

## Adaptation to apparent motion in crowding condition

Reza Rajimehr<sup>a,\*</sup>, Maryam Vaziri-Pashkam<sup>a</sup>, Seyed-Reza Afraz<sup>a,b</sup>, Hossein Esteky<sup>a,b</sup>

<sup>a</sup> School of Cognitive Sciences (SCS), Institute for Studies in Theoretical Physics and Mathematics (IPM), Niavaran,  
P.O. Box 19395-5746, Tehran, Iran

<sup>b</sup> Research Laboratory for Brain and Cognitive Sciences, Shaheed Beheshti University, Tehran, Iran

Received 17 April 2003; received in revised form 17 October 2003

### Abstract

Visual adaptation has been successfully used for studying the neural activity of different cortical areas in response to visual stimuli when observers do not have explicit conscious access to those stimuli. We compared the orientation selective adaptation to apparent motion and its effect on the perception of stimuli with bistable apparent motion in crowded and non-crowded conditions. In the crowding paradigm conscious access to a visual stimulus is severely impaired when it is flanked by other similar stimuli in the peripheral visual field. As expected, adaptation to the target stimulus occurred in the non-crowded condition in all of the individual subjects ( $n = 4$ ;  $P < 0.001$ ). Although in the crowded condition subjects were not able to discriminate the target stimulus, adaptation to that stimulus was still preserved ( $P < 0.001$ ). There was no significant difference between the adaptations in the two conditions of the apparent motion ( $P > 0.05$ ). Imaging studies have shown that V5 cortex is the earliest visual area that specifically responds to apparent motion. Our results suggest that in certain conditions V5 may be activated while there is no explicit conscious access to the apparent motion.

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**Keywords:** Apparent motion; Crowding; Adaptation; Awareness

### 1. Introduction

Motion is one of the most important visual attributes, which is processed in multiple levels of visual hierarchy. In some special conditions we perceive motion in a visual scene where there is no physical movement. For example, if two stimuli are briefly flashed in rapid succession, with appropriate spatial and temporal displacements, observers will report seeing an *illusory motion* between the two stimuli. This perceptual phenomenon is called apparent motion. Neurophysiological and imaging studies have shown that higher visual areas are involved in the processing of this kind of illusory motion (Goebel, Khorram-Sefat, Muckli, Hacher, & Singer, 1998; Kaneoke, Bundou, Koyama, Suzuki, & Kakigi, 1997; Kawakami, Kaneoke, & Kakigi, 2000; Mikami, 1991; Mikami, Newsome, & Wurtz, 1986; Newsome, Mikami, & Wurtz, 1986).

An important question is whether illusory moving stimuli can modulate the functional properties of such higher areas in the absence of explicit conscious perception of those stimuli.

To address this question, we measured orientation selective adaptation to the apparent motion in a *crowding* paradigm. Crowding effect is a phenomenon in which existence of similar visual distractors near the target stimulus in the peripheral visual field impairs explicit conscious access of the observer to that stimulus (Toet & Levi, 1992; Wilkinson, Wilson, & Ellemberg, 1997). Our main question was whether orientation selective adaptation to apparent motion is preserved when the adapting stimulus is flanked by crowding distractors. The preservation of adaptation under crowding and without explicit conscious perception of the apparent moving stimulus imply that, at least the first cortical area involved in the processing of apparent motion can be activated while the observer is not aware of that stimulus.

To study the orientation selective adaptation to apparent motion, we used *motion quartet*, a bistable apparent motion stimulus for which either a horizontal

\* Corresponding author. Tel.: +98-21-2294035; fax: +98-21-2290151.

E-mail address: [rajimehr@ipm.ir](mailto:rajimehr@ipm.ir) (R. Rajimehr).

or vertical motion pattern can be perceived. Kruse, Stadler, and Wehner (1986) have shown that prolonged presentation of a stimulus with a specific orientation of apparent motion adapts the subject's perception. In such conditions subjects see a motion quartet (test stimulus) moving in the opposite orientation compared to the adapting stimulus.

