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Orientation-selective adaptation to crowded illusory lines

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Abstract. Visual adaptation has been successfully used as a psychophysical tool for studying the functional organisation of visual awareness. It has been shown that orientation-selective adaptation to a grating pattern occurs in crowded conditions. In such conditions, simultaneous presentation of flanking distractors pushes the target stimulus out of conscious perception and severely impairs orientation discrimination in the periphery of the visual field. In the present study, orientation-selective adaptation to illusory lines induced by two line gratings abutting each other with a phase shift was examined in crowded and non-crowded conditions. To rule out the effects of lower level adaptations we used an animation paradigm in which the orientations of the two line gratings were altered repeatedly during adaptation phase without any change in the orientation of the resulting illusory line. Although performance of subjects in reporting the orientation of crowded illusory lines was at chance level, orientation-selective adaptation was preserved for crowded as well as non-crowded adapting targets. Two control experiments demonstrated that adaptation to endpoints of real lines at the location of abutting grating lines had minimal effect on the adaptation to illusory lines; and changes in the configuration of endpoints could not be responsible for better performance when adapting and test stimuli were different. We conclude that a crowding effect occurs after illusory lines have been processed in the visual stream. Since illusory lines seem to be represented at relatively early stages of visual processing (eg area V2), adaptation to crowded illusory stimuli suggests that neuronal activation in those early stages is not necessarily correlated with conscious perception.

1 Introduction

Simultaneous presentation of flanking distractors on a radial spatial array impairs target discrimination in the periphery of the visual field; this spatial interaction is called 'crowding' or 'lateral masking' (Toet and Levi 1992; Wilkinson et al 1997). Task performance drops to chance level under severely crowded conditions even with unlimited exposure time. It seems that a crowded target does not gain access to the observer's awareness, although an unconscious averaging of crowded signals could happen (Parkes et al 2001).

When observers are adapted to a simple grating patch either alone or with grating flankers, and are then tested at target location for detection of a briefly presented grating patch, either at the same or at an orthogonal orientation, orientation-specific adaptation is observed in both cases even when perceptual awareness of orientation had been confounded by crowding. These results suggest that a crowding effect as a consequence of insufficient attentional resolution occurs later than orientation processing in the visual stream (He et al 1996).

'Visual adaptation' has been successfully used for determining whether visual disappearance phenomena such as crowding effect or binocular rivalry occur in higher-level cortical areas than the primary visual cortex (Blake and Fox 1974; He et al 1996). Adaptation to orientation in a crowded condition or the suppression phase of binocular rivalry suggests that these phenomena occur later than V1 where neurons respond selectively to orientation signals. Such conditions also indicate that V1 activation does not necessarily determine conscious perception and V1 neurons could be selectively active even in the absence of awareness.

In addition, orientation-selective adaptation and tilt aftereffect occur for invisible patterns (He and MacLeod 2001). These observations imply that extremely fine details, even ones that are too fine to be perceptually seen, can penetrate the visual system without awareness. This evidence supports the idea that V1 activation does not always have reciprocal correlation with conscious perception.

Exploring cortical regions that are not a neural correlate of consciousness (NCC) is an important method in studying the locus of awareness (Crick and Koch 1998). Hence, addressing the question whether cortical regions responsible for detection of illusory lines (eg V2) could have selective activation and adaptation to their preferred stimuli without awareness (similar to what has been shown to happen in V1) could be informative whether those regions are not an NCC.

The stimuli used in our experiments consisted of two line gratings abutting each other with a phase shift, thus eliciting the perception of an illusory horizontal or vertical line between the two sets of gratings (Soriano et al 1996). Neurophysiological experiments have shown that illusory contours may be represented at relatively early stages in the visual system such as area V2 (Peterhans et al 1982; von der Heydt et al 1984). The responses of V2 neurons to an illusory contour can even be stronger than to a real contour (Baumgartner et al 1984).

To determine the correlation of activation of such areas with conscious perception, we measured orientation-selective adaptation to illusory lines in crowded condition and compared it with that in non-crowded condition. In addition, the results of our experiments could decide whether crowding effect occurred later than the level of illusory line processing.

2 General methods

2.1 *Observers*

Observers were five medical students (two females and three males) participating voluntarily in 2 h sessions. Their ages ranged from 22 to 24 years. All subjects were trained psychophysical observers with normal or corrected-to-normal vision, but were naïve to the purpose of the experiment. In each experiment, subjects completed 5 blocks consisting of 64 randomised trials.

