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# Selective enhancement of orientation tuning before saccades

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1 **Abstract**

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

17 **Precis**

18 Combining a time-resolved reverse-correlation technique with statistical modeling, we show  
19 that planning a saccadic eye movement involves dynamic changes in perception, including a  
20 feature-specific increase in gain and finer orientation tuning that is selective to the movement  
21 target.

22

## 1 **Introduction**

2 The active observer is equipped with a powerful tool to constrain processing of visual  
3 information before imminent eye movements: *the pre-saccadic shift of attention* (see Rolfs,  
4 2015, and Zhao et al., 2012, for reviews). A tight coupling between attention and the planning  
5 of saccadic eye movements (Remington, 1980; Shepherd, Findlay, & Hockey, 1986)  
6 prioritizes visual information at the saccade's target and deteriorates information processing  
7 elsewhere in the visual field (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995;  
8 Kowler et al., 1995). This selection mechanism becomes effective within only 60 ms of an  
9 instruction to move the eyes (Rolfs & Carrasco, 2012), and is thus considerably faster than  
10 the 300 ms it takes to wilfully deploy covert attention (Ling & Carrasco, 2006; Müller &  
11 Rabbitt, 1989).

12 While much effort has been devoted to delineating the mechanisms of covert  
13 attention (Carrasco, 2011), surprisingly little research has addressed the mechanism  
14 underlying pre-saccadic attentional selection. Candidate mechanisms suggested by  
15 psychophysical experiments include a change in perceptual feature tuning, filtering sensory  
16 information most similar to the target (Li, Barbot & Carrasco, 2016). An alternative (or  
17 additional) mechanism is an increase in the gain of neural responses to stimuli at the  
18 saccade target. Indeed, neurons in V4—a key visual area in the extrastriate portion of the  
19 ventral stream—increase their response to stimuli in their receptive field when a saccade is  
20 about to target that stimulus, whereas a saccade directed away from the stimulus has no  
21 effect on the pre-saccadic neural response (Moore et al., 1998).

22 In general, a gain increase of responses in single cells tuned to a specific feature  
23 value results in a narrowing of tuning curves at the neural population level (Treue & Martinez-  
24 Trujillo, 1999; Martinez-Trujillo & Treue, 2004), in particular, for neurons that are highly  
25 feature-selective to begin with (Hembrook-Short, Mock, & Briggs, 2017). Changes in gain  
26 and tuning are thus not mutually exclusive and may both contribute to spatially specific  
27 enhancement of visual performance in visual discrimination tasks before an eye movement.

1 In the case of planning a saccade while attending to a target orientation, both feature-based  
2 and spatial attention are involved. While feature-based attention acts across the visual field  
3 and depends on the task set, spatial attention arises at the saccade target once the eye  
4 movement is cued. Observed changes in tuning curves before a saccade are thus due to the  
5 deployment of spatial attention, but may interact with feature-based attention. Characterizing  
6 how pre-saccadic attention shapes ongoing visual processing is essential for computational  
7 models in vision (Hamker et al., 2008; Miconi & VanRullen, 2016) and enables a deeper  
8 understanding of visual selection at different levels of analysis.

9         Here, we examine the time course of perceptual orientation tuning before saccade  
10 onset. In a recent study that pursued a similar research question, participants had to detect  
11 low contrast Gabors embedded in visual noise (Li, Barbot & Carrasco, 2016). By relating  
12 orientation and spatial frequency information in the noise to detection reports (see also Wyart  
13 et al., 2012), these authors revealed orientation tuning curves that narrowed with time over  
14 the last 50 ms before saccade onset. Concurrently, the gain of high-spatial frequencies  
15 increased over time. Whereas this study compared orientation tuning during covert shifts of  
16 attention with those observed before saccades, we focus strictly on pre-saccadic attention.  
17 However, using a reverse correlation paradigm, typically used to characterize neural tuning  
18 curves (Ringach, 1998; Ringach et al., 1997), we probed target detection at both the saccade  
19 target and a location in the opposite hemifield, allowing us to assess the obligatory nature of  
20 pre-saccadic tuning changes and their selectivity to the saccade target. We then employed  
21 General Additive Mixed Modelling (GAMM) to assess the temporal dynamics of perceptual  
22 orientation tuning before saccades. Thus, by using a different experimental paradigm and  
23 analysis tool, the present study seeks to replicate and expand upon previously reported  
24 changes in tuning before saccades by contrasting tuning curves at two locations in the visual  
25 field. We find that non-target locations exhibited weak orientation tuning. In stark contrast,  
26 perceptual processing at the saccade target showed a steadily increasing gain that was  
27 accompanied by finer orientation tuning right before saccade onset.