We compared orientation selective adaptation to apparent motion in crowded and non-crowded conditions. The crowding paradigm was designed with multiple distractors, which severely impaired the orientation discrimination in the adapting stimulus and dropped the subject's performance to the chance level. In addition, to investigate the pure effect of apparent motion on the perception of the test stimulus compared to possible effects of other visual patterns in the stimuli, *flicker stimuli* were used during the adaptation period as a control condition (see Section 2.4 for details).

## 2. Methods

### 2.1. Subjects

Four subjects, three males and one female, aged between 24 and 32 years, participated voluntarily in the experiment. All subjects were trained psychophysical observers with normal or corrected-to-normal vision. They, however, were naive with respect to the purpose of the experiment.

### 2.2. Apparatus

The stimuli were programmed in Delphi V.6, on a Pentium III 800 MHz PC. Images were displayed on a RGB color monitor, 800H×600V pixel resolution, 60 Hz frame rate (795FT Plus, LG: Korea). The subjects were placed in a dark room with their heads fixed on a chin and forehead rest. They viewed the displays binocularly. The distance between eyes and the monitor screen was 50 cm. Data was analyzed using SPSS V.11.

### 2.3. Stimuli

Each stimulus was a horizontal or vertical rectangular patch  $2.28 \times 1.14^\circ$  in size. They were embedded in a light gray background containing circular black spots  $0.17 \times 0.17^\circ$  in size, flashing in specific locations. According to the temporal and spatial displacements of the spots inside the patches we had three types of stimuli (see Fig. 1).

#### 2.3.1. Apparent moving stimuli

In the *apparent moving stimuli* two spots appeared for 200 ms in two adjacent corners of an imaginary rectangular frame inside a dark gray patch. Immediately

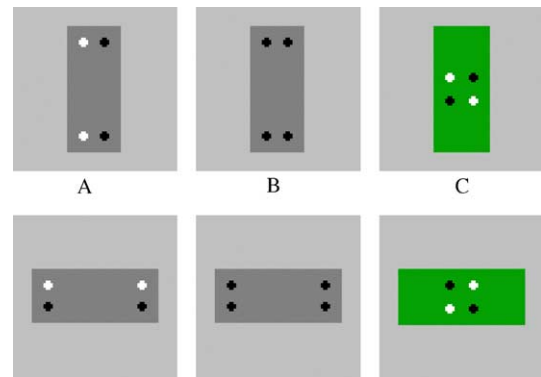


Fig. 1. Stimuli used in this study. (A) Apparent moving stimuli in which two spots appeared in one side of an imaginary rectangular frame inside the horizontal or vertical dark gray patch in a light gray background, these spots disappeared, and immediately two other spots were presented in the other side of the imaginary rectangle. (B) Flicker stimuli in which four circular black spots were located in four corners of an imaginary rectangle inside a horizontal or vertical dark gray patch in a light gray background. These spots repeatedly disappeared and reappeared in the same locations. (C) Motion quartet stimuli in which two spots appeared in two opposite corners of an imaginary square, inside the center of horizontal or vertical rectangular green patch, then disappeared and immediately reappeared in two other opposite corners. The black and white spots indicate the spot positions on successive frames. (For interpretation of the references in colour in this figure legend, the reader is referred to the web version of this article.)

after the spots disappeared two other spots were presented in the other corners of the imaginary rectangle for 200 ms. This alternation continued with the frequency of 2.5 Hz. The imaginary rectangle was  $2.06 \times 1.03^\circ$  in size. It lied vertically in the vertical patch and horizontally in the horizontal patch. The orientation of the apparent motion was either horizontal or vertical.

This type of stimulus was used as adapting stimulus in the adaptation phase of our experiment (Section 2.4). We used apparent motion in a rectangular frame instead of a square frame in order to enhance the adaptation effect of the apparent motion (Hock, Schoner, & Hochstein, 1996).