2.2 *Apparatus*

The stimuli were presented on a Pentium III 800 MHz PC. Images were displayed on a RGB colour monitor, 800 (width) $\times$ 600 (height) pixel resolution, 60 Hz frame rate (795FT Plus; LG, South Korea). The subjects, placed in a dark room, with their heads fixed in a chin-and-forehead rest, viewed the displays binocularly. The distance between their eyes and the screen was 50 cm.

We used DMDX package for windows (http://www.u.arizona.edu/~kforster/dmdx/DMDX%20Timing.pdf) for programming the psychophysical experiments and SPSS 10.0 for statistical analysis of data.

3 Experiment 1

3.1 *Methods*

In this experiment orientation-selective adaptation to illusory lines in crowded and non-crowded conditions was studied. The displays used are shown in figure 1. Each trial began with the presentation of a fixation point for 800 ms followed by presentation of the adapting stimulus for 4 s (adaptation phase), followed immediately by presentation of the test stimulus for 580 ms (test phase), and ended with a 5 s period of blank screen as inter-trial interval. The fixation point was a small red dot during the adaptation phase

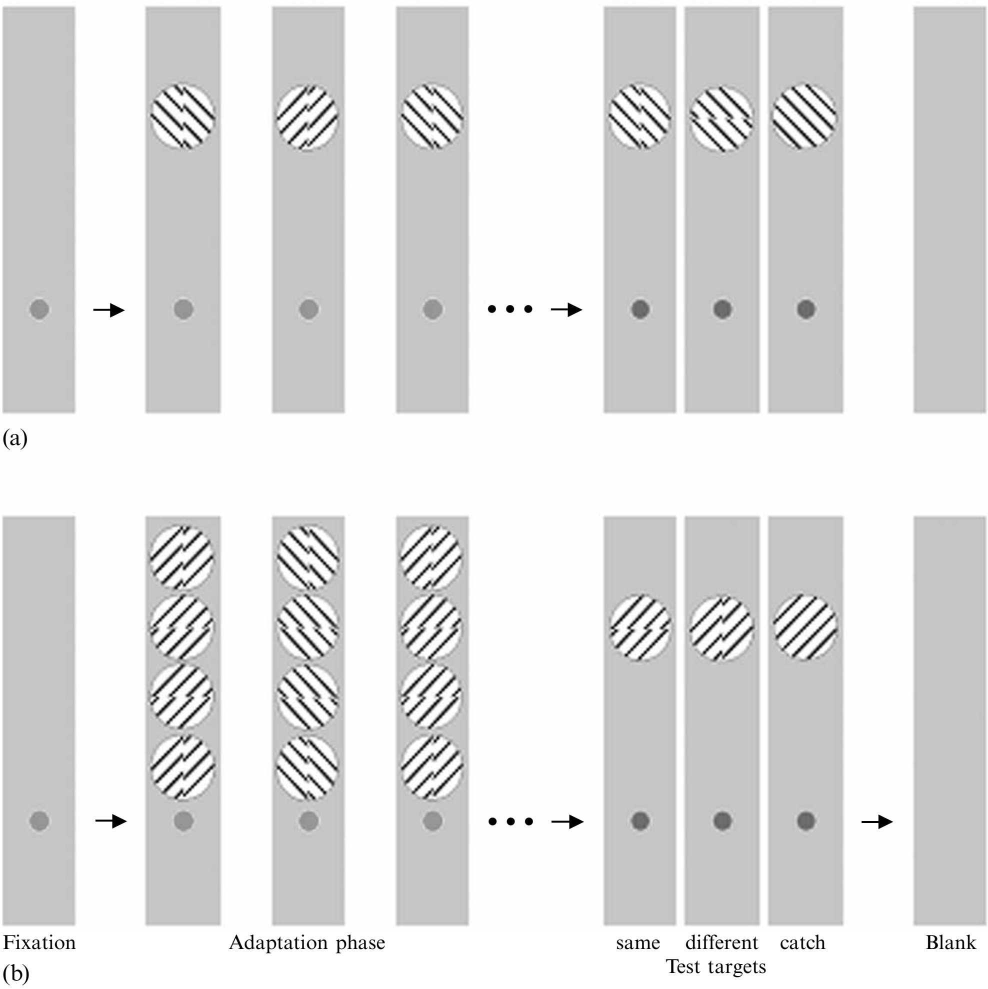

Figure 1. Experiment 1. Adaptation to non-crowded (a) and crowded (b) illusory lines. Each trial consisted of four phases: fixation, animation/adaptation, test target presentation, and blank presentation. Eight grating patches, whose orientations changed every 500 ms, comprised an animation in the adaptation phase in both crowded and non-crowded trials lasting for 4 s. Orientation of the test target illusory line was either the same as, or different from, that of the (spatially) corresponding adapting illusory line. In some trials (catch trials), the test target did not have any illusory line.

that turned to green in the test phase. Observers were asked to fixate on the fixation point, maintain their fixation through the trial, and report the orientation of the illusory line in the test patch (appearing in the periphery of their visual field) at the end of the trial.