1

## 2 **Method**

3 *Participants.* We tested nine observers (mean age 22.3 years, SD  $\pm$ 3.1 years, three females,  
4 one left-handed) in five experimental sessions (one training and four test sessions with  $\sim$ 1  
5 hour per session), with at least one night between consecutive sessions. In the training  
6 session, observers were instructed to familiarize themselves with the eye-movement task  
7 throughout the first blocks and to do the perceptual task simultaneously with the saccade  
8 task only in subsequent blocks. Therefore, data from the training session was excluded from  
9 further analysis. All participants were naïve as to the purpose of the study and signed  
10 informed consent prior to their participation. Participants had normal or corrected-to-normal  
11 vision and received 7€ per session as compensation for their participation and an additional  
12 7€ after completion of all five sessions. The study was conducted in accordance with the  
13 Declaration of Helsinki (2008).

14

15 *Materials and procedure.* Observers were seated in a dark, quiet room. Their head was  
16 positioned on a chin rest in order to minimize head movements. The experiment was  
17 displayed at a distance of 57 cm on a 23.6" ViewPixx/3D screen (1920 x 1080 pixels; VPixx  
18 Technologies Inc., Saint Bruno, QC, Canada) with 10 bits of resolution on each of the RGB  
19 channels and a refresh rate of 120 Hz. We recorded eye position of the participant's  
20 dominant eye (determined beforehand using a hole-in-a-card test) with a sampling rate of  
21 1000 Hz using an Eyelink 1000 Desktop Mount (SR Research, Ottawa, ON, Canada). A  
22 DELL precision T3600 workstation with a Debian 8 operating system running Matlab  
23 (Mathworks, Natick, MA, USA), the Psychophysics toolbox 3 (Brainard, 1997; Kleiner et al.,  
24 2007; Pelli, 1997) and the Eyelink toolbox (Cornelissen, Peters, & Palmer, 2002) was used to  
25 control stimulus presentation, response collection, and online gaze control. Perceptual  
26 reports were collected via key press using a ResponsePixx (VPixx Technologies Inc., Saint  
27 Bruno, QC, Canada).

1           The participants' task was to detect either a horizontal or vertical Gabor patch, as  
2 defined in the beginning of a block, in a fast sequence of randomly oriented Gabors. We  
3 presented a fixation point (white circle with black contour) with a diameter of 0.6 degrees of  
4 visual angle (dva) on a grey background (**Figure 1a**). In addition, we displayed two circular  
5 black placeholders (3 dva diameter) at an eccentricity of 6 dva to the left and to the right from  
6 the central fixation point. After 800 ms of successful fixation (i.e., no blinks; eye positions  
7 were within a distance of 1.5 dva from the fixation point), the stimulus sequence was  
8 presented at a speed of 30 Hz (~33 ms per stimulus). The sequence consisted of up to  
9 twelve Gabor patches (depending on the saccade latency on a given trial; see below) with  
10 100% contrast, randomly assigned spatial frequencies between 1 and 4 cycles per degree  
11 (cpd), a random phase, and 1° SD Gaussian envelope. Each Gabor patch had one out of 10  
12 possible orientations distributed uniformly from 0° to 162°, in steps of 18°. Each Gabor patch  
13 had a randomly assigned orientation such that—given the median saccade latency—the  
14 sequence contained the target orientation in 47% of all trials. Due to this random assignment,  
15 the target orientation could be presented more than once in the orientation sequence.  
16 Simultaneously with sequence onset, we displayed a central *movement cue*, a small black  
17 line (length = 0.25 dva, thickness = 0.085 dva,) extending from the fixation symbol, pointing  
18 to one of the two placeholders and prompting participants to move their eyes immediately to  
19 the indicated location. The sequence of stimuli and the movement cue were removed as  
20 soon as the onset of the eye movement was detected (i.e., eye positions were outside a  
21 radius of 1.5 dva from the fixation point *after* the presentation of the movement cue). Another  
22 600 ms after the presentation of the movement cue, we presented a response cue: one of  
23 the two locations was highlighted by changing the color of the placeholder from black to  
24 white. Observers had to report whether they detected a target stimulus (i.e., a Gabor with  
25 defined target orientation) at the highlighted location by pressing one of two buttons.  
26 Importantly, the movement cue was uninformative with respect to the location of the  
27 response cue. As a consequence, in 50% of the trials the movement cue and response cue

1 indicated the same location and in 50% of the trials the movement cue pointed to the location  
2 opposite from the response cue. Across the experiment, the direction of the saccade,  
3 therefore, was uncorrelated to the perceptual task, and participants were explicitly instructed  
4 to monitor both test locations.

5 A single session consisted of 24 blocks (with 32 trials per block) and we ran 12 blocks  
6 for each the horizontal and vertical target orientation, which were randomly interleaved. Trials  
7 in which the saccade was not made within 400 ms after cue presentation or in which  
8 participants blinked during the trial were aborted. All aborted trials were repeated in a  
9 randomized order at the end of each block. Each observer completed a total of 3,072 trials in  
10 the course of the four test sessions.

