Peri-saccadic visual sensitivity is higher in the upper visual field

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Abstract

Visual neural processing is distributed among a multitude of sensory and sensory-motor brain areas exhibiting varying degrees of functional specializations and spatial representational anisotropies. Such diversity raises the question of how perceptual performance is determined, at any one moment in time, during natural active visual behavior. Here, exploiting a known dichotomy between the primary visual cortex and superior colliculus in representing either the upper or lower visual field, we asked whether peri-saccadic visual sensitivity is dominated by one or the other spatial anisotropy. Humans detected peri-saccadic upper visual field stimuli significantly better than lower visual field stimuli, contrary to known perceptual superiority in the lower visual field during steady-state gaze fixation. Consistent with this, peri-saccadic superior colliculus visual responses were also significantly stronger in the upper visual field than in the lower visual field. Thus, peri-saccadic visual sensitivity reflects oculomotor, rather than visual, map spatial anisotropies.

Introduction

Natural active visual behavior is characterized by frequent saccadic eye movements used to scan our environment. At the time of saccades, vision is not necessarily completely halted[1-9], but it is certainly altered. For example, visual sensitivity can be strongly suppressed peri-saccadically[3, 10-13], and spatial localization perceptual performance is grossly distorted[14-16]. Temporal judgements are additionally affected by saccades[17]. This evidence suggests that peri-saccadic vision is phenomenologically fundamentally different from vision during steady-state gaze fixation. In hindsight, this idea makes plenty of sense: peri-saccadic vision takes place in exact temporal synchrony with large saccade-related activity bursts in multiple cortical and subcortical areas, including the superior colliculus (SC), that drive the eye movements[18-24].

The fact that peri-saccadic vision transpires at the same time as saccade motor commands leads to a question about the neural substrates supporting this special, albeit fleeting, kind of vision. In particular, it is well known that perceptual performance during steady-state fixation is superior in the lower visual field[25-28], and increasing evidence suggests that the primary visual cortex (V1) exhibits neural tissue anisotropies that might explain such perceptual asymmetry[29, 30]. On the other hand, the SC's visual representation preferentially favors the upper visual field instead[31], with neurons exhibiting higher and earlier visual sensitivity for stimuli above the retinotopic horizon than below it. If both V1 and SC neurons interact to coordinate visually-guided behavior, how might such divergent anisotropies in these two functionally and anatomically related brain areas determine perceptual performance, and particularly during the peri-saccadic interval? Answering this and related questions is important for better understanding how functional specializations in different visual and motor structures[32] can all work together to give rise to coherent behavioral outcomes.

We approached this problem by studying peri-saccadic visual sensitivity. It is generally accepted that the sensitivity of the visual system to brief peri-saccadic flashes is strongly suppressed[3, 6, 10, 11, 33]. However, residual visual processing still takes place at the time of saccades[1, 2, 9], allowing us to ask whether such processing is more sensitive in the upper or lower visual fields. We first asked human subjects to generate horizontal saccades, and we presented upper or lower visual field peri-saccadic flashes, which were near the vertical retinotopic meridian at the time of peak saccadic suppression. We found that, despite expected saccadic suppression, residual visual sensitivity was significantly higher in the upper visual field than in the lower visual field. This result was categorically different from our expectation that perceptual sensitivity should have been better in the lower visual field[25]. However, it was in line with the anisotropy that exists in the oculomotor system, symbolized by the SC's preference for upper visual field stimuli[31]. Therefore, we next inspected SC visual responses in rhesus macaque monkeys around the time of saccades. With similar stimuli to those used for the humans, we found that SC peri-saccadic visual responses were again still higher in the upper rather than the lower visual field. Our results suggest that peri-saccadic visual sensitivity reflects oculomotor, rather than visual, map anisotropies. This observation might imply prioritization for detecting extra-personal stimuli for rapid orienting or evasive responses exactly at the time at which perception may be most compromised by saccades.

Results

Peri-saccadic perceptual sensitivity is higher for upper visual field stimuli

We first asked whether human perceptual sensitivity around the time of saccades is different for upper or lower visual field peri-saccadic stimuli. In a first experiment (Experiment 1; diffuse attention), subjects generated approximately 12 deg horizontal saccades to the right or left of central fixation (Fig. 1A). At different times relative to saccade onset, a brief flash lasting approximately 16.7 ms was presented. The flash was centered horizontally at the midpoint between the initial fixation target location and the final desired saccade endpoint (that is, halfway along the intended saccade vector), and it consisted of two vertically-aligned image patches (each at 5 deg above or below the screen center). One patch was the target to be detected by the subjects, and it was either a horizontal or vertical gabor grating. The other patch was an irrelevant distractor without inherent orientation information (it was a superposition of two orthogonal gabors, with the total pattern tilted by 45 deg; Methods). Across trials, the oriented patch was placed either above (upper visual field target location) or below (lower visual field target location) the horizontal meridian, and the other patch was at the vertically-symmetric position. The subjects were instructed to report the orientation of the target flash (horizontal or vertical), and we assessed whether their performance differed as a function of target location.

Across 20 subjects, we found that peri-saccadic perceptual performance was consistently better for upper visual field target locations when compared to lower visual field target locations. Specifically, Fig. 1B shows the time course of the proportion of correct trials in this experiment for targets flashed above (yellow) or below (blue) the horizontal meridian. During pre- and post-saccadic intervals long before or after the eye movements, performance was close to ceiling levels. However, in the critical peri-saccadic interval in which saccadic suppression was to be expected[6, 11, 12], we found that the proportion of correct trials was significantly higher in the upper visual field than in the lower visual field (red asterisks; GLMM, main effect of target gabor location, p<0.01, FDR corrected; see Methods). Therefore, peri-saccadic perception was significantly better in the upper visual field, unlike known lower visual field superiority of perceptual performance in the absence of saccades[25, 27, 28].

