Perceptual evidence for saccadic updating of color stimuli

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In retinotopically organized areas of the macaque visual cortex, neurons have been found that shift their receptive fields before a saccade to their postsaccadic position. This saccadic remapping has been interpreted as a mechanism contributing to perceptual stability of space across eye movements. So far, there is only limited evidence for similar mechanisms that support perceptual stability of visual objects by remapping the representation of object features across saccades. In our present study, we investigated whether color stimuli presented before a saccade affected the perception of color stimuli at the same spatial position after the saccade. We found that the perceived hue of a postsaccadically flashed stimulus was systematically shifted toward the color of a presaccadically presented stimulus. This finding would be in accordance with a saccadic remapping process that preactivates, prior to a saccade, the neurons that represent a stimulus after the saccade at this very location. Such a remapping of visual object features could contribute to the stable perception of the visual world across saccades.

Introduction

During everyday vision, the characteristic pattern of eye traces includes sequences of stable fixations and fast eye movements (Yarbus, 1961). The latter lead to shifts of the retinal image and bring relevant parts of the visual scene into the center of finest visual resolution for further analysis. Consequently, in retinotopic areas of the visual cortex, the representations shift with every eye movement. Despite these frequent and abrupt changes in the neuronal representation, the perception of our visual environment remains stable.

One mechanism that has been proposed to contribute to this perceptual stability is saccadic updating or remapping. In such a case, the shift of a receptive field is anticipated prior to saccade execution. This predictive remapping was first reported for the monkey lateral intraparietal area (Duhamel, Colby, & Goldberg, 1992) and later on for the superior colliculus (Walker, Fitzgibbon, & Goldberg, 1995), the frontal eye field (Umeno & Goldberg, 1997), and visual cortical areas V2, V3, and V3A (Nakamura & Colby, 2002). While some neurons respond to a presaccadic stimulation of their future receptive field not until the saccade is executed, others respond with their normal visual latency to stimulus onset, i.e., even before the eyes have started to move.

Updating has been found in the dorsal pathway of the visual cortex, which processes spatial information. For the ventral pathway, which predominantly processes information about visual objects, we would expect that updating mechanisms involve a preactivation of the postsaccadic representation of visual object features. While direct evidence for updating in the ventral pathway is missing, neurons in area V4 have been found to show a presaccadic increase in activity when the saccade target is in their receptive field (Fischer & Boch, 1981; Moore, Tolias, & Schiller, 1998). Furthermore, presaccadic receptive field shifts have been observed in this area (Tolias et al., 2001). Even in primary visual cortex, correlations between pre- and postsaccadic activity have been observed (Khayat, Spekreijse, & Roelfsema, 2004a, 2004b). In addition, evidence for spatial updating has recently been found not only in human parietal cortex (Merriam, Genovese, & Colby, 2003) but also in human cortical areas V1, V2, V3, V3A, and hV4 (Merriam, Genovese, & Colby, 2007).

As an alternative explanation to remapping, perceptual stability could also be based on craniotopic representations of space that were found in parietal cortex in close vicinity to retinotopic representations (Duhamel, Bremmer, BenHamed, & Graf, 1997; Galletti, Battaglini, & Fattori, 1993; Krekelberg, Kubischik, Hoffmann, & Bremmer, 2003; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, &

Bremmer, 2005). In these areas, some visual neurons' receptive fields do not move when the eyes move. However, the perisaccadic dynamics of these representations have not been investigated.

Evidence for transsaccadic integration of visual features comes from recent psychophysical studies. Melcher and Morrone (2003) showed that sensitivity for the detection of postsaccadic coherent motion was higher when the motion was consistent with motion information shown prior to the saccade. Furthermore, Prime, Niemeier, and Crawford (2006) reported that observers were able to indicate the crossing points of oriented lines presented before and after saccade execution. The authors hypothesized that this perceptual behavior could be based on recurrent feedback connections between both dorsal and ventral stream and occipital cortex. Melcher (2005, 2007) recently found perceptual evidence for transsaccadic integration in the ventral pathway. Observers were adapted presaccadically with tilt, form or face stimuli, and showed adaptation after-effects for test stimuli presented postsaccadically at the same spatial position. For tilt adaptation at the initial fixation, after-effects were even reported for test stimuli presented at the saccade target prior to saccade execution, indicating a predictive remapping. Jüttner and Röhler (1993) showed an influence of presaccadically presented Landolt rings on the perception of the orientation of postsaccadically presented rings. Yet, since incorrect responses were likewise biased toward the orientation of the presaccadic stimulus, Jüttner (1997) hypothesized a shift in the decision criterion in an evaluation of the postsaccadic stimulus under a presaccadic context.

