Predictive remapping of visual features precedes saccadic eye movements

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The frequent occurrence of saccadic eye movements raises the question of how information is combined across separate glances into a stable, continuous percept. Here I show that visual form processing is altered at both the current fixation position and the location of the saccadic target before the saccade. When human observers prepared to follow a displacement of the stimulus with the eyes, visual form adaptation was transferred from current fixation to the future gaze position. This transfer of adaptation also influenced the perception of test stimuli shown at an intermediate position between fixation and saccadic target. Additionally, I found a presaccadic transfer of adaptation when observers prepared to move their eyes toward a stationary adapting stimulus in peripheral vision. The remapping of visual processing, demonstrated here with form adaptation, may help to explain our impression of a smooth transition, with no temporal delay, of visual perception across glances.

Human visual perception involves brief periods of steady fixation separated by rapid, jerking shifts in gaze position. These saccadic eye movements, which typically occur two to three times every second, dramatically change the position at which objects in the world are projected onto the retina[1,2]. Perception of the visual world, however, is smooth and continuous, with no illusions that stable objects are moving or any periods of perceived blindness after each saccade before retinal reafference. There have been three main explanations as to why perception appears to be continuous across eye movements. The first is that eye movements are essentially ignored, with perception beginning anew on each fixation. This idea is supported by studies showing failures to notice changes across saccades[3,4]. The second theory is that changes in receptive fields around the time of saccades[5–7] might allow visual information to be remapped from one neuron to another. A third possibility is that visual stability is mediated by neurons whose receptive fields are head centered (craniotopic)[8] or in external spatial coordinates (spatiotopic)[9,10], rather than in retinal coordinates.

To distinguish between these potential explanations for stable and continuous visual perception, I used adaptation aftereffects to measure any transfer of visual information around the time of saccadic eye movements. Typically, this procedure involves presenting an adapting stimulus and then, after a delay, a brief test stimulus in the same location[11–14]. By varying the temporal and spatial presentation of the adaptor and test stimulus, it was possible to test the predictions of each of the three theories.

RESULTS

These experiments used the tilt adaptation aftereffect (TAE), which persists longer than a single fixation, but also has a well-constrained spatial extent[11–14]. After a brief adaptation to a strongly tilted adaptor, observers tend to see a test stimulus presented at that location as tilted in the opposite direction. On each trial, the adapting stimulus (tilted $-20°$ or $20°$) was presented for 3 s, followed by a delay and then a brief (50 ms) test stimulus. The observer's task was to judge whether the test had been oriented to the left or right. Control trials without a saccade allowed me to measure the maximum effect of the TAE for each observer as well as the spatial extent of the aftereffect (**Supplementary Fig. 1** online). On these trials, observers showed a typical TAE, with the magnitude of the effect varying as a function of the distance of the adaptor and test stimuli.

In the first experiment, the adaptor was presented at the initial fixation position. Then, after a short, random delay of 100–200 ms, the position of the fixation point was displaced by $10°$ to the other side of the screen (**Fig. 1**). The displacement of the fixation point served as a cue to make a saccadic eye movement to the new target. Because there is a temporal delay between the appearance of a visual cue and the onset of the saccadic eye movement[1,2], I was able to vary the timing of the test stimulus so that it would be presented either before or after the saccade. In one condition, the test (50 ms) was displayed at the initial fixation position, whereas in the second condition, the test was presented at the saccadic target.

The onset of the cue to make a saccade led to two opposite effects, depending on whether the test was shown at the initial fixation point or at the future fixation location. For tests at fixation, the intention to make an eye movement led to a marked decrease in the TAE ($F_{4,4} = 11.31$, $P < 0.001$), by nearly 80%, before saccadic onset (**Fig. 2a**, squares). There was also a reduction in the TAE for trials in which the adaptor and test were spatially separated by $4°$ (**Fig. 2a**, circles).