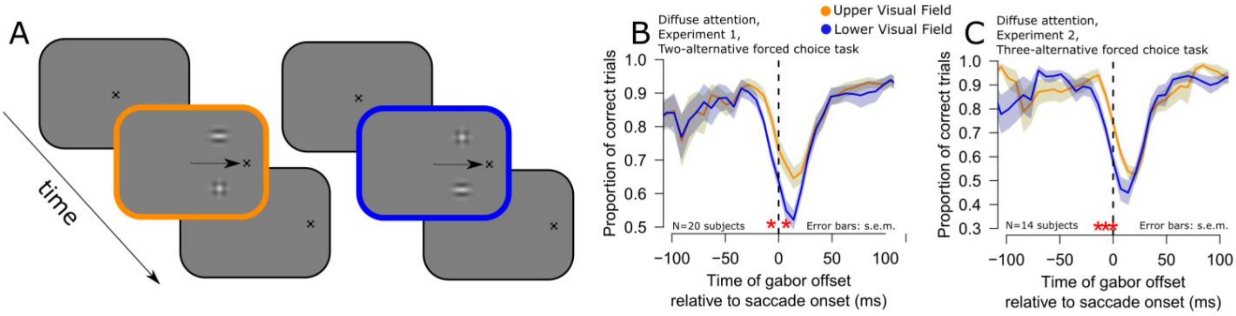

Figure 1 Better peri-saccadic perceptual performance in the upper visual field. (A) Subjects generated ~12 deg horizontal saccades (schematized by an arrow in the figure). At different times relative to saccade onset, two image patches appeared briefly, one above and one below the horizontal meridian (Methods). One patch was an oriented gabor grating (the target), and the other was a distractor with no orientation information. The subjects reported the orientation of the target gabor, and we assessed whether the subjects' responses were better when the target appeared in the upper (yellow) versus lower (blue) visual field. **(B)** Time course of perceptual performance relative to saccade onset for targets in the upper (yellow) or lower (blue) visual field in Experiment 1 (diffuse attention condition; Methods). Red asterisks indicate significant differences between the two curves (GLMM, main effect of target gabor grating location, p<0.01, FDR corrected). **(C)** Similar analysis for Experiment 2 (diffuse attention condition; Methods). Here, chance performance was at 0.33 proportion of correct trials, instead of 0.5. In both cases, peri-saccadic perceptual performance was significantly higher in the upper rather than the lower visual field. Figures 2, 3 describe eye movement and visual stimulation controls that we analyzed in order to rule out other potential alternative explanations for different perceptual performance in the upper and lower visual fields.

This result was also highly robust: we replicated the same observation in a second experiment (Experiment 2, diffuse attention), in which we increased task difficulty. Specifically, in this second experiment (Methods), the target could have one of 3 different orientations, and we tested 14 subjects with it. The increased task difficulty allowed us to obtain a higher dynamic range of potential correctness results, minimizing ceiling and/or floor effects in the critical peri-saccadic interval. Once again, we found that perceptual performance at the times near saccade onset (i.e. during peri-saccadic suppression of visual sensitivity) was consistently better for upper rather than lower visual field target locations (Fig. 1C, red asterisks; GLMM, main effect of target gabor location, p<0.01, FDR corrected; see Methods).

Note that in both peri-saccadic experiments in Fig. 1, the flashes were designed to be symmetric around the horizontal meridian, minimizing visual differences between the upper and lower visual field trials. In control analyses, we also explicitly confirmed that the flashes appeared at similar times and retinotopic positions relative to the ongoing saccades, and that the saccades themselves were similar across the two conditions of upper versus lower visual field targets. Specifically, Fig. 2A, B shows the horizontal saccade trajectories in the two experiments for upper and lower visual field target positions. The trajectories were largely overlapping. Moreover, in Fig. 2C, D, we plotted the distributions of saccade amplitudes in the two conditions, with no differences in the saccade sizes between upper and lower visual field target trials. Similarly, both saccadic reaction times (Fig. 2E, F) as well as gabor offset times relative to saccade onset times (Fig. 2G, H) in the two experiments were the same for upper and lower visual field targets. Statistically, the distributions of saccadic reaction times, saccadic amplitudes, and gabor grating offset times relative to saccade onset times did not differ between trials with upper or lower visual field targets (Kolgomorov-Smirnov test, p>0.05, corrected, 6 comparisons overall, for Experiment 1 and Experiment 2). Therefore, the differences in peri-saccadic perceptual performance seen in Fig. 1 cannot be attributed to systematically different saccade parameters between upper and lower visual field target trials.

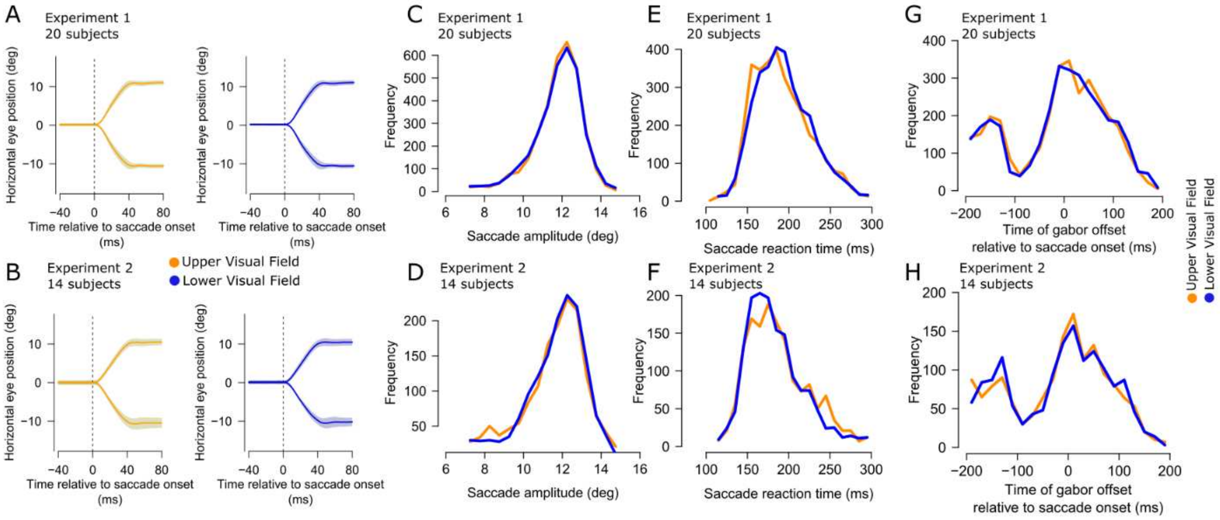

Figure 2 Similarity of eye movement metrics and timings between the upper and lower visual field target locations giving rise to differential peri-saccadic performance in Fig. 1. (A, B) Mean horizontal eye position traces for Experiment 1 (**A**) and Experiment 2 (**B**), separated by target location. Error bars denote two standard deviations. The saccades were similar whether the target appeared in the upper or lower visual field. **(C, D)** Saccade amplitude histograms in each experiment, again separated by upper or lower visual field target location. There was no systematic difference between the saccades for the different target locations. **(E, F)** Saccadic reaction times in each experiment were also similar for upper or lower visual field targets. **(G, H)** This implies that even the times of the gabor gratings relative to saccade onsets were matched between upper and lower visual field targets. Note that the dip in the histogram in each experiment is a known outcome of saccadic inhibition[34-37], but it was, critically, no different between the two conditions.