The aim of our current study was to investigate whether transsaccadic integration, being based on either predictive remapping or craniotopic mapping, could be found also for a primary object feature in visual perception, i.e., color, which is predominantly processed in ventral visual areas (Komatsu, 1998; Wandell & Wade, 2003; Zeki, 1990). Accordingly, we tested whether the appearance of postsaccadic color stimuli was affected by presaccadically presented color stimuli at the same spatial locations. If updating mechanisms would exert a preactivating or facilitating effect on those neurons with receptive fields corresponding to the postsaccadic retinal position of the stimulus that preferentially encode the stimulus color, then these neurons should show a stronger response to a postsaccadic stimulus. Thus, the appearance of the postsaccadic stimulus should be shifted toward the color of the presaccadic stimulus. Such a finding would provide evidence for predictive remapping in the ventral stream of the visual cortex. Accordingly, we measured color appearance under different presaccadic color configurations in a forced-choice experiment: subjects had to compare two simultaneously presented postsaccadic test stimuli. Critically, the postsaccadic stimuli were presented at the same spatial positions, not at the same retinal positions, as the presaccadic stimuli.

Methods

Participants

Five observers participated in the experiment; one was an author while the other observers were naive as to the goals of the study. All subjects had normal or corrected-to-normal vision and were color normals as assessed with the Ishihara (2006) plates test. All observers gave informed written consent prior to participating in the experiment.

Stimuli

Stimuli were displayed on a 22-in. CRT monitor (Phillips Brilliance 202 P7). Luminance of the phosphor pixels (P22) of the monitor declined exponentially to the tenth of the maximum within less than 5 ms. Resolution was set to 1152×864 at 100 Hz. Stimulation was controlled by a C++ program based on the template toolbox distributed with the eye tracking software (see below).

The background was set to a neutral gray (CIE $(x, y) = (0.315, 0.321)$) with a luminance of 20.1 cd/m^2.

Initial fixation (FP) and saccade targets (ST) were presented 5.3° left and right from the center of the screen, respectively. The resulting saccade amplitude of 10.6° has been shown to be in the typical range during scene perception in large displays (von Wartburg et al., 2007), and this metric made it possible to change the stimuli during saccade execution.

In addition to fixation and saccade targets, a 4×2 array of eight black (0.2 cd/m^2) circles were displayed throughout the trials to indicate positions on the screen where stimuli could appear (Figure 1). The circles had a diameter of 1.9°, a spacing of 2.6°, and a center distance of 5.3° from the possible fixation locations. Stimuli were colored disks that filled two or four of the circles. Stimulus colors were isoluminant with the background. Isoluminance was determined by heterochromatic flicker photometry for one of the subjects (MW) and the same values were used for all subjects. Note, however, that exact isoluminance was not critical for the purpose of the experiment. Preview colors were red (CIE $(x, y)_{pr} = (0.396, 0.321)$) or yellow (CIE $(x, y)_{py} = (0.377, 0.420)$). Test patch hues varied between reddish (CIE $(x, y) = (0.394, 0.336)$) and yellowish (CIE $(x, y) = (0.382, 0.401)$) in nine approximately equidistant steps, which were also approximately equidistant in CIE Luv space. The chromaticity in the center of this color scale (CIE $(x, y)_r = (0.390, 0.366)$) was chosen as reference against which other chromaticities had to be compared.