At the future target position, there was a strong boost in the TAE before the saccade (**Fig. 2b**, squares). Normally, there is no TAE for a

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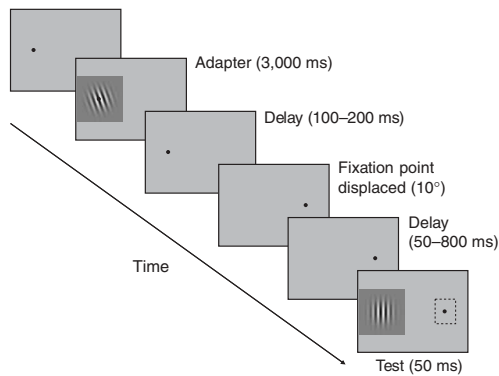
Figure 1 Design of the first experiment. The adaptor was shown either at the fixation point or at a position 4° or 7° above or below. After a blank delay, the fixation point was displaced 10° to the other side of the screen. This displacement served as the cue to make a saccade to the new fixation position. The test stimulus was then shown for 50 ms at either the initial fixation position (as shown in the figure) or the saccadic target (shown by the empty box). The timing of the test stimulus was varied across trials so that it could occur either before or after the saccade (see Methods).

test stimulus presented 10° in the periphery (**Supplementary Fig. 1**). Shortly after the presentation of the saccade cue, however, the TAE increased to more than 60% of its full magnitude ($F_{4,4} = 11.20$, $P < 0.001$). Thus, the progressive decrease in the TAE at fixation was accompanied by a simultaneous growth in the aftereffect at the future fixation position. These results suggest that adaptation was transferred from the current to the future fixation position before the saccade. There was little transfer of TAE for trials with a 4° vertically offset adaptor (**Fig. 2b**, circles), indicating that the remapping of the TAE was spatially selective ($F_{4,4} = 0.66$, $P = 0.973$). After the saccade, a portion of the full TAE was found at the original fixation position, consistent with previous reports of spatiotopic integration[15,16].

Notably, a shift in spatial attention was not sufficient to transfer TAE to a new location (**Supplementary Fig. 2** online). This is consistent with single-unit recording studies showing that remapping of receptive fields is directly linked with the eye movement itself[17,18]. It should also be noted that the change in adaptation at the initial fixation and saccadic target cannot be explained by a failure to perceive the brief test stimulus. Had observers missed the brief test stimulus entirely, they might have been led to guess or to base their judgments on other information, such as a visible aftereffect from the adaptation period[11]. There is no evidence either for increased guessing or for observers perceiving a visible afterimage (**Supplementary Fig. 3** and **Supplementary Discussion** online).

The first experiment examined the event in which eye movements are used to follow a target that changes retinal position, which is a situation that occurs frequently in everyday viewing as a result of motion of either the observer or the target. Trans-saccadic perception might also be important, however, when an object remains in the same relative spatial location and the eye moves. After such an eye movement, an object previously viewed with central vision may be displaced toward a peripheral location on the retina. Likewise, a saccadic target

viewed in the periphery could, after the eye movement, be located at the center of fixation. In the case of stationary objects and the moving eye, previous studies suggest two possible mechanisms that might allow the visual system to transfer information across saccades.

The first potential mechanism is presaccadic changes in receptive fields. Individual neurons in the lateral intraparietal area[5,6] and frontal eye fields (FEFs)[18,19] may respond to their current or their future receptive fields, or even both. Such studies have not revealed, however, whether or how such brain regions directly influence visual perception. Given the role of the lateral intraparietal area and FEFs in saccade generation, remapping may serve to maintain accurate sequences of saccades by predicting the retinal coordinates of future saccade targets. If so, then remapping might be important for the oculomotor system, but have no role in conscious perception. A proportion of neurons in visual areas also show changes in their receptive fields around the time of saccades[7]. Again, however, it is not clear from such studies whether the pattern of changes in the activity of the ensemble of neurons actively alters visual perception.

A second possible explanation for trans-saccadic integration is the presence of spatiotopic receptive fields, which may be able to combine
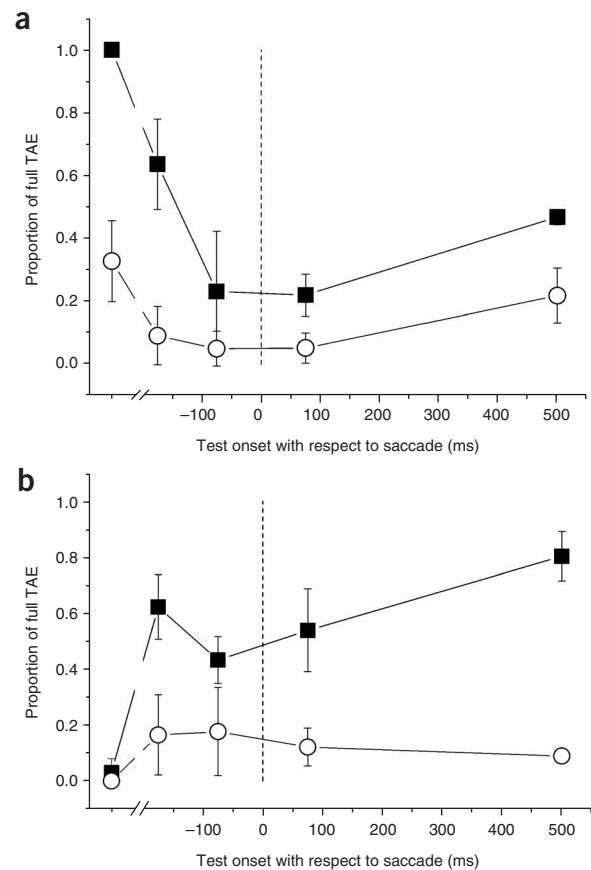