We also considered whether potential saccadic curvature might have differed sufficiently between the two conditions to influence the results of Fig. 1. That is, it could be argued that the retinotopic position of the flash might have been systematically closer to the fovea for upper versus lower visual field target flashes (perhaps due to saccadic curvature), which would have conferred a slight acuity advantage for the upper visual field targets. However, this was again not the case. In Fig. 3A, B, we plotted the distance of the gabor grating from the fovea at the time of its offset in the two conditions (upper versus lower visual field target locations), and in the two experiments. There was clear overlap in this distance between the two target locations. Moreover, since the flash sometimes happened during the eye movements themselves, we also plotted the retinal slip of the flash in Fig. 3C, D.

Again, such slip was similar whether the target flash was in the upper or lower visual fields, and this was the case in both experiments. Therefore, the retinal conditions of the flashes were similar for upper and lower visual field targets, meaning that the results of Fig. 1 were not trivially explained by systematically different retinotopic stimulation between conditions.

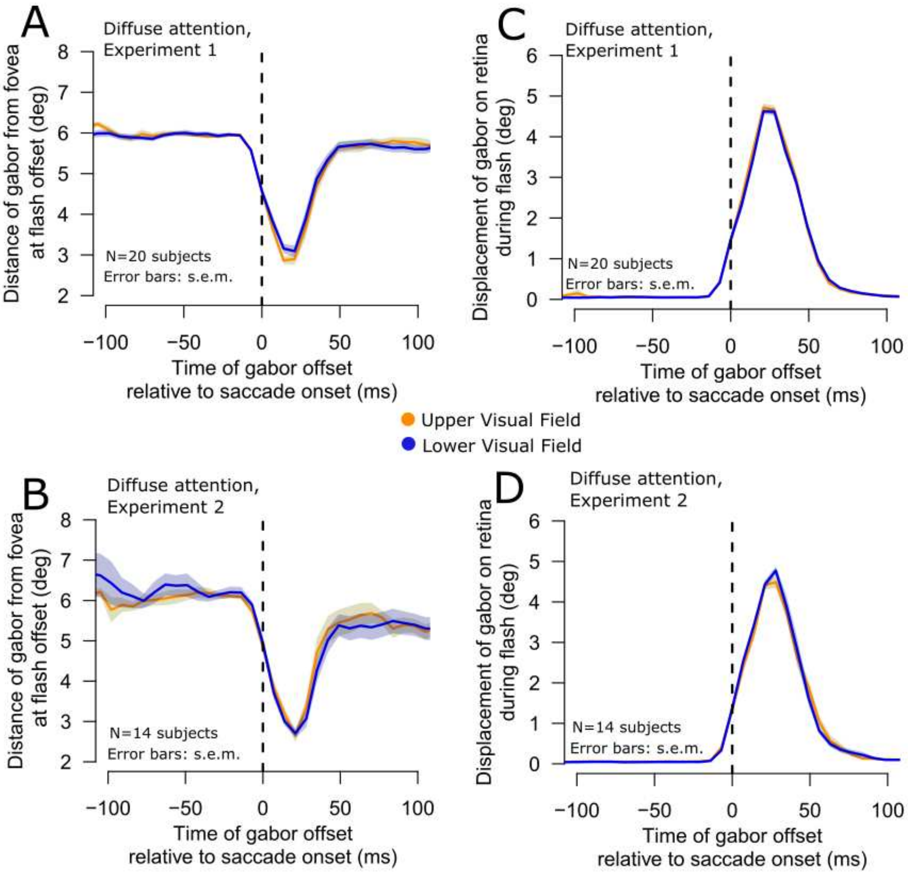

Figure 3 Similarity of retinal stimulation by the flashed gabor patches in the upper and lower visual field target trials. (A, B) In each experiment, we plotted the distance of the target gabor grating from the fovea as a function of time from saccade onset. During the saccade, the patches were closest to the fovea because the flash was always midpoint along the saccade path and timed to frequently occur peri-saccadically. However, and most critically, the distance to the fovea was not different for upper and lower visual field targets (compare yellow and blue curves in each panel). Therefore, the results of Fig. 1 were not due to a visual acuity benefit for upper visual field targets due to retinal eccentricity. Error bars denote s.e.m. **(C, D)** Similar analysis but for the retinal slip of the images during their onset (that is, the displacement of the gabor during its presentation). Because the eye was moving during a saccade, the grating slipped in position on the retina. However, once again, such retinal slip was the same for upper (yellow) and lower (blue) visual field targets in both experiments.

Valid prior knowledge of upper or lower visual field target location does not alter the result

Perhaps the strongest evidence that better upper visual field peri-saccadic perceptual performance was a robust phenomenon emerged when we gave our subjects, within contiguous blocks of trials, valid prior knowledge about the upcoming target location. Specifically, in approximately one quarter of all trials in each experiment (Methods), the subjects were explicitly told that the current block of trials had primarily only upper visual field targets (with 97% probability). Similarly, in another one quarter of the trials, the subjects were informed that the current block of trials had primarily lower visual field target locations (with 97% probability). We called these blocked trials the "focused attention" trials. In both cases, visual sensitivity in the peri-saccadic interval was still higher in the upper visual field than in the lower visual field. This result is shown in Fig. 4. That is, even when the subjects fully knew in advance that a target was going to appear in the lower visual field, their peri-saccadic sensitivity to such a target was still lower than their sensitivity for targets in the upper visual field. In fact, statistical analysis in each experiment (including both diffuse versus focused trial comparisons) revealed that there was neither a main effect of attentional instruction nor an interaction effect between gabor grating position and attentional instruction (Fig. 4 A,B, red asterisks; GLMM, main effect of target gabor location, p<0.01, FDR corrected; see Methods). Note also that eye movement control analyses in the focused attention conditions (as in Fig. 2, 3) again ruled out any eye movement or retinal stimulation explanations of the results. Thus, even valid advance knowledge of target position did not eliminate the observation of stronger peri-saccadic perceptual sensitivity in the upper visual field.

