Selective enhancement of orientation tuning before saccades

Sven Ohl*
Department of Psychology, Humboldt-Universität zu Berlin, Germany
Bernstein Center for Computational Neuroscience, Berlin, Germany

Clara Kuper*
Department of Psychology, Humboldt-Universität zu Berlin, Germany
Bernstein Center for Computational Neuroscience, Berlin, Germany
Freie Universität, Berlin, Germany

Martin Rolfs
Department of Psychology, Humboldt-Universität zu Berlin, Germany
Bernstein Center for Computational Neuroscience, Berlin, Germany

Saccadic eye movements cause a rapid sweep of the visual image across the retina and bring the saccade's target into high-acuity foveal vision. Even before saccade onset, visual processing is selectively prioritized at the saccade target. To determine how this presaccadic attention shift exerts its influence on visual selection, we compare the dynamics of perceptual tuning curves before movement onset at the saccade target and in the opposite hemifield. Participants monitored a 30-Hz sequence of randomly oriented gratings for a target orientation. Combining a reverse correlation technique previously used to study orientation tuning in neurons and general additive mixed modeling, we found that perceptual reports were tuned to the target orientation. The gain of orientation tuning increased markedly within the last 100 ms before saccade onset. In addition, we observed finer orientation tuning right before saccade onset. This increase in gain and tuning occurred at the saccade target location and was not observed at the incongruent location in the opposite hemifield. The present findings suggest, therefore, that presaccadic attention exerts its influence on vision in a spatially and feature-selective manner, enhancing performance and sharpening feature tuning at the future gaze location before the eyes start moving.

Introduction

The active observer is equipped with a powerful tool to constrain processing of visual information before imminent eye movements: *the presaccadic shift of attention* (see Rolfs, 2015, and Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012, for reviews). A tight coupling between attention and the planning of saccadic eye movements (Remington, 1980; Shepherd, Findlay, & Hockey, 1986) prioritizes visual information at the saccade's target and deteriorates information processing elsewhere in the visual field (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995). This selection mechanism becomes effective within only 60 ms of an instruction to move the eyes (Rolfs & Carrasco, 2012), and is thus considerably faster than the 300 ms it takes to wilfully deploy covert attention (Ling & Carrasco, 2006; Müller & Rabbitt, 1989).

While much effort has been devoted to delineating the mechanisms of covert attention (Carrasco, 2011), surprisingly little research has addressed the mechanism underlying presaccadic attentional selection. Candidate mechanisms suggested by psychophysical experiments include a change in perceptual feature tuning, filtering sensory information most similar to the target (Li, Barbot, & Carrasco, 2016). An alternative (or additional) mechanism is an increase in the gain of neural responses to stimuli at the saccade target. Indeed, neurons in V4—a key visual area in the extrastriate portion of the ventral stream—increase their response to stimuli in their receptive field when a saccade is about to target that stimulus, whereas a saccade directed away from the stimulus has no effect

Citation: Ohl, S., Kuper, C., & Rolfs, M. (2017). Selective enhancement of orientation tuning before saccades. *Journal of Vision*, *17*(13):2, 1–11, doi:10.1167/17.13.2.

doi: 10.1167/17.13.2 Received July 14, 2017; published November 1, 2017 ISSN 1534-7362

on the presaccadic neural response (Moore, Tolias, & Schiller, 1998).

In general, a gain increase of responses in single cells tuned to a specific feature value results in a narrowing of tuning curves at the neural population level (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999), in particular, for neurons that are highly feature-selective to begin with (Hembrook-Short, Mock, & Briggs, 2017). Changes in gain and tuning are thus not mutually exclusive and may both contribute to spatially specific enhancement of visual performance in visual discrimination tasks before an eye movement. In the case of planning a saccade while attending to a target orientation, both feature-based and spatial attention are involved. While feature-based attention acts across the visual field and depends on the task set, spatial attention arises at the saccade target once the eye movement is cued. Observed changes in tuning curves before a saccade are thus due to the deployment of spatial attention, but may interact with feature-based attention. Characterizing how presaccadic attention shapes ongoing visual processing is essential for computational models in vision (Hamker, Zirnsak, Calow, & Lappe, 2008; Miconi & VanRullen, 2016) and enables a deeper understanding of visual selection at different levels of analysis.

Here, we examine the time course of perceptual orientation tuning before saccade onset. In a recent study that pursued a similar research question, participants had to detect low contrast Gabors embedded in visual noise (Li et al., 2016). By relating orientation and spatial frequency information in the noise to detection reports (see also Wyart, Nobre, & Summerfield, 2012), these authors revealed orientation tuning curves that narrowed with time over the last 50 ms before saccade onset. Concurrently, the gain of high-spatial frequencies increased over time. Whereas this study compared orientation tuning during covert shifts of attention with those observed before saccades, we focus strictly on presaccadic attention. However, using a reverse correlation paradigm, typically used to characterize neural tuning curves (Ringach, 1998; Ringach, Hawken, & Shapley, 1997), we probed target detection at both the saccade target and a location in the opposite hemifield, allowing us to assess the obligatory nature of presaccadic tuning changes and their selectivity to the saccade target. We then employed general additive mixed modeling (GAMM) to assess the temporal dynamics of perceptual orientation tuning before saccades. Thus, by using a different experimental paradigm and analysis tool, the present study seeks to replicate and expand upon previously reported changes in tuning before saccades by contrasting tuning curves at two locations in the visual field. We find that nontarget locations exhibited weak orientation tuning. In stark contrast, perceptual processing at the saccade target showed a steadily increasing gain that was accompanied by finer orientation tuning right before saccade onset.