#### 2.3.2. Motion quartet

In the *motion quartet* stimuli two spots appeared for 200 ms in two opposite corners of an imaginary square ( $1.03 \times 1.03^\circ$  in size), inside the center of a rectangular green patch. Then the spots disappeared and immediately reappeared in two other opposite corners of the motion quartet for 200 ms. This alternation continued with the frequency of 2.5 Hz. The motion in this type of stimulus can be seen as two pairs of horizontally or vertically moving spots. The motion quartet was used as test stimulus in our experiment (see Section 2.4).

The dark gray patches in the adapting stimuli and green patches in the test stimuli were isoluminated using

*heterochromatic flicker photometry* (Ives, 1912; Wagner & Boynton, 1972).

### 2.3.3. Flicker stimuli

In the *flicker stimuli* four spots were presented in four corners of an imaginary rectangle inside a horizontal or vertical dark gray rectangular patch. These spots disappeared and reappeared in the same locations with the frequency of 2.5 Hz. The size of spots, patch and imaginary rectangle were similar to those in the apparent moving stimuli. This type of stimulus was used in the adaptation phase of the control condition (see Section 2.4).

### 2.4. Procedure

Each trial of the experiment contained two phases: *adaptation phase*, and *test phase*. The adapting stimulus was a crowded or non-crowded apparent moving stimulus, which was randomly distributed in each experimental block. In non-crowded trials the adapting target stimulus was presented alone, 11.3° above the fixation point. In crowded trials an additional 14 apparent moving stimuli (distractors) were presented around the adapting target stimulus (see Fig. 2). The distractors orientations of motion were selected randomly. The border-to-border distance of the stimulus patches was 0.28°. The test stimulus was a motion quartet at the location of the adapting target stimulus, which appeared after the adapting stimulus without any delay. The color of adapting and test patches was different (gray and

green, respectively) to cue subjects about the initiation of test phase (note that, especially for non-crowding trials it is difficult for the viewer to find out when the test phase is started). The duration of the adaptation phase and the test phase were 5 and 1.2 seconds, respectively.

In each trial subjects were asked to fixate at a small red circle (fixation point) in the middle of the display, and give two responses: one in the adaptation phase and another in the test phase. In the adaptation phase subjects had to report the orientation (horizontal or vertical) of apparent motion in the target stimulus (anytime during this phase) by pressing one of two buttons on a computer keyboard with the index and the middle finger of their right hands. In the test phase they had to report the perceived orientation of the motion quartet by pressing one of two other buttons on the computer keyboard with the index and the middle finger of their left hands. A *two-alternative forced-choice* (2AFC) procedure was used in both phases.

Each experimental block contained 50 trials with a 2 second inter-trial interval. Each subject was trained with one experimental block and was tested with 12 experimental blocks, six blocks with horizontal patches and six blocks with vertical patches (see Fig. 2). The subjects were instructed and trained about the location of the target in the crowding display.

It is possible that orientation of the dark gray patch and that of the imaginary frame of the apparent motion affect the subjects' judgment about the orientation of the motion quartet. To rule out this possibility a control experiment was designed. In this control experiment a flicker stimulus, either crowded or non-crowded, was presented in the adaptation phase at the same location as the target stimulus for 5 s. Apparent moving stimuli were used as distractors in the crowded condition like the main experiment. The adapting flicker stimulus was followed by a motion quartet in a test phase, quite the same as the previous experiment. Subjects had to report the perceived orientation of the motion quartet in the test phase.

### 3. Results

The data collected from the responses of the subjects in the adaptation phase were used to compare visibility of the target stimulus in crowded and non-crowded conditions. As Fig. 3 shows, there was a robust crowding during the adaptation phase in crowded trials so that the subjects' performance dropped to the chance level in these trials. The percent corrects of the subjects were significantly better in non-crowded conditions compared with crowded conditions for both vertical and horizontal patches separately ( $p < 0.0001$ ,  $\chi^2$  test). The performance of the subjects in crowded trials was not