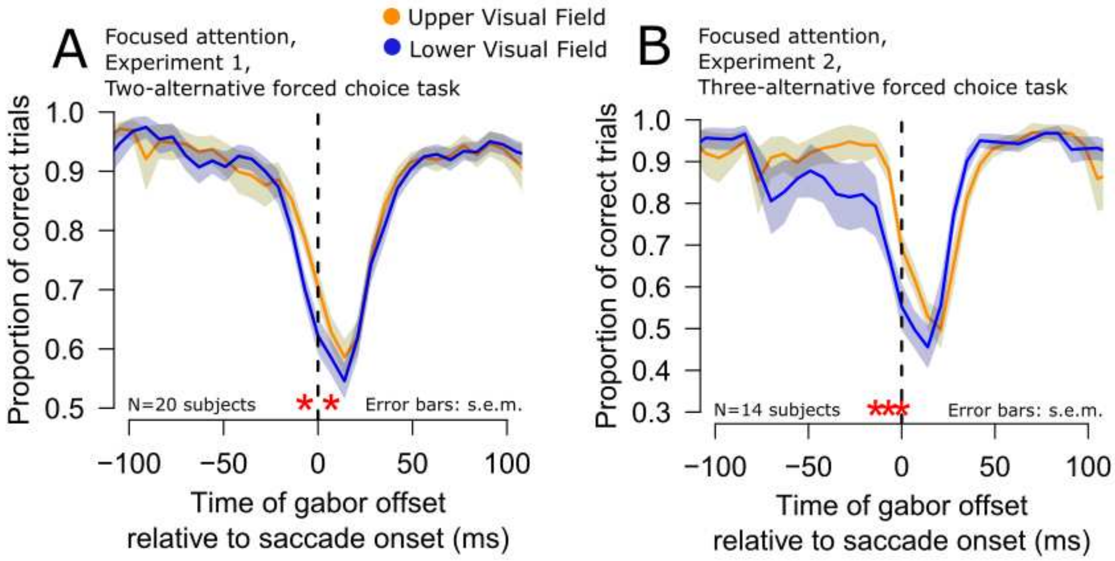

Figure 4 Persistence of the upper visual field peri-saccadic perceptual advantage even with full advance prior knowledge of target location. (A, B) In both experiments, peri-saccadic upper visual field performance was still better than lower visual field performance (red asterisks) even with valid prior knowledge of target location (Methods). All other conventions are similar to those in Fig. 1.

Of course, the results of Fig. 4 were not entirely only a negative result (with respect to the blocking manipulation of target position). For example, when we compared perceptual performance long before saccade onset (-200 to -70 ms from saccade onset) in the diffuse and focused attention conditions, both experiments were suggestive of a perceptual benefit when prior knowledge about target location was provided. For example, in Experiment 1, the subjects exhibited 88% average correct rates with prior knowledge of target location (focused attention trials) when compared to 86% average correct rates without prior knowledge (p=0.055, paired t-test). In Experiment 2, the average correct rates were 91% and 88% in the diffuse and focused attention trials, respectively (p=0.017, paired t-test). Therefore, the lack of influence of advanced prior knowledge on peri-saccadic perceptual performance alluded to above (Fig. 4) was primarily restricted to the peri-saccadic interval.

Peri-saccadic superior colliculus visual sensitivity is also higher for the upper visual field

The results so far suggest that peri-saccadic perceptual sensitivity in humans is better in the upper visual field, a result that is directly opposite of how perceptual sensitivity normally manifests during maintained gaze fixation[25, 27, 28]. This implies that peri-saccadic perceptual sensitivity may be dominated by pathways other than the classic visual cortical systems exhibiting anisotropies favoring the lower visual field[29, 30]. Interestingly, unlike the visual cortex, the SC does preferentially process upper, rather than lower, visual field stimuli during fixation[31]. Therefore, we wondered whether peri-saccadic visual sensitivity in the SC was still better in the upper visual field, consistent with our perceptual results above (e.g. Fig. 1). In other words, we investigated whether neural peri-saccadic sensitivity patterns were similar to the perceptual results.

We analyzed the visual responses of 115 SC neurons that we knew exhibited saccadic suppression for stimuli appearing immediately in the wake of microsaccades[38]. We chose this particular dataset (Methods) to carefully analyze for visual field asymmetries because of two primary reasons. First, microsaccades are an effective means to study saccadic suppression in the SC[38, 39] because microsaccades are genuine saccades[40, 41], and because they have the advantage of not moving visual response fields (RF's) too much due to their small size. Therefore, presenting stimuli to the RF's with and without the rapid eye movements (to assess suppression of visual sensitivity relative to baseline) is experimentally simple with microsaccades. Second, in this data set, we used stimuli presented directly in the post-movement interval after the microsaccades[38], allowing us to avoid (as much as possible) the visual effects of retinal image displacements during the movements themselves.

We first assessed that the recorded neurons were similarly distributed across the upper and lower visual fields. Figure 5A shows the RF hotspot directions in deg, relative to the horizontal cardinal axis, for all of the recorded neurons. Negative numbers indicate neurons representing the lower visual field, and positive numbers indicate neurons with RF hotspots above the horizontal meridian. From the figure, it can be seen that the two populations of neurons were equally sampled across the upper and lower visual fields. Similarly, in Fig. 5B, we plotted the amplitudes of microsaccades occurring near stimulus onset (and thus associated with peri-saccadic suppression), which were similar in the sessions in which we recorded neurons with either upper or lower visual field RF's. Therefore, the eye movement characteristics were similar regardless of whether we recorded upper or lower visual field SC neurons.

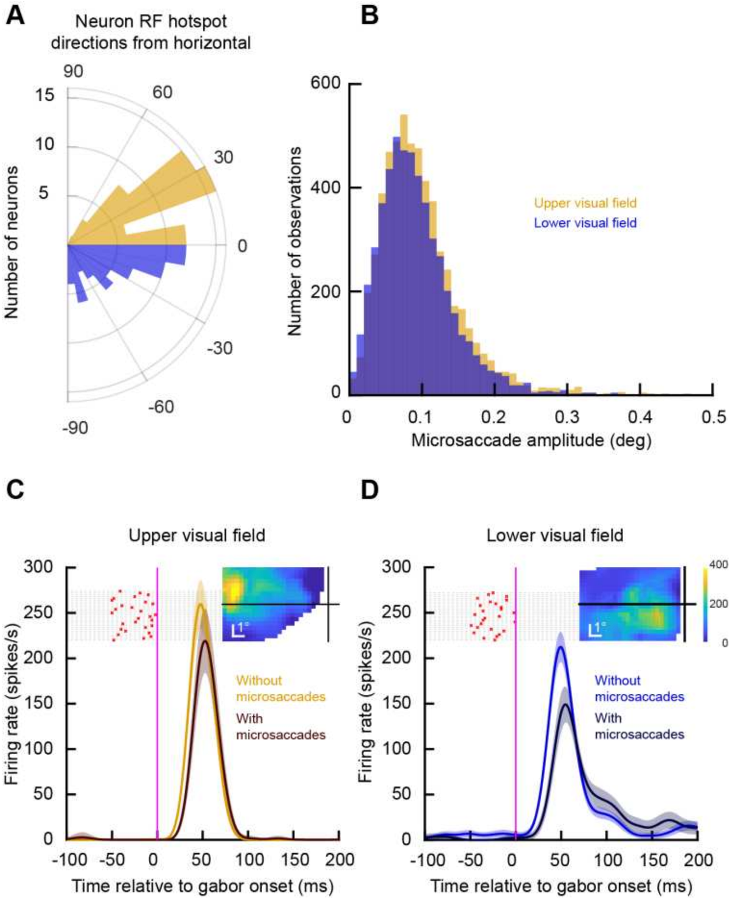

Figure 5 Higher upper visual field peri-saccadic sensitivity in SC neurons. (A) Distribution of RF hotspot locations from our recorded population, expressed as a direction from the horizontal meridian. Approximately half of the neurons had RF hotspots in the upper visual field (yellow), and the rest had hotspots in the lower visual field. **(B)** We assessed peri-saccadic suppression by evaluating visual sensitivity for stimuli appearing near the time of microsaccades[38, 39]. Here, we characterized the microsaccade amplitudes for the two groups of sessions that we compared (in which we recorded either upper or lower visual field SC neurons). The eye movement amplitudes were matched across the two groups. **(C)** Example upper visual field SC neuron responding to the onset of a low spatial frequency gabor grating (0.56 cpd). The saturated yellow curve shows the neuron's visual response in the absence of nearby microsaccades (Methods), and the darker curve shows the same neuron's visual response when the stimulus appeared immediately in the wake of microsaccades (individual microsaccade onset times are shown as a trial raster of red crosses in the background of the figure). The inset shows the RF location of this neuron, indicating that it preferentially represented a part of the upper visual field. Error bars denote 95% confidence intervals. **(D)** Similar to **C** but for a neuron preferring the lower visual field (see RF map in the inset). Not only did the neuron have lower baseline visual sensitivity (saturated blue curve)[31], but its suppressed visual response (darker curve) was also more strongly reduced than in the neuron in **C**. Thus, SC visual neural sensitivity was still higher in the upper visual field during peri-saccadic intervals.

When we then inspected the neurons' visual responses themselves, we observed consistently higher peri-saccadic SC visual sensitivity in the upper visual field neurons than in the lower visual field neurons. Consider, for example, the pair of neurons shown in Fig.

5C, D. In Fig. 5C, the neuron had an upper visual field RF (the RF map is shown in the inset). Its visual response to a low spatial frequency grating of 0.56 cpd was mildly suppressed when the grating appeared immediately after microsaccades. Specifically, the yellow curve shows the neuron's average firing rate in the absence of microsaccades near stimulus onset (Methods), and the darker curve shows the average firing rate when the grating appeared immediately after microsaccades (individual microsaccade times across different trials from this condition are shown as red crosses in the figure). The neuron's response was suppressed in association with microsaccades, as expected but such suppressed response was still robust and peaking above 200 spikes/s. On the other hand, the neuron in Fig. 5D represented a lower visual field location (its RF map is shown in the inset). Not only was its baseline visual response (in the absence of nearby microsaccades) weaker than the baseline response of the neuron in Fig. 5C[31], but its peri-saccadically suppressed response (dark curve) was also more strongly affected by the eye movements. In other words, the neuron experienced stronger saccadic suppression than the neuron in the upper visual field, consistent with our perceptual results above. Thus, if anything, the spatial anisotropy in the SC in terms of upper versus lower visual field neural sensitivity[31] was amplified even more during peri-saccadic intervals.

We confirmed this by isolating a measure of saccadic suppression, and confirming that it was stronger for lower rather than upper visual field SC neurons. Across the population, we normalized each neuron's activity by its strongest no-microsaccade visual response to any of the five different spatial frequencies that we tested[38]; that is, we picked the spatial frequency that evoked the strongest peak response, and we normalized all trials' firing rate measurements by this value (Methods). We then normalized each neuron's peri-saccadically suppressed visual response using the very same normalization factor, and we averaged across neurons. For the neurons preferring the upper visual field (Fig. 6A), the population generally preferred low spatial frequencies[42] in its baseline no-microsaccade activity (yellow curve; error bars denote 95% confidence intervals). However, the tuning curves were broader than in the lower visual field neurons (Fig. 6B, blue curve). For example, the upper visual field neurons were more sensitive to 4.44 cpd gratings than the lower visual field neurons, consistent with prior observations[31]. Most importantly for the current study, for the peri-saccadically suppressed visual bursts (dark curves in Fig. 6), similar observations persisted. That is, the upper visual field neurons had broader tuning curves than the lower visual field neurons in the peri-saccadic interval, and they were suppressed less than the lower visual field neurons at the low spatial frequencies. For example, at the lowest spatial frequency (0.56 cpd), there was significantly weaker saccadic suppression in the upper visual field neurons (Fig. 6A) than in the lower visual field neurons (Fig. 6B); this is evidenced by the larger difference between the blue and dark blue curves in Fig. 6B than between the yellow and dark yellow curves in Fig. 6A ($p = 0.038$, two-sample t-test).

At higher spatial frequencies, the saccadic suppression effect was expectedly weakened overall[38], but this weakening again happened more so for the upper visual field neurons than for the lower visual field neurons (for example, the difference between the curves at 2.22 and 4.44 cpd was smaller in the upper visual field, panel A, than in the lower visual field, panel B). Coupled with the fact that the neurons were themselves more sensitive in the upper visual field in the no-microsaccade trials[31] (e.g. Fig. 5), this suggests that there was consistently higher peri-saccadic visual sensitivity in the SC visual bursts in the upper visual field.

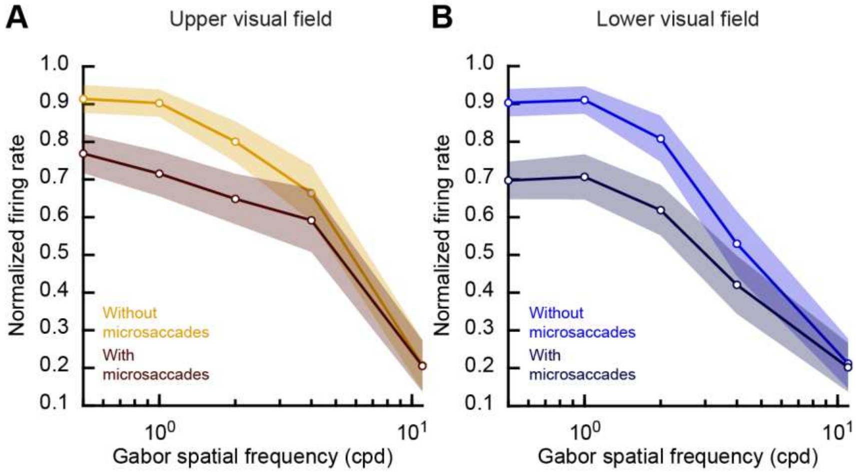

Figure 6 Broader peri-saccadic SC population tuning curves in the upper visual field. (A) Average population tuning curve of the upper visual field neurons without eye movements (saturated yellow) and peri-saccadically (dark). Error bars denote 95% confidence intervals. In both curves, we normalized each neuron's activity to the peak visual response for the preferred spatial frequency (Methods). Lower spatial frequencies experienced more suppression than higher spatial frequencies, as expected[38]. **(B)** Same analysis but for the lower visual field neurons. In baseline (saturated blue), the neurons were more low-pass in nature than the upper visual field neurons in **A**[31]. For example, the tuning curves dropped sharply at 4.44 cpd when compared to the neurons in **A**. This difference persisted for the peri-saccadic tuning functions (that is, there was stronger saccadic suppression in the darker curve when compared to **A**); also see Fig. 7.

We also confirmed the above interpretations by plotting the neural peri-saccadic suppression time course profiles, like we did for the human experiments above. We found consistently higher relative sensitivity in the upper visual field neurons than in the lower visual field neurons, as can be seen in Fig. 7 for the case of 0.56 cpd grating stimuli. To obtain this figure, we calculated the normalized firing rate for each trial in which the gabor grating appeared in the interval from -50 ms to 140 ms relative to movement onset (see Methods). We then plotted the mean normalized firing rate at each time bin for neurons in the upper (yellow) versus lower (blue) visual fields. Values lower than one indicated a reduction in firing rate, which took place for both upper and lower visual field neurons (indicating peri-saccadic suppression). Most critically, and consistent with Figs. 5, 6, the peak suppression was stronger by about 10% for the neurons in the lower visual field (blue) compared to the neurons in the upper visual field (yellow). Similar trends were observed for higher spatial frequencies, but they got progressively weaker and weaker as expected from Fig. 6 and ref. [38]. We conclude that peri-saccadic visual neural sensitivity is consistently higher in the upper visual field, similar to our conclusion with our human perceptual results.

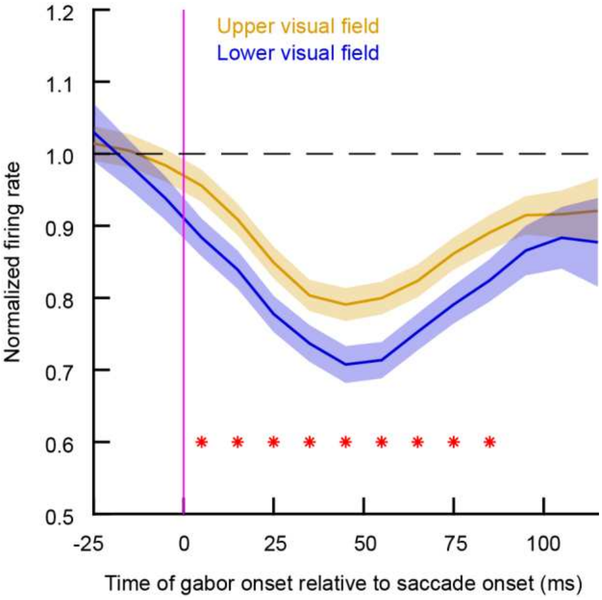

Figure 7 Milder suppression in upper visual field SC neurons in peri-saccadic times. The figure shows the time course of visual neural sensitivity in the SC for low spatial frequencies (Methods). Upper visual field neurons (yellow) experienced milder saccadic suppression, and were therefore more sensitive, than lower visual field neurons (blue). Such an effect was temporally locked to the saccades, as in Fig. 1B, C. Thus, coupled with overall higher visual sensitivity in upper visual field SC neurons, these results suggest that during peri-saccadic intervals, the anisotropy between upper and lower visual field SC sensitivity is even larger than in the absence of eye movements.

Discussion

In this study, we started with human perceptual experiments in which we flashed images at approximately the upper and lower vertical retinotopic meridians (Fig. 3) during saccades. For these particular presentations (that is, peri-saccadically), perception was paradoxically better in the upper visual field than in the lower visual field (e.g. Fig. 1), despite strong saccadic suppression. That is, at the time of strong peri-saccadic perceptual suppression[3, 10, 11, 33], perceptual performance violated a well-known observation that lower vertical meridian vision is better than upper vertical meridian vision[25-28]. We then investigated visual neural sensitivity in the SC, and we again found higher sensitivity in the upper visual field. Thus, during peri-saccadic epochs, visual performance may actually reverse its superiority for the lower visual field and reflect, instead, better processing of upper visual field locations.

When considering active vision, the existence of spatial anisotropies in neural circuits and behavior is intriguing, in general. In particular, not only is visual performance better in the lower visual field[25-28], but attentional performance is as well[43, 44] . Moreover, cortical visual areas may have anisotropies that are in line with such behavioral anisotropies favoring the lower visual field[29, 30]. However, for the oculomotor system, opposite anisotropies exist. First, the SC strongly favors upper visual field visual stimuli[31]. Second, saccadic reaction times are faster in the upper visual field[31, 45-47]. And, third, saccadic landing positions are also more accurate in the upper visual field[31], likely reflecting significantly smaller movement fields in the SC upper visual field representation[31]. However, if that is indeed the case, how does vision operate during peri-saccadic intervals? We found that it behaves more like the oculomotor anisotropy, as in being better in the upper visual field, than the visual cortical anisotropy. This dichotomy is interesting to consider from a broader perspective, especially when discussing more general questions regarding the role of the SC in cognition in general. For example, increasing evidence suggests that the SC may be a controller of visual attentional modulations in the cortex[48-54]. However, if this is the case, then how might one reconcile the opposite anisotropies that the SC and visual cortices exhibit?

One possibility might be that the pattern of feedback that the SC provides to the cortex is combined to serve either attention or perceptual performance at strategic times. For example, it may be the case that larger visual RF’s in the lower visual field representation of the SC aid multiple smaller RF’s in the cortex to be functionally bound together during directed covert attention to a given location. This could jointly modulate the normally separate cortical RF’s. Thus, the opposite anisotropy between the SC and visual cortex may actually be functionally useful during gaze fixation. In the case of peri-saccadic vision, the opposite anisotropy may be useful in an additional manner: to favor detecting far, extra-personal stimuli (e.g. aerial threats) exactly at the time in which perception may be most compromised by saccadic suppression. This can aid in quick orienting or evasive responses. Thus, it may be favorable to have better peri-saccadic vision in the upper visual field, like in the SC, than in the lower visual field, like in the cortex. This, in turn, might mean that the gain of feedback from the SC to the cortex, which may be useful for saccadic suppression[55], is higher for lower visual field locations than upper visual field locations (that is, causing stronger saccadic suppression).

We find this idea useful, and plausible, in placing our results in the context of other recent observations related to active vision. For example, we recently found that SC saccade-related bursts are stronger in the lower visual field, not the upper visual field[31, 56]. Interestingly, saccade kinematics were not different for upper and lower visual field saccades, suggesting that the SC motor bursts do not necessarily dictate movement kinematics[56]. Instead, we think that they may modulate the gain of feedback to the cortex, perfectly supporting our observations of stronger saccadic suppression in the lower visual field. Indeed, there is evidence that feedback projections from the SC to the frontal cortex may target inhibitory neurons[57, 58], and inactivation of the SC during saccades renders saccade-related frontal cortical bursts stronger rather than weaker[59]. All of this evidence suggests that there may be asymmetric gain feedback to the cortex from the SC, which causes stronger saccadic suppression in the lower visual field. One prediction of the above idea, therefore, is that we should also observe stronger peri-saccadic visual sensitivity in the upper visual field in cortical visual areas, not just in the SC, but this idea remains to be tested.