Method

Participants

We tested nine observers (mean age 22.3 years, $SD \pm 3.1$ years, three females, one left-handed) in five experimental sessions (one training and four test sessions with ~1 hr per session), with at least one night between consecutive sessions. In the training session, observers were instructed to familiarize themselves with the eye movement task throughout the first blocks and to do the perceptual task simultaneously with the saccade task only in subsequent blocks. Therefore, data from the training session was excluded from further analysis. All participants were naive as to the purpose of the study and signed informed consent prior to their participation. Participants had normal or corrected-to-normal vision and received 7€ per session as compensation for their participation and an additional 7€ after completion of all five sessions. The study was conducted in accordance with the Declaration of Helsinki (2008).

Materials and procedure

Observers were seated in a dark, quiet room. Their head was positioned on a chin rest in order to minimize head movements. The experiment was displayed at a distance of 57 cm on a 23.6-in. ViewPixx/3D screen (1920 × 1080 pixels; VPixx Technologies Inc., Saint Bruno, QC, Canada) with 10 bits of resolution on each of the RGB channels and a refresh rate of 120 Hz. We recorded eye position of the participant's dominant eye (determined beforehand using a hole-in-a-card test) with a sampling rate of 1000 Hz using an Eyelink 1000 Desktop Mount (SR Research, Ottawa, ON, Canada). A Dell precision T3600 workstation with a Debian 8 operating system running Matlab (Mathworks, Natick, MA), the Psychophysics Toolbox 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) and the Eyelink toolbox (Cornelissen, Peters, & Palmer, 2002) was used to control stimulus presentation, response collection, and online gaze control. Perceptual reports were collected via key press using a ResponsePixx (VPixx Technologies Inc., Saint Bruno, QC, Canada).

The participants' task was to detect either a horizontal or vertical Gabor patch, as defined in the beginning of a block, in a fast sequence of randomly oriented Gabors. We presented a fixation point (white

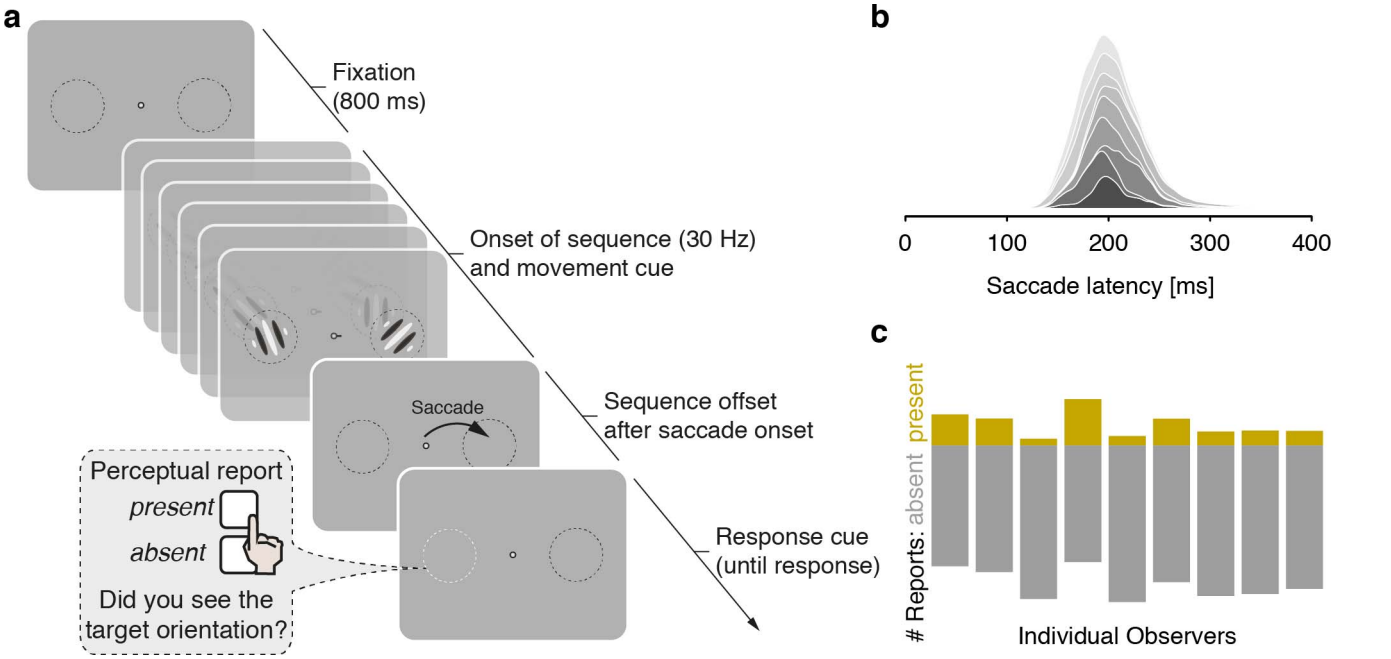

Figure 1. Experimental procedure, results, and model predictions. (a) At two locations, we presented random sequences of oriented Gabor patches at 30 Hz, along with a movement cue pointing to one of the two locations. Gabors and movement cue were removed after online detection of saccade onset. After saccade landing, a response cue appeared and highlighted the test location. Movement cue and response cue were uninformative with respect to each other; the location of the response cue was equally often congruent or incongruent with the saccade target. The observer's task was to report on the presence of a target orientation (horizontal or vertical, as defined at the beginning of each block of trials) at the highlighted location. The figure shows an example of a trial probing the incongruent location. (b) Stacked densities of saccade latencies for each individual observer. (c) Number of present (gold) versus absent (gray) reports for each individual participant.

circle with black contour) with a diameter of 0.6 degrees of visual angle (dva) on a gray background (Figure 1a). In addition, we displayed two circular black placeholders (3 dva diameter) at an eccentricity of 6 dva to the left and to the right from the central fixation point. After 800 ms of successful fixation (i.e., no blinks; eye positions were within a distance of 1.5 dva from the fixation point), the stimulus sequence was presented at a speed of 30 Hz (~33 ms per stimulus). The sequence consisted of up to 12 Gabor patches (depending on the saccade latency on a given trial; see below) with 100% contrast, randomly assigned spatial frequencies between 1 and 4 cycles per degree (cpd), a random phase, and 1° *SD* Gaussian envelope. Each Gabor patch had one out of 10 possible orientations distributed uniformly from 0° to 162°, in steps of 18°. Each Gabor patch had a randomly assigned orientation such that—given the median saccade latency—the sequence contained the target orientation in 47% of all trials. Due to this random assignment, the target orientation could be presented more than once in the orientation sequence. Simultaneously with sequence onset, we displayed a central *movement cue*, a small black line (length = 0.25 dva, thickness = 0.085 dva) extending from the fixation symbol, pointing to one of the two placeholders and prompting participants to move their eyes immediately to the indicated location. The sequence of stimuli and the movement cue were removed as soon as the onset of the eye movement was detected (i.e., eye positions were outside a radius of 1.5 dva from the fixation point *after* the presentation of the movement cue). Another 600 ms after the presentation of the movement cue, we presented a response cue: One of the two locations was highlighted by changing the color of the placeholder from black to white. Observers had to report whether they detected a target stimulus (i.e., a Gabor with defined target orientation) at the highlighted location by pressing one of two buttons. Importantly, the movement cue was uninformative with respect to the location of the response cue. As a consequence, in 50% of the trials the movement cue and response cue indicated the same location and in 50% of the trials the movement cue pointed to the location opposite from the response cue. Across the experiment, the direction of the saccade, therefore, was uncorrelated to the perceptual task, and participants were explicitly instructed to monitor both test locations.

A single session consisted of 24 blocks (with 32 trials per block), and we ran 12 blocks for each the horizontal and vertical target orientation, which were randomly interleaved. Trials in which the saccade was not made within 400 ms after cue presentation or in which

participants blinked during the trial were aborted. All aborted trials were repeated in a randomized order at the end of each block. Each observer completed a total of 3,072 trials in the course of the four test sessions.

Data analysis

For inferential statistics, we computed a GAMM for a binomial dependent variable (Hastie & Tibshirani, 1990). The GAMM allows us a nonparametric prediction of observers' reports (absent = 0, present = 1) from the orientation of the Gabor at a time point before saccade onset. The predictor variables in a GAMM are modeled as smooth functions (i.e., penalized regression splines), with an estimated complexity (i.e., estimated degrees of freedom) and the significance of their (possibly nonlinear) influence on reports is assessed. The GAMM is a powerful statistical tool that offers several advantages for the analysis of the present data. First, it is agnostic with respect to the shape of the tuning curves and their dynamics before the saccade. Second, it allows us to estimate the development of tuning curves at two locations for all observers in a single regression model. This is particularly helpful as we expected very weak (or even no) tuning for some conditions, which often impedes estimates of parameters in a time window dominated by noise. Third, the GAMM enables us to study the development of orientation tuning in a continuous fashion, where predictors at different time points are computed simultaneously in order to estimate a smooth (possibly nonlinear) evolution. This approach typically decreases the unreliability of (independently fitted) parameter estimates for data in arbitrarily defined time windows. In our GAMM, we included the predictors stimulus orientation and time of presentation before saccade onset, and the interaction of these two factors, Stimulus Orientation × Time. We restricted the analysis to a time window from a stimulus offset of −170 to 0 ms before saccade onset, as the median latency of saccades was 200 ms (Figure 1b) and the duration of a single stimulus was 33.3 ms. Moreover, we added the parametric factor congruency as a treatment contrast (0 = opposite hemifield; 1 = saccade target location) to the model; therefore, the predictors stimulus orientation, time, and their interaction predict perceptual reports for the incongruent location only (providing a baseline). To predict reports for the congruent location, we included the two-way interactions Time × Congruency, Orientation × Congruency, and the three-way interaction of Orientation × Time × Congruency. Note that the treatment of the two levels of congruency is arbitrary: Using congruent location as the baseline would yield identical results. Finally, for all nonparametric terms we also added their random effects (i.e., their interaction with participants) to the model. Statistical analyses were performed using the *mgcv* package (Wood, 2003, 2006, 2011) in the R environment (R Version 3.2.3, R Core Team, 2014). For inferential statistics of saccade parameters, we used repeated-measures analyses of variance (rmANOVA).

Saccades were detected offline by first transforming raw eye positions into two-dimensional velocity space, and then classifying successive eye positions as saccades when they exceeded the median velocity by 5 *SD*s for a minimum duration of 8 ms (Engbert & Mergenthaler, 2006). We merged two events classified as saccades into a single saccade when they were separated by less than 20 ms. We defined the response saccade as the first saccade with a distance between landing position and center of the saccade target smaller than 3.6 dva (i.e., 60% of the target's eccentricity). Trials were rejected from further analyses when (a) they included blinks or missing samples in the eye recordings or (b) they included saccades with an amplitude larger than 1 dva before execution of the response saccade. A total of 26,520 trials (96%) entered the final data analysis.

Results

We assessed perceptual orientation tuning before saccades using a reverse correlation approach in combination with a GAMM, enabling a nonparametric and nonlinear analysis of orientation tuning and its progression before saccades. We determined the relative influence of a range of stimulus orientations, displayed before saccade onset, on the detection of a target orientation at the saccade target and at an incongruent location. Similar approaches in electrophysiological studies in monkeys—that did not include perceptual reports—have shown a presaccadic enhancement of neural responses to stimuli at the saccade target, but no effect at a location opposite the saccade target (Moore et al., 1998).