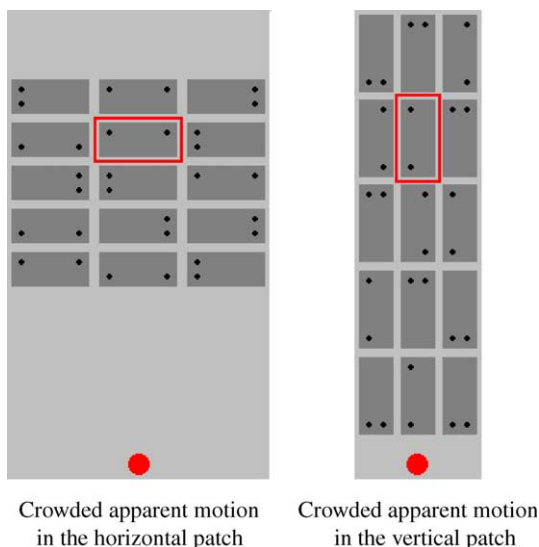


Fig. 2. Apparent moving stimuli in the crowded condition. Fourteen distractors were added to the display around the adapting target stimulus (the red rectangle around the target stimulus is only for illustration purpose). (For interpretation of the references in colour in this figure legend, the reader is referred to the web version of this article.)

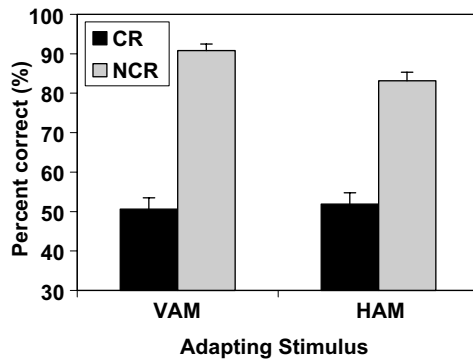


Fig. 3. Bars represent orientation discrimination performances in crowded (CR) and non-crowded (NCR) conditions. VAM: adapting vertical apparent motion inside the horizontal patch, and HAM: adapting horizontal apparent motion inside the vertical patch. Error bars represent one standard error of mean.

significantly above the chance level for both vertical and horizontal patches ( $P > 0.05$ ,  $\chi^2$  test).

The data collected from the test phase were used to measure the amount of orientation selective adaptation in the crowded and non-crowded trials. Hock et al. (1996) have shown that adaptation to apparent motion stimuli enhances by increasing aspect ratio of the moving spots. The aspect ratio is defined as the distance between the two spots in one side of an imaginary rectangle divided by the range of the apparent motion. Thus, in order to achieve the optimal adaptation to apparent motion, only trials in which the adapting target stimulus moved vertically in horizontal rectangular patches (aspect ratio = 2), and the trials with horizontal apparent motion in vertical adapting target patches (aspect ratio = 2) were analyzed. The other two conditions with “aspect ratio = 1/2” were excluded.

To measure the amount of the adaptation we defined the *adaptation index* as

$$\text{Adaptation index} = D/T \times 100$$

where  $D$  was the number of trials in which the perceived orientation in the motion quartet was *different* from the orientation of the apparent motion in the target apparent moving stimulus and  $T$  was the total number of trials.

The adaptation index in both crowded and non-crowded conditions of selected apparent moving stimuli with “aspect ratio = 2”, was significantly above 50% ( $P < 0.001$ ,  $\chi^2$  test) (see Fig. 4). This means that subjects preferred to perceive the orientation in the motion quartet, opposite to that in the target apparent moving stimuli. There was no significant difference between the adaptation indices in the two crowded and non-crowded conditions ( $P > 0.05$ ,  $\chi^2$  test).

There was no significant adaptation in the data collected from the control experiment with adapting flicker stimuli (either with horizontal patches or vertical pat-

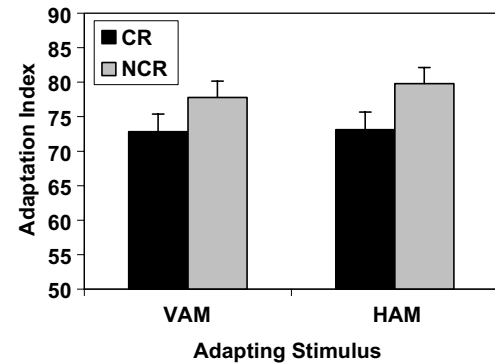


Fig. 4. Adaptation index for crowded (CR) and non-crowded (NCR) adapting stimuli. Error bars represent one standard error of mean.

