and spatiotopic representation of the visual world (D'Avossa et al., 2006; Duhamel, Bremmer, Benhamed, & Graf, 1997). While each of these theories can explain certain aspects of the trans-saccadic stability issue, the discovery of predictive remapping (Duhamel, Colby, & Goldberg, 1992; Sommer & Wurtz, 2006), the activity increase of many neurons in retinotopic brain areas when saccades are about to bring stimuli into their receptive fields, suggests a more comprehensive and plausible framework for understanding trans-saccadic perception (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Melcher & Colby, 2008).

Predictive remapping was observed in the lateral parietal area (Colby, Duhamel, & Goldberg, 1995; Duhamel et al., 1992; Wang et al., 2016), the frontal eye field (Goldberg & Bruce, 1990; Sommer & Wurtz, 2006), the superior colliculus (Walker, Fitzgibbon, & Goldberg, 1995), and extrastriate visual cortex (Nakamura & Colby, 2002). In anticipation of a saccade, neurons in these brain areas were shown to have a normal, current receptive field and a future receptive field (i.e., the spatial location where the receptive field will be after the intended saccade). Remapping could occur even before the saccade onset, reflected as a combination of neuronal activity increase in the future receptive field and concurrent decrease in the current receptive field.

Although predictive remapping is thought to contribute to visual stability by updating the internal image with each saccade, details of predictive remapping remain to be thoroughly investigated. Some researchers propose that visual stability is based on remapping of attention pointers (Cavanagh et al., 2010; Joiner, Cavanaugh, & Wurtz, 2011; Mirpour & Bisley, 2012, 2016; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). They propose that a map of attentionally significant locations is updated before saccades. Once a saccade is completed, feature information can be selectively extracted from these locations. In other words, presaccadic activity of remapping neurons conveys only spatial information, but not feature information. On the other hand, some other researchers argue that feature information along with spatial information is remapped before saccades, which is implemented by a predictive activity transfer from neurons that initially encode the stimulus to neurons whose receptive fields will encompass the stimulus location after the saccade. (Harrison, Retell, Remington, & Mattingley, 2013; Melcher, 2007; Melcher & Colby, 2008; Subramanian & Colby, 2014; Szinte, Jonikaitis, Rolfs, Cavanagh, & Deubel, 2016). Therefore, whether presaccadic activity of remapping neurons conveys feature information (e.g., orientation, motion direction, or contrast) is still under intense debate.

Melcher (2007) used the tilt aftereffect (TAE) to measure any transfer of visual orientation adaptation from the current fixation position to the saccadic target location around the time of saccades. Several visual adaptation aftereffects, including TAE, MAE (motion aftereffect), and TEAE (contrast threshold elevation aftereffect), are especially suitable for studying predictive feature remapping because these aftereffects are highly specific to adapted features, well constrained in spatial extent, and persist longer than a typical fixation (Anstis, Verstraten, & Mather, 1998; He & MacLeod, 2001; Melcher, 2005). In Melcher's study, after a brief adaptation to a tilted grating presented at the initial fixation point, participants 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. Melcher found that the intention to make a saccade simultaneously triggered a reduction of the TAE magnitude at the initial fixation point and a TAE increase at the saccadic target location, even before saccades. He suggested that the orientation adaptation (or orientation information) could be transferred from the initial fixation point to the future fixation point (i.e., the saccadic target location) before saccades, therefore providing evidence for predictive feature remapping. Recently, Rolfs et al. (2011) argued that, in Melcher's experiments, TAE was measured at the location (the reversed remapped location) opposite to the actual remapped location of the adapting stimuli (see Figure 1), and they believe that these experiments did not actually study the behavioral correlates of predictive remapping (but see also Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014; Zirnsak & Moore, 2014).

