

Predictive feature remapping before saccadic eye movements

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Saccadic eye movements cause rapid and dramatic displacements of the retinal image of the visual world, yet our conscious perception of the world remains stable and continuous. A popular explanation for this remarkable ability of our visual system to compensate for the displacements is the predictive feature remapping theory. The theory proposes that, before saccades, the representation of a visual stimulus can be predictively transferred from neurons that initially encode the stimulus to neurons whose receptive fields will encompass the stimulus location after the saccade. Visual adaptation aftereffect experiments performed by Melcher (2007) provided psychophysical evidence for this theory. However, it was argued that the visual aftereffects were not measured at the “appropriate” remapped location (Rols, Jonikaitis, Deubel, & Cavanagh, 2011). Therefore, whether the remapped representation contains feature information (e.g., orientation, motion direction, or contrast) is still a subject of intense debate. Here, to explore the nature of the predictive transfer during trans-saccadic perception, we measured visual aftereffects (tilt aftereffect, motion aftereffect, and threshold elevation aftereffect) at the appropriate remapped location of adapting stimuli before saccades. We observed a significant tilt

aftereffect and motion aftereffect, but little threshold elevation aftereffect. Furthermore, the tilt aftereffect and motion aftereffect exhibited spatial specificity. These findings provide strong evidence for the predictive feature remapping theory and suggest that intermediate visual processing stages (i.e., extrastriate visual cortex) might be critical for feature remapping. Finally, we propose that the feature remapping process might also contribute to the spatiotopic representation of visual features.

Introduction

The visual system must rapidly update its internal representations of the visual world during saccades. One way to accomplish this is through predictive remapping (Milner & Reddy, 2003; Milner, Reddy, & Murray, 2001; Milner, Reddy, & Williams, 2000), which occurs before saccades (Milner, 1982), and another way is through post-saccadic recalibration (Mays & Young, 1991).

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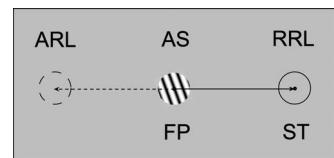


Figure 1. Appropriate remapped location of visual adaptor. In Melcher's study (2007), subjects adapted to a tilted grating presented at the initial fixation point. Then they were asked to make a saccade and judge the orientation of a test grating briefly presented at either the initial fixation point or the saccadic target location. According to Rolfs et al. (2011), the visual adaptor (i.e., the tilted grating) at the initial fixation point activates neurons that encode the adaptor's expected retinal location after the saccade. The remapping vector (dashed arrow) actually opposes the saccade vector (solid arrow). Therefore, the appropriate remapped location of the adaptor corresponds to the retinal position that the adaptor will have only following the saccade. FP: fixation point; ST: saccadic target; ARL: appropriate remapped location; AS: adapting stimulus; and RRL: reversed remapped location.