Another interesting insight from our SC results is that within the SC itself, the visual anisotropy between the upper and lower visual fields is magnified peri-saccadically. That is, not only are neurons less sensitive in the lower visual field in baseline fixation (Fig. 5), but they also experience stronger saccadic suppression in the peri-movement intervals (Figs. 6, 7). Therefore, the already strong disparity in visual sensitivity between the upper and lower visual fields in the SC[31] is rendered even stronger peri-saccadically.

Finally, it is interesting to consider that even full prior knowledge of target location (Fig. 4) did not necessarily alter our observations in the perceptual experiments. This suggests that fundamental mechanisms governing peri-saccadic vision operate under practically all conditions, irrespective of attention. This might have a useful ecological purpose, as mentioned above. At the time during which vision is most compromised by saccades, it might be most useful to utilize whatever remaining residual visual abilities, under all behavioral contexts, to detect extra-personal stimuli (which primarily reside in the upper visual field) and rapidly react to them.

Methods

Experiments 1 and 2 were psychophysical experiments on human participants. The third experiment consisted of analyzing neurophysiological recordings from two rhesus macaque monkeys. The human experiments were approved by the University of Glasgow Research Ethics Committee, and the participants received a compensation of £6 per testing hour. Written informed consent was also obtained, in accordance with the 1964 Declaration of Helsinki. The monkey experiments were approved by the Regierungspräsidium Tübingen, under licenses CIN3/13 and CIN04/19G, and the experiments complied with European and national laws governing animal research.

A total of 34 human subjects aged between 18 and 38 years took part in the behavioral experiments (Experiment 1: 20 subjects, 14 females; Experiment 2: 14 subjects, 8 females). All subjects self-reported as being free from neurological impairments. All subjects also had normal or corrected to normal vision and were naïve to the purposes of the experiment. The neurophysiological analyses were performed on an existing data set from ref. [38], which we re-analyzed here from the perspective of visual field asymmetries. The monkeys in that study were two adult, male rhesus macaques aged 7 years.

In what follows, we first describe the human experiments, and we then report on the neurophysiological analyses.

Human laboratory setup and behavioral tasks

Stimuli were presented on a 24-inch LCD monitor (1920 x 1024 pixels) at 60 Hz. Subjects were seated with their head resting on a chin and forehead rest to reduce head movements. Eyes were horizontally and vertically aligned with the center of the screen at a distance of 65 cm. Eye movements were recorded with the EyeLink 1000 system (detection algorithm: pupil and corneal reflex; 1000 Hz sampling; saccade detection was based on 30 deg/s velocity and 9500 deg/s^2 acceleration thresholds). Subjects' responses were recorded on a standard keyboard. A five point-calibration on the horizontal and vertical axes was performed at the beginning of each experimental run. The programs for stimulus presentation and data collection were written in MATLAB (MathWorks) using the Psychophysics Toolbox Version 3[60, 61], and Eyelink Toolbox extensions[62].

Stimuli included a fixation point measuring 0.7 degrees of visual angle (deg), which was jumped to instruct saccade generation. Target stimuli were gabors with a spatial frequency of 0.9 cycles per deg, gaussian envelope with σ 3.5 deg (see Fig. 1A). Distractor stimuli consisted of the sum of two gabors (one horizontal and one vertical), tilted by 45 degrees (see Fig. 1A).

Each subject took part in two behavioral sessions, in non-consecutive days (day 1 and day 2). The experiment consisted of a gabor discrimination task, adapted from ref. [3]. During the first session (day 1) each subject completed three training runs before a fourth experimental phase. Day 2 started directly with the experimental runs, without training runs. Each session lasted approximately 1.2 hours.

On the first experimental day, the subjects first engaged in three training phases, each lasting approximately 4-5 minutes. For the first phase, the subjects were shown a fixation spot that jumped right or left by 12 deg, and they generated visually-guided saccades. We measured their baseline reaction times during this phase. For the second phase, the subjects maintained gaze fixation, and two image patches (like in Fig. 1A) were flashed for 1 frame (~16.7 ms) either on the right or left side of the fixation spot (at a horizontal eccentricity of 6 deg). The patches were each at 5 deg above or below the horizontal meridian, and one of them was the target patch, while the other was the distractor patch. They both had a contrast of 40%. In Experiment 1, the target could have two orientations (horizontal or vertical), and in Experiment 2, it could have 3 orientations (horizontal, vertical, and oblique with direction +/-15 deg from the horizontal). Subjects practiced reporting the target orientation during fixation. Then, we moved to the third phase, in which we reduced the patch contrasts to 30% instead of 40%. We then started the main experiments.

Each experimental run consisted of 55 trials. Each subject took part in a variable number of experimental runs, ranging between 15 and 20 in two non-consecutive days. At the beginning of each run, a five point-calibration on the horizontal and vertical axes was performed. During each run, drift correction was applied every 7 trials. For each trial, subjects maintained central fixation and pressed the spacebar to initiate a trial. After a variable interval between 750 ms and 1250 ms, the central fixation spot disappeared and a target fixation point was presented at 12 deg eccentricity, horizontally, randomly to the left or right with respect to central fixation. Subjects were asked to perform a saccade as quickly and accurately as possible towards the target fixation point. At a variable interval from the requested saccade signal, we presented the target-distractor configuration (flash) on the same side as the requested saccade, for 1 frame or ~16.7 ms (see Fig. 1A)[1, 2, 63-65]. The flash time interval was centered on the subject's median saccadic reaction time estimated from the first training phase. We aimed at sampling behavioral performance around three main moments around the peri-saccadic interval: a) before saccade onset, presenting the target-distractor configuration 110 ms before the expected saccade onset time, as estimated from median saccadic reaction times; b) around saccade onset, presenting the target-distractor configuration at the expected saccade onset; and c) After saccade onset, presenting the target-distractor configuration 30ms after the expected saccade onset. In Experiment 1, subjects reported one of two orientations as above, and in Experiment 2, they reported one of three orientations. Subjects were instructed to aim for accurate responses, not fast response times.

In each experiment, we had either a diffuse attention set of trials or a focused attention block of trials. In 50% of the experimental runs, the subjects were told that the target could either appear in the upper or lower visual field. In 25% of the runs, the subjects were told that the target will appear in the upper visual field with 97% probability. And, in the final 25% of the runs, the subjects were told that the target will appear in the lower visual field with 97% probability. We randomly varied the order with which the diffuse and focused blocks of trials that were run across individuals. That is, for some subjects, the diffuse block could start first followed by the two focused blocks, whereas for other subjects, one focused block could be finished first, then the diffuse block, and then the other focused block. Each subject was told which block they were running before they started their sessions.