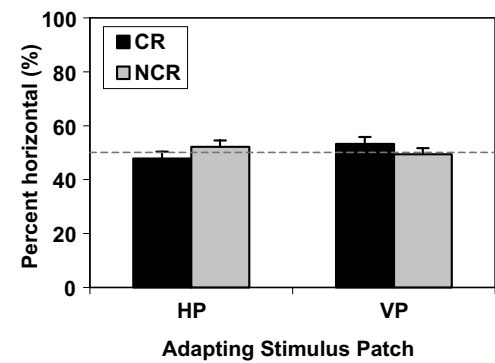


Fig. 5. Results of control experiment with flicker adapting stimuli for horizontal patches (HP) and vertical patches (VP). Perceived orientation of motion quartet in the test phase was shared equally between horizontal and vertical orientations in both crowded and non-crowded conditions. Error bars represent one standard error of mean.

ches). Subjects reported horizontal and vertical orientations for the motion quartets equally ( $P > 0.05$ ,  $\chi^2$  test) after 5 s of presenting flicker stimuli in crowded or non-crowded conditions (see Fig. 5).

#### 4. Discussion

The results of the main experiment showed that adaptation to apparent motion was preserved in crowded as well as non-crowded conditions. As explained previously we did not use apparent moving stimuli in the usual square frame (“aspect ratio = 1”). Instead, we used a rectangular frame. In this way, half of the stimuli had “aspect ratio = 2” and half of them had “aspect ratio = 1/2”, and we included only stimuli with “aspect ratio = 2” in the analysis to have a strong adaptation. Therefore we selected trials with vertical apparent motion from the blocks with horizontal patches and trials with horizontal apparent motion from the blocks with vertical patches. Thereby, one could claim that the bias in the perception of motion quartet measured in the

main experiment may be caused by the orientation of dark gray rectangular patches in the adapting stimuli or the green rectangular patches in the test stimuli. Furthermore the spacing of the black spots inside the rectangular patches may induce perception of a horizontal or vertical imaginary rectangle, which can bias the perception of the test stimulus. In the control experiment (with flicker adapting stimuli) gray rectangular patches in the adaptation phase, green rectangular patches in the test phase and spacing of the black spots were the same as the selected trials of the main experiment. However there was no perceptual bias in the perception of the test stimulus in the control experiment. These results show that the adaptation in the main experiment is purely based on the apparent motion of the spots.

Earlier studies using the binocular rivalry paradigm demonstrated that information not available to the observers' awareness (because of rivalry suppression) could still induce or prime the perception of apparent motion (Blake, Ahlstrom, & Alais, 1999; Wiesenfelder & Blake, 1991). Wiesenfelder and Blake (1991) have shown that a long range displacement of a given spot can induce motion perception in a specific direction even when the initial location of the spot is invisible due to the suppression phase of binocular rivalry. Furthermore, using an ambiguous motion display, Blake et al. (1999) revealed that the direction of apparent motion can be effectively primed by a local real motion when the priming motion itself is suppressed from awareness by binocular rivalry. These studies indicate that mechanisms underlying apparent motion perception have access to the spatial location and real motion information while they are perceptually invisible. However, in both studies subjects had a clear perception of the apparent motion itself. Using the crowding paradigm, we pushed the apparent motion out of explicit conscious perception. Our results suggest that apparent motion information—by itself—could be registered in the visual system in the absence of awareness.

Crowding effect may be due largely to insufficient *spatial attentional resolution* (He, Cavanagh, & Intriligator, 1997). In consistence to this theory, there are some studies indicating that visual information of target and distractors in a crowding display are pooled together before they reach consciousness (Levi, Hariharan, & Klein, 2002; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). He, Cavanagh, and Intriligator (1996) have studied orientation selective adaptation in the crowding condition to show that crowding is a high-level phenomenon, which occurs at the level of *attentional selection* not at an early *sensory* level. In their experiments they asked the human observers to report the orientation of a single grating in the periphery of their visual field while it was flanked by other similar gratings. In this crowding condition the observers are no longer aware of the orientation of the target stimulus.

