When circles become triangular: how transsaccadic predictions shape the perception of shape

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Human vision is characterized by a consistent pattern of saccadic eye movements. With each saccade, internal object representations change their retinal position and spatial resolution. This raises the question as to how peripheral perception is affected by imminent saccadic eye movements. Here, we suggest that saccades are accompanied by a prediction of their perceptual consequences (i.e., the foveation of the target object). Accordingly, peripheral perception should be biased toward previously associated foveal input. In this study, we first exposed participants to an altered visual stimulation where one object systematically changed its shape during saccades. Subsequently, participants had to judge the shape of briefly presented peripheral saccade targets. The results showed that targets were perceived as less curved for objects that previously changed from more circular in the periphery to more triangular in the fovea. Similarly, shapes were perceived as more curved for objects that previously changed from triangular to circular. Thus, peripheral perception seems to depend not solely on the current input but also on memorized experiences, enabling predictions about the perceptual consequences of saccadic eye movements.

Keywords: eye movements; prediction; anticipation; transsaccadic memory; peripheral vision

Introduction

Visual perception is established by a consistent pattern of eye movements. In primates, fixations are interrupted by fast ballistic eye movements, the so-called saccades, several times each second. This, in evolutionary terms, old “saccade-and-fixate” strategy guarantees that the high-resolution foveal region is brought to interesting spots for detailed visual sampling. As a consequence, with each new fixation, objects change their retinal position and, owing to the visual system's nonhomogeneity, their spatial resolution as well.

While saccadic eye movements are the key to our remarkable visual abilities, they also pose several challenges to our visual system that need to be overcome to assure stable and detailed perception. First, the retinal motion of objects caused by saccades needs to be ignored to distinguish it from real object motion. Second, object information before and after a saccade needs to be linked to establish object correspondence. As will be elaborated, the solutions implemented by the visual system to tackle these problems may lead to specific perceptual effects accompanying saccadic eye movements, which provide informative clues about visual perception.

Saccadic eye movements and visual perception

The question as to how saccades affect visual perception has been a subject of investigation since the early days of experimental psychology. For example, it has been shown that vision is strongly impaired during the short time it takes to complete a saccade, an effect known as saccadic suppression. In functional terms, saccadic suppression may help to ignore retinal object motion caused by saccades. Conversely, perceptual improvements occur at the current and future retinal saccade target location shortly before the saccade. These
location-specific saccadic-enhancement effects have been suggested to reflect the (partly predictive) allocation of attentional resources.\textsuperscript{9,10,12} In functional terms, saccadic enhancement may help to link object information across saccades (see Ref. 3).

In addition to these more or less inherent perceptual effects of saccadic eye movements, visual perception is also specifically modulated by previous saccade-contingent experience. For example, color perception is modified after wearing spectacles that introduced an artificial coupling of eye movements and color changes.\textsuperscript{13} Moreover, we recently showed that the perception of spatial frequency in the periphery is modified after experiencing an artificial coupling of eye movements and changes in spatial frequency of saccade target objects.\textsuperscript{3} More specifically, participants in the study of Herwig and Schneider first underwent a 30-min acquisition phase where, unnoticed by participants, one object systematically changed its spatial frequency during the saccade. In the following test phase, the frequency of peripheral saccade targets was perceived as higher for objects that previously changed from low in the periphery to high in the fovea. Similarly, the frequency of peripheral targets was perceived as lower for objects that previously changed from high to low. This result indicates that peripheral visual perception is specifically biased toward previously associated post-saccadic foveal input. Such influences of anticipated effects on presaccadic visual processing fit well with the idea that perception depends, in large measure, on memorized experiences enabling predictions about future events.\textsuperscript{14–16} Accordingly, we proposed a \textit{transsaccadic feature prediction} mechanism accompanying saccadic eye movements. This mechanism is thought to be based on past experience and enables the visual system to predict visual features of objects across saccades.\textsuperscript{3,17}

This study

Up to now, effects of transsaccadic feature prediction on visual perception have been exclusively reported for surface features (i.e., color and texture) that are known to play an important role in establishing object correspondence while moving the eyes.\textsuperscript{18,19} As a consequence, it is not known whether visual features other than color and texture are predicted across saccadic eye movements. Given that relatively precise information about the visual form of a saccade target object is also retained across a saccade,\textsuperscript{20} shape features might be a likely candidate for a transsaccadic prediction mechanism. Thus, this study was conducted to test whether the perception of visual shape in the periphery is partly based on predicted post-saccadic foveal input. To this end, we adopted the paradigm of Herwig and Schneider (see Ref. 3) and introduced an artificial coupling of eye movements and visual form changes of saccade target objects. More precisely, for half the participants, unfamiliar associations were established by changing the shape of one object (swapped object, hereafter) during the saccade from more circular to triangular. For the other half of participants, the swapped object changed its shape from more triangular to circular. If peripheral shape perception is subject to a transsaccadic feature-prediction mechanism, one and the same shape should be perceived differently for previously swapped objects compared with previously unswapped objects.