Gaze direction was monitored with an infrared eye tracking system (SR Research Eye Link II) running at 500 Hz. Saccade detection thresholds were set to
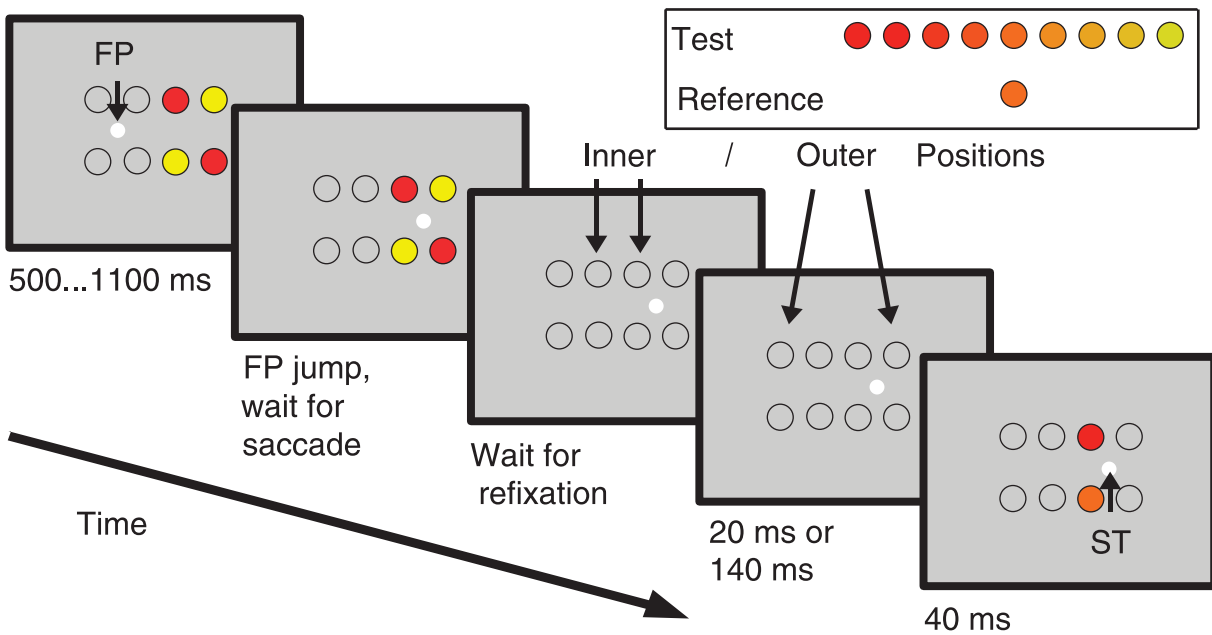
Figure 1. Stimulus sequence. Eight circle outlines and four color patches in a red-yellow checkerboard arrangement appeared at trial start around the saccade target (ST) position. In control trials, all circles were filled with the neutral gray of the background. After a variable time interval (500 … 1100 ms), the fixation point disappeared and ST appeared, and the observer had to execute a saccade to ST. At saccade onset, the color patches disappeared. Twenty or 140 ms after refixation, two colored test patches were flashed for 40 ms. The chromaticities of the patches were chosen from a set of nine equiluminant chromaticities along a line between the chromaticities of the red and the yellow presaccadic color patches (inset). The observer had to report which of the two postsaccadic patches was perceived as more yellowish.

$v = 22°$/s and $a = 5000°$/s^2. Pre- and postsaccadic gaze had to be within a virtual control window of 1.6° by 1.6° centered on the fixation or saccade target. Trials in which refixation did not achieve the required accuracy were aborted and repeated later in the session.

Procedure

Observers were seated 54 cm in front of the monitor screen. Head position was maintained stable by the use of a chin rest.

Observers fixated the initial FP to the left or right of the center of the screen and started the trial with a button press. Eight black circles and four circular color patches (preview stimuli) filling the four circles farthest away from the FP appeared on the screen. Two of the stimuli were red, two were yellow, in a checkerboard arrangement (see Figure 1). Observers had been instructed to ignore these presaccadic stimuli to prevent them from actively memorizing the specific stimulus layout in each trial. After a variable duration (500 … 1100 ms) the FP jumped to the saccade target position and the observers' task was to make a saccade to this position. When the saccade was detected by the eye tracking system, the color patches were turned off, leaving only the eight circles on the display. After refixation, two test patches