Saccade parameters in our task did not vary between conditions. Saccade latency was unaffected by congruency between the saccade direction and the probed location, $F(1, 8) = 2.24$, $p = 0.173$; congruent: 203.6 ± 0.3 ms, incongruent: 203.2 ± 0.3 ms). Similarly, saccade amplitude was not affected by congruency, $F(1, 8) = 2.5$, $p = 0.149$; congruent: 6.27 ± 0.01 dva, incongruent: 6.25 ± 0.01 dva).

In general, the perceptual task was very difficult with observers reporting the presence of a target stimulus in only 13.3% of the trials on average (18.8% on target present trials and 9.4% in target absent trials, 14.7% in trials probing the congruent location and 11.9% in trials probing the incongruent location; Figure 1c). Critically, the probability to report the presence of the target orientation depended on stimulus orientation.

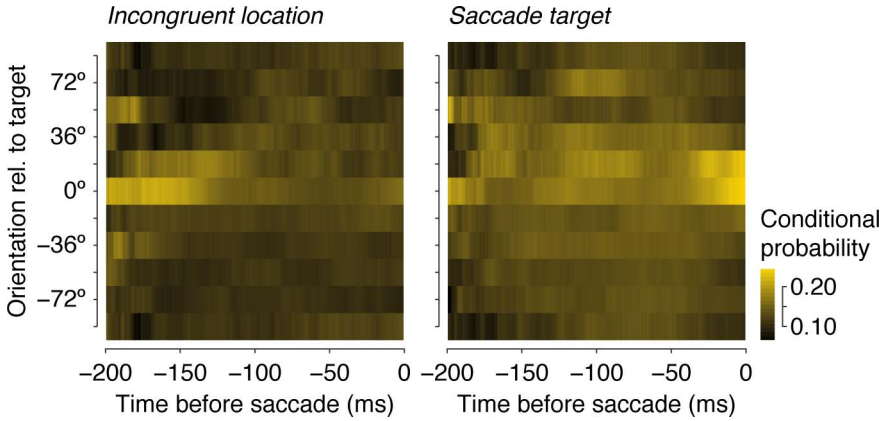

Figure 2. Mean probability of reporting the presence of a target orientation, conditional on a presented orientation in a given time window before saccade onset. Probabilities are shown for the saccade target location (right panel) and the incongruent location (left panel), respectively. Computation of single tiles in the heat map are based on all stimuli of the respective orientation that had their offset in a 33-ms time window ending at the indicated point in time.

Stimuli whose orientation matched the target orientation had the strongest influence on reporting the presence of a target orientation, both at the saccade target and the incongruent location (Figure 2), and this influence decreased for more dissimilar orientations, providing evidence for perceptual orientation tuning. Right before saccade onset, the probability for reporting the presence of a target orientation was elevated for near-target orientations at the saccade target as compared to the incongruent location. This suggests that saccades influence the dynamics of orientation tuning in a spatially selective manner.

We assessed the significance of orientation tuning before saccades at the saccade target (congruent location) and at the location in the opposite hemifield (incongruent location) using a GAMM, including parametric terms, smooth terms, and random effects (Table 1; see Method for detailed model setup). More specifically, when the target detection was probed at the incongruent location, we observed a significant influence of stimulus orientation on the perceptual report (estimated degrees of freedom [*edf*] = 5.85, $X^2 = 22.41$, $p = 0.002$). The probability of reporting target presence did not vary across time before saccade onset (*edf* = 1.00, $X^2 = 0.16$, $p > 0.250$). However, we observed a significant interaction of time and orientation at the incongruent location (*edf* = 7.77, $X^2 = 45.44$, $p < 0.001$). Closer inspection of Figure 3 (top right) suggests that this interaction arises from a time-limited orientation tuning 160 ms before the saccade that vanishes within 20 ms (see also Figure 4).

Importantly, tuning curves develop very differently for trials in which participants were asked about the presence of a target orientation at the saccade target. Overall, congruency did not influence the probability of reporting the presence of the target orientation (coefficient = 0.29, $z = 1.06$, $p > 0.250$). However, the tuning to the target orientation was significantly different between congruent and incongruent locations (*edf* = 6.75, $X^2 = 67.93$, $p < 0.001$), with a much more distinct tuning profile at the saccade target than at the opposite location (Figure 3, bottom-left). Moreover, before saccade onset, this orientation tuning evolved differently at the saccade target location than in the opposite hemifield (*edf* = 3.86, $X^2 = 44.98$, $p < 0.001$; Figure 3, bottom right). Note that the negative deflection for target orientations here (Figure 3, bottom right) must not be mistaken for a suppressive influence for stimuli close to the target orientation; instead, this partial effect rides on top of all other partial effects (Figure 3, top row and bottom left) and is the

Model term	Estimate	Statistic	*p* value
Parametric terms	Coefficient	*z* value	
Intercept	−2.26	−7.31	<0.001
Congruency	0.29	1.06	>0.250
Smooth terms	*edf*	X^2	
Orientation	5.85	22.41	0.002
Time	1.00	0.16	>0.250
Orientation × Time	7.77	45.44	<0.001
Orientation × Congruency	6.75	67.93	<0.001
Time × Congruency	1.80	2.13	>0.250
Orientation × Time × Congruency	3.86	44.98	<0.001
Random effects			
Orientation	8.64	13.59	<0.001
Time	3.99	7.95	<0.001
Orientation × Time	0.009	0.007	>0.250
Orientation × Congruency	42.58	165.23	<0.001
Time × Congruency	3.94	7.75	<0.001
Orientation × Time × Congruency	17.53	58.42	<0.001

Table 1. Results from the general additive mixed modeling.