Methods

Participants

Sixteen participants, whose ages were between 21 and 33 years, took part in this study. Ten of the participants were female. Informed written consent was obtained from each participant before the experiment, and they received reimbursement for their participation. All participants reported normal or corrected-to-normal vision and were naive with respect to the aim of the study.

Apparatus and stimuli

Participants performed the experiment in a dimly lit room and stimuli were presented on a 19-in display monitor running at 100 Hz at a distance of 71 cm. The screen's resolution was set to 1024 × 786 pixels, which corresponded to physical dimensions of 36 cm (width) × 27 cm (height). Eye movements were recorded with a video-based tower-mounted eye tracker (Eye Link1000, SR Research, Ontario, Canada) with a sampling rate of 1000 Hz. In all participants, the right eye was monitored, and the head was stabilized by a forehead-and-chin rest. The central fixation stimulus was a black “+” character (0.3° × 0.3°, line width 2 pixels) (see Fig. 1). As potential saccade targets, we used equiluminant red and green stimuli (31 cd/m²) of different shapes. More precisely, two-dimensional (2D) shapes were created by choosing five intermediate steps of a transformation of a circle (radius = 0.74°) into an equilateral triangle.
triangular shape (side length = 1.6°). The different shapes are defined by the curvature of their sides ($\kappa = 0.74^\circ$/radius), which range from 0 for the triangle to 1 for the circle. In this study, we used shapes with curvatures of 0.27, 0.4, 0.53, 0.66, and 0.79 (Fig. 1D). All stimuli were presented on a gray background with a mean luminance of 30 cd/m$^2$.

**Procedure and design**

The experiment was run in a single session of about 45 min and comprised an acquisition phase and a test phase (Fig. 1A and B). Before each phase, a nine-point grid calibration procedure was applied. Each trial of the acquisition phase started (following a variable fixation interval of 500–1000 ms) with the presentation of a red and a green object that appeared at 6° to the left and right of the screen’s center at random. Participants were instructed to saccade to either the red or the green object, depending on their own choice, but to look at each object about equally often. Feedback regarding the number of saccades to the red and green object was provided every 48 trials. Importantly, the peripheral red and green object differed in their shape, with one object being more triangular ($\kappa = 0.27$) and the other object being more circular ($\kappa = 0.79$). Note that the shape of the objects was task irrelevant. The mapping of color and peripheral shape was fixed for each participant but counterbalanced across participants. For subgroup A, we consistently replaced the more circular object ($\kappa = 0.79$) with a more triangular object ($\kappa = 0.27$) of similar color during the saccade, whereas for subgroup B, we replaced the more triangular object ($\kappa = 0.27$) with a more circular object ($\kappa = 0.79$) during the saccade. That is, different shapes of one saccade target object with a particular color (swapped object) were presented to the presaccadic peripheral and post-saccadic foveal retina. Thus, for subgroup A, the swapped object always changed its shape from more
circular to triangular, whereas for subgroup B, the swapped object always changed its shape from more triangular to circular (Fig. 1C). For both subgroups, saccades to the peripheral object with the other color (normal object, hereafter) did not lead to a replacement. Thus, for the normal object, the same shape was presented to the presaccadic peripheral and postsaccadic foveal retina. Following the saccade, both objects were presented for 250 ms and then replaced with a blank screen for 1500 ms’ duration. With this manipulation, we could ensure that participants always foveated objects with the same shape. The shape of the swapped and the normal object only differed before the saccade in the periphery. The acquisition phase consisted of 240 trials, which were run in five blocks of 48 trials each. In the test phase (Fig. 1B), participants had to saccade as fast and accurately as possible to a target object, which appeared 6° to the left or right of the fixation stimulus. When no saccade was made within 350 ms after target onset, the trial was aborted and participants received an error message asking them to execute the eye movement faster. The target object was either red or green and varied in shape. In two-thirds of the trials, we presented a target object with a curvature of 0.53. In the remaining third of the trials, the target object’s curvature was 0.27, 0.4, 0.66, or 0.79. These later catch trials were inserted to prevent participants from noticing the uniformity of the target object’s curvature. To ensure that targets were only presented to the peripheral retina, we replaced them with a fixation stimulus as soon as the eyes started to move. Five hundred milliseconds after completion of the saccade, a test object was presented at the previous and now foveated saccade target location. The participants’ task was to match the shape of this foveally presented test object to the shape of the presaccadic peripheral target object. The shape of the test object was chosen at random among the five different curvatures (0.27, 0.4, 0.53, 0.66, and 0.79), but could be incrementally changed in steps of 0.13° by pressing the up- or downward pointing arrow keys on the keyboard (for a related procedure, see Ref. 3). Pressing the Enter key terminated the trial. The test phase consisted of 192 trials, which were run in four blocks of 48 trials each.