were flashed with a delay of 20 ms or 140 ms after saccade offset for 40 ms at the two positions either to the left or to the right of the ST. The retinal positions of the possible test positions corresponded to the four circles around initial fixation which were not color-filled. The chromaticity of one of the stimuli (reference) was the reference chromaticity (see above). The other stimulus (test) had a chromaticity that was chosen randomly from the set of nine possible values. The observers indicated whether the upper or the lower of the two patches appeared more yellowish by pressing one of two buttons. Which of the two stimuli was displayed on top of the other and whether the stimuli were displayed right or left of the ST varied pseudo-randomly from trial to trial. Likewise, arrangement of presaccadic red and yellow stimuli and the direction of the saccade were varied from trial to trial. Depending on saccade direction, the possible flash positions left or right of ST were inner or outer with respect to saccade execution (Figure 1). This ambiguity was introduced to keep subjects unaware of the specific distribution of presaccadic colors, and thus to reduce a possible influence of attention or expectation on the decision process (Jüttner, 1997). Furthermore, this arrangement made it possible to estimate the influence of perisaccadic retinal stimulation. In trials with test presentation at the outer positions, the retinal area illuminated presaccadically by the test stimuli was swept across the

inner object positions. Due to delays by saccade detection and screen refresh, in some trials the color patches were still present at these positions during the saccade. In case the postsaccadic sensory input had been integrated with this perisaccadic stimulation, the perceived color should have been shifted toward the presaccadic colors of the inner patches in these trials. The inner patches always were the counterpart to the presaccadic colors at the test positions. If, on the other hand, perisaccadic retinal stimulation induced an afterimage, postsaccadic perception should be shifted toward the presaccadic color of the outer patches (Webster & Mollon, 1991). The two different postsaccadic delays of the test patch presentation were chosen to test for the time course of the hypothesized transsaccadic integration.

In control trials, no presaccadic stimuli were presented. Control measurements were performed only with a 20-ms postsaccadic delay of stimulus onset. Measurements were performed in blocks of 54 or 72 trials each, with several blocks per session. The total number of valid trials per subject was 1080, including six repetitions per stimulus configuration.

Data analysis

By fitting psychometric functions to the responses, the points of subjective equivalence between the postsaccadic reference and test patch were estimated (Wachtler, Albright, & Sejnowski, 2001) depending on the presaccadic color configuration. Trials with postsaccadic patches in inner columns and outer columns and different postsaccadic delay times were analyzed independently. Responses from trials with leftward and rightward saccades as well as those with the reference stimulus in the top and the bottom row were pooled for analysis to average out possible observer-specific or systematic perceptual asymmetries (e.g., Levine & McAnany, 2005). Saccadic trials in which the presaccadic color stimuli had not been turned off at the end of saccade execution (less than 5% of saccadic trials) were discarded from analysis. Psychometric functions were analyzed using psignifit version 2.5.6 (http://bootstrap-software.org/psignifit/), a software package that implements the maximum-likelihood method described by Wichmann and Hill (2001a). Confidence intervals were found by the percentile bootstrap method implemented by psignifit, based on 10.000 simulations (Wichmann & Hill, 2001b). Significance of threshold shifts was tested by computing the probability that the threshold difference of the two independent data sets was smaller than differences of thresholds of bootstrapped data sets based on the psychometric function that was fitted to a combination of the data sets of the two conditions. Therefore, 10.000 Monte Carlo simulations of independent and combined data sets were performed, as implemented in the same toolbox.

Results

Mean saccadic latencies ranged from 175 ms to 194 ms (observer SM: 175 ± 31 ms; RH: 178 ± 27 ms; JF: 184 ± 25 ms; CM: 194 ± 38 ms; MW: 179 ± 20 ms). The saccade duration was about 59 ms (observer SM: 59 ± 4 ms; RH: 59 ± 8 ms; JF: 58 ± 5 ms; MW: 67 ± 7 ms; CM: 53 ± 5 ms). The mean delay between saccade start and extinction of the presaccadic color patches was 30 ± 10 ms (all values mean $\pm$ SD). Thus the visual stimuli disappeared during the saccade.