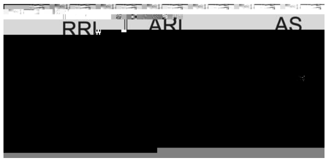

Figure 1. Appropriate remapped location of visual adaptor. In Melcher's study (2007), subjects adapted to a tilted grating presented at the initial fixation point. Then they were asked to

Here, to further test the predictive feature remapping theory, we measured the TAE, MAE, and TEAE at the

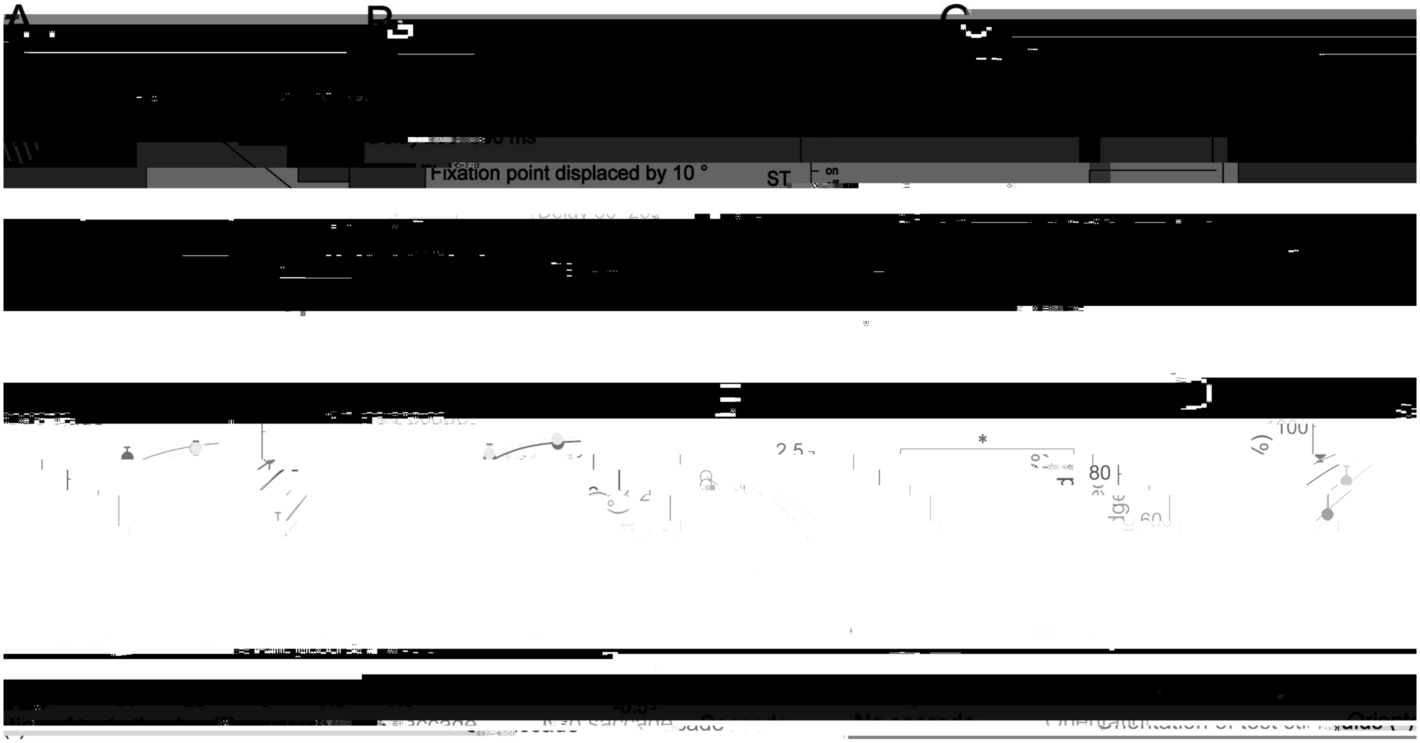

Figure 2. Stimuli, procedure, time course of events, and results in Experiment 1. (A) The spatial location and the remapped location of the grating adaptor. Subjects made a saccade from the fixation point to the saccadic target. The saccade direction and the remapping direction are shown by the solid 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

appropriate or "actual" remapped location of adapting stimuli before saccades as proposed by Rolfs et al. (2011; Figure 2A). If feature information (orientation, motion direction, and contrast) could be predictively remapped, we expect to detect adaptation aftereffect at the appropriate remapped location before saccades. Since these aftereffects are mediated by brain areas at different processing levels (Georgeson, 2004; Kohn, 2007; Webster, 2015), this approach provides a comprehensive characterization of predictive feature remapping during trans-saccadic perception.