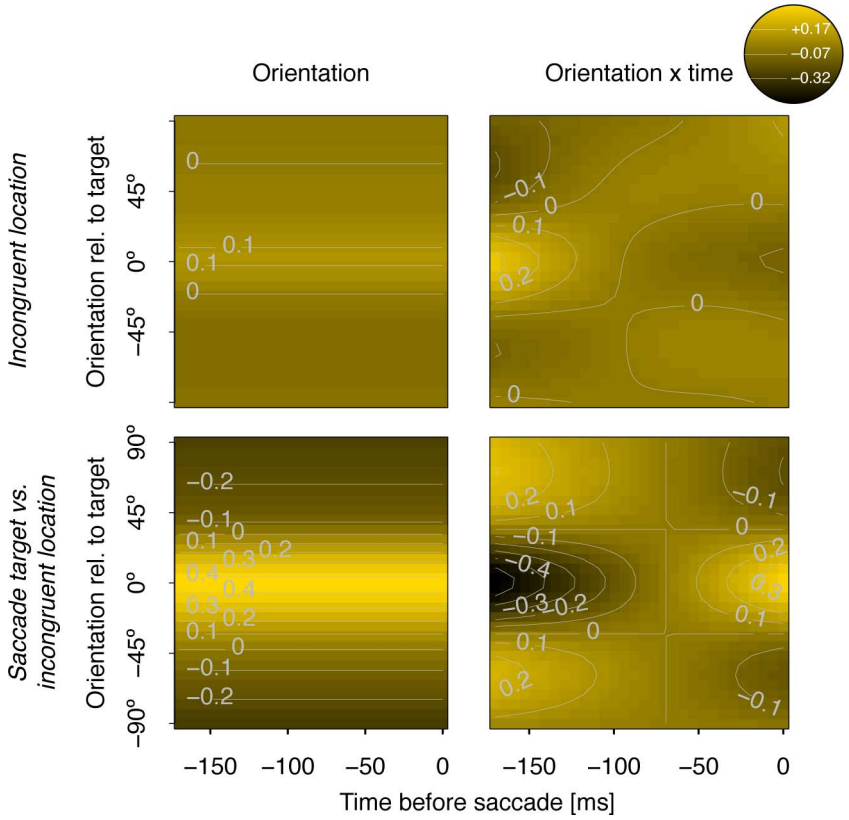

Figure 3. Partial effects of the binomial GAMM in logit units including contour lines (gray). The panels display partial effects from the GAMM. Hence, the bottom panels display the difference (i.e., the contrast-coded factor) between saccade target and incongruent location as a function of stimulus orientation and stimulus offset relative to saccade onset.

consequence of a continuous increase in tuning over time at the saccade target (see Figure 4a, reflecting the sum of all partial effects).

While Figure 3 illustrates the evolution of orientation tuning over time at the incongruent location (top row) and at the saccade target *relative* to the incongruent location (bottom row), Figure 4a visualizes predicted orientation tuning curves over time for the saccade target and the incongruent location independently. At the incongruent location, the initial tuning for reporting the presence of a target orientation washed out over time. In stark contrast, at the saccade target, orientation tuning strongly unfolds over time. Testing the time course of present reports given the target orientation at the incongruent location versus the saccade target, we observed a significant enhancement at the saccade target starting 106 ms before saccade onset (all ts[8] > 2.3, all ps < 0.05; Figure 4b).

Next, we investigated whether the enhancement at the saccade target can be accounted for by an increase in gain or by changes in the width of the tuning profile. To this end, we examined the progression of orientation tuning before saccades by comparing orientation tuning curves obtained at 100, 50, and 0 ms (Figure 4c) before saccade onset to tuning at the earliest time point (i.e., 170 ms before saccade onset). A change in tuning width is evident if the ratio of two tuning curves is not fixed at a constant (i.e., a multiplicative gain change), but instead shows a maximum for the preferred feature value and a minimum at orientations whose influence is reduced. However, in the present study tuning curves are a mixture of a uniform baseline and a tuning curve. When comparing the ratio of two tuning curves with nonzero baselines, any significantly reduced response at intermediate orientations (e.g., similar to a Mexican hat shape) provides clear evidence for an increase in tuning; in contrast, pure increases in gain result in a positive deflection (ratios > 1) of the ratio around the maximum of the tuning curve. Figure 4c shows that—with time approaching the onset of the saccade—both of these patterns become evident. Orientation tuning increased at the saccade target as early as 100 ms before saccade onset (maximum ratio at 18° > 1; $t[8] = 3.79$, $p = 0.005$), with no clear evidence for a decrease at intermediate orientations suggests a pure increase in gain for a sharpening of the tuning profile. Similarly, the comparison at 170 and 50 ms before saccade onset yielded a significant enhancement (maximum ratio at 3.6° > 1; $t[8] = 4.76$, $p = 0.001$), but no significant decrease at intermediate orientations. Finally, we assessed the progression of orientation tuning over the longest interval from 170 to 0 ms before saccade onset. There,