For each presaccadic stimulus configuration, we determined the chromaticity of the postsaccadic stimulus at the same screen location that was perceptually equivalent to the reference stimulus. We fitted psychometric functions to the fraction of "yellower" responses as a function of test chromaticity and determined the shift of the 50% point depending on the presaccadic stimulus. Figure 2 shows the psychometric functions for all observers. Overall Goodness of fit was computed for all curves using deviance D (Dobson, 1990; Wichmann & Hill, 2001a). Comparing the D values of the data sets with distributions of D^* generated by a bootstrap method using the parameters of the fitted curve, all D values except for one curve were in 95% confidence intervals, indicating acceptable goodness of fit of the collected data with logistic shaped functions. For some curves, singular points had to be omitted as outliers (determined by a jackknife procedure; see Wichmann & Hill, 2001a).

Black curves in Figure 2 indicate the responses in trials without presaccadic color patches, i.e., the baseline condition. The small shifts with respect to the reference chromaticity were not systematic across observers. Red (yellow) curves show data for trials with red (yellow) presaccadic patches at the screen position of the postsaccadic test patch.

In the 20-ms delay condition, response functions for presaccadic red and yellow patches were shifted significantly relative to each other for observers SM, RH, JF, and MW at inner test positions and for observers SM, RH, MW, and CM at outer test positions, indicating a significant difference ($p < 0.05$) in the perceptual point of subjective color equivalence with different presaccadic color configurations. For red previews at the test position, the preview at the reference stimulus position was yellow. In this case physically more yellow test stimuli were necessary to be perceived as same hue as the reference stimulus, and vice versa, as if pre- and postsaccadic colors at the same spatial (not retinal) position were perceptually mixed. Differences in the 140-ms delay condition were smaller but significant except for data of observer RH in the outer and observer MW and CM in the inner condition. For observer JF, the appearance shift in the outer condition was in the reversed direction.

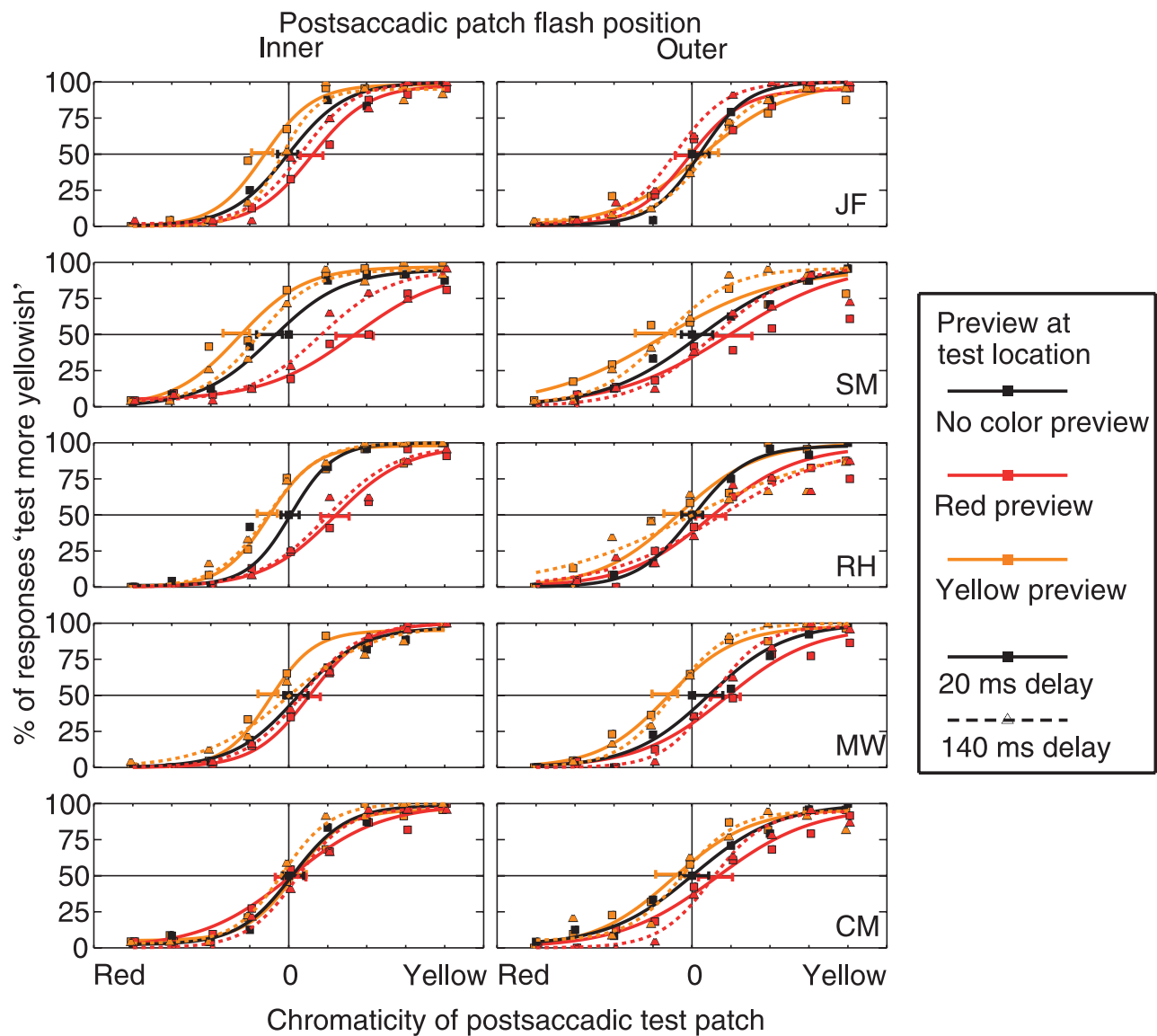Figure 3 shows averaged shifts of the points of subjective equivalence for the 20-ms delay and the 140-ms delay