However, the orientation-specific adaptation (a V1 phenomenon) is not affected by crowding. Their results suggest that crowding happens at areas higher than the site of adaptation (V1) in the visual stream. Using the same logic, adaptation to apparent motion in the crowding condition leads us to suggest that crowding effect also occurs at a stage later than the first cortical area involved in the apparent motion detection.

However, there are also other theories that interpret crowding in the term of ordinary lateral masking (Mansfield, Legge, & Ortiz, 1998; Townsend, Taylor, & Brown, 1971; Wolford & Chambers, 1984). These theories imply that visual information of a crowded target is blocked in the early sensory level by flankers. Our finding that crowding cannot impair adaptation to the apparent motion provides further evidence for the idea that crowding is not an ordinary masking and under severe crowding, the information of apparent motion can reach higher visual areas responsible for apparent motion detection.

Another important point which should be considered is the possible role of attention in relation to our findings. It has been shown that attention is required for apparent motion perception (Battelli et al., 2001; Verstraten, Cavanagh, & Labianca, 2000). At first glance, our results look inconsistent with this idea. Traditionally a close relationship is considered between attention and consciousness, so given that attention is necessary for apparent motion perception, how could we explain our results when subjects had no conscious access to the apparent motion stimulus? Two possible explanations could be proposed here: (1) although explicit perception of apparent motion may need attention, its detection and adaptation at the cellular level does not necessarily need attention. (2) There might be subliminal attentional modulation of the crowded target when it is not explicitly perceived. Consistently, a recent study (Montaser-Kouhsari and Rajimehr, unpublished data) shows that adaptation to a crowded target is attenuated when visual attention is drawn away from the crowding display.

Human motion complex (hMT+) or V5 cortex is involved in the processing of motion information (Tootell et al., 1995; Watson et al., 1993; Zeki, 1991; Zeki et al., 1991). There are some neurophysiological experiments implying that neuronal substrates for apparent motion processing are distributed over multiple cortical levels including early visual areas and middle temporal (MT) cortex (Mikami, 1991; Mikami et al., 1986; Newsome et al., 1986). These studies indicate that MT neurons are involved in the long-range (1.0° and more) apparent motion processing while neurons in the primary visual cortex have directional selective responses only to short-range (mainly around 0.5°) apparent motion. Imaging studies in humans confirm that V5 is the *first* area in the visual pathway, which responds to long-range apparent

motion (Goebel et al., 1998; Kaneoke et al., 1997; Kawakami et al., 2000). There is some recent evidence demonstrating the contribution of parietal regions to the apparent motion detection in the *bistable motion* displays (Battelli et al., 2001; Williams, Elfar, Eskandar, Toth, & Assad, 2003). It has been shown that attentional mechanisms have a critical role in the perception of bistable apparent motion (Cavanagh, 1992). Therefore, the involvement of parietal areas in the above-mentioned studies might be due to the attentional load of the task (not to apparent motion detection per se). Also another study by Zhuo et al. (2003) shows the activation of the anterior-temporal lobe corresponding to the interaction between apparent motion and shape of the stimuli. Taken together, it seems that V5 is the first site in the visual pathway which responds selectively to the direction of apparent motion. The fact that orientation selective adaptation to apparent motion occurs even when the adapting stimulus is pushed out of the explicit conscious perception in severe crowding implies that neural representation of apparent motion (probably in V5) does not necessarily require awareness. This result is consistent with the results obtained by Goebel, Muckli, Zanella, Singer, and Stoerig (2001). Their fMRI studies on hemianopic patients show that sustained V5 activation occurs without visual awareness.

Further studies are needed to explore the mechanisms and locus of high-level motion perception in crowding conditions.

## Acknowledgements

We wish to thank Patrick Cavanagh and two anonymous reviewers for their insightful comments on the manuscript. This work was supported by the School of Cognitive Sciences, Iranian Institute for Studies in Theoretical Physics and Mathematics (IPM), Tehran, Iran.

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