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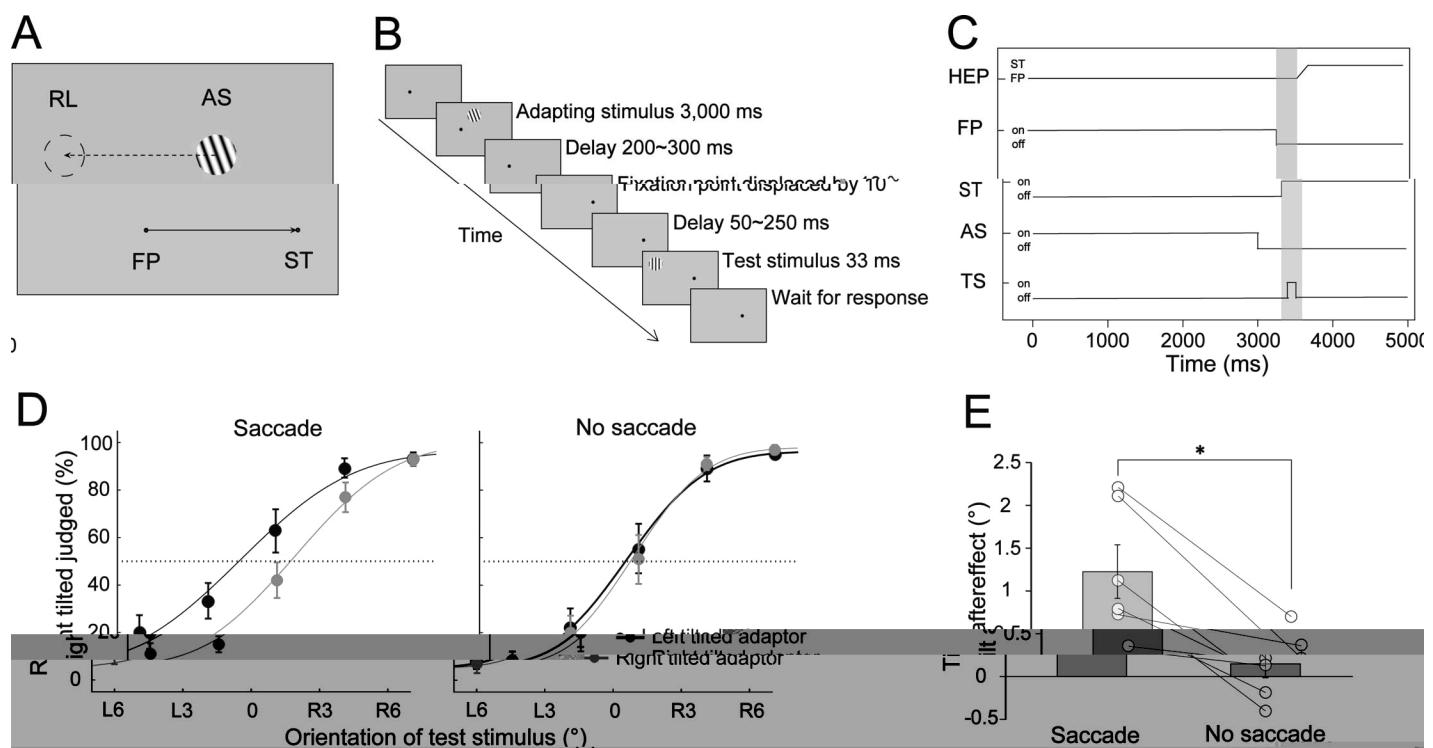
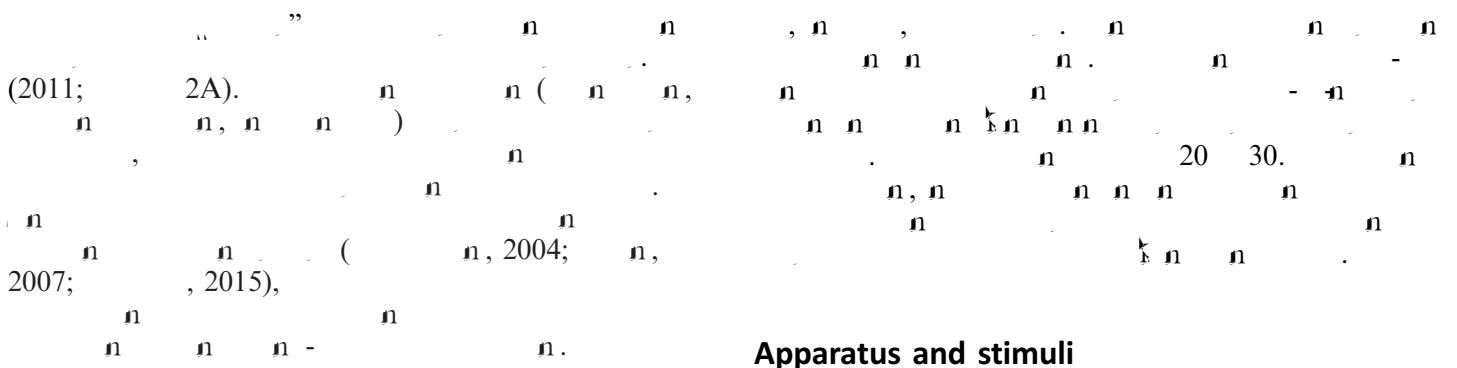


Figure 2. Stimuli, procedure, time course of events, and results in Experiment 1. (A) The spatial location and the remapped location of the grating adaptor. Subjects made a saccade from the fixation point to the saccadic target. The saccade direction and the remapping direction are shown by the solid arrow and the dashed arrow, respectively. Test stimuli were presented at the remapped location before saccades. (B) Schematic description of a trial for measuring the TAE. (C) Time course of events in a trial. RL: remapped location; HEP: horizontal eye position; FP: fixation position; ST: saccadic target; AS: adapting stimulus; and TS: test stimulus. (D) Psychometric functions showing orientation judgments after adapting to the left or right tilted adaptor. The abscissa refers to the orientation of test stimuli. L and R indicate that a test stimulus was left or right tilted. The ordinate refers to the percentage of trials in which subjects indicated that a test stimulus was right tilted. (E) TAE magnitudes in the saccade and no-saccade conditions. Data are plotted for each subject (lines and circles) as well as the group means (bars). The asterisk indicates a statistically significant difference between the two conditions (* $p < 0.05$). Error bars denote 1 SEM calculated across subjects for each condition.