Figure 2. Psychometric functions. Rows show data of different subjects, with data for inner and outer postsaccadic test positions in columns. Solid lines and squares indicate the condition with 20-ms delay between saccade end and test patch onset; triangles and dashed lines correspond to the 140-ms delay condition. Colors indicate the presaccadic patch color at the test patch position (black: blank control). The shifts of the 50% points indicate the chromaticity of the test stimulus that would have been perceptually equivalent to the reference stimulus. Note that presaccadic colors at the spatial locations of test and reference were always different. Error bars at the 50% point indicate 95% confidence intervals, as estimated with a bootstrap simulation (shown only for the 20-ms condition).

conditions computed across all observers. Color shift s was measured as fraction of the color difference between point of subjective equality c_s and the chromaticity of the reference c_r and the average chromaticity of reference and presaccadic stimulus c_p. This compares the observed appearance shift to the shift that would occur if pre- and postsaccadic stimuli would contribute equally to the appearance of the postsaccadic test. We took into account that the presaccadic stimuli at the test and reference positions had different colors by dividing by a factor of two, which yields $s = |c_s - c_r| / |c_r + c_p|$. This measure is analogous to the Brunswik (1928) ratio, which is commonly used to quantify perceptual shifts. The shifts were

significant for both the 20-ms and the 140-ms delay condition and in the magnitude of about 10%. The effect was smaller for the outer positions and the longer postsaccadic delays, but differences were not significant (Kruskal–Wallis test across conditions, $p > 0.05$).

With two subjects we performed two further control experiments. The first control experiment was implemented to determine whether or not the effect depended on the assignment of color to an object, which can be expected to remain stable during a saccade. In this experiment, the circle outlines were extinguished after saccade detection to disturb object identity assignments across the saccade. Otherwise, the protocol was identical
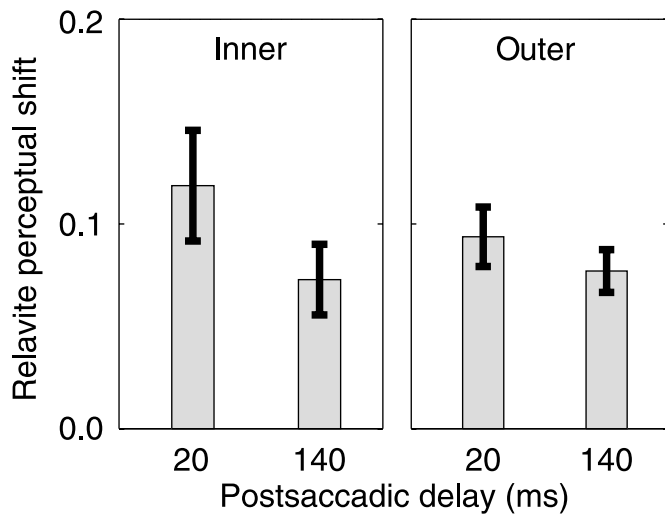
Figure 3. Averaged perceptual shifts. Perceptual shifts averaged across all subjects are shown for 20-ms postsaccadic delay and 140-ms delay. Shifts were measured as ratio of the color difference between point of subjective equality to the chromaticity of the reference and the average chromaticity of reference and presaccadic stimulus. A value of 1 indicates an equal contribution of pre- and postsaccadic color to the perceived hue (see main text). Left: test at inner locations, right: test at outer locations. Error bars indicate standard error.

to the main experiment. For both subjects, the shifts in the control condition were similar to those in the main experiment (see Supplementary data), indicating that spatial or feature-based, not object-based mechanisms underlie the integration of color stimuli across saccades.

In the second control experiment, we used simulated saccades to investigate the influence of retinal motion. Subjects had to fixate throughout the trial, while the initial color stimuli and the circle outlines were moved horizontally, the color stimuli were turned off, and afterward were followed by two flashed test stimuli. Temporal and spatial configurations of the stimulus display were adjusted to achieve similar retinal stimulation as in the saccade experiments. The motion of the stimulus pattern took place over five screen refreshes. The successive stimulus positions during this period were adjusted to the average saccade dynamics as measured in the main experiment. To mimic the distribution of cessation times of presaccadic stimulus colors in saccade trials, color fillings were turned off at the second, third, or fourth frame, respectively, chosen randomly. In this experiment, we observed, for both inner and outer test positions, an appearance shift toward the color of the patches nearer to fixation, which during the simulated saccade swept across the retinal positions of the test (see Supplementary data). This is in contrast to the shifts observed with real saccades, which depend on the presaccadic color at the spatial location of the test. Thus, retinal motion cannot explain the effects observed in the main experiment.

Discussion

Our data show significant effects of presaccadically presented colored stimuli on the color appearance of postsaccadic test stimuli at the same spatial position. Shifts in appearance of postsaccadic stimuli indicated a mixture of pre- and postsaccadic hues. The appearance shifts declined after saccade execution, but, unlike other perisaccadic perceptual effects (Ross, Morrone, Goldberg, & Burr, 2001), were still observed 140 ms after saccade termination. The results demonstrate transsaccadic integration of color and are compatible with the integration of previously reported time courses of remapping activity (Nakamura & Colby, 2002). The magnitude of the color appearance shifts in our experiment is 1.5 times the discrimination threshold in the fixation condition. These results seem compatible with the finding that 50% or fewer cells in retinotopically organized areas exhibit remapping activity (Nakamura & Colby, 2002). Typically, objects in the visual environment do not change during a saccade. It may therefore be a useful strategy for the visual system to preactivate presaccadically those neurons in retinotopically organized areas that have receptive fields at the postsaccadic retinal position of a visual object.

Pre- and postsaccadic stimuli in our experiments were presented at different retinal locations. Our results therefore cannot be explained by temporal integration or contrast effects (Brenner, Granzier, & Smeets, 2007) but indicate active mechanisms of saccadic updating. Similar shifts were found for a motor learning situation where stimulus color changes were correlated with saccade direction (Bompas & O'Regan, 2006). Finally, our observed shifts in hue perception cannot be explained by postsaccadic enhancement of chromatic contrast sensitivity (Burr, Morrone, & Ross, 1994); however, both effects may have a similar neuronal basis.

Perisaccadic retinal stimulation

Perception of isoluminant chromatic stimuli is only weakly affected by saccadic suppression (Burr et al., 1994; Uchikawa & Sato, 1995). Therefore, timing of stimulus presentation with respect to the saccade was critical in our experiments to prevent stimulation by receptive fields shifting across stimulus patches during the saccade. Due to delays in saccade detection and variability in saccade durations, this was not always possible for the stimuli at "outer" positions (Figure 1). However, because of the checkerboard configuration of the presaccadic patches, these perisaccadic stimulating color patches were yellow when the presaccadic stimulus was red, and vice versa. Therefore, additive transsaccadic integration of these stimuli should have led to

a reduction or even reversal of the perceptual shifts induced by the presaccadic stimuli. A contrast effect (i.e., afterimage) should have led to a stronger shift. However, in these trials with testing at "outer" positions, a perceptual shift being about 10% smaller in size was found. But this difference was not significant (Kruskal–Wallis test, $p > 0.05$).

Neuronal correlates

Spatiotopic representations in visual cortex have been reported for the dorsal pathway (Duhamel et al., 1997; Galletti et al., 1993). Cells in these areas have large receptive fields and are not color selective. To provide a basis for a map-like visual buffer, spatiotemporal binding to the feature contents in other areas would be necessary. To obtain the reported results would require integration of pre- and postsaccadic color information, e.g., by perceptual coupling of decaying presaccadic with incoming postsaccadic activity in the ventral stream, or by temporal integration in a downstream module that is involved in the decision process in the task, or even directly in the retinotopic representations (see below). Prime, Tsotsos, Keith, and Crawford (2007) found nearly perfect transsaccadic memory for up to four objects. But in their experiment it was the explicit task to memorize as many presaccadic objects as possible to detect postsaccadic changes, whereas we instructed our subjects to ignore the presaccadic colors. This makes it unlikely that memory played an important role in the decision process in our experiments, even though the test positions were arranged around the saccade target.

As an alternative explanation, the reported transsaccadic perceptual integration could be evoked by means of selective remapping of presaccadic information in retinotopically organized areas. At saccade onset, this transfer could selectively preactivate pools of neurons that are tuned to the corresponding presaccadic value of a coded feature (e.g., color). Since color is represented in the cortex by a population code (Wachtler, Sejnowski, & Albright, 2003), many neurons with overlapping color selectivities will encode the stimuli in our experiments, which varied between red and yellow. If a red stimulus was presented presaccadically, those neurons with preferences for reddish colors would be preactivated and would respond stronger to the appearance of the postsaccadic stimulus. Thus, the overall activity pattern of the neurons encoding this stimulus would be biased toward red. Consequently, the postsaccadic stimulus would look more reddish compared to the same stimulus presented without a red presaccadic stimulus.

Previous psychophysical studies of updating mostly used tasks that required processing primarily in the dorsal pathway (Melcher & Morrone, 2003; Prime et al., 2006). In our study, we used a color appearance task. While color information is used for the processing of spatial and

motion information in the dorsal pathway (Dobkins & Albright, 1994; Gegenfurtner et al., 1994; Toth & Assad, 2002), so far there is no indication for processing of chromatic signals relevant for color appearance judgments outside the ventral pathway (Heywood & Kentridge, 2003; Zeki, 1980). A previous approach to test object-selective remapping in ventral pathway reported a transfer of adaptation after-effects (Melcher, 2005, 2007). These findings are in line with our results because in both cases, the effects can be interpreted as integration of a remapped presaccadic activity state with postsaccadic input. In Melcher's design, however, the visual system was adapted for at least three seconds, followed by a delay of several hundred milliseconds before the saccade was initiated. Therefore, the system was in a post-adaptation situation. In our experiments, on the other hand, presaccadic stimuli were displayed for 1100 ms or less and were present until saccade onset. A mechanism to explain the effect could be a selective gain increase or preactivation of the representation of the region around the saccade target as reported by Moore et al. (1998). Recently, Hamker, Zirnsak, Calow, and Lappe (2008) proposed a model whose predictions are consistent with reported perceptual distortions of space and shifts of receptive fields during saccades. An essential mechanism of the model is an oculomotor feedback signal that acts on retinotopically organized neuronal maps prior to a saccade. It is conceivable that the results of our experiments could be explained by a similar mechanism that acts on feature-specific representations. Taken together, we consider the results of our study as evidence that updating mechanisms for object features occur not only under adaptation conditions but are also involved in processing of dynamically changing visual input under natural viewing conditions.

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