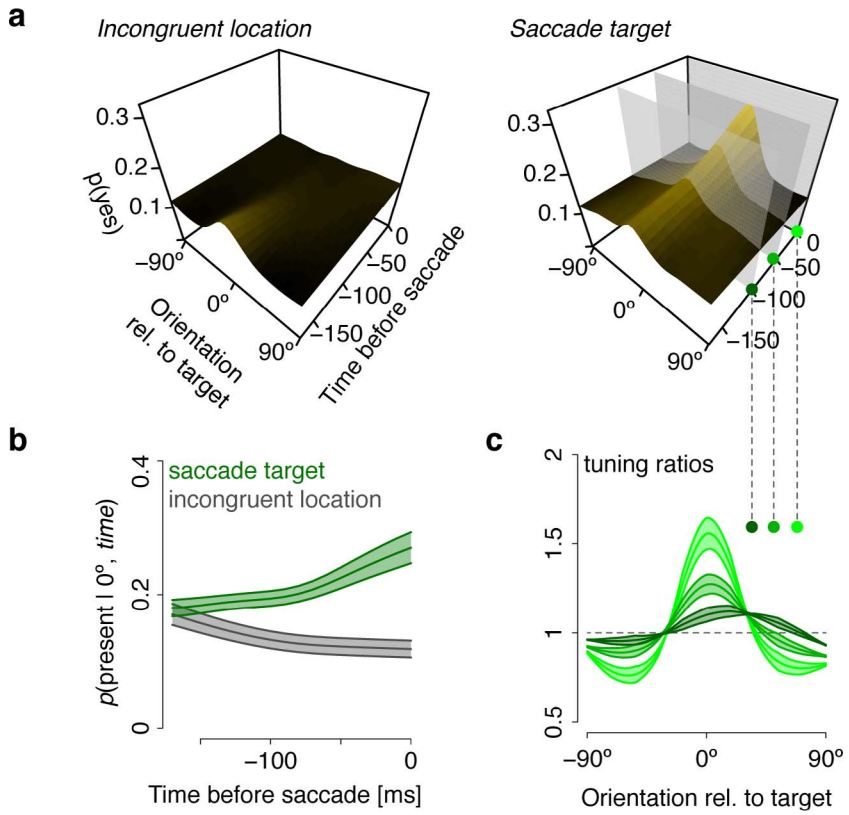

Figure 4. Predictions from the GAMM. (a) Predicted orientation tuning curves for the incongruent location and the saccade target location. (b) The probability of a present report as a function of the target orientation's presentation time before a saccade, based on GAMM predictions ($M \pm 1$ *SEM*) for the incongruent location (gray) and the saccade target (green). (c) Comparison of orientation tuning curves at 100, 50, and 0 ms before saccade onset, expressed as a ratio of model predictions at these points in time relative to orientation tuning at 170 ms before saccade onset (displayed as $M \pm 1$ *SEM*).

we observed the strongest increase in the probability to report the presence of a target orientation for stimuli that carried the target (or very similar) orientation (maximum ratio at $1.8° > 1$; $t[8] = 5.74$, $p < 0.001$). In contrast to the previous ratios of tuning curves, we observed a Mexican hat–shaped profile for this comparison, indicating a sharpening of the tuning profile (Figure 4c). Testing the minimum of this Mexican hat profile at −59.4° against the most extreme orientation (−90°) also showed a significant deviation, suggesting that the orientation tuning at the saccade target is indeed refined briefly before movement onset ($t[8] = 3.4$, $p = 0.009$). Thus, at the saccade target location, we observe both a progressive increase in the gain of orientation tuning as well as a sharpening of selectivity for the target orientation right before the onset of the saccade.

Discussion

Based on participants' reports of target orientations in a rapidly updating stream of oriented stimuli, we obtained time-resolved orientation tuning curves before saccadic eye movements at two locations in the visual field. Time-locked to saccade onset, these curves show a spatially selective increase in gain of orientation tuning at the saccade target starting within 100 ms before saccade onset and, in addition, finer tuning right before saccade onset. Orientation tuning in the opposite hemifield did not undergo such evolution, suggesting that presaccadic attention is prioritizing relevant features in a spatially selective manner.

The deployment of covert spatial attention increases the gain of visual responses in V4 neurons (McAdams & Maunsell, 1999). Similarly, saccades enhance visual responses of V4 neurons encoding the saccade target (Moore et al., 1998). In line with these studies, we observed an increase in the gain of orientation tuning starting as soon as 100 ms before saccade onset. Nevertheless, a saccade-related increase in gain alone cannot account for the orientation tuning we observed at the earliest time point examined at 170 ms before saccade onset. Orientation tuning, however, can result from deploying feature-based attention as a consequence of keeping the target orientation fixed and informing observers about the orientation at the beginning of the block. Such a task set efficiently shapes feedforward processing of incoming visual

signals (Zhang & Luck, 2009). We observed, in addition, finer orientation tuning right before the saccade, which can be explained by an interaction of feature-based attention and a saccade-related shift of spatial attention. Indeed, the feature-similarity gain model (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999) predicts that a multiplicative modulation of individual neural tuning curves will result in sharper tuning of the population response. Hence, in the present study, finer tuning right before saccade onset could result from a saccade-related increase in gain that modulates orientation tuning established by feature-based attention.

Using a different reverse-correlation approach than ours, Li and colleagues (2016) compared orientation tuning during fixation and overt attention shifts. Their findings concur with ours in that they observed enhanced orientation tuning for stimuli at the target of a saccade, which reached its peak in the last 50 ms before movement onset. In addition, they report evidence for a gain increase in the processing of high spatial frequency information before saccades. Indeed, it seems possible that the enhanced orientation tuning observed by Li et al. (2016) is a direct consequence of the increase in gain for high spatial frequencies. Given the low-contrast stimuli used in their study, and provided that contrast sensitivity varies with spatial frequency in a nonlinear fashion (Campbell & Robson, 1968), a simple contrast-gain mechanism may account for the observed changes in orientation tuning. This account, however, fails to explain the present data. In our study, we find an increase in tuning for stimuli presented at full contrast, when an increase in contrast sensitivity is not expected to further enhance performance. Instead, the sharpening of orientation tuning observed here, becoming evident within 50 ms of saccade onset, occurs in addition to an increase in the gain of orientation tuning, which starts somewhat earlier. Thus, based on entirely different approaches and stimulus regimes, our results and those by Li et al. (2016) converge onto a coherent picture of presaccadic attention as a selection process that involves several mechanisms to enhance stimulus encoding in early visual processing.