11 *Data analysis.* For inferential statistics, we computed a GAMM for a binomial dependent  
12 variable (Hastie & Tibshirani, 1990). The GAMM allows us a non-parametric prediction of  
13 observers' reports (absent = 0, present = 1) from the orientation of the Gabor at a time point  
14 before saccade onset. The predictor variables in a GAMM are modeled as smooth functions  
15 (i.e., penalized regression splines), with an estimated complexity (i.e., estimated degrees of  
16 freedom) and the significance of their (possibly non-linear) influence on reports is assessed.  
17 The GAMM is a powerful statistical tool that offers several advantages for the analysis of the  
18 present data. First, it is agnostic with respect to the shape of the tuning curves and their  
19 dynamics before the saccade. Second, it allows us to estimate the development of tuning  
20 curves at two locations for all observers in a single regression model. This is particularly  
21 helpful as we expected very weak (or even no) tuning for some conditions, which often  
22 impedes estimates of parameters in a time window dominated by noise. Third, the GAMM  
23 enables us to study the development of orientation tuning in a continuous fashion, where  
24 predictors at different time points are computed simultaneously in order to estimate a smooth  
25 (possibly nonlinear) evolution. This approach typically decreases the unreliability of  
26 (independently fitted) parameter estimates for data in arbitrarily defined time windows. In our  
27 GAMM, we included the predictors *stimulus orientation*, *time of presentation* before saccade

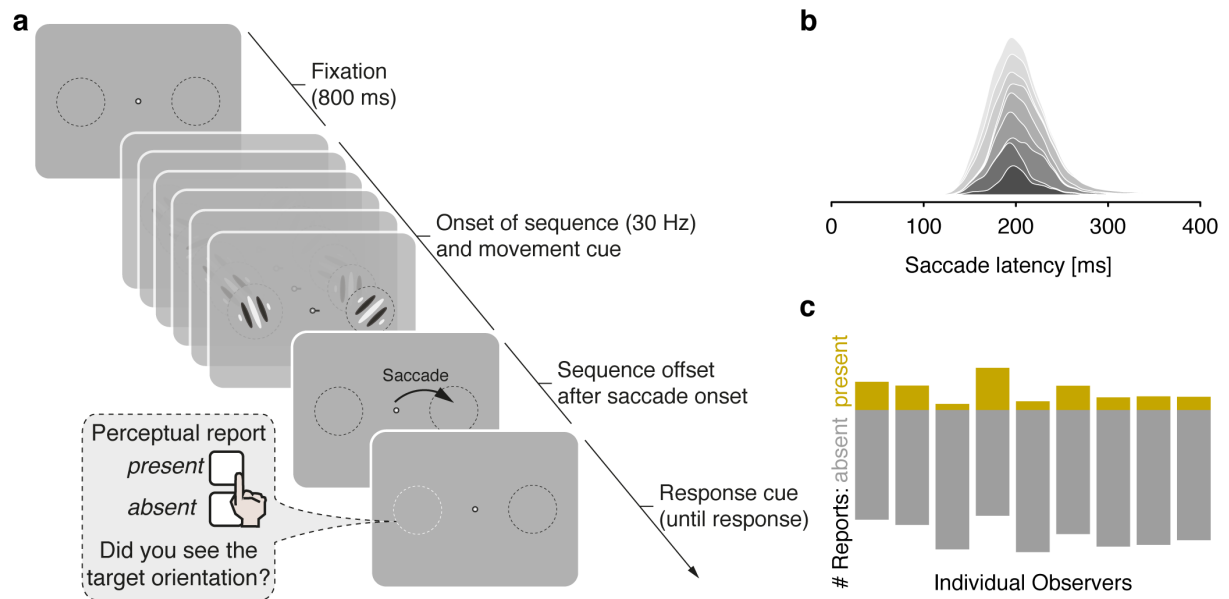


1 onset, and the interaction of these two factors, *stimulus orientation x time*. We restricted the  
2 analysis to a time window from a stimulus offset of -170 ms to 0 ms before saccade onset, as  
3 the median latency of saccades was 200 ms (**Figure 1b**) and the duration of a single  
4 stimulus was 33.3 ms. Moreover, we added the parametric factor *congruency* as a treatment  
5 contrast (0 = opposite hemifield; 1 = saccade target location) to the model; therefore, the  
6 predictors *stimulus orientation*, *time* and their interaction predict perceptual reports for the  
7 *incongruent* location only (providing a baseline). To predict reports for the *congruent* location,  
8 we included the two-way interactions *time x congruency*, *orientation x congruency*, and the  
9 three-way interaction of *orientation x time x congruency*. Note that the treatment of the two  
10 levels of congruency is arbitrary: using congruent location as the baseline would yield  
11 identical results. Finally, for all non-parametric terms we also added their random effects (i.e.,  
12 their interaction with participants) to the model. Statistical analyses were performed using the  
13 *mgcv* package (Wood, 2006; 2003; 2011) in the R environment (R Version 3.2.3, R Core  
14 Team, 2015). For inferential statistics of saccade parameters, we used repeated-measures  
15 analyses of variance (rmANOVA).