Methods

Subjects

Twenty-four subjects participated in the study. Thirteen subjects were female and eleven were male. Their ages ranged from 18 to 26 years. All subjects had normal or corrected-to-normal vision and gave informed consent to participate in the experiment.

Apparatus and stimuli

The experiments were conducted in a dark room. A 17-inch CRT monitor (EIZO ColorEdge CG2176) was used to display the stimuli. The resolution of the monitor was set to 1024 × 768 pixels. The distance between the monitor and the subjects was approximately 60 cm. The subjects were seated in a comfortable chair with their head supported by a chin rest. A chin rest was used to ensure that the subjects' heads remained stable during the experiments. The subjects' eyes were aligned with the center of the monitor. A camera was positioned above the monitor to record the subjects' eye movements. The subjects' horizontal eye position (HEP) was recorded at 100 Hz using a high-resolution camera (Photron FASTCAM SA5). The subjects' vertical eye position (VEP) was recorded at 100 Hz using a low-resolution camera (Photron FASTCAM SA5).

$$\begin{aligned}
 & \frac{n}{n} - \frac{n}{n} = 10 \quad \frac{k}{k} = 40 \quad \left(\frac{n}{n} \right) \frac{k}{k} \\
 & \frac{n}{n} - \frac{n}{n} = 2 \quad \frac{k}{k} = \frac{n}{n} \quad 2-A_C
 \end{aligned}$$

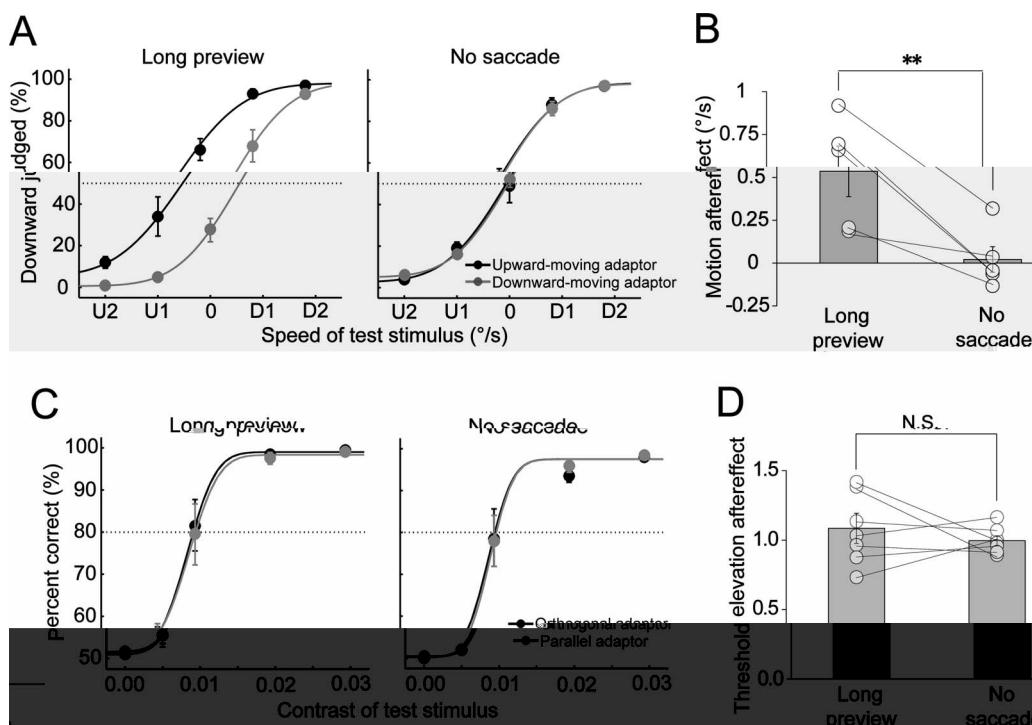


Figure 4. Results of Experiments 3 and 4. (A) Psychometric functions showing motion direction judgments after adapting to the upward- or downward-moving adaptor. The abscissa refers to the direction of test stimuli. U and D indicate that a test stimulus moved upward or downward. The ordinate refers to the percentage of trials in which subjects indicated that a test stimulus moved downward. (B) MAE magnitudes in the long-preview and no-saccade conditions. (C) Psychometric functions showing contrast detection performance after parallel or orthogonal adaptation. (D) TEAE magnitudes in the long-preview and no-saccade conditions. Data are plotted for each subject (lines and circles) as well as the group means (bars). Asterisks indicate a statistically significant difference between two conditions (** $p < 0.01$). Error bars denote 1 SEM calculated across subjects for each condition.