In contrast to Li et al. (2016), we were not interested in comparing covert and overt attention shifts, but in comparing the specificity of the effects of saccade preparation on orientation tuning to the saccade target. Our results show that reshaping of orientation tuning occurs exclusively at the saccade target. It is worth noting that in the present study, the saccade target was uninformative as to the test location. This orthogonal manipulation of movement cue and response cue rendered both locations equally task-relevant. This experimental feature goes beyond previous studies of the time course of presaccadic attention shifts (e.g., Li et al., 2016; Rolfs & Carrasco, 2012), in which the movement cue unequivocally identified the subsequent test location. Nevertheless, we observed similar mechanisms underlying the presaccadic attention shift as these previous studies suggested. This result shows that a valid movement cue is not a necessary condition for observing changes in gain and tuning before saccades, underscoring that the presaccadic attention shift selects information in an obligatory fashion, and with no need of a conscious strategic allocation of resources following a valid cue.

It may appear surprising that perception at the saccade target is best just before movement onset—at a point in time at which visual sensitivity is known to deteriorate (Volkmann, Schick, & Riggs, 1968). Based on our data and that of previous studies (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel, 2008; Li et al., 2016; Montagnini & Castet, 2007; Rolfs & Carrasco, 2012; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011), we contend that an enhanced processing of saccade targets protects these locations from suppression (see also Khan, Blohm, Pisella, & Munoz, 2015). In fact, protecting stimuli at the saccade target from subsequent visual interference is not limited to presaccadic visual perception but is also observed in visual memory (Hanning, Jonikaitis, Deubel, & Szinte, 2016; Ohl & Rolfs, 2017) suggesting a general mechanism that fortifies action-relevant locations in visual processing and storage.

Orientation tuning is the key characteristic of early visual processing in primary visual cortex (Hubel & Wiesel, 1962, 1968). The dynamics of neural orientation tuning can be well characterized by reverse correlation, showing that tuning develops within 30 to 45 ms after stimulus onset and persists for another 40 to 85 ms (Ringach et al., 1997). A similar methodological approach—on the basis of which we also developed our paradigm—has been introduced to study perceptual orientation tuning during fixation. This similarity of the experimental approach provides an interface for the comparison of neural tuning in macaque cortex and human perception (Ringach, 1998). Saccades have been shown to enhance neural orientation tuning for preferred orientations at the saccade target and leave selectivity at the location in the opposite hemifield unaltered (Moore et al., 1998). Moreover, microstimulation of neurons in oculomotor brain regions (frontal eye fields, superior colliculus, lateral intraparietal sulcus) results in similar perceptual benefits and neural enhancement at corresponding retinotopic locations in visual cortex (Cavanaugh & Wurtz, 2004; Moore & Armstrong, 2003; Moore & Fallah, 2001, 2004; Muller, Philiastides, & Newsome, 2005; see Moore & Zirnsak, 2017, for review), providing a potential neural mechanism underlying the presaccadic attention shift and the findings of our study.

Conclusion

Assessing the mechanisms by which saccades change how we perceive contributes to a comprehensive answer to basic questions of active human sensory information processing. Here we showed that in the short time window from the onset of saccade planning to the execution of the eye movement, the presaccadic attention shift is reflected in spatially selective changes in perceptual orientation tuning. This perceptual effect resembles the saccade-contingent selective enhancement of neural firing at the target of saccadic eye movements. Reshaping sensory tuning at the goal of the saccade occurs even before the eyes move—a mechanism that may contribute to the continuity in visual processing across saccadic eye movements.

Keywords: eye movements, saccades, pre-saccadic attention, orientation tuning

Acknowledgments

This research was supported by a DFG Emmy Noether grant (RO 3579/2–1) to M. R. and a DFG research grant to S. O. and M. R. (OH 274/2-1 and RO 3579/6-1). The authors declare no competing financial interests.

*SO and CK contributed equally to this article.
Commercial relationships: none.
Corresponding author: Sven Ohl.
Email: sven.ohl@bccn-berlin.de.
Address: Department of Psychology, Humboldt Universität zu Berlin, Germany.

References

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *The Journal of Physiology*, *197*(3), 551–566.

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484–1525, doi:10.1016/j.visres.2011.04.012.

Castet, E., Jeanjean, S., Montagnini, A., Laugier, D., & Masson, G. S. (2006). Dynamics of attentional deployment during saccadic programming. *Journal of Vision*, *6*(3):2, 196–212, doi:10.1167/6.3.2. [PubMed] [Article]

Cavanaugh, J., & Wurtz, R. H. (2004). Subcortical modulation of attention counters change blindness. *Journal of Neuroscience*, *24*(50), 11236–11243.

Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers*, *34*(4), 613–617.

Deubel, H. (2008). The time course of presaccadic attention shifts. *Psychological Research*, *72*(6), 630–640.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences*, *103*(18), 7192–7197.

Hamker, F. H., Zirnsak, M., Calow, D., & Lappe, M. (2008). The peri-saccadic perception of objects and space. *PLoS Computational Biology*, *4*(2), e31, doi:10.1371/journal.pcbi.0040031.