Figure 2 The proportion of full TAE measured for test stimuli presented at varying time periods before or after the saccade. In the first experiment, the adaptor was always shown at (squares) or near fixation. Circles show performance on trials in which the adaptor was shown 4° above or below fixation. No TAE was found on trials in which the adaptor was shown 7° in the periphery under any condition, and thus only data from the 0° and 4° offsets are presented in the figure. Full TAE was measured in control trials in which there was no offset of the fixation point and thus no saccade. No change in the TAE as a function of time was found in the control trials ($F_{4,4} = 0.19$, $P = 0.689$). (**a**) Average proportion of TAE for trials in which the test stimulus was shown at the initial fixation position. (**b**) Average proportion of full TAE for trials in which the test stimulus was shown at the saccadic target. The dotted vertical line indicates saccade onset. Symbols show mean and s.e.m. for five observers.

presaccadic and postsaccadic information about the same spatial location. Spatiotopic and craniotopic receptive fields have been found in many areas[8–10], including human motion-processing areas that have been directly implicated in perception[10]. Unlike in remapping, which involves the transfer of information from one neuron to another, a single spatiotopic neuron could respond to the same stimulus in two different retinal positions. Previous studies of trans-saccadic perception, however, have typically examined a single, post-saccadic test period, and thus have not tested for presaccadic changes.

To distinguish between the two possible mechanisms of perceptual integration, I carried out a second experiment to test the situation in which the adapting stimulus was presented peripherally at the future saccadic target. At the beginning of each trial, the observer maintained fixation while the adaptor was shown for 3 s on the other side of the display (10°). Then, after a random delay (100–200 ms), the fixation point was displaced to the position that had previously been occupied by the adaptor. Note that only a portion of the TAE is expected to transfer across the saccade under these conditions[16]. If, as suggested in the first experiment, trans-saccadic adaptation involves an active remapping process before saccade onset, then I can make a counter-intuitive prediction: the TAE at the saccadic target should be reduced before the onset of the eye movement. Thus, although there was a presaccadic increase in adaptation at the target in the first experiment, here I would expect that remapping would transfer some of the TAE away from neurons with the target in the presaccadic receptive field to those with the target in the postsaccadic receptive field. If trans-saccadic perception is mediated by spatiotopic receptive fields, without any active remapping of visual processing, then the decrease in TAE should be evident only after the saccade; spatiotopic information is not relevant before the saccade when adaptor and test are still in the same retinal location.

Consistent with the remapping hypothesis, the TAE was reduced by more than half at the saccadic target even before the onset of the eye movement (**Fig. 3a**). Overall, the TAE was decreased for stimuli presented after the saccadic cue, both before and after the saccade ($F_{4,4} = 12.97$, $P < 0.001$). The postsaccadic TAE at the longest delay (56%) was similar to that found when the adaptor and test were spatially matched across the saccade in the first experiment (48%), as well as to the spatiotopic TAE reported in a recent experiment (58%)[16]. In addition to providing further evidence of presaccadic changes in perception, the results of this second experiment also argue against an attention-based explanation, as the presaccadic TAE was reduced at the saccadic target rather than increased by the shift of attention to the target location. The results also speak against the possibility that a visible aftereffect from the adaptor (which can be found for tilted gratings under some conditions)[11] was responsible for trans-saccadic TAE. In this experiment, any lingering visual aftereffect (which none of the observers reported) would have been displaced 10° in the periphery, and thus would be unlikely to explain the strong TAE at the new fixation position after the saccade.

The transfer of the TAE before saccades in both experiments raises the question of whether remapping occurs between two discrete locations. The existence of neurons sensitive to both adaptor and test locations might, in theory, lead to a measurable TAE for targets presented in intermediate positions between the fixation and the saccadic target. In fact, the pattern of mislocalization immediately before saccades[20,21] has been interpreted as evidence that space and time might compress toward the saccadic target, perhaps as a result of presaccadic remapping[21,22]. However, a recent study of FEF neurons found no evidence that neurons with receptive fields in the inter-
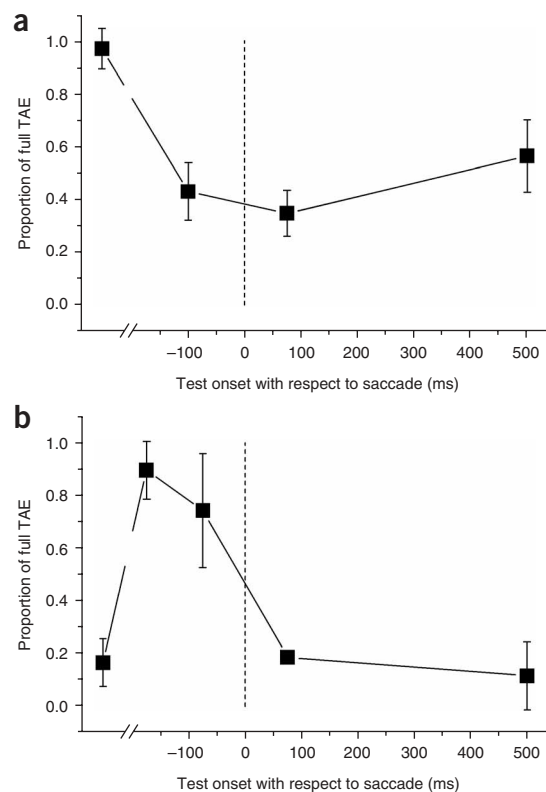

Figure 3 The proportion of full TAE as a function of the timing of the test stimulus in experiments 2 and 3. In both experiments, there was no vertical offset of the adaptor. (**a**) Average proportion of TAE when the adaptor was presented 10° in the periphery at the future saccadic target. In this experiment, the test was always presented at the position of the saccadic target. (**b**) Average proportion of TAE for trials in which the adaptor was shown at the initial fixation position and the test was presented at the intermediate position in between the initial fixation and the saccadic target. The fixation and target were separated by 10°. All other details are as in **Figure 2**.

mediate positions were affected by remapping[18]. To investigate these conflicting reports, I tested whether the intermediate spatial location, between the current and future fixation positions, would also show a saccade-related change in the TAE. Indeed, there was a TAE at the middle position before the saccadic onset ($F_{4,4} = 15.76$, $P < 0.001$), but this effect disappeared after the completion of the saccade (**Fig. 3b**). Notably, participants reported (see Methods) that the test stimuli presented in the middle location was perceived as shifted toward the initial fixation position before the saccade (mean: 0.91°, standard error: 0.13°), compared with tests presented after the saccade ($t_9 = 7.26$, $P < 0.001$). The perceived shift was too small to have placed the stimulus within the functional extent of the adaptation at fixation. Instead, the large change in TAE at the intermediate position before the saccade may reflect the remapping process or a bias in the updating of spatial location across saccades.

DISCUSSION

The findings here demonstrate that visual form adaptation transfers its spatial location depending on the position of the planned saccade target. The results provide further evidence that postsaccadic perception does not begin anew, but rather takes into account previous visual experience[23]. In the case of visual aftereffects, as investigated in this study, adaptation is thought to alter the neural processing of

subsequently viewed stimuli in a way that can enhance sensitivity to changes[24]. It is an example of how previous experience can be incorporated into perception across separate fixations, in this case by predicting what the eye will see after it lands. Such presaccadic changes might help to explain the rapid reallocation of attention across saccades[25], as well as providing a clue as to why no 'blank interval' is consciously perceived during retinal reafference.

Perceptual remapping, like the updating of neuronal receptive fields[17–19], was linked directly to the saccadic eye movement itself, rather than to a shift in attention. This provides further evidence that spatial updating is a primary mechanism for ensuring perceptual stability across saccades, and gives new insight into the process that links presaccadic and postsaccadic perception. At the same time, the perceptual effects for intermediate positions found here contrast with a recent report measuring remapping of receptive fields in FEFs, raising the question of how the remapping of individual neurons in the oculomotor system is related to overall visual processing in extrastriate cortex. The exact implications of saccade-related changes in receptive fields have remained a matter of debate because of the great variability in the temporal and spatial characteristics of saccade-linked changes, as well as the fact that previous studies have not tested the visual selectivity or perceptual consequences of the activity of individual neurons. The current results show that changes in receptive fields are mirrored by a specific perceptual effect: visual adaptation is remapped before saccades. Such presaccadic changes in visual processing may underlie the seamless transition across separate glances that is a hallmark of visual perception.