Data analysis

Results

Experiment 1: Predictive remapping of orientation before saccade

$t(5) = 3.92, p < 0.01$

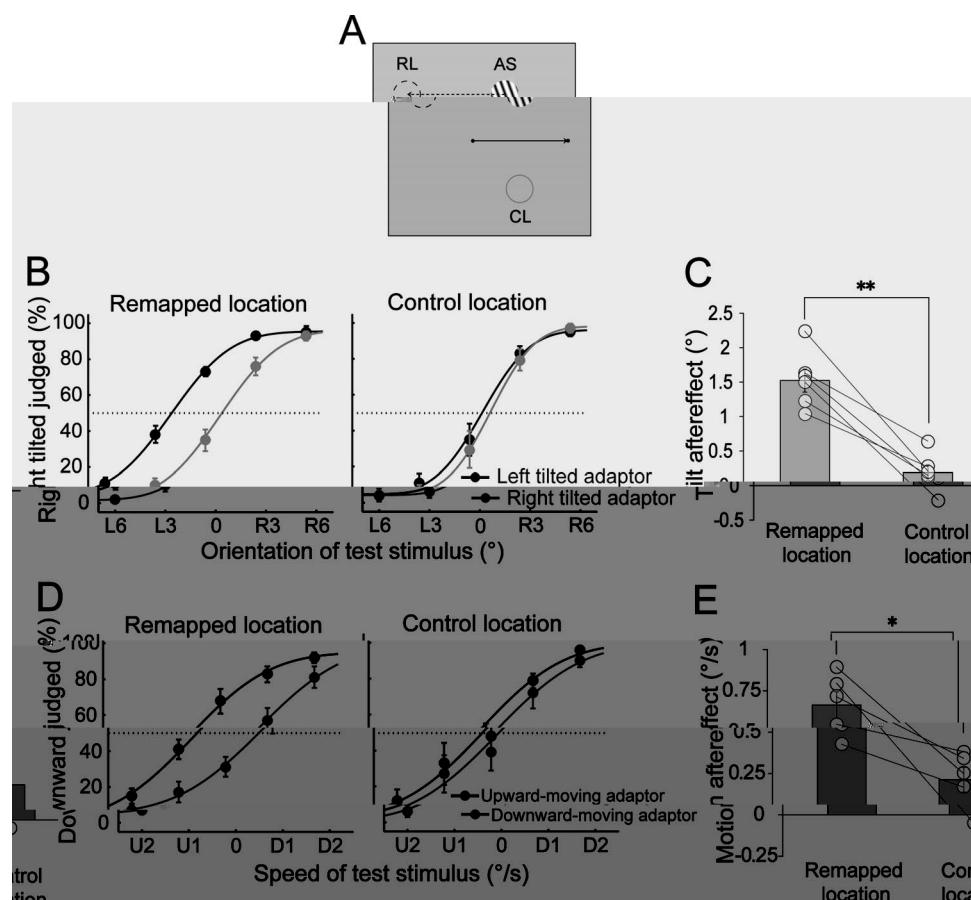


Figure 5. Results of Experiments 5 and 6. (A) The spatial location and the remapped location of the grating adaptor and the control location. RL: remapped location; AS: adapting stimulus; and CL: control location. (B) Psychometric functions showing orientation judgments after adapting to the left or right tilted adaptor. The abscissa refers to the orientation of test stimuli. L and R indicate that a test stimulus was left or right tilted. The ordinate refers to the percentage of trials in which subjects indicated that a test stimulus was right tilted. (C) TAE magnitudes at the remapped location and the control location. (D) Psychometric functions showing motion direction judgments after adapting to the upward- or downward-moving adaptor. The abscissa refers to the direction of test stimuli. U and D indicate that a test stimulus moved upward or downward. The ordinate refers to the percentage of trials in which subjects indicated that a test stimulus moved downward. (E) MAE magnitudes at the remapped location and the control location. Data are plotted for each subject (lines and circles) as well as the group means (bars). Asterisks indicate a statistically significant difference between two conditions ($*p < 0.05$; $**p < 0.01$). Error bars denote 1 SEM calculated across subjects for each location.