16 Saccades were detected offline by first transforming raw eye positions into 2D velocity  
17 space, and then classifying successive eye positions as saccades when they exceeded the  
18 median velocity by 5 SDs for a minimum duration of 8 ms (Engbert & Mergenthaler, 2006).  
19 We merged two events classified as saccades into a single saccade when they were  
20 separated by less than 20 ms. We defined the response saccade as the first saccade with a  
21 distance between landing position and center of the saccade target smaller than 3.6 dva (i.e.,  
22 60% of the target's eccentricity). Trials were rejected from further analyses when a) they  
23 included blinks or missing samples in the eye recordings or b) they included saccades with  
24 an amplitude larger than 1 dva before execution of the response saccade. A total of 26,520  
25 trials (96%) entered the final data analysis.

26

27



1

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

12

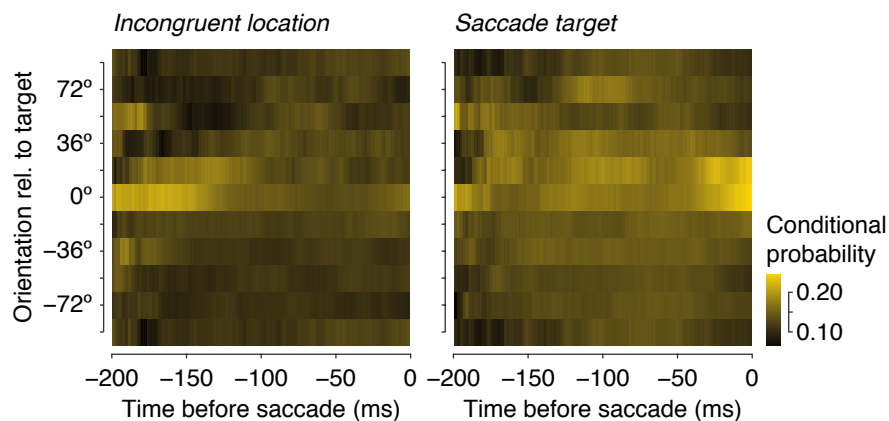
### 13 **Results**

14 We assessed perceptual orientation tuning before saccades using a reverse correlation  
 15 approach in combination with a general additive mixed model (GAMM), enabling a non-  
 16 parametric and non-linear analysis of orientation tuning and its progression before saccades.  
 17 We determined the relative influence of a range of stimulus orientations, displayed before  
 18 saccade onset, on the detection of a target orientation at the saccade target and at an  
 19 incongruent location. Similar approaches in electrophysiological studies in monkeys—that did  
 20 not include perceptual reports—have shown a pre-saccadic enhancement of neural  
 21 responses to stimuli at the saccade target, but no effect at a location opposite the saccade  
 22 target (Moore, Tolias, & Schiller, 1998).

23 Saccade parameters in our task did not vary between conditions. Saccade latency  
 24 was unaffected by congruency between the saccade direction and the probed location ( $F(1,$

1 8) = 2.24,  $p = 0.173$ ; congruent:  $203.6 \pm 0.3$  ms, incongruent:  $203.2 \pm 0.3$  ms). Similarly,  
2 saccade amplitude was not affected by congruency ( $F(1, 8) = 2.5$ ,  $p = 0.149$ ; congruent:  $6.27$   
3  $\pm 0.01$  dva, incongruent:  $6.25 \pm 0.01$  dva).

4 In general, the perceptual task was very difficult with observers reporting the  
5 presence of a target stimulus in only 13.3% of the trials on average (18.8% on target present  
6 trials and 9.4% in target absent trials, 14.7% in trials probing the congruent location and  
7 11.9% in trials probing the incongruent location; **Figure 1c**). Critically, the probability to  
8 report the presence of the target orientation depended on stimulus orientation. Stimuli whose  
9 orientation matched the target orientation had the strongest influence on reporting the  
10 presence of a target orientation, both at the saccade target and the incongruent location  
11 (**Figure 2**), and this influence decreased for more dissimilar orientations, providing evidence  
12 for perceptual orientation tuning. Right before saccade onset, the probability for reporting the  
13 presence of a target orientation was elevated for near-target orientations at the saccade  
14 target as compared to the incongruent location. This suggests that saccades influence the  
15 dynamics of orientation tuning in a spatially selective manner.