METHODS

Subjects. Five participants with normal vision participated in the experiment. Informed written consent was obtained for all observers.

Materials. Stimuli were presented on a Sony F520 monitor and viewed from a distance of 60 cm. Experiments were run with MATLAB software (Mathworks) and displayed using VSG graphics (Cambridge Research Graphics). The adaptor and test both subtended 4°. The stimulus display was refreshed on the screen at 60 Hz.

Eye position was sampled using a Viewpoint eye tracker (Arrington Research) at 60 Hz. The position of the eye on each frame was recorded for each trial and saved for offline analysis. Saccadic onset was calculated by hand for each trial and used to sort the trials into six time periods (bins): (i) saccadic latencies that were too brief (less than 150 ms after the fixation point moved) or too long (more than 400 ms after the fixation point moved), which were discarded from further analysis, (ii) trials in which the target was presented 50–149 ms before the saccade, (iii) trials in which the target was presented 150–250 ms before the saccade, (iv) perisaccadic trials in which the test was shown within a window of time from 50 ms before to 49 ms after the saccade, which were not included in this analysis, (v) trials in which the stimulus was presented 50–150 ms after the saccade and (vi) trials in which the test was presented more than 150 ms after the saccade. There were only a handful of trials in which an observer forgot to make the saccade, and these were excluded from further analysis.

Procedure. The observers were extensively trained in the saccade task before the beginning of data collection. In the training session, the timing of the saccadic eye movement with respect to the cue and the test stimulus was measured, and feedback was given to ensure that the saccade had not been made before the fixation cross was moved to the new position. The distribution of saccadic eye movements was determined to calculate the optimal timing of the test stimulus and avoid perisaccadic presentation of the stimulus.

On each trial, the starting fixation point was randomly assigned to either the left or right side of the display, at a distance of 5° from the center of the screen. The observer initiated each trial by pressing a button when ready. The adaptor was then presented. In experiment 1, the adaptor was presented at fixation or at a point 4° or 7° above or below fixation. This served to map the spatial extent of the TAE. In experiment 2, the adaptor was shown at the future saccadic target position, whereas it was shown at the initial fixation point for Experiment 3. The adaptor was tilted 20° in orientation, with half of the trials containing a grating tilted to the left and half containing one tilted to the right. After the delay, the test stimulus was presented in one of five orientations: –2°, –1°, 0°, 1° or 2°. In experiment 1, the test was shown at either the initial fixation or at the saccadic target. In experiment 2, the test was shown at the saccadic target, whereas in experiment 3 it was shown in between the initial fixation and target locations. The participant was cued to report whether the test was tilted to the left or to the right after each trial and gave his or her response by pressing a keyboard button and then the enter key.

As found previously, perceived tilt was biased in the direction opposite that of the adaptor[12–14]. For individual observers, the TAE was calculated for each experimental condition and each bin in the saccade trials, except for excluded trials. The proportion of trials in which the observer responded "Tilted to the left" for each of the five tilt orientations was plotted and a curve was fit to estimate the 50% point at which the stimulus was perceived on an equal number of trials to be tilted to the right or the left. Leftward and rightward tilted adapters were plotted separately to measure the distance between the two psychophysical curves. Given that each observer had a different maximum TAE, the TAE in each condition and for each participant was converted to a "Proportion of full TAE" measure[16]. For example, the maximum TAE for an observer might be 3°, in which case a 1° TAE in a specific condition would be scored as 0.33 of the full TAE. This allowed for a cross-participant measure of the how the TAE changed in a particular spatial location as a result of the experimental manipulations. The full TAE for this group of observers ranged from 1.76° to 3.12°.

In addition to the three main experiments that measured tilt adaptation, there was an additional experiment that examined the perceived location of a test stimulus flashed in the intermediate location between the initial fixation position and the saccadic target. In a separate block of trials, observers were asked to report both the tilt and the location of the test stimulus (the tilt judgment was discarded from further analysis). This spatial localization test measured the illusion in the apparent position of central test stimuli before the saccade. Participants reported whether the test position was nearer to the pre- or postsaccadic fixation point using a button press. The true position of the test stimulus was varied from a central location (between the two fixation positions) in steps of 1° of visual angle, ranging from –3° to 3°. The data for each position was plotted to determine the 50% point at which observers were equally likely to respond that the target was nearer to fixation or that it was located nearer to the saccadic target.

Note: Supplementary information is available on the Nature Neuroscience website.

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