Methods

Subjects

A total of thirty-four naive subjects (18 male and 16 female) participated in the study. The numbers of subjects in Experiments 1–6 were six, five, five, seven, six, and five, respectively. None of them was involved in more than one experiment. Participants were right-handed with reported normal or corrected-to-normal vision and had no known neurological or visual disorders. Their ages ranged from 20 to 30. Participants gave written, informed consent in accordance with the procedures and protocols approved by the human subject review committee of Peking University.

Apparatus and stimuli

Visual stimuli were presented on a uniform gray background at a viewing distance of 57 cm. The background luminance was 43.4 cd/m^2 in Experiment 4 and 10.5 cd/m^2 in other experiments. The display was an IIYAMA color graphic monitor (model: HM204DT; refresh rate: 60 Hz; resolution: 1024 × 768; size: 22 in.). In Experiment 4, stimuli were rendered with a video card with 8-bit input resolution and 14-bit output resolution using Cambridge Research System

Bits++. The output luminance of the display monitor was linearized using a look-up table in conjunction with photometric readings from a colorCAL colorimeter (Cambridge Research System). Subjects' head position was stabilized using a chin and head rest. We used an SMI iView X™ Hi-Speed 500 eye tracker to monitor eye position and the SMI BeGaze™ Eye Tracking Analysis Software to process eye movement data. The velocity threshold for saccade detection was set as 30°/s.

In Experiments 1, 2, and 5, adapting stimuli were two circular patches of sinusoidal gratings with a randomized phase (radius: 1.96°; contrast: 1.0; spatial frequency: 1.5 cycles/°; orientation: −20° or +20°; "−" and "+" indicate that a grating was left or right tilted; Figure 2A). Test stimuli were similar to the adapting stimuli, except that their contrast was 0.2, and they were oriented at one of five angles (−6°, −3°, 0°, 3°, 6°).

In Experiment 3 and 6, adapting stimuli were two 100% coherent RDKs (random dot kinematograms) consisting of 150 dots (contrast: 1.0; diameter: 0.08°). The dots moved at a velocity of 4°/s, either upward or downward, within a virtual circular area subtending 5.88° in diameter. Test stimuli were similar to the adapting stimuli, except that their contrast was 0.08 and they moved at one of five speeds (2°/s upward, 1°/s upward, 0°/s, 1°/s downward, 2°/s downward).

In Experiment 4, adapting stimuli were two circular patches of sinusoidal gratings with a randomized phase (radius: 1.96°; contrast: 1.0; spatial frequency: 1.5 cycles/°; orientation: 0° or 90°). Test stimuli were otherwise identical to the adapting stimuli except that their orientation was 0° and their contrast was one of five values (0, 0.005, 0.01, 0.02, and 0.03). In all the experiments, the centers of adapting and test stimuli were 7.07° away from the initial fixation point, in either the upper right or the upper left direction (Figure 2A). Test stimuli were presented at the remapped location of adapting stimuli.

Design

For all the experiments in the study, we used a method of constant stimuli to measure visual aftereffects at the remapped location of adapting stimuli. In an adaptation block, there was only one adaptor. Before the presentation of test stimuli, subjects experienced 30-s preadaptation and 3-s topping-up adaptation.

Experiment 1 measured the tilt aftereffect (TAE). There were two experimental conditions: the "saccade" condition and the "no saccade" condition. Each condition had 10 blocks of 40 trials (five blocks for each adaptor). A saccade block began with a preadaptation at the upper right of the initial fixation point (Figure 2A). In a trial, after a topping-up adaptation and a 200–300-ms blank interval, the position of the fixation point was displaced by 10° to the other side of the screen, which served as a cue for participants to make a saccadic eye movement to the new position of the fixation point. Following the displacement, after a 50–250-ms blank interval, a test stimulus was presented for 33 ms at the upper left of the initial fixation position (i.e., the remapped location of the adaptor). At the end of the trial, subjects were asked to make a two-alternative-forced-choice (2-AFC) response to indicate that the test stimulus was left or right tilted (Figure 2B). Since human saccade latency is about 200 ms (Robinson, 1964), it is very likely that the test stimulus appeared before the onset of the saccade. Note that only trials in which a test stimulus appeared before saccade onset were included for data analysis. In a block, each of the five test stimuli was presented eight times. Blocks in the no-saccade condition were similar to the saccade blocks, except that there was no displacement of the fixation point and hence no saccade was triggered.