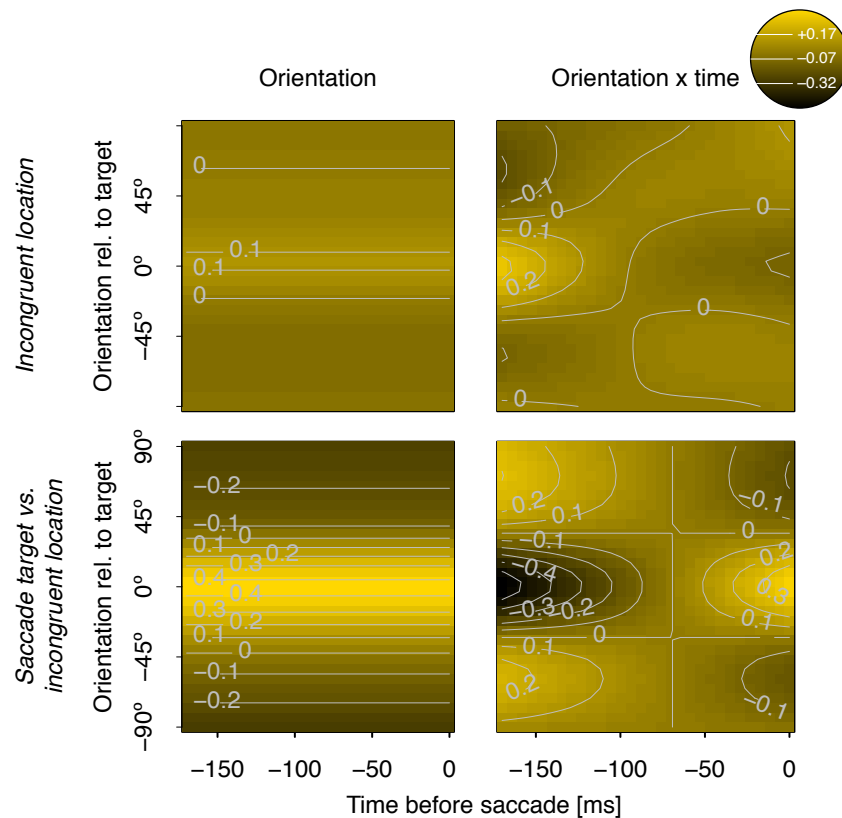


16

17 **Fig. 2.** Mean probability of reporting the presence of a target orientation, conditional on a presented  
18 orientation in a given time window before saccade onset. Probabilities are shown for the saccade  
19 target location (right panel) and the incongruent location (left panel), respectively. Computation of  
20 single tiles in the heatmap are based on all stimuli of the respective orientation that had their offset in a  
21 33 ms long time window ending at the indicated point in time.  
22

23 We assessed the significance of orientation tuning before saccades at the saccade  
24 target (congruent location) and at the location in the opposite hemifield (incongruent location)

1 using a GAMM, including parametric terms, smooth terms, and random effects (**Table 1**; see  
 2 **Methods** for detailed model setup). More specifically, when the target detection was probed  
 3 at the incongruent location, we observed a significant influence of stimulus orientation on the  
 4 perceptual report (estimated degrees of freedom (edf) = 5.85,  $X^2 = 22.41$ ,  $p = 0.002$ ). The  
 5 probability of reporting target presence did not vary across time before saccade onset (edf =  
 6 1.00,  $X^2 = 0.16$ ,  $p > 0.250$ ). However, we observed a significant interaction of time and  
 7 orientation at the incongruent location (edf = 7.77,  $X^2 = 45.44$ ,  $p < 0.001$ ). Closer inspection  
 8 of **Figure 3** (top-right) suggests that this interaction arises from a time-limited orientation  
 9 tuning 160 ms before the saccade that vanishes within 20 ms (see also **Figure 4**).



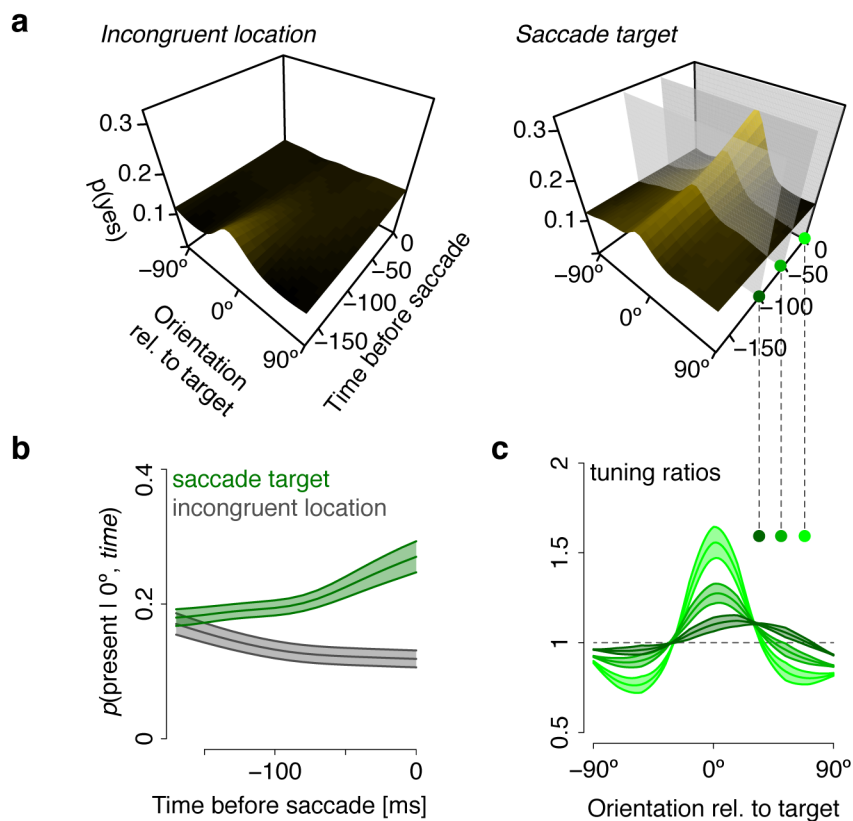
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11 **Fig. 3.** Partial effects of the binomial GAMM in logit units including contour lines (grey). The panels  
 12 display partial effects from the GAMM. Hence, the bottom panels display the difference (i.e., the  
 13 contrast-coded factor) between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

15

16 Importantly, tuning curves develop very differently for trials in which participants were  
 17 asked about the presence of a target orientation at the saccade target. Overall, congruency  
 18 did not influence the probability of reporting the presence of the target orientation (coefficient

1 = 0.29,  $z = 1.06$ ,  $p > 0.250$ ). However, the tuning to the target orientation was significantly  
 2 different between congruent and incongruent locations (edf = 6.75,  $X^2 = 67.93$ ,  $p < 0.001$ ),  
 3 with a much more distinct tuning profile at the saccade target than at the opposite location  
 4 (**Figure 3**, bottom-left). Moreover, before saccade onset, this orientation tuning evolved  
 5 differently at the saccade target location than in the opposite hemifield (edf = 3.86,  $X^2 =$   
 6 44.98,  $p < 0.001$ ; **Figure 3**, bottom-right). Note that the negative deflection for target  
 7 orientations here (**Figure 3**, bottom right) must not be mistaken for a suppressive influence  
 8 for stimuli close to the target orientation; instead, this partial effect rides on top of all other  
 9 partial effects (**Figure 3**, top row and bottom left) and is the consequence of a continuous  
 10 increase in tuning over time at the saccade target (see **Figure 4a**, reflecting the sum of all  
 11 partial effects).  
 12



13

14 **Fig. 4.** Predictions from the GAMM. **a** Predicted orientation tuning curves for the incongruent location  
 15 and the saccade target location. **b** The probability of a *present* report as a function of the target  
 16 orientation's presentation time before a saccade, based on GAMM predictions (Mean  $\pm$  1SEM) for the  
 17 incongruent location (gray) and the saccade target (green). **c** Comparison of orientation tuning curves  
 18 at 100 ms, 50 ms, and 0 ms before saccade onset, expressed as a ratio of model predictions at these

1 points in time relative to orientation tuning at 170 ms before saccade onset (displayed as Mean  $\pm$   
2 1SEM).  
3

4 While **Figure 3** illustrates the evolution of orientation tuning over time at the  
5 incongruent location (top row) and at the saccade target *relative* to the incongruent location  
6 (bottom row), **Figure 4a** visualizes predicted orientation tuning curves over time for the  
7 saccade target and the incongruent location independently. At the incongruent location, the  
8 initial tuning for reporting the presence of a target orientation washed out over time. In stark  
9 contrast, at the saccade target, orientation tuning strongly unfolds over time. Testing the time  
10 course of present reports given the target orientation at the incongruent location vs. the  
11 saccade target, we observed a significant enhancement at the saccade target starting 106  
12 ms before saccade onset (all  $t(8) > 2.3$ , all  $p$ s  $< 0.05$ ; **Figure 4b**).

13 Next, we investigated whether the enhancement at the saccade target can be  
14 accounted for by an increase in gain or by changes in the width of the tuning profile. To this  
15 end, we examined the progression of orientation tuning before saccades by comparing  
16 orientation tuning curves obtained at 100 ms, 50 ms, and 0 ms (**Figure 4c**) before saccade  
17 onset to tuning at the earliest time point (i.e., 170 ms before saccade onset). A change in  
18 tuning width is evident if the ratio of two tuning curves is not fixed at a constant (i.e., a  
19 multiplicative gain change), but instead shows a maximum for the preferred feature value and  
20 a minimum at orientations whose influence is reduced. However, in the present study tuning  
21 curves are a mixture of a uniform baseline and a tuning curve. When comparing the ratio of  
22 two tuning curves with non-zero baselines, any significantly reduced response at  
23 intermediate orientations (e.g., similar to a Mexican-hat shape) provides clear evidence for  
24 an increase in tuning; in contrast, pure increases in gain result in a positive deflection (ratios  
25  $> 1$ ) of the ratio around the maximum of the tuning curve. **Figure 4c** shows that—with time  
26 approaching the onset of the saccade—both of these patterns become evident. Orientation  
27 tuning increased at the saccade target as early as 100 ms before saccade onset (maximum  
28 ratio at  $18^\circ > 1$ ;  $t(8) = 3.79$ ,  $p = 0.005$ ), with no clear evidence lack of a decrease at