Hanning, N. M., Jonikaitis, D., Deubel, H., & Szinte, M. (2016). Oculomotor selection underlies feature retention in visual working memory. *Journal of Neurophysiology*, *115*(2), 1071–1076.

Hastie, T. J., & Tibshirani, R. J. (1990). *Generalized additive models* (Vol. 43). London: Chapman & Hall/CRC.

Hembrook-Short, J. R., Mock, V. L., & Briggs, F. (2017). Attentional modulation of neuronal activity depends on neuronal feature selectivity. *Current Biology*, *27*(13), 1878–1887.

Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, *57*(6), 787–795.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of Physiology*, *160*(1), 106–154.

Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *The Journal of Physiology*, *195*(1), 215–243.

Khan, A. Z., Blohm, G., Pisella, L., & Munoz, D. P. (2015). Saccade execution suppresses discrimination at distractor locations rather than enhancing the saccade goal location. *European Journal of Neuroscience*, *41*(12), 1624–1634.

Kleiner, M., Brainard, D. H., Pelli, D. G., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3. *Perception*, *36*(14), 1–16.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E.

(1995). The role of attention in the programming of saccades. *Vision Research*, *35*(13), 1897–1916.

Li, H.-H., Barbot, A., & Carrasco, M. (2016). Saccade preparation reshapes sensory tuning. *Current Biology*, *26*(12), 1564–1570, doi:10.1016/j.cub.2016.04.028.

Ling, S., & Carrasco, M. (2006). Sustained and transient covert attention enhance the signal via different contrast response functions. *Vision Research*, *46*(8), 1210–1220.

Martinez-Trujillo, J. C., & Treue, S. (2004). Feature-based attention increases the selectivity of population responses in primate visual cortex. *Current Biology*, *14*(9), 744–751.

McAdams, C. J., & Maunsell, J. H. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *The Journal of Neuroscience*, *19*(1), 431–441.

Miconi, T., & VanRullen, R. (2016). A feedback model of attention explains the diverse effects of attention on neural firing rates and receptive field structure. *PLoS Computational Biology*, *12*(2), e1004770, doi:10.1371/journal.pcbi.1004770.

Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision*, *7*(14):8, 1–16, doi:10.1167/7.14.8. [PubMed] [Article]

Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, *421*(6921), 370–373.

Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences*, *98*(3), 1273–1276.

Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *Journal of Neurophysiology*, *91*(1), 152–162, doi:10.1152/jn.00741.2002.

Moore, T., Tolias, A. S., & Schiller, P. H. (1998). Visual representations during saccadic eye movements. *Proceedings of the National Academy of Sciences*, *95*(15), 8981–8984.

Moore, T., & Zirnsak, M. (2017). Neural mechanisms of selective visual attention. *Annual Review of Psychology*, *68*(1), 47–72, doi:10.1146/annurev-psych-122414-033400.

Müller, H. J., & Rabbitt, P. M. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception and Performance*, *15*(2), 315–330.

Muller, J. R., Philiastides, M. G., & Newsome, W. T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proceedings of the National Academy of Sciences*, *102*(3), 524–529, doi:10.1073/pnas.0408311101.

Ohl, S., & Rolfs, M. (2017). Saccadic eye movements impose a natural bottleneck on visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *43*(5), 736–748.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442.

R Core Team (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Remington, R. W. (1980). Attention and saccadic eye movements. *Journal of Experimental Psychology: Human Perception and Performance*, *6*(4), 726–744.

Ringach, D. (1998). Tuning of orientation detectors in human vision. *Vision Research*, *38*(7), 963–972.

Ringach, D. L., Hawken, M. J., & Shapley, R. (1997). Dynamics of orientation tuning in macaque primary visual cortex. *Nature*, *387*, 281–284.

Rolfs, M. (2015). Attention in active vision: A perspective on perceptual continuity across saccades. *Perception*, *44*(8–9), 900–919, doi:10.1177/0301006615594965.

Rolfs, M., & Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. *Journal of Neuroscience*, *32*(40), 13744–13752, doi:10.1523/JNEUROSCI.2676-12.2012.

Rolfs, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. *Nature Neuroscience*, *14*(2), 252–256.

Shepherd, M., Findlay, J. M., & Hockey, R. J. (1986). The relationship between eye movements and spatial attention. *The Quarterly Journal of Experimental Psychology Section A*, *38*(3), 475–491, doi:10.3758/BF03202407.

Treue, S., & Martinez-Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, *399*(6736), 575–579.

Volkmann, F. C., Schick, A. M., & Riggs, L. A. (1968). Time course of visual inhibition during voluntary saccades. *Journal of the Optical Society of America*, *58*(4), 562–569.

Wood, S. N. (2003). Thin plate regression splines. *Journal of the Royal Statistical Society Series B*, *65*(1), 95–114, doi:10.2307/3088828.

Wood, S. (2006). *Generalized additive models: An introduction with R*. London: Chapman & Hall/CRC.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society Series B*, *73*(1), 3–36, doi:10.2307/41057423.

Wyart, V., Nobre, A. C., & Summerfield, C. (2012). Dissociable prior influences of signal probability and relevance on visual contrast sensitivity. *Proceedings of the National Academy of Sciences*, *109*(9), 3593–3598, doi:10.1073/pnas.1204601109.

Zhang, W., & Luck, S. J. (2009). Feature-based attention modulates feedforward visual processing. *Nature Neuroscience*, *12*(1), 24–25, doi.org/10.1038/nn.2223.

Zhao, M., Gersch, T. M., Schnitzer, B. S., Dosher, B. A., & Kowler, E. (2012). Eye movements and attention: The role of pre-saccadic attention in perception, memory and the control of saccades. *Vision Research*, *74*, 40–60, doi:10.1016/j.visres.2012.06.017.