Experiment 2 was designed to examine whether there was TAE at the remapped location when the test stimuli were presented before the onset of a saccadic cue. The key manipulation of this experiment was to display the saccadic target for a variable duration before the test stimuli and the saccadic cue (Figure 3A). There were three experimental conditions: the "long preview" condition, the "short-preview" condition, and the no-saccade condition. Each condition had 10 blocks of 40 trials (five blocks for each adaptor). A long preview or short preview block began with a preadaptation at the upper right of the initial fixation point. In a long preview or short preview trial, after a topping-up adaptation, a saccadic target was presented 10° to the other side of the screen, followed by an 800–1200-ms (the long preview condition) or 300–400-ms (the short preview condition) interval. During the interval, a test stimulus was presented for 33 ms at the upper left of the initial fixation point. The gap between the onset of the saccadic target and the onset of the test stimulus was 400–800 ms (the long preview condition) or 100–150 ms (the short preview condition). Then the initial fixation point disappeared, which served as a cue to make a saccadic eye movement to the saccadic target. After the saccade, subjects were asked to make a 2-AFC judgment to indicate that the test stimulus was left or right tilted. In a block, each of the five test stimuli was presented eight times. Blocks in the no saccade condition were similar except that the initial fixation point remained on the screen throughout blocks, and no saccade was made.

Experiment 3 measured the motion aftereffect (MAE). There were two experimental conditions: the long preview condition and the no-saccade condition.

Each condition had 10 blocks of 40 trials (five blocks for each adaptor). The procedure of Experiment 3 was similar to that of Experiment 2 except that both the adapting and test stimuli were RDKs. Following adaptation, subjects were asked to make a 2-AFC

For all the experiments, the orders of experimental conditions and test stimuli were randomized. Subjects were given one practice block for each experimental