1 intermediate orientations suggests a pure increase in gain for a sharpening of the tuning  
2 profile. Similarly, the comparison at 170 ms and 50 ms before saccade onset yielded a  
3 significant enhancement (maximum ratio at  $3.6^\circ > 1$ ;  $t(8) = 4.76$ ,  $p = 0.001$ ), but no significant  
4 decrease at intermediate orientations. Finally, we assessed the progression of orientation  
5 tuning over the longest interval from 170 ms to 0 ms before saccade onset. There, we  
6 observed the strongest increase in the probability to report the presence of a target  
7 orientation for stimuli that carried the target (or very similar) orientation (maximum ratio at  
8  $1.8^\circ > 1$ ;  $t(8) = 5.74$ ,  $p < 0.001$ ). In contrast to the previous ratios of tuning curves, we  
9 observed a Mexican-hat shaped profile for this comparison, indicating a sharpening of the  
10 tuning profile (**Figure 4c**). Testing the minimum of this Mexican-hat profile at  $-59.4^\circ$  against  
11 the most extreme orientation ( $-90^\circ$ ) also showed a significant deviation, suggesting that the  
12 orientation tuning at the saccade target is indeed refined briefly before movement onset ( $t(8)$   
13  $= 3.4$ ,  $p = 0.009$ ). Thus, at the saccade target location, we observe both a progressive  
14 increase in the gain of orientation tuning as well as a sharpening of selectivity for the target  
15 orientation right before the onset of the saccade.

16

1 **Table 1.** Results from the GAMM.

Model term	estimate	statistic	p-value
<i>Parametric terms</i>			
	coefficient	z-value	
Intercept	-2.26	-7.31	<0.001
Congruency	0.29	1.06	>0.250
<i>Smooth terms</i>			
	edf	$\chi^2$	
Orientation	5.85	22.41	0.002
Time	1.00	0.16	>0.250
Orientation x Time	7.77	45.44	<0.001
Orientation x congruency	6.75	67.93	<0.001
Time x congruency	1.80	2.13	>0.250
Orientation x time x congruency	3.86	44.98	<0.001
<i>Random effects</i>			
Orientation	8.64	13.59	<0.001
Time	3.99	7.95	<0.001
Orientation x Time	0.009	0.007	>0.250
Orientation x congruency	42.58	165.23	<0.001
Time x congruency	3.94	7.75	<0.001
Orientation x time x congruency	17.53	58.42	<0.001



## 1 **Discussion**

2 Based on participants' reports of target orientations in a rapidly updating stream of oriented  
3 stimuli, we obtained time-resolved orientation tuning curves before saccadic eye movements  
4 at two locations in the visual field. Time-locked to saccade onset, these curves show a  
5 spatially selective increase in gain of orientation tuning at the saccade target starting within  
6 100 ms before saccade onset and, in addition, finer tuning right before saccade onset.  
7 Orientation tuning in the opposite hemifield did not undergo such evolution, suggesting that  
8 pre-saccadic attention is prioritizing relevant features in a spatially selective manner.

9         The deployment of covert spatial attention increases the gain of visual responses in  
10 V4 neurons (McAdams, & Maunsell, 1999). Similarly, saccades enhance visual responses of  
11 V4 neurons encoding the saccade target (Moore et al., 1998). In line with these studies, we  
12 observed an increase in the gain of orientation tuning starting as soon as 100 ms before  
13 saccade onset. Nevertheless, a saccade-related increase in gain alone cannot account for  
14 the orientation tuning we observed at the earliest time point examined at 170 ms before  
15 saccade onset. Orientation tuning, however, can result from deploying feature-based  
16 attention as a consequence of keeping the target orientation fixed and informing observers  
17 about the orientation at the beginning of the block. Such a task set efficiently shapes  
18 feedforward processing of incoming visual signals (Zhang & Luck, 2009). We observed, in  
19 addition, finer orientation tuning right before the saccade, which can be explained by an  
20 interaction of feature-based attention and a saccade-related shift of spatial attention. Indeed,  
21 the feature-similarity gain model (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo,  
22 1999) predicts that a multiplicative modulation of individual neural tuning curves will result in  
23 sharper tuning of the population response. Hence, in the present study, finer tuning right  
24 before saccade onset could result from a saccade-related increase in gain that modulates  
25 orientation tuning established by feature-based attention.

