 1985). In the case of our stimulus configuration it might be argued that the edge of the artificial scotoma could act as a virtual contour and in that capacity produce a shift in bar position, even though the scotoma and the test bar triad were presented at different times. Though average screen brightness was made the same inside and outside the artificial scotoma (see Materials and Methods), the latter had clearly visible edges before filling-in occurred. We therefore created an illusory contour of approximately equal visibility where the lower edge of the artificial scotoma had been located (Fig. 1c). This stimulus was then presented alternately with the three-bar bisection stimulus, with the center bar positioned near the virtual border as in the experiments with the artificial scotoma. No significant shift was observed in either observer (M.K. -0.65 ± 0.51 , G.W. -0.75 ± 0.78).

It might also be argued that the shift is caused by a difference in test bar sensitivity between the random dot pattern and the inside of the scotoma. We compared the threshold of the three-bar bisection, a psychophysical measure of judgement precision, in the control and experimental portions of the experiment and

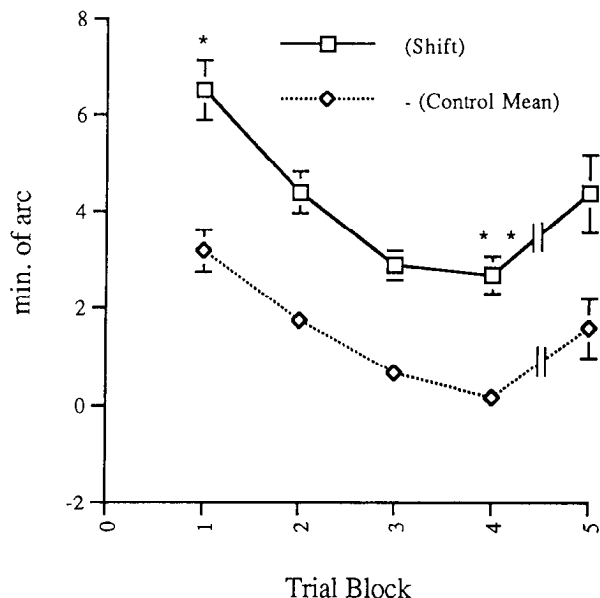


Figure 4. The learning effect. Over the course of many weeks, the original offset bias in the mean of the control portion of the experiment had almost disappeared for subject M.K., indicating that the observer had become more accurate in performing the three-bar bisection task. During this same time period, the mean of the scotoma condition remained much more stationary. Since the shift is defined as a difference in means between the scotoma and control conditions, the changing control condition caused a corresponding decline in the shift over time. Nevertheless, the effect was still strong even after the control bias disappeared. The last block (#5) was taken after 1 month without performing trials, indicating that the improvement was reversible. This "learning" indicated long-term changes in positional judgements taking place over the course of several months, in addition to the short-term changes referred to as "shifts." The data points marked with asterisks represent data points with the same markings in the two previous figures.

found no significant differences that were induced by the scotoma (Table 1). The magnitude of the thresholds has little to do with the significance of the shifts. As evidenced by the error bars, use of a large number of trials produces highly significant shifts whatever the threshold values.

We also measured the shift using the inverse of the conditioning stimulus. The area previously corresponding to the sco-

toma was filled with the random dot pattern while the surrounding area was blank. The control consisted of an entirely blank screen. Observers reported a shift away from the random dot pattern of $5.61' \pm 0.64$ and $2.47' \pm 0.48$ for subjects M.K. and G.W., respectively. These shifts were in a direction opposite to those seen for the initial conditioning stimulus with the bars in an identical position, though slightly smaller in magnitude. This finding provides additional evidence that the shift is not caused by an interaction with the edge of the scotoma, since such a mechanism would not be consistent with a shift in the reverse direction.

To explore further the dependency of the shift on the conditioning stimulus, a series of oriented bars (Fig. 1*d*) was substituted for the random dot pattern. The experiment was performed at four different bar orientations, including one where the angle, and thus direction of movement, of each bar was randomized. All four orientation patterns yielded significant shifts, although smaller than with the random dot pattern. No correlation was found between the magnitude of the shift and the correspondence in orientation of the test bars and the bars in the background (average M.K. 2.60 ± 0.48 , G.W. 2.40 ± 0.55). However, the randomly oriented bars produced a larger shift than the iso-oriented bars (M.K. 3.85 ± 0.49 , G.W. 2.71 ± 0.65).

A small artificial scotoma within a dynamic noise pattern slowly fades until the occlusion appears to be filled with the random dots (Ramachandran and Gregory, 1991; Spillman and Kurtenbach, 1992). Over a period of several seconds, the random dot pattern appears to encroach the scotoma until the occlusion is no longer visible. We studied the relationship between this process, known as filling-in, and our shifts using a slightly different protocol (Procedure 2, Materials and Methods). The smaller scotoma facilitated the target fading process and the addition of a "deconditioning" stimulus allowed examination of the short-term temporal nature of the shift. While the previous experiments allowed a buildup of the shift between trials, the new ones sought to find the shifts occurring within single conditioning periods. In effect, between trials, we sought to reset the system to its default state by presenting stimuli throughout the visual field, allowing us to study the effects of very short conditioning periods. Even after only 1 sec of exposure to an artificial scotoma, there was a substantial shift in perceived position of the central bar, with a more prominent

Table 1. Psychophysical thresholds (min of arc)

Data point	M.K.		G.W.	
	Experimental	Control	Experimental	Control
Eccentricity				
4.0	-1.37 ± 0.13	-1.23 ± 0.12	-2.22 ± 0.24	-1.79 ± 0.17
5.0	-1.79 ± 0.20	-1.82 ± 0.18	-1.97 ± 0.20	-2.07 ± 0.22
6.0	-2.96 ± 0.30	-2.56 ± 0.26	-2.97 ± 0.24	-3.02 ± 0.23
8.0	-3.22 ± 0.34	-3.64 ± 0.37	-4.68 ± 0.50	-5.10 ± 0.64
Bar position				
1.0	-2.34 ± 0.24	-2.44 ± 0.25	-3.03 ± 0.35	-4.05 ± 0.46
0.0	-2.17 ± 0.17	-2.18 ± 0.24	-2.91 ± 0.27	-3.64 ± 0.35
-0.5	-2.56 ± 0.23	-2.38 ± 0.24	-2.47 ± 0.23	-2.51 ± 0.24
-1.0	-2.07 ± 0.13	-2.37 ± 0.18	-3.25 ± 0.34	-3.37 ± 0.33
-2.0	-2.48 ± 0.23	-2.39 ± 0.22	-3.02 ± 0.36	-3.22 ± 0.37
-2.5	-2.35 ± 0.27	-2.32 ± 0.25	-2.66 ± 0.22	-2.54 ± 0.25

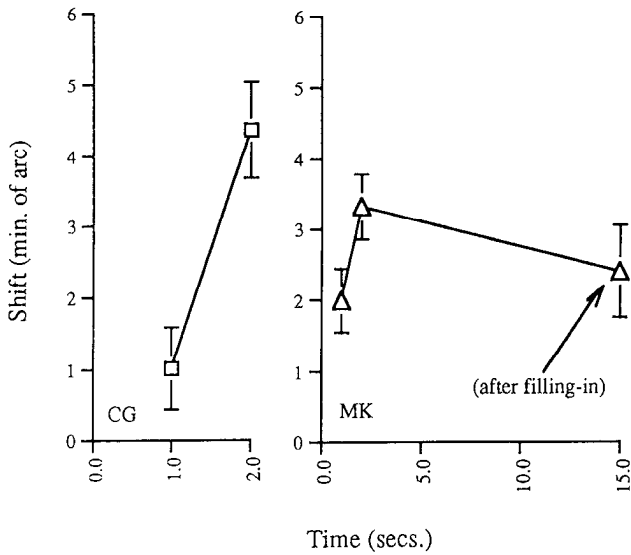


Figure 5. The temporal nature of the shift. The points were obtained through a different protocol (Procedure 2, Materials and Methods) that sought to examine the shift over single conditioning periods. The final point, labeled *after filling-in*, was obtained after the target had completely faded from view during each trial. The results indicated that a strong shift was apparent even after only 1 sec of conditioning, but the shift has not yet reached its maximum.

effect seen after 2 sec (Fig. 5). Filling-in took an average of approximately 15 sec under our observation conditions, and at that time the shift is not greatly different.

Further experiments were performed to test the relationship between our shift and filling-in. Since a moving scotoma disrupts the fill-in process, we tested the shift while jittering the scotoma horizontally over a distance of 0.25° at 2 Hz and obtained shifts

of $3.36' \pm 0.48$ and $4.67' \pm 0.59$ for subjects M.K. and G.W., respectively. Shifts were slightly smaller than they were with a stationary scotoma, but were still maintained even when the filling-in process was disrupted.

Discussion

Our results provide further evidence that the ability to localize a given object in space is dependent on contextual influences. The experiments reported here show that spatial localization can be artificially biased by a small, reversible scotoma and that this bias is a separate phenomenon from the positional alterations of concurrently presented contextual stimuli (Badcock and Westheimer, 1985).

The shift effect we observed is strongly dependent on the spatial and temporal characteristics of the stimulus used to create it. Moving the test stimulus even slightly relative to the scotoma often resulted in dramatic changes to both the magnitude and direction of the shift, with the effect falling off abruptly when the middle bar was moved to a position outside the scotoma. The disappearance of the shift when the bars are centered within the scotoma indicates that the mechanism that causes the positional bias is symmetric through the middle of the scotoma.

It is tempting to attribute this mechanism to the RF expansions inside artificial scotomata that have been previously reported by Pettet and Gilbert (1992) in anesthetized cats. Although little is known about the exact neural mechanisms that underlie spatial localization, it is reasonable to postulate that this differential RF expansion would cause significant distortion in the perception of position. If one treats an ensemble of cells as representing a series of labeled lines each signaling a particular position in space, the system's determination of an object's location would depend on the relative activity of the different labeled lines activated by the stimulus. The estimate of position

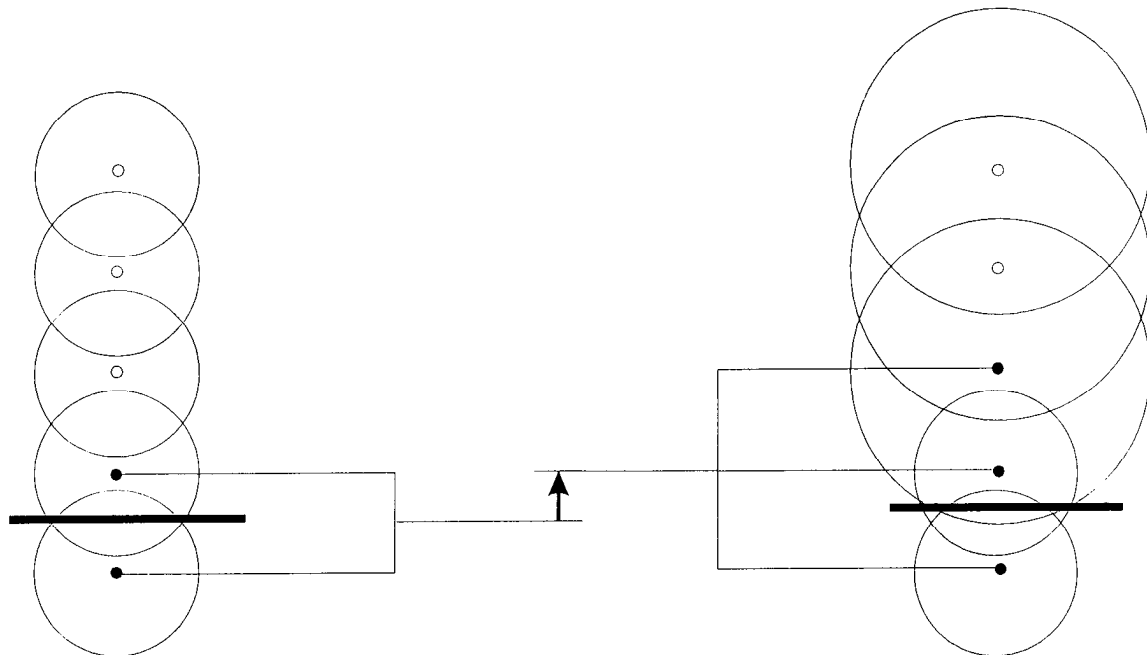


Figure 6. RF expansion as a mechanism for the shift effect. *Large circles* represent individual RFs. *Left*, Preexpansion RFs. The two lower RFs are both stimulated by the bar, and each one signals that the bar is located at the center of its RF. The perceived location is estimated by averaging these two values. *Right*, Postexpansion RFs. Because the RFs at the *top* have enlarged, an additional RF is stimulated by the bar, biasing the perceived position toward the top of the diagram. The *arrow* shows the predicted shift.

would represent an average, or vector sum, of the positions signaled by the activated lines (Fig. 6). During RF expansion, an additional set of lines are activated on one side of the stimulus for objects located near the scotoma boundary.

RF expansion was originally observed immediately following lesions to the retinal photoreceptor layer (Gilbert and Wiesel, 1992), which led to the artificial scotoma experiments mentioned above. With this more extended loss of visual input, there is in the longer term a rearrangement of cortical topography, such that RFs inside the silenced cortical area rearrange themselves to receive input from the surround (Kaas et al., 1990; Heinen and Skavenski, 1991; Chino et al., 1992; Gilbert and Wiesel, 1992).

There are several further points of correspondence between the effects of various stimuli in the psychophysical work presented here and previous work with artificial scotomata (Pettet and Gilbert, 1992). The orientation of bars used as a conditioning stimulus showed no consistent correlation to RF expansion and had no obvious role in the perceived shift. The relative efficiency of stimulus patterns such as randomly oriented bars and dynamic random dots in inducing RF expansions was similar to their relative effectiveness in producing perceptual shifts.

The shift is strongly dependent on eccentricity as well, increasing rapidly moving away from the fovea. In establishing the cortical mechanism of the shift, it is tempting to relate the dependence on eccentricity with cortical parameters such as average RF size and magnification factor; however, the rate of change of the shift is considerably faster than either of these two measures (Hubel and Wiesel, 1974; Dow et al., 1981). If the perceived shift is dependent, as postulated, on the ratio of RF expansions within artificial scotomata, the dependency on eccentricity would suggest that the amount of plasticity in the cortex is not constant across the visual field.

We would postulate that the anatomical basis for the shift is the plexus of long-range horizontal connections of pyramidal cells in the primary visual cortex (Gilbert and Wiesel, 1979, 1983, 1989; Rockland and Lund, 1982, 1983; Martin and Whitteridge, 1984; for review, see Gilbert, 1992). These cells allow integration of information over cortical distances that are much larger than the classical model of the RF and may serve as a relay for contextual information between local subsets of cells. Although these influences are normally subthreshold, the artificial scotoma may cause an adaptation of inhibition, unmasking normally inactive input from farther away in the visual field. RFs in the interior of the scotoma that do not normally respond to the test bars would be potentiated in their expanded state, responding to positions outside the original RF.

During the course of the experiment, we stumbled on a secondary finding, which is a separate phenomenon from our shift. There appears to be a distinct improvement effect in the performance of the three-bar hyperacuity task over many sets of trials. Through the course of more than 10^4 presentations of the test bars in an identical location, performance on the control half of the original experiment improved dramatically over a 3 month period in the most active of our observers (M.K.). This improvement is evident in the marked data points of Figures 2 and 3, which were obtained under identical conditions, but have very different values. The marked point in Figure 3 was obtained before the corresponding point in Figure 2 and shows a considerably greater shift value. There was originally an offset bias in the control condition (which of course does not show up in our

data because they represent the difference between the control and artificial scotoma conditions), but this approached zero at the end of the 3 month period (Fig. 4). During this same time period, experimental values declined only slightly, possibly because variations such as moving the scotoma relative to the test stimulus resulted in slightly different stimuli between experimental runs, while the control experiment, which did not include a scotoma, remained the same. Similar results to the original state were obtained by switching the stimulus to the opposite hemifield ($5.72' \pm 0.81$), indicating that the improvement in the task was specific to visual field position. This improvement appeared to be reversible. The control mean returned to half its original value within 1 month of cessation of the task. A small improvement in thresholds was also observed for the control, but the change was much smaller than the corresponding change in the mean.

An improvement of psychophysical threshold, a measure of precision, has been reported in the fovea with as few as 2000–2500 presentations (McKee and Westheimer, 1978), and the findings of Poggio et al. (1992) show that improvement occurs for accuracy judgements as well. Although physiological models for this type of improvement have not yet been documented in the visual cortex, a similar phenomenon has been observed in the auditory system. The cortical area that responds to the training frequency of a discrimination task is greatly enlarged compared to untrained animals and neurons within this region are more sharply tuned (Recanzone et al., 1993). Repeated stimulation of a small region of somatosensory cortex also yields similar cortical changes (Jenkins et al., 1990). It seems likely that a similar phenomenon may be occurring in the visual cortex, allowing the processing system to better judge the location of the line segments. This improvement suggests that in addition to the short-term dynamic changes in RF size, occurring over a time scale of 1 sec, there are more enduring changes in response to repetitive perceptual tasks that develop and last for weeks and months.

The present psychophysical work predicts stimulus-dependent behaviors of RFs not yet reported in physiological studies. The negative shifts obtained from the inverse conditioning stimulus seem to indicate that RFs can be made smaller by preferentially stimulating the interior of their RFs or that RFs outside the patch are expanding toward the interior. The short time course of the induction of the shift suggests a lower limit for RF plasticity than has been documented in the physiological experiments. Changing the temporal duration of the random dot pattern caused significant deviations in the shift. The results indicated that the shift reached a peak around 2 sec and fell off at longer conditioning periods. These results also suggest that filling-in and the observed shift are distinct phenomena. The filling-in process occurred gradually over a period of about 15 sec. If the positional shifts or their underlying cellular processes accounted for the disappearance of the scotoma, the shift would increase with longer periods of conditioning. On the contrary, the shift was smaller after a full fill-in had taken place than after only 2 sec of conditioning. The relatively minor differences between moving and stationary scotomata reinforce the distinction between filling in and positional shifts, since fill-in does not occur with moving scotomata.

Our results call for a different way of thinking about sensory RFs. Physiological studies have shown that RF plasticity can occur over time courses as small as a few minutes, while the present work proposes that this reorganization may occur within

a single second. These findings suggest that RF characteristics are stimulus dependent, changing from second to second in response to their local context. Intersecond cortical dynamics may also help to explain other contextual influences in vision perception such as illusory contours and the tilt illusion. It is tempting to relate the changes in cortical circuits early in the visual pathway suggested by these experiments to processes underlying the storage of more complex percepts in higher-order cortical areas.

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