$=0.011$, $t(5)=3.82$, $p=0.012$.

Experiment 2: Time-dependent predictive remapping of orientation

and $t(5)=3.82$, $p=0.012$ ($t(5)=3.82$, $p=0.012$).

(B & C, 1969; B & C, 2003; B & C, 2005; B & C, 1973; B & C, 1979),

0.878. $t(4)=8.14$, $p < 0.01$, $t(4)=3.97$, $p = 0.017$,

$t(4)=0.16$, $p = 0.878$. $t(4)=0.16$, $p = 0.878$.

n : $t(4) = 7.05, p < 0.01$; n : $t(4) = 3.67, p = 0.021$ (3C n 3). n , A n n n n n n , t(4) = 6.08, p < 0.01.

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Experiment 3: Predictive remapping of motion direction before saccade

A n n n n ,
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n n n n n A n n -
t n n , t(4) = 3.62, p = 0.022, A n n -
n n - n n , t(4) = 0.28, p = 0.791.
, t A n n -
n n n n - n n n n , t(4)
= 4.58, p = 0.01 (4A n 4B).

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2003; , , & , 2003;
, 1995; n & B n , 2003). ,
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Experiment 4: Contrast information cannot be predictively remapped

A n n n n n n n n n n n ,
t n - n n n n n n n n n , t(6) = 0.779, p =
0.465, n - n n n n n n n , t(6) = 0.105, p =
0.919. , t n n n n n n n ,
t(6) = 0.723, p = 0.497 (4C n 4).

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Experiments 5 and 6: Location specificity of predictive feature remapping

A n n n n n n n n n n n n ,
n n n n n n n n n n n n ,
A n A n n n n n n n n n n ,
n n n n n n n n n n n n ,
 $t(5) = 9.07, p < 0.001$, n - n t n n ,
 $t(5) = 1.67, p = 0.155$, , t n n ,
A n A n n n n n n n n n n ,
 $t(5) = 6.66, p < 0.001$ (5B n 5C). n n n n n n ,
A n A n n n n n n n n n n ,
 $t(4) = 8.20, p < 0.001$, n n n n n ,
 $t(4) = 2.88, p = 0.045$. , t n n ,
A n A n n n n n n n n n n ,
 $t(4) = 3.95, p = 0.017$ (5 n 5). n n n n n n ,
n n n n n n .

Discussion

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(2011) n n n n n ,

- et al., 2011), which includes the visual system (Fig. 1). In addition, the work of Johnson et al. (2011) also presents a review of the literature on visual system development in children and adolescents.
- The visual system undergoes extensive growth during the first year of life. During this period, the eye increases in size by 30% and the visual system becomes increasingly complex. The optic nerve, which connects the eye to the brain, grows rapidly, reaching its full size by approximately 18 months of age. The lens of the eye also undergoes significant changes, becoming more transparent and allowing for better focusing of light onto the retina. The retina itself continues to develop, with the outer nuclear layer increasing in thickness and the inner nuclear layer becoming more organized. The macula, the central part of the retina responsible for sharp, central vision, begins to form during this time.
- In addition to the growth of the eye and visual system, the brain also undergoes significant development during the first year of life. The brain increases in weight by approximately 40% during this period, with the visual cortex (the part of the brain responsible for processing visual information) growing particularly rapidly. This growth is driven by the establishment of new connections between neurons in the visual cortex and the other parts of the brain involved in vision, such as the thalamus and the cerebellum.
- As the child continues to grow and develop, the visual system continues to mature. By the age of 2, the visual system has reached a level of maturity similar to that of an adult, although some fine-tuning of visual processing still occurs. For example, the ability to recognize faces and objects becomes more refined, and the visual system becomes more efficient at processing complex visual stimuli. The development of the visual system continues throughout childhood and adolescence, with the visual cortex becoming increasingly specialized and the overall efficiency of the visual system improving over time.
- The visual system is a complex and dynamic system, with many different components working together to allow us to see clearly. The development of the visual system is a remarkable process that involves the coordinated growth and maturation of the eye, brain, and other neural structures. By understanding the development of the visual system, we can gain a deeper appreciation for the complexity of vision and the importance of maintaining good eye health throughout our lives.

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Keywords: feature remapping, saccade, psychophysics, adaptation, visual aftereffect

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