**Data analysis**

Saccade onsets were detected using a velocity criterion of 30 °/s. In the acquisition phase, we discarded 4% of trials where the saccadic latency was <100 ms or >1000 ms. In the test phase, only trials with target objects presented with a curvature of 0.53 were analyzed. We discarded 5% of these test trials where the saccade latency was <100 ms or >350 ms.

**Results**

**Acquisition phase**

During acquisition, participants looked at the to-be-swapped object and the normal object about equally often (49.3% vs. 50.7%). Moreover, they did not take longer to saccade to the to-be-swapped object (M = 308 vs. 311 ms). Swapping occurred during the saccade (mean delay after saccade onset (±SD) was 29.3 (±3.8) ms; mean saccade duration was 43.9 (±8.4) ms).

**Test phase**

Mean shape judgments and saccadic latencies of the test phase were analyzed as a function of the within-subjects factor object status during acquisition (normal vs. swapped) and the between-subjects factor change direction (circular to triangular vs. triangular to circular).

The 2 (status) × 2 (direction) mixed analysis of variance (ANOVA) on judgment data revealed a significant interaction of status and direction \( (F(1, 14) = 17.057, P = 0.001, \eta^2_p = 0.55) \), which is depicted in Figure 2. As can be seen in this figure, and as was corroborated by separate tests for each direction subgroup, participants of subgroup A judged the shape of peripheral objects that were swapped during acquisition from circular to triangular to be less curved than that of objects that were not swapped during acquisition \( (t(7) = 2.633, P = 0.034) \). Conversely, participants of subgroup B judged the shape of peripheral objects that were swapped during acquisition from triangular to circular to be more curved than that of objects that were not swapped during acquisition \( (t(7) = -3.326, P = 0.013) \).

Neither the main effect of status nor the main effect of direction reached significance (all \( Fs < 0.04, Ps > 0.864 \)). The analysis of latencies (mean saccadic latency was 176 (±40) ms) showed no significant effects (all \( Fs < 1.51, Ps > 0.239 \)).

In addition, we fitted the shape judgments for each participant (Fig. 3) with a Gaussian function \( \left( y = a \times e^{-(x-b)/c^2}\right) \) using the Curve-fitting Toolbox of Matlab (R2013b) to test for
differences in three parameters: $a$ (representing the amplitude of the Gaussian distribution), $b$ (representing the centroid), and $c$ (representing the peak’s width). Significant effects mirroring the previous analysis were found for parameter $b$, the centroid of the Gaussian function, the interaction of status and direction ($F(1, 14) = 15.119, P = 0.002, \eta^2_p = 0.52$). Separate tests revealed that, in subgroup A, parameter $b$ was higher for previously swapped objects (triangle to circle, $M = 0.52$) than for normal objects ($M = 0.48; t(7) = −2.77, P = 0.028$). Conversely, in subgroup B, parameter $b$ was lower for previously swapped objects (circle to triangle, $M = 0.48$) than for normal objects ($M = 0.52; t(7) = 2.75, P = 0.028$). No significant effects were found for parameters $a$ or $c$. Goodness of fit was excellent ($R^2$ triangle to circle, normal ($M = 0.97$) and swapped ($M = 0.97$), circle to triangle normal ($M = 0.99$) and swapped ($M = 0.99$)).

**Discussion**

The past decades witnessed a great deal of research confirming that perception and action are tightly interrelated.\textsuperscript{15,22–25} This is particularly true for the oculomotor system, which can be considered as a fundamental action as well as a perceptual device.\textsuperscript{26,27} Accordingly, each saccadic eye movement has profound effects on visual perception.
ranging from suppression effects around the time of the saccade\(^5\text{-}^7\) to location- and object-specific enhancement effects.\(^9\text{-}^{10}\) Here, we focused special emphasis on perceptual effects of saccades that are due to previous experience. More precisely, we suggested that saccadic eye movements are accompanied by a prediction of their perceptual consequences (i.e., the foveation of the target object).
Such transsaccadic predictions are assumed to be based on previous learning linking pre- and postsaccadic input.\textsuperscript{3,17,28,29} If this holds true, it should be possible to bias predictions by creating new and unfamiliar associations of peripheral and foveal patterns. In this study, we established such unfamiliar associations by changing the shape of objects during the saccade.