Human data analysis

Only trials where a valid eye movement was executed entered the next stage of analysis. Valid eye movements had to be performed towards the landing fixation point and be between 7 deg and 15 deg in amplitude. Eye movement reaction time had to be between 100 ms and 300 ms, and with saccade duration shorter than 90 ms. For Experiment 1, 24% of trials were excluded based on these criteria, on average, across subjects. For Experiment 2, 32% of trials were excluded based on these criteria, on average, across subjects.

For perceptual reports, we computed the timing of the gabor offset relative to saccade onset by subtracting the time when the target-distractor configuration (flash) disappeared from the moment of saccade onset. According to this convention, negative values represent stimuli that were presented before the onset of the eye movement, while positive values represent stimuli that were (partially or in full) presented after saccade onset.

We also computed the distance traveled by the eyes while the target-distractor configuration (flash) was presented (‘Displacement of gabor on retina during flash’) by subtracting the eye position measured when the target-distractor configuration (flash) disappeared on screen from the eye position measured when the target-distractor configuration (flash) appeared on screen. This measure captures the distance traveled by the eyes over the target-distractor configuration, or the retinal slip of the flash, thus capturing potential saccade kinematic differences between experimental conditions that could account for discrimination performance during the peri-saccadic interval.

Finally, we computed the distance between the fovea and the target gabor when the target-distractor configuration disappeared from screen (‘Distance of gabor from fovea at flash offset’). This measure captures the distance between the fovea and the target gabor when the target-distractor configuration disappeared from screen, allowing us to assess potential differences in proximity of the fovea to the target gabor that could account for discrimination performance during the perisaccadic interval.

Data were analyzed using the R software for statistical computing[66]. The data were analyzed with a Generalized Linear Mixed Model (GLMM)[67], based on the Generalized Linear Model framework proposed by McCullagh and Nelder[68]. Main effects and interaction between conditions for proportion of correct trials (binary outcome, 0-1) were tested using the logit function as link function (logistic regression model). Main effects and interaction between conditions for displacement of gabor on retina during flash and distance of gabor from fovea at flash offset were tested using the identity function (linear regression model). A subject numerical identifier was used as a random effect variable.

For each participant, we used a moving time window of 30 ms, shifting its center by 7 ms at every iteration. For every time window, we ran one GLMM for each dependent variable (proportion of correct trials, displacement of gabor on retina during flash and distance of gabor from fovea at flash offset, 3 models overall) and tested the main effect and interaction of the independent variables (gabor position and attentional state). The p values of each test were corrected by the number of time windows that entered the analysis by means of false discovery rate (FDR)[69] at a $p<0.01$ level.

We used the Kolmogorov-Smirnov test to assess potential differences between distributions in the upper visual field and lower visual field experimental conditions for saccade reaction time, saccade gabor offset relative to saccade onset, and saccade amplitude.

Monkey neurophysiology

We analyzed the neural data presented in ref. [38]. In that study, we documented saccadic suppression in the SC, but we did not explore effects of upper versus lower visual field locations. Here, we re-analyzed the same data from the perspective of visual field asymmetries. The behavioral and neurophysiological methods were described previously[38].

Briefly, the monkeys fixated a small, central fixation spot. At some point during gaze fixation, a vertical gabor grating of different spatial frequencies (0.56, 1.11, 2.22, 4.44, and 11.11 cpd) and high contrast (100%) appeared within a recorded neuron's RF and stayed there for a few hundred milliseconds. The monkeys were rewarded for simply maintaining fixation on the fixation spot until trial end. Because the stimulus stayed on for a prolonged period (unlike in the human experiments), we only analyzed trials in which the stimulus onset event happened after microsaccades. This interval is still an interval in which peri-saccadic suppression of the evoked visual burst still takes place[13, 38, 39]. Also, prior to running the main task, we mapped the RF's using standard delayed and memory-guided saccade tasks. This allowed us to identify the RF hotspots and classify them as being in either the upper or lower visual field (Fig. 5A). All microsaccades were also detected previously in the original study[38]. Here, we assessed their amplitude distributions across the upper and lower visual field sessions (Fig. 5B), to ensure their similarity.

One main goal of the analysis was to investigate suppression of visual sensitivity around the time of microsaccades, and to determine if such modulation was different for neurons located in the upper or in lower visual field. To perform such analysis, for each neuron, we analyzed the neural activity following the stimulus onset in the mapping task, to determine the neuron's RF hotspot location as the region of the visual field giving most activity. Once the hotspot was determined, upper visual field neurons were defined when the vertical component of the hotspot location was bigger than zero. All other neurons were labeled as lower visual field neurons. Then, we divided the data into two groups depending on whether saccades were executed or not during a critical interval around the stimulus presentation. In particular, no-saccade trials were defined as all the trials which did not have any saccades present between -100 to 100 ms around gabor onset. If a saccade was present in the time interval above, it was considered a saccade trial, and we assessed saccade time relative to stimulus onset time for evaluating time courses of neural suppression.

Spatial frequency tuning curves (i.e., responses for each given spatial frequency) were described previously[31, 38], but in this, study we analyzed how saccades influenced these curves differently when the RF was either in the upper or lower visual field. To test the effect of saccadic suppression in the upper and lower visual fields, we computed a measure of “normalized firing rate”. First, we calculated, for each trial, the peak firing rate between 30 and 150 ms after stimulus onset. Then, for each neuron and spatial frequency condition, we averaged the peak firing rate in trials in which no saccades were detected. This value was then normalized by dividing the averages of each spatial frequency condition by the preferred spatial frequency response of that neuron, giving as a result the average tuning curve when no saccades were present. Similarly, for each neuron and spatial frequency, we averaged all the trials in which the gabor stimulus was presented 40 to 100 ms after saccade onset. The average peak firing rate at each spatial frequency condition was then normalized by the peak firing rate for the preferred spatial frequency response of the trials with no saccades. Doing so, values lower than one indicated suppression of neural activity because of saccade generation.

To summarize the time courses of saccadic suppression of SC visual bursts in the upper and lower visual fields (e.g. Fig. 7), we selected all the trials in which the gabor stimulus was presented between -50 to 140 ms relative to saccade onset. We then smoothed the data by applying a running average window of 50 ms on the normalized peak firing rate (relative to the baseline firing rate of for that spatial frequency) and by moving the average time window in steps of 10 ms. This analysis was performed only for the lower spatial frequency grating (0.56 cpd), which was the one used in the behavioral experiment reported above. To statistically test the difference between the upper and lower visual fields, we ran a series of two-sample independent t-tests at each bin of the two curves, and we adjusted the alpha level with Bonferroni correction.

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Competing interests

The authors declare no competing interests.

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