Each adapting or test stimulus consisted of two line gratings (both oriented either at 45° or at 135°) abutting each other with a phase shift. There was an illusory vertical or horizontal border between the two sets of gratings in each grating patch. Each patch subtended 2.86 deg of visual angle and had four real lines with 0° tilt angle (angle between the two line gratings) and 0° lateral alignment (the amount of lateral misalignment between the two line gratings). Line spacing (distance between two lines in each grating) was 0.45 deg and line width was 0.11 deg.

In adaptation phase, the adapting target patch was either presented alone (non-crowded condition) or with flanking patches (crowded condition). In the crowded condition, there were three distractors—one above and the other two below the target. The eccentricity of the target patch in both conditions was 8.5° above the fixation point. Centre-to-centre distance between two adjacent patches in the radial array was 3 deg.

Since we intended to study the 'pure' adaptation to 'illusory' lines, orientation-specific adaptation of the 'real' grating lines had to be avoided as well as retinal adaptation. To rule out the effects of lower-level adaptations, an animated stimulus display was used in the adaptation phase. In this animation, the orientation of tilted real lines inside adapting target patch changed to the orthogonal orientation repeatedly (seven times in every 4 s of the adaptation phase) but the orientation of illusory lines remained the same (see figure 1). Real grating lines of distractor patches in the crowding trials also changed in the same way. The orientations of illusory lines of target and distractor patches (which were constant during animation period) were randomised across trials. As a result, there was no adaptation to tilted real lines while our stimuli could still induce the perception of illusory lines with constant orientations during the 4 s of adaptation phase so that the cells or synapses encoding illusory lines were adapted because there was no change in the location and orientation of illusory lines.

The test target patch was presented after the animated adaptation phase. It was placed at the same location as the adapting target patch (see figure 1). The orientation of the illusory line in the test target was either the same or different from that of the adapting orientation in the corresponding location. In one-third of the trials, which we called the 'catch trials', the test target patch had no illusory line (ie an oriented grating with no phase shift inside the patch). Subjects were asked to report the orientation of the illusory line (while fixating on the fixation dot) with one of the two alternative keys on the computer keyboard and not to respond when the catch stimulus was presented. As there was a prolonged gaze time during the experiment, subjects were allowed to interrupt the experiment (by pressing the 'escape' key on the keyboard) whenever they felt tired and then resume the experiment until the end of the block.

3.2 *Results*

The results for all subjects showed that orientation-specific adaptation to illusory lines was preserved when the target was crowded as well as when it was non-crowded. The percentage of correct responses for 'same adapt–test' condition—where adapting and test illusory lines had the same orientations—was lower than in the 'different adapt–test' condition in both crowded (χ^2 test, $p < 0.001$) and non-crowded (χ^2 test, $p < 0.001$) trials, showing that recognition of an illusory line is more difficult when the visual system is adapted to the same illusory orientation (see figure 2). Comparison

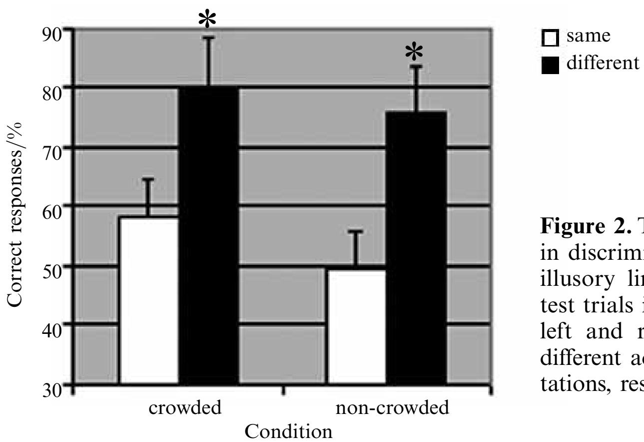

Figure 2. The percentage of correct responses in discrimination of the orientation of a test illusory line in same and different adapt–test trials in experiment 1. In each condition, left and right bars refer to the same and different adapting and test illusory line orientations, respectively. Bars represent ±1 SEM.

of adaptation indices (ie the percentage of correct responses to the 'different adapt – test' minus that to the 'same adapt – test' condition) between crowded and non-crowded trials did not show a significant difference (χ^2 test, $p = 0.15$), although adaptation was slightly stronger in non-crowded trials.

Subjects had three choices (vertical, horizontal, or 'catch-response') for reporting the orientation of the test illusory line of which only one was correct in each trial. The percentage of 'error catch-responses' (where subjects had mistakenly reported a non-catch trial as a catch one) was significantly higher in the 'same adapt – test' condition than in the 'different adapt – test' condition in both crowded and non-crowded trials (χ^2 test, $p < 0.05$). Figure 3 shows the distribution of 'error catch-responses' in non-catch trials.

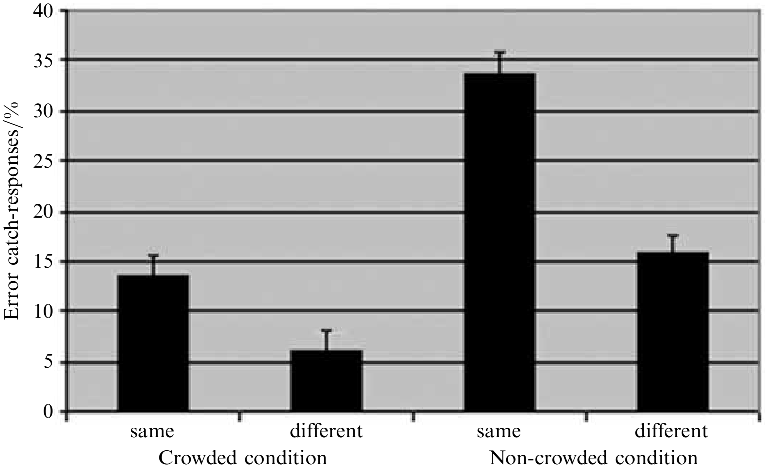

Figure 3. Distribution of 'error catch-responses' in non-catch trials. Bars represent ± 1 SEM.

'Same adapt – test' condition consisted of two states based on the orientation of the illusory line in adapting and test patches (either both vertical or horizontal). Similarly, 'different adapt – test' condition also consisted of two states (adapting vertical – test horizontal or vice versa). The percentage of correct illusory line orientation responses in each of these four states is shown in figure 4. In each state, the percentage of correct responses was approximately similar in the crowded and non-crowded conditions (χ^2 test, $p = 0.76$).

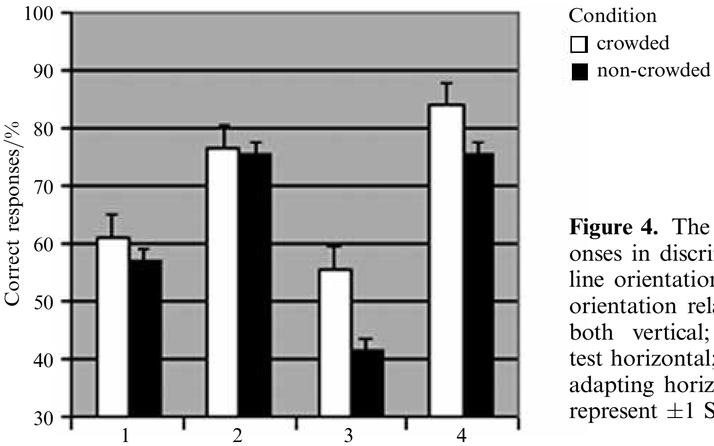

Figure 4. The percentage of correct responses in discrimination of the test illusory line orientation with respect to differential orientation relations: (1) adapting and test both vertical; (2) adapting vertical and test horizontal; (3) both horizontal; and (4) adapting horizontal and test vertical. Bars represent ± 1 SEM.

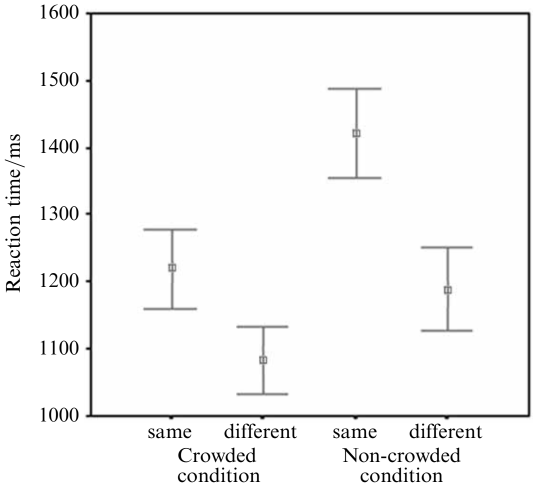

Figure 5. Plot of the reaction times in the four groups of data. Bars represent ±1 SEM.

Analysis of the reaction times was also consistent with the results of the percentage of correct data. As shown in figure 5, subjects had longer reaction times in 'same adapt–test' condition compared to 'different adapt–test' condition in both crowded and non-crowded trials (t-test, $p < 0.001$).

In the analysis of all catch trials (see figure 6), there were no tendencies for responses towards horizontal or vertical orientation and there was no significant difference between horizontal and vertical responses (χ^2 test, $p > 0.05$).

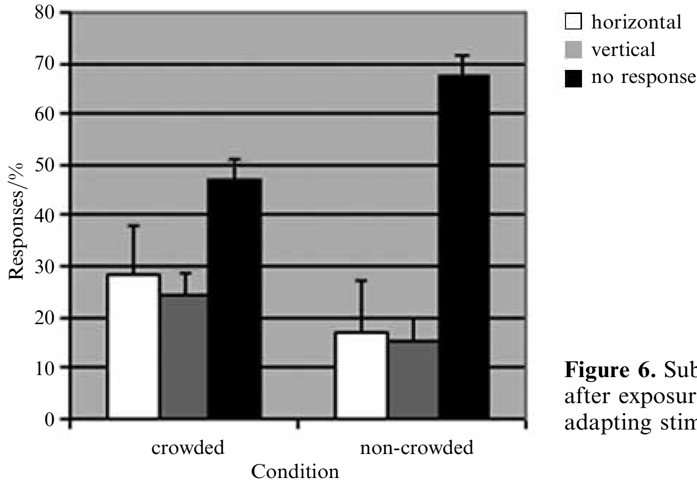

Figure 6. Subjects' responses to catch trials after exposure to crowded or non-crowded adapting stimuli. Bars represent ±1 SEM.

4 Experiment 2

4.1 *Methods*

In order to ensure that in crowded trials the orientation of the illusory line in the target patch was completely crowded (ie subjects were at chance level), the magnitude of crowding of illusory lines in adapting target patches was measured in the second experiment. Three distractors, one above and two below, were added to the target patch in crowded trials. The eccentricity of the target from the fixation and the distance between centres of the patches were the same as in experiment 1 (see figure 7). To ensure severe crowding, subjects were allowed to view the crowded stimuli for 4 s.

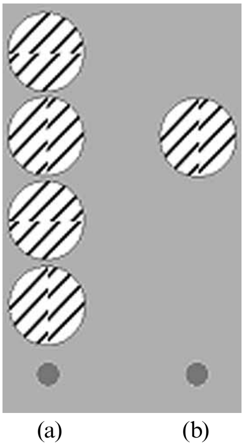

Figure 7. Examples of crowded (a) and non-crowded (b) stimuli used in experiment 2. Illusory lines were maintained crowded by adding three adjacent distractors around the target.

The remaining details were the same as in experiment 1 except that no test stimulus was presented here. Animation paradigm was also used during the 4 s of stimulus presentation. Subjects had to report the orientation of the illusory line in the target patch.

4.2 *Results*

The results of this experiment demonstrated a robust crowding effect for our stimulus arrangement. Performance of the subjects in discriminating the orientation of the target illusory lines dropped to chance level in crowded trials and the difference between performances in crowded and non-crowded trials was significant (χ^2 test, $p < 0.001$). Performance in crowded trials was not significantly above chance level (χ^2 test, $p > 0.05$). Figure 8 shows the percentage of correct responses in each condition (crowded versus non-crowded).

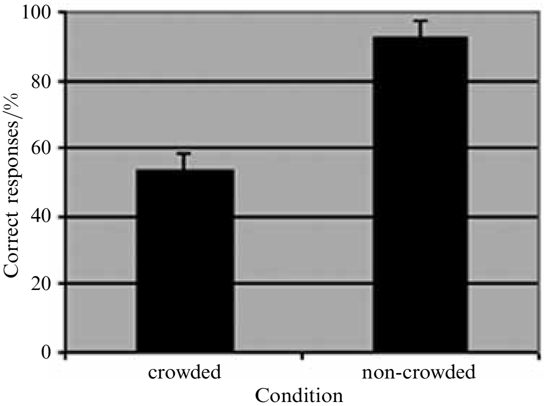

Figure 8. The percentage of correct responses in orientation discrimination of illusory lines in crowded and non-crowded conditions in experiment 2. Subjects responded to crowded targets at approximately chance level even with a long exposure time. Bars represent ±1 SEM.

5 Experiment 3

5.1 *Methods*

One may conclude that the difference between performances in the same and different adapt – test trials in experiment 1 is due to adaptation to endpoints of real lines at the location where the grating lines abut. To rule out this possibility, we weakened the induction of illusory lines, rearranging the real lines by changing the running direction at the location where the grating lines abut. In this way, the number of endpoints as well as the magnitude of the phase shift were not altered (see figure 9), yet it was more difficult to perceive the orientation of the illusory lines. If orientation-specific adaptation to illusory lines was attenuated by this rearrangement, we could conclude

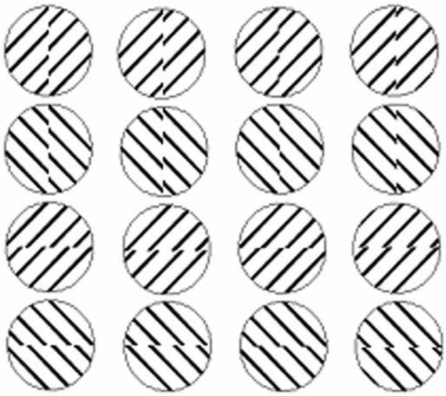

Figure 9. Four categories of stimuli used in experiment 3. Phase shifts in categories 1 and 2 were similar. Phase shifts in categories 3 and 4 were also similar but smaller than in categories 1 and 2. Categories with equal phase shift differed only in the running direction at the location where the grating lines abut. Each row of stimuli (a, b, c, and d) represents an illusory line orientation (horizontal or vertical) with a specific grating orientation (45° or 135°).

that there is a positive correlation between illusory-line perception and adaptation to illusory lines in the stimuli used in our experiments.

As shown in figure 9, stimuli in categories 1 and 2 had an equal phase shift. Note that stimuli used in experiment 1 belonged to category 2. These two categories were different in their arrangement of real lines. To show that this type of rearrangement weakened the visibility of illusory lines in the periphery, its effect on illusory line perception was tested for another phase shift. Categories 3 and 4 in figure 9 had a similar phase shift (less than that of stimuli in categories 1 and 2) and an equal number of endpoints but differed in their arrangement of real lines. To show that different categories of line arrangements induced illusory lines of different perceptual strength, subjects' ability to discriminate illusory line orientations was initially measured for each category of stimuli separately. In each trial, one grating patch containing an illusory line was presented in the periphery (in the same eccentricity as the target patch in the previous experiments) for 580 ms. Subjects had to discriminate the orientation of the illusory line. Orientations of the grating lines in each patch did not provide a clue for the subject since any orientation of the grating lines (45° or 135°) could have induced either of the two alternative illusory line orientations (vertical or horizontal) in a random fashion (see figure 9). In the second step of this experiment, we tested orientation-selective adaptation to illusory lines in the non-crowded condition using the four stimulus categories described above as adapting stimuli. The stimuli used in experiment 1 were used as test stimuli and the adaptation method was the same as that in experiment 1.

5.2 *Results*

As shown in figure 10, stimulus category 2 resulted in higher percentage of correct responses in discriminating illusory line orientation and induced the strongest perception of an illusory line. Performance of categories 2 and 4 was significantly better than that of categories 1 and 3, respectively (χ^2 test, $p < 0.05$), with no significant difference between categories 2 and 4. In line with our findings, Soriano et al (1996) demonstrated earlier that phase manipulation in abutting gratings was an important factor affecting the illusory line perception. The better illusion induction for category 2 in comparison to category 1, and also for category 4 in comparison to category 3, could be explained by the fact that there are four 'misaligned' endpoints in categories 2 and 4 but only three in categories 1 and 3, the total number of endpoints being equal in all categories (see note in figure 9).

Stimulus category 1 did not show any orientation-specific adaptation to illusory lines (see figure 11), while it was shown in experiment 1 that stimulus category 2 had a robust adaptation to illusory lines.

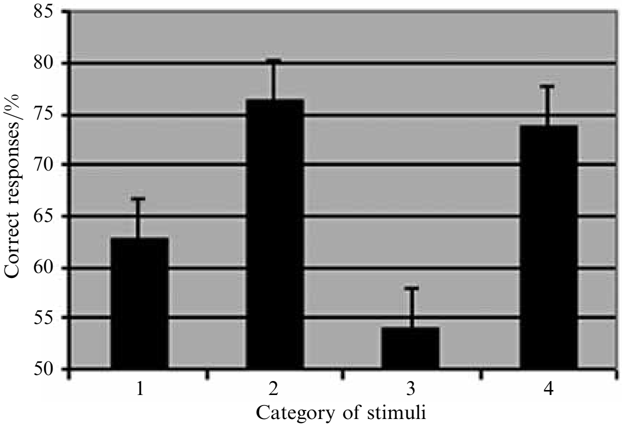

Figure 10. The percentage of correct orientation discrimination of illusory lines in the four stimulus categories of experiment 3. The best performance was observed for category 2. Bars represent ± 1 SEM.

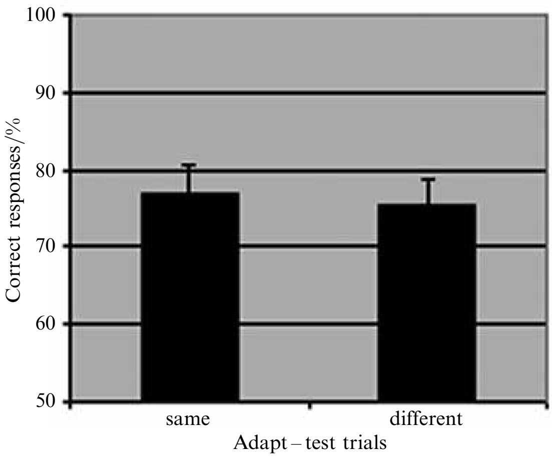

Figure 11. The percentage of correct responses in non-crowded same adapt – test and different adapt – test trials when category 1 stimuli were used as the adapting stimuli. Bars represent ± 1 SEM.

We defined 'adaptation index' (AI) as the difference between the percentage of correct responses in 'different adapt – test' trials (DAT) and that in 'same adapt – test' trials (SAT).

$$\text{Adaptation Index} = \text{DAT} - \text{SAT} .$$

AI was calculated for the four categories of stimuli with the following results: AI (category 1) $= -1.66$; AI (category 2) $= 26.15$; AI (category 3) $= -2.48$; AI (category 4) $= 15.12$.

There was a significant positive correlation between the percentage of illusory line perceptions and AI for different categories of stimuli (Pearson correlation coefficient $r = 0.924$; t-test, $p < 0.05$) (figure 12).

6 Experiment 4

6.1 *Methods*

Orientation of the illusory line in the test stimulus was different from that in the adapting stimulus in 'different adapt – test' adaptation trials of experiments 1 and 3, and this changed the configuration of the endpoints at the time of test stimulus presentation. One might argue that this change could have acted as a clue for discriminating the orientation of the illusory lines and provided an uncontrolled source of bias in our experiments, thus leading to better performance in 'different adapt – test' trials without

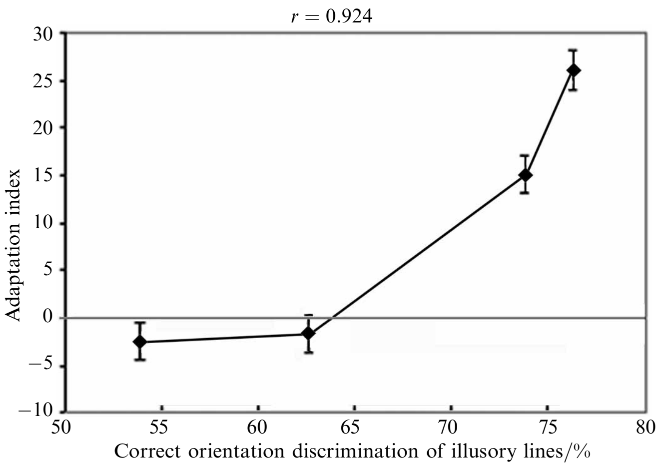

Figure 12. Correlation between the percentage of correct orientation discrimination of illusory lines and adaptation index in experiment 3. Adaptation index was defined as the difference between the percentage of correct responses in different and same adapt – test trials. Bars represent ± 1 SEM.

there really having been any adaptation. Therefore we performed a control experiment to ensure that the better performance in 'different adapt – test' trials was not due to change in the configuration of endpoints.

To account for the effect of such bias, we performed an orientation-discrimination experiment at the same eccentricity as that used in the previous experiments by presenting a test target after brief presentation of the pre-test stimulus. The test target and pre-test stimuli were exactly the same abutting gratings as those described in experiment 1. The illusory line orientation of the test target stimulus was either same as, or different from, that of the pre-test stimulus. As in experiment 1, in one-third of the trials, the so-called catch trials, the test target had no illusory line. The pre-test and test target stimuli were presented for 500 and 580 ms, respectively. Subjects had to report the orientation of the test illusory line. In this condition, there was no visual adaptation because the pre-test stimulus was presented for a short time only.

6.2 *Results*

As shown in figure 13, performance of the subjects in discrimination of the orientation of the test illusory line did not show an improvement in the rapid-change condition, with no significant difference between performances of subjects in the rapid-change and no-change conditions (χ^2 test, $p > 0.05$).

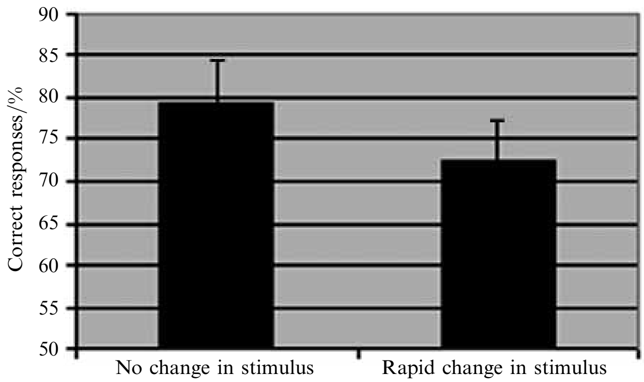

Figure 13. The difference between the percentages of correct responses in rapid-change and no-change conditions in experiment 4 was not significant. Bars represent ± 1 SEM.

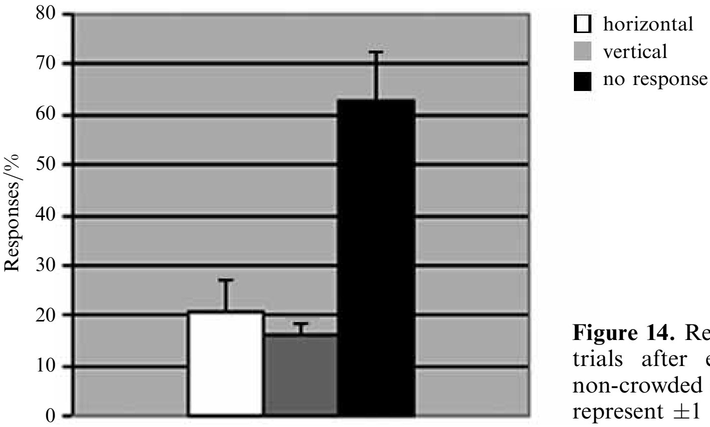

Figure 14. Responses of subjects to catch trials after exposure to non-adapting/non-crowded stimuli in experiment 4. Bars represent ± 1 SEM.

We found no-response tendencies towards horizontal and vertical orientations in the analysis of catch trials with non-adapting stimuli (see figure 14), and the percentage of 'horizontal' responses (though slightly higher) was not significantly different from that of 'vertical' responses in catch trials (χ^2 test, $p > 0.05$).

7 Discussion

The results of experiment 1 clearly demonstrated that orientation-selective adaptation to illusory lines is preserved even when there is no evidence of conscious access to it. Such an adaptation occurs efficiently both in the crowded and in the non-crowded conditions. Adaptation to real lines could mimic the results of adaptation to illusory ones; therefore lower-level adaptations (eg in LGN or V1) were bypassed by using an animation paradigm during adaptation period, and adaptation to endpoints of real lines still remained at the locations where the grating lines abutted. As experiment 3 showed, even such adaptation to endpoints, occurring probably in V1, could not be responsible for the adaptation to illusory lines.

The two orientations of the real lines alternated during the animation period, so adaptation to one orientation would accumulate with each alternation. This average adaptation develops in time and may cause lower-level adaptations to remain. Since this alternation occurs for two orthogonal orientations, opponent inhibitory interactions among neuronal populations in the primary visual cortex responding to those orientation signals prevent any such average adaptation.

Our results also revealed that adaptation to illusory lines could not be explained by a rapid change in stimulus presentation and the configuration of the endpoints. There was no response bias for different orientations, so the results of adaptation to illusory lines could not have been produced by the response bias of the subjects either.

Adaptation to illusory lines could be due to repeated firing of neurons or neuronal populations in response to illusory contours (abutting gratings) presented at their preferred orientation for a long exposure time (4 s in our experiments). Continuous neural firing decreases the orientation sensitivity maximally at the adapting orientation. In a significant portion of adaptation trials the test illusory line faded and the test patch looked as a grating patch without an illusory line.

Our findings are consistent with two important conclusions:

(i) Assuming a feedforward manner for visual information processing where area V2 is the first area involved in the detection of illusory lines (Peterhans et al 1982; von der Heydt et al 1984), we could conclude that crowding effect occurs after processing of illusory contours in some area higher than V2.

(ii) Since cortical area V2 is considered to be the first area involved in the processing of illusory lines, preservation of the adaptation to crowded illusory lines suggests that at least area V2 could be activated by a stimulus feature (illusory line orientation, as is in our study) when there is no conscious perception of that feature. Therefore, activation of V2 neurons is not strictly correlated with conscious perception.

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