The present results clearly indicate that peripheral shape perception is biased toward previously associated foveal input. That is, peripheral shapes were perceived as less curved in objects that previously changed from more circular in the periphery to more triangular in the fovea. Similarly, shapes were perceived as more curved for objects which previously changed from triangular to circular. While the observed biases in peripheral shape perception were rather small, they were, however, highly consistent. Please note that comparable magnitudes have been observed previously\textsuperscript{3} and, that given the short acquisition phase of only 30 min pitted against a lifetime of previous learning in an unaltered visual environment, the small magnitude is not surprising. Moreover, using an unspeeded postsaccadic report to assess presaccadic perception allows the possibility that the biases have their locus at a memorial rather than a perceptual stage. While this concern pertains to almost all tests of presaccadic perception, and while these stages are not always clearly distinguishable,\textsuperscript{30} a simultaneous matching task might be suited to assess peripheral perception more directly.

The present finding extends existing evidence for transsaccadic prediction of surface features\textsuperscript{3,13} to another class of visual features, namely contour features that are crucial for shape perception and object recognition. At the neural level, processing of object features occurs in the ventral pathway through numerous levels in a recurrent network from the primary visual cortex (V1) to the inferior temporal cortex (IT).\textsuperscript{31} This raises the question of what the exact visual level of transsaccadic feature prediction is. Curvature, as an advanced shape property, has been shown to be prominently represented in area V4.\textsuperscript{32} V4 is an important intermediate stage in the ventral pathway supporting object recognition and has been shown to be modulated by attention and saccade preparation.\textsuperscript{33} Moreover, area V4 is also known to be highly relevant in color and surface perception.\textsuperscript{34,35} At the behavioral level, changing mid-level features like object shape across the saccade diminishes postsaccadic identification.\textsuperscript{20} On the contrary, low-level visual properties such as luminance or contrast are known to be abstracted from transsaccadic memory.\textsuperscript{36} Taken together, all these different observations indicate that mid-level visual features may play critical roles for transsaccadic prediction. This idea fits well with theoretical and computational models assuming a crucial role of such mid-level features in the control of saccadic eye movements.\textsuperscript{37,38}

In general, the prediction of visual object features across saccades can have multiple effects on perception as well as on action control. First, transsaccadic predictions probably conceal acuity limitations in the periphery, which might explain why the visual field seems to be uniformly detailed most of the time.\textsuperscript{3,39} Second, predicting the perceptual consequences of eye movements probably also leads to the temporal predating of saccadic eye movements, because the predicted foveal perceptual pattern before saccade execution is confused with the actual visual impression after the saccade.\textsuperscript{40} Finally, transsaccadic predictions may also affect saccade execution, as suggested by recent findings showing that eye movements during visual search and face perception are directed toward their predicted visual effects.\textsuperscript{3,17,29}

It is essential, however, to keep note of the main functions of transsaccadic prediction. On the one hand, predicting foveal input allows the establishment of object correspondence across saccades.\textsuperscript{37} Given the nonhomogeneity of the visual system and possible oculomotor errors, this process is of utmost importance for \textit{saccade monitoring} (i.e., the postsaccadic evaluation of failure or success of the saccadic eye movement). On the other hand, transsaccadic predictions are essential for \textit{saccade target selection}, as suggested by ideomotor-inspired theories of action control.\textsuperscript{3,29,41} According to ideomotor theory, actions are assumed to be selected with respect to their intended and anticipated perceptual effects.\textsuperscript{15,23,42} For actions performed by the oculomotor system such as saccades, these effects ultimately lie in the foveation of the saccade target.

**Conclusions and future perspectives**

The main goal of this study was to investigate how past experience associated with making saccadic eye movements modulates peripheral perception. The
results provide support for the idea that peripheral perception is biased toward previously associated foveal input. In particular, peripheral objects were perceived to be more triangular or circular if their shape were contingently changed in a preceding acquisition phase. Thus, peripheral perception seems to depend not solely on the current input but also on memorized experiences enabling predictions about the perceptual consequences of saccadic eye movements.

An important next step will be to further specify the level of transsaccadic feature prediction by systematically varying different low-, mid-, and high-level visual features across saccades. Progress along this line may help to identify the visual areas involved in transsaccadic prediction. A further interesting point for future research is the comparison of factors influencing the acquisition and application of transsaccadic associations. For example, while testing object correspondence seems to be based on the application of associations for transsaccadic prediction, breaking object continuity across saccades does not prevent the acquisition of these associations. Finally, another line for future research will be to determine whether predictions pertain to saccade target objects alone or whether other relevant objects (e.g., objects in visual working memory) are also subject to transsaccadic prediction.

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[Correction added on March 10, 2015, after first online publication: In the final paragraph of the Conclusions and future perspectives section, the citation of reference 43 was changed to “37” in the fourth and fifth sentences.]

Conflicts of interest

The authors declare no conflicts of interest.

References