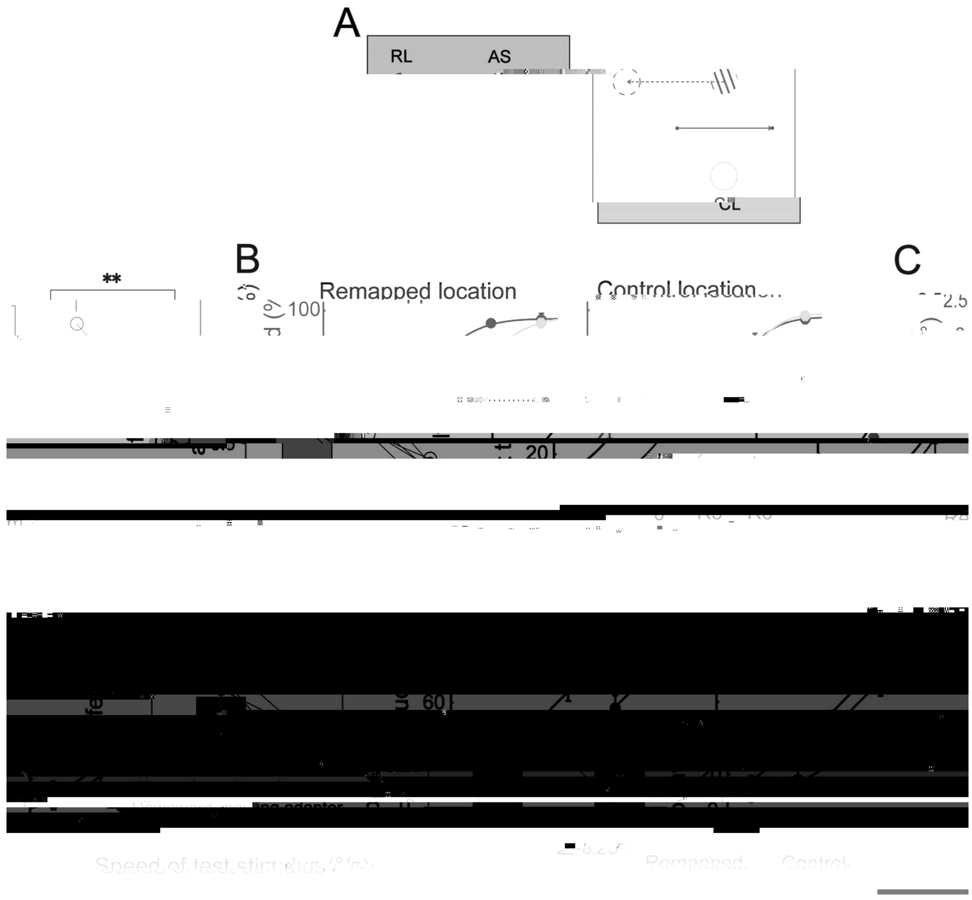

Figure 5. Results of Experiments 5 and 6. (A) The spatial location and the remapped location of the grating adaptor and the control location. RL: remapped location; AS: adapting stimulus; and CL: control location. (B) Psychometric functions showing orientation judgments after adapting to the left or 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.

$= 0.011$, but little TAE in the no-saccade condition, $(5) = 0.92$, $= 0.398$. Moreover, a paired test showed that the magnitude of the TAE in the saccade condition was significantly larger than that in the no-saccade condition, $(5) = 3.82$, $= 0.012$ (Figure 2D and 2E). These results demonstrated that the orientation information could be predictively remapped before saccades. Given the dependence of TAE on early and intermediate visual cortical areas (Blakemore & Campbell, 1969; Boynton & Finney, 2003; Fang, Murray, Kersten, & He, 2005; Maffei, Fiorentini, & Bisti, 1973; Movshon & Lennie, 1979), the predictive remapping of orientation during trans-saccadic perception might entail these areas.

Experiment 2: Time-dependent predictive remapping of orientation

Although Experiment 1 has shown that orientation information could be transferred before saccades, it remains unknown whether this transfer process is time dependent. Here we displayed the saccadic target for a variable duration before the test stimuli and the saccadic cue, therefore manipulating the preview time (Figure 3A). At the remapped location of the adapting stimuli, one-sample tests showed significant TAEs in the long-preview condition, $(4) = 8.14$, < 0.01, and the short-preview condition, $(4) = 3.97$, $= 0.017$, but little TAE in the no saccade condition, $(4) = 0.16$, $= 0.878$. Moreover, paired tests showed that both the TAE magnitudes in the long preview condition and the short preview condition were significantly larger than that in the no saccade condition: long preview versus no saccade: $(4) = 7.05$, < 0.01; and short preview versus no saccade: $(4) = 3.67$, $= 0.021$ (Figure 3C and 3D). Furthermore, the TAE magnitude in the long preview condition was significantly larger than that in the short preview condition, $(4) = 6.08$, < 0.01. These results revealed that the predictive remapping effect increased with the latency of the planned saccade, suggesting that the orientation remapping process is time dependent.

Experiment 3: Predictive remapping of motion direction before saccade

To examine whether motion direction could be predictively represented before saccades, we measured the MAE at the remapped location of the motion adaptors. In Experiments 3–6, we adopted the long preview protocol from Experiment 2 because of its effectiveness in generating the transferred TAE. One-sample tests showed a significant MAE in the long-preview condition, $(4) = 3.62$, $= 0.022$, but little MAE in the no-saccade condition, $(4) = 0.28$, $= 0.791$. Moreover, a paired test showed that the MAE magnitude in the long-preview condition was significantly larger than that in the no-saccade condition, $(4) = 4.58$, $= 0.01$ (Figure 4A and 4B). These results demonstrated that the motion direction information could be remapped before saccades. It is well known that MAE originates in early and intermediate visual cortical areas, especially area MT (Kohn & Movshon, 2003; Seiffert, Somers, Dale, & Tootell, g thatJTf*.33uTJ0-1.Fte0.01 & 4Be,cationiblgnitud(331cades,7-330.6(the)-333.4(pred movements. They revealed a robust increase in visual performance at the remapped, future retinal locations of a sequence of movement goals occurring before the onset of saccades. They attributed the performance increase to attentional pointers to the remapped locations updated by a predictive remapping process. Notably, our study here provided clear evidence that, at the remapped location, in addition to the spatial

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