26         Using a different reverse-correlation approach than ours, Li and colleagues (2016)  
27 compared orientation tuning during fixation and overt attention shifts. Their findings concur

1 with ours in that they observed enhanced orientation tuning for stimuli at the target of a  
2 saccade, which reached its peak in the last 50 ms before movement onset. In addition, they  
3 report evidence for a gain increase in the processing of high-spatial-frequency information  
4 before saccades. Indeed, it seems possible that the enhanced orientation tuning observed by  
5 Li et al. (2016) is a direct consequence of the increase in gain for high spatial frequencies.  
6 Given the low-contrast stimuli used in their study, and provided that contrast sensitivity varies  
7 with spatial frequency in a nonlinear fashion (Campbell & Robson, 1968), a simple contrast-  
8 gain mechanism may account for the observed changes in orientation tuning. This account,  
9 however, fails to explain the present data. In our study, we find an increase in tuning for  
10 stimuli presented at full contrast, when an increase in contrast sensitivity is not expected to  
11 further enhance performance. Instead, the sharpening of orientation tuning observed here,  
12 becoming evident within 50 ms of saccade onset, occurs in addition to an increase in the  
13 gain of orientation tuning, which starts somewhat earlier. Thus, based on entirely different  
14 approaches and stimulus regimes, our results and those by Li et al. (2016) converge onto a  
15 coherent picture of pre-saccadic attention as a selection process that involves several  
16 mechanisms to enhance stimulus encoding in early visual processing.

17 In contrast to Li et al. (2016), we were not interested in comparing covert and overt  
18 attention shifts, but in comparing the specificity of the effects of saccade preparation on  
19 orientation tuning to the saccade target. Our results show that reshaping of orientation tuning  
20 occurs exclusively at the saccade target. It is worth noting that in the present study, the  
21 saccade target was uninformative as to the test location. This orthogonal manipulation of  
22 movement cue and response cue rendered both locations equally task-relevant. This  
23 experimental feature goes beyond previous studies of the time course of pre-saccadic  
24 attention shifts (e.g., Rolfs & Carrasco, 2012; Li et al., 2016), in which the movement cue  
25 unequivocally identified the subsequent test location. Nevertheless, we observed similar  
26 mechanisms underlying the pre-saccadic attention shift as these previous studies suggested.  
27 This result shows that a valid movement cue is not a necessary condition for observing

1 changes in gain and tuning before saccades, underscoring that the pre-saccadic attention  
2 shift selects information in an obligatory fashion, and with no need of a conscious strategic  
3 allocation of resources following a valid cue.

4         It may appear surprising that perception at the saccade target is best just before  
5 movement onset—at a point in time at which visual sensitivity is known to deteriorate  
6 (Volkman, Schick, & Riggs, 1968). Based on our data and that of previous studies (Castet,  
7 Jeannean, Montagnini, Laugier, & Masson, 2006; Montagnini & Castet, 2007; Deubel, 2010;  
8 Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; Rolfs & Carrasco, 2012; Li, Barbot, & Carrasco,  
9 2016), we contend that an enhanced processing of saccade targets protects these locations  
10 from suppression (see also Khan, Blohm, Pisella, & Munoz, 2015). In fact, protecting stimuli  
11 at the saccade target from subsequent visual interference is not limited to pre-saccadic visual  
12 perception but is also observed in visual memory (Ohl & Rolfs, 2017; Hanning, Jonikaitis,  
13 Deubel, & Szinte, 2016) suggesting a general mechanism that fortifies action-relevant  
14 locations in visual processing and storage.

15         Orientation tuning is the key characteristic of early visual processing in primary visual  
16 cortex (Hubel & Wiesel, 1962; 1968). The dynamics of neural orientation tuning can be well  
17 characterized by reverse correlation, showing that tuning develops within 30 ms to 45 ms  
18 after stimulus onset and persists for another 40 ms to 85 ms (Ringach et al., 1997). A similar  
19 methodological approach—on the basis of which we also developed our paradigm—has  
20 been introduced to study perceptual orientation tuning during fixation. This similarity of the  
21 experimental approach provides an interface for the comparison of neural tuning in macaque  
22 cortex and human perception (Ringach, 1998). Saccades have been shown to enhance  
23 neural orientation tuning for preferred orientations at the saccade target and leave selectivity  
24 at the location in the opposite hemifield unaltered (Moore et al., 1998). Moreover,  
25 microstimulation of neurons in oculomotor brain regions (frontal eye fields, superior colliculus,  
26 lateral intraparietal sulcus) results in similar perceptual benefits and neural enhancement at  
27 corresponding retinotopic locations in visual cortex (Cavanaugh & Wurtz, 2004; Moore &

1 Armstrong, 2003; Moore & Fallah, 2001; 2004; Muller, Philiastides, & Newsome, 2005; see  
2 Moore & Zirnsak, 2017, for review), providing a potential neural mechanism underlying the  
3 pre-saccadic attention shift and the findings of our study.

4

## 5 **Conclusion**

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

15

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