Superior colliculus peri-saccadic field potentials are dominated by a visual sensory preference for the upper visual field

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Summary

The primate superior colliculus (SC) is critical for saccade generation[1-9], but it also possesses a rich visual processing repertoire[10,11]. A now-acknowledged property of the SC is that it does not represent all visual field locations equally: besides foveal magnification[12,13], SC neurons representing the upper visual field show significantly stronger and earlier visual responses than neurons representing the same retinotopic eccentricities in the lower visual field[14-16]. Intriguingly, saccade-related motor bursts in the same neurons exhibit the opposite asymmetry: SC motor bursts are stronger in the lower rather than upper visual field[14,17]. Here, and motivated by evidence of sensory signals embedded within the motor bursts themselves[11,17-21], I asked whether a visual sensory preference for the upper visual field in the SC still manifests itself peri-saccadically, despite the weaker motor bursts. Since SC local field potentials (LFP's) exhibit saccade-related modulations[18,22-24], I specifically investigated whether they reflect the visual[14-16] or motor[14,17] spiking asymmetries. As expected, LFP's exhibited strong peri-saccadic negativity at the time of motor bursts[18,22-24]. Critically, such negativity was much larger in the SC's upper visual field representation, and it matched the asymmetry in stimulus-evoked LFP negativity. Peri-saccadic LFP modulations thus reflected the SC's sensory preference for the upper visual field, and they were unambiguously dissociated from peri-saccadic spiking asymmetries. This dissociation persisted even with saccades towards a blank, suggesting that topographic location was a critical determinant. My results suggest that at the time of saccades, the SC network possesses a clear sensory-related signal, potentially relevant for processes beyond just online saccade control.

Results

Stronger peri-saccadic field potential deflections in the upper visual field

We previously documented an asymmetry in the SC's representation of the upper and lower visual fields[14]. Here, I revisited the same database[14], but now focusing on peri-saccadic LFP modulations. To better orient the readers, I first summarize how the stimulus-evoked LFP's behaved. Figure 1A reproduces earlier results[14], demonstrating that visually-evoked LFP modulations were stronger (more negative) in the upper visual field. Note that in each experiment, the appearing stimulus was always placed at the best response field (RF) location of the recorded neurons[14]. The inset, again reproduced from ref. [14], shows that this upper/lower visual field LFP asymmetry was consistent with the asymmetry in SC visual response firing rates. Figures 1B, C, in turn, remind that the LFP asymmetry was step-like across the horizontal meridian[14], suggesting a potential quadrant-based discontinuity.

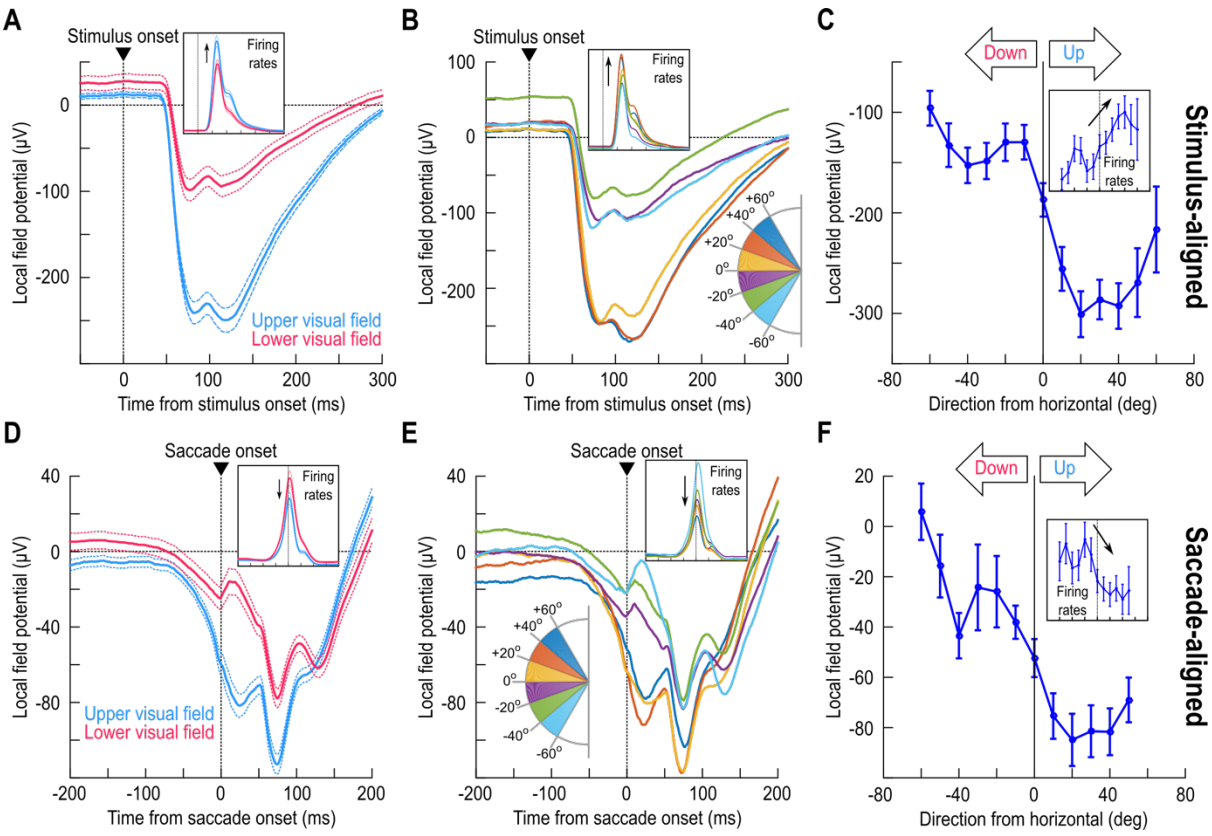

Figure 1 Peri-saccadic local field potential (LFP) deflections in the superior colliculus (SC) reflect their visual counterparts. (A) Stimulus-evoked LFP deflections after the brief appearance of a small white spot at the preferred response field (RF) location[14]. Blue shows the average for all electrode tracks in the SC's upper visual field representation; red shows results from the lower visual field representation. The inset shows the corresponding single-neuron firing rates[14]. LFP negativity deflections were much stronger in the upper visual field representation[14]. **(B, C)** The same data but now separated as a function of direction from the horizontal axis represented by the SC sites. There was a step-like discontinuity across the horizon[14]. **(D)** Similar to **A** but now for data aligned to saccade onset towards a visible spot. Even though the motor bursts were weaker in the upper visual field[14,17] (inset), the LFP negativity deflections were still much stronger for the upper visual field, consistent with the stimulus-evoked effects in **A**. **(E, F)** The same discontinuity across the horizontal meridian seen in **B**, **C** was also evident peri-saccadically (0-50 ms from saccade onset in **F**; Methods). Note how the insets in **B**, **E** as well as **C**, **F** show directly opposing dependencies in the spiking activity between the visual and motor epochs; in contrast, the LFP's show the same dependencies. Error bars in all panels denote SEM. **A**-**C** were reproduced with permission from our earlier study[14] for easier direct visualization next to **D**-**F**. All insets were also reproduced[14].

Peri-saccadically, we previously noted that SC motor bursts are actually weaker in the upper visual field[14,17], an opposite asymmetry from the visual bursts. Does that mean that LFP negativity would also be smaller? Using a delayed, visually-guided saccade task (Methods), I plotted in Fig. 1D average peri-saccadic LFP modulations across all tested electrode tracks. Like in the stimulus-evoked analyses (Fig. 1A), I classified electrode tracks according to whether they penetrated the SC's upper (blue) or lower (red) visual field representation. Also like in the stimulus-evoked analyses, the saccade target was always at the best RF location of the session[14]. There was much larger peri-saccadic LFP negativity in the upper visual field representation ($p=9.4\times10^{-9}$; t-test for the interval 0-50 ms from saccade onset,

comparing upper and lower visual field electrode tracks). This was despite the weaker motor bursts (inset). Thus, peri-saccadically, aggregate SC network activity reflected the strong visual sensory preference for the upper visual field, and not the weaker simultaneously-occurring motor bursts.

Given this dissociation, and given that LFP signals might reflect the influence of synaptic and other network activity[25-32], these results suggest that SC peri-saccadic sensory information could act to weaken motor bursts. Interestingly, we recently found a potential inverse relationship between image preference at stimulus versus saccade onset in visual-motor SC neurons: for some image manipulations, if a neuron fired more for one image feature in its visual burst, it tended to also have weaker saccade bursts for the same feature[18].

Remarkably, the visual field asymmetry in peri-saccadic LFP negativity also exhibited a step-like discontinuity across the horizon: just like in the stimulus-evoked LFP's (Fig. 1B), all tested electrode tracks in the upper visual field had similar peri-saccadic LFP negativity amplitude, which was larger (in absolute value) than all tested electrode tracks in the lower visual field (Fig. 1E). This can also be seen in Fig. 1F; here, I measured the LFP amplitude in the interval 0-50 ms from saccade onset. There was a similar dependence to the stimulus evoked modulations in Fig. 1B, C ($p=6.72\times10^{-10}$; one-way ANOVA across the shown angular direction bins). Again, this dependence was the opposite of that in the spiking activity (inset).

It is also worthwhile to consider the magnitude of the peri-saccadic LFP asymmetry. From Fig. 1D, F, I calculated the LFP amplitude in the interval 0-50 ms from saccade onset; it was ~3.1 times larger (in absolute value) in the upper visual field. This was similar to the stimulus-evoked LFP asymmetry of Fig. 1A-C (peak LFP amplitude in the interval 30-100 ms from stimulus onset being ~2.5 times larger in the upper visual field[14]). Thus, despite the quantitative and qualitative differences in visual field asymmetries for stimulus-evoked versus saccade-related spiking, the LFP asymmetries were both qualitatively and quantitatively similar.

The peri-saccadic LFP asymmetry was also present in all ranges of tested eccentricities and directions. For example, just like we did earlier for stimulus-evoked effects[14], I measured LFP amplitude in the interval 0-50 ms from saccade onset and plotted it as a function of either eccentricity or direction bins represented by the electrode tracks. I also did the same analyses, which were not documented in the earlier study[14], for the motor burst spiking. In every eccentricity (Fig. 2A) and direction (Fig. 2B) bin, motor bursts were weaker in the upper visual field[14,17] ($p=0.0155$ and $p=0.276$ for main effects of upper/lower visual field and eccentricity, respectively, in Fig. 2A; $p=0.0001$ and $p=0.2289$ for main effects of upper/lower visual field and direction from horizontal, respectively, in Fig. 2B; two-way ANOVA in each case; Methods). This effect was reversed for LFP's, and also significantly amplified (Fig. 2C, D) ($p=0$ and $p=0.5393$ for main effects of upper/lower visual field and eccentricity, respectively, in Fig. 2C; $p=0$ and $p=0.4986$ for main effects of upper/lower visual field and direction from horizontal, respectively, in Fig. 2D; two-way ANOVA in each case). Thus, the asymmetry in the SC's peri-saccadic LFP's was the same as that in both the spiking and LFP sensory-driven responses (Fig. 1)[14].

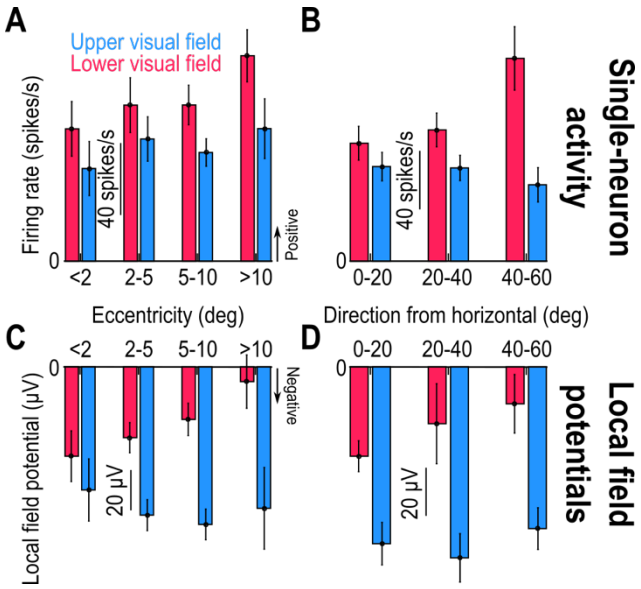

Figure 2 Consistency of the results of Fig. 1 across tested eccentricities and directions. (A, B) For all single neurons from the database, I binned them according to the eccentricity (**A**) or direction from horizontal (**B**) of their RF hotspots (similar binning to what we had done with visually-evoked LFP measurements in our earlier study[14]). This confirmed the consistently weaker motor bursts in the upper visual field[17]. In each bin, the measurements were made in the interval 0-50 ms from saccade onset. **(C, D)** For peri-saccadic LFP's, there was always a stronger negativity for the upper visual field, like in the stimulus-evoked deflections (Fig. 1) and opposite the spiking asymmetry of **A**, **B**. Error bars denote SEM. Figures S1, S2 document similar results when measuring pre-saccadic activity.

I also checked LFP and spiking modulations in the immediate pre-saccadic interval[3,23,33]. The LFP's, but not the spikes, still reflected the sensory preference for the upper visual field (Figs. S1, S2).

Visual field location as a defining feature

In light of our recent observations that there is a sensory representation embedded within both SC motor bursts and peri-saccadic LFP's[18], the results above imply that stimulus location may itself be considered a visual feature. If so, then it is the SC neurons' topographic location, and not stimulus presence per se, that should matter. To confirm this, I analyzed data from memory-guided saccades with no visible saccade target (Methods).

The difference in peri-saccadic LFP negativity for upper and lower visual fields persisted. Figure 3A, B shows peri-saccadic LFP's for both visually-guided and memory-guided saccades. In the upper visual field, the memory condition caused a substantial shift in pre-saccadic LFP voltage (Fig. 3A; the interval before saccade onset; black arrow). This shift, which could reflect working memory[34], and which was also previously observed[22], was essentially absent in the lower visual field (Fig. 3B; the interval before saccade onset; black arrow). This corroborates the idea of significant functional differences in the SC's upper and

lower visual field representations[14,15]. More importantly, peri-saccadically, the amplitude of the deflection from pre-saccadic baselines was bigger in the upper than lower visual field, consistent with Figs. 1, 2. This is better appreciated after applying a baseline shift (Fig. 3C; Methods): there was still a clearly stronger negativity for upper visual field sites ($p=0.0021$; t-test for the interval 0-50 ms from saccade onset, comparing upper and lower visual field electrode tracks), which was also present in different direction bins (Fig. 3D). Indeed, at all tested eccentricity (Fig. 3E) and direction (Figs. 3F, S3) bins, there was stronger peri-saccadic LFP negativity for the upper visual field ($p=0.004$ and $p=0.4981$ for main effects of upper/lower visual field and eccentricity, respectively, in Fig. 3E; $p=0.0118$ and $p=0.2461$ for main effects of upper/lower visual field and direction from horizontal, respectively, in Fig. 3F; two-way ANOVA in each case). Thus, SC topographic location was the critical feature.

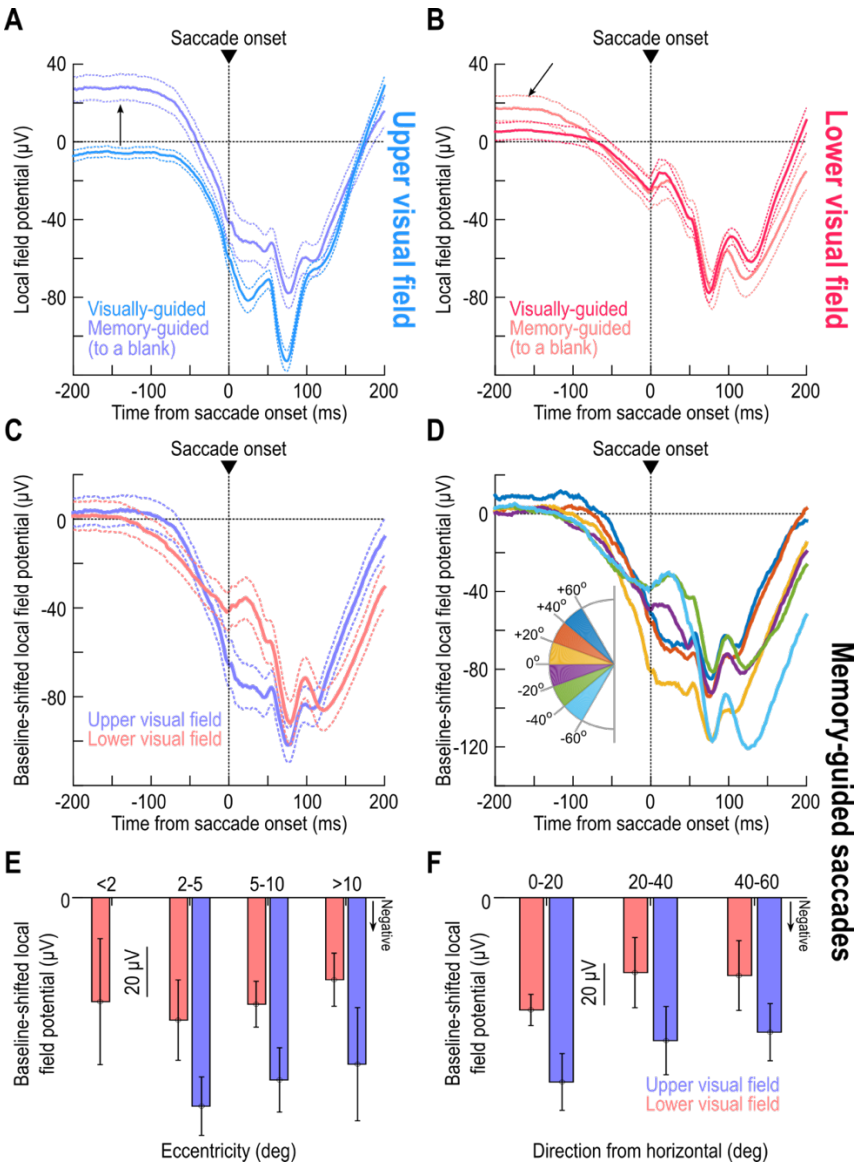

Figure 3 Stronger upper visual field peri-saccadic LFP modulations even in the absence of a visible saccade target. (A) Peri-saccadic LFP's for upper visual field electrode tracks with and without a visible target (the visible target curve is the same as that in Fig. 1D). Long before the saccade (upward arrow), the memory condition elevated LFP voltages[22]. However, the peri-saccadic deflection magnitude was similar in the two curves. **(B)** Same as **A** but for the lower visual field. Here, the memory condition had a much weaker effect long before saccade onset (oblique arrow). Importantly, the peri-saccadic deflection was still similar in both conditions. **(C)** Applying a baseline shift in the memory condition (Methods) revealed a similar peri-saccadic asymmetry between the upper and lower visual fields in the absence of a visible saccade target; there was stronger negativity in the upper visual field. **(D)** Same as Fig. 1E but for the memory condition (after baseline shift). Upper visual field tracks had consistently stronger peri-saccadic LFP negativity. For example, compare the yellow and purple traces (sites straddling the horizontal meridian), especially in the peri-saccadic interval. **(E, F)** Same as Fig. 2C, D, but for the memory condition, again showing stronger negativity in the upper visual field (the missing bar for <2 deg eccentricity means no data). Error bars in all panels indicate SEM. Also see Fig. S3.

Upper visual field saccades to a blank are still associated with weaker motor bursts

Armed with the results of Figs. 1-3, I could now predict that SC motor bursts should be weaker in the upper visual field even for memory-guided saccades. I confirmed this: I consistently observed weaker saccade-related motor bursts for upper visual field SC neurons (Figs. 4, S4) (p=0.0126 and p=0.2251 for main effects of upper/lower visual field and eccentricity, respectively, in Fig. 4C; p=0.0008 and p=0.2898 for main effects of upper/lower visual field and direction from horizontal, respectively, in Fig. 4D; two-way ANOVA in each case).

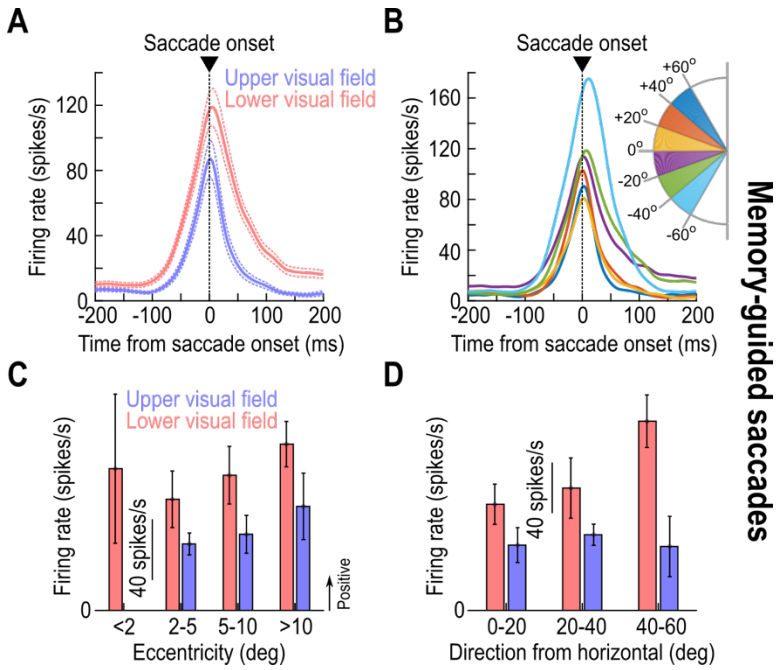

Figure 4 Weaker motor bursts in the upper visual field in the absence of a visible saccade target. (A, B) Like the insets of Fig. 1D, E but for the memory-guided saccade task. **(C, D)** Like Fig. 2A, B but for memory-guided saccades. Motor bursts in the upper visual field were weaker than in the lower visual field, which is opposite the peri-saccadic LFP asymmetries (Fig. 3). Error bars denote SEM. Also see Fig. S4.

Therefore, all results suggest that peri-saccadic SC network activity: (1) reflects the strong sensory preference for the upper visual field (Figs. 1, 2)[14]; (2) is accompanied by weaker spiking bursts[14,17] (Fig. 4); and (3) is a function of SC topography (Figs. 3, 4). Thus, sensory tuning in SC movement commands[18] extends to the domain of visual field asymmetries.

Discussion

If SC peri-saccadic LFP modulations directly reflect spiking activity in saccade-related motor bursts, as might be generally assumed[22], then I should have observed weaker peri-saccadic negativity for the upper visual field SC representation, concomitant with weaker motor bursts[14,17]. I found the opposite: peri-saccadic LFP modulations reflected the SC's sensory, rather than motor, preference. I believe that these results add to our recent evidence[18] of sensory tuning in SC motor bursts.

The fact that LFP's can be dissociated from spiking activity has been observed before, even in the SC itself, albeit in the context of signal timing. Specifically, in stimulus-evoked responses, LFP modulations normally lead stimulus-driven spiking in both the SC[23] and frontal eye fields (FEF)[35], suggesting that the spiking activity might reflect the local network's processing of incoming sensory signals. On the other hand, peri-saccadically, LFP modulations lag the onset of spiking motor bursts[23,35,36]. Thus, the timing relationship between LFP's and spiking is flipped peri-saccadically. In my case, I found an even more remarkable dissociation: peri-saccadic LFP modulations reflected the SC's stimulus-evoked preferences (whether in LFP's or spiking) and not the motor burst preferences. Thus, SC sensory preferences for the upper retinotopic visual field seem omnipresent in LFP's.

I interpret my results as being consistent with our recent observations of a sensory signal embedded within SC motor bursts[18]. In line with this, we do know that SC motor bursts vary as a function of visual field location[14,17]. However, there is one difference that is worth noting here: while SC visual responses are stronger for upper visual field stimuli[14], saccade-related motor bursts are weaker[14,17]. This suggests a model in which SC network activity is actively reformatted[37,38] between the visual and motor epochs, and I believe that such reformatting could happen for a variety of reasons beyond saccade control. For example, one kind of reformatting could help downstream areas to correctly distinguish between SC visual and motor bursts, which is important in order to avoid unwanted saccades at the time of "visual" spikes[18,39-41]. My results add another distinct possibility: the reformatting could be relevant for corollary discharge and its influences on peri-saccadic vision. That is, if there is a sensory signal present in the SC peri-saccadically[18], and if this signal is not relevant for controlling the eye movements themselves[17], then this signal could be part of what is relayed[42-45] from the SC to other brain areas. In turn, this signal could alter peri-saccadic vision in strategic ways[15,46]. Interestingly, we recently found that peri-saccadic visual sensitivity becomes momentarily better in the upper visual field, which is opposite from how it behaves without saccades[15]. Thus, a peri-saccadic sensory signal in the SC could be used to transitorily alter well-known visual field perceptual asymmetries[47-49].

Finally, the fact that I observed the same effects with memory-guided saccades suggests that topographic location is what matters, and it is also consistent with the idea that visual location is itself an important "feature" for vision. This observation is also in line with the idea that LFP's might reflect local anatomy and connectivity[25-29,31,32], especially if one were to consider that the SC might amplify its anatomical representation of the upper visual field[14]. Indeed, for recording sites away from the eye movement endpoints, peri-saccadic LFP modulations are much smaller in amplitude[50] than what I observed here.

In all, my results motivate further studies of peri-saccadic visual field asymmetries, both perceptually and at the neural level.

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Declaration of interests

I declare no competing interests.

Supplemental information

Figures S1-S4.

Methods

Database

I analyzed data from the same database as that described in our earlier publication[14]. Briefly, the database consisted of SC neuronal recordings from two adult, male rhesus macaque monkeys (*macaca mulatta*) performing standard visual and oculomotor tasks. The recordings were performed using penetration of the SC with a single, tungsten microelectrode per session. In the previous publication[14], we analyzed spiking activity (firing rates) and local field potential (LFP) modulations in the stimulus-evoked epoch, to characterize visual responses in the SC. We also analyzed spiking activity in the saccade-related motor burst epoch, but only when the saccade target was visible (in the delayed, visually-guided saccade task; see below). Here, I analyzed LFP modulations in the peri-saccadic motor burst epoch; these modulations were never analyzed or documented previously. I also used the LFP results to motivate testing spiking motor bursts for saccades in the absence of a visual target (in the memory-guided saccade task; see below). Again, these analyses were not documented previously elsewhere.

In what follows, I briefly describe the behavioral tasks relevant for this study, as well as the neurophysiological signals used. I also detail the analysis methods that I followed in the current study.

All of the original experiments were approved by ethics committees at the regional governmental offices of the city of Tübingen[14].

Delayed, visually-guided and memory-guided saccade tasks

I analyzed SC spiking activity and LFP modulations around the time of saccadic eye movements generated by the monkeys during two distinct behavioral tasks.

In the first task, the saccades were visually-guided, and delayed by an explicit instruction. Specifically, the monkeys first fixated a small white spot presented over a gray background for 300-1000 ms. Then, another small white spot appeared at an eccentric location, and it remained on until the end of the trial. 500-1000 ms after the onset of the eccentric spot, the initial fixation spot was extinguished, instructing the monkeys to generate a visually-guided (albeit delayed) saccade to the (still visible) eccentric spot.

In the second task variant, the memory-guided saccade paradigm, the eccentric spot was only presented for ~50 ms. Then, after some memory delay (300-1000 ms), the initial fixated spot was removed, instructing the monkeys to generate a memory-guided saccade towards the remembered location of the brief flash. The target reappeared only after a few hundred milliseconds of stable post-saccadic fixation. Thus, the saccade in this task variant was now generated without a visible target (towards a blank).

The saccade target location was at a fixed position per session in the memory-guided saccade task, which was chosen based on the mapped response field (RF) hotspot location[14]. The latter was inferred from the delayed, visually-guided saccade task, in which we varied

target location from trial to trial[12,14]. However, in the analyses of the current study, I picked only saccades towards the RF hotspot location[14], especially because we do know that peri-saccadic LFP modulations are much weaker at SC sites far away from the movement endpoints[50]. Indeed, I used exactly the very same trials per session as those used to describe the motor bursts of the visually-guided saccades in the previous study[14].

Electrophysiological signals used

I analyzed firing rates and LFP modulations.

The firing rates were obtained from the spike times using convolution with a Gaussian kernel having 10 ms standard deviation parameter.

The LFP's were obtained from wide-band electrode signals that were sampled at 40 KHz and then filtered in hardware to a bandwidth of 0.7Hz-6KHz. We further filtered the signals in software as follows. First, we removed the 50, 100, and 150 Hz harmonics of the line noise using an IIR notch filter. Then, we applied a zero-phase-lag low-pass filter with 300 Hz cutoff frequency. Finally, we down-sampled the signals to 1 KHz[14].

The motor bursts (firing rates) of the delayed, visually-guided saccades were analyzed previously[14]. Thus, I used the same sessions and same trials as in the previous analyses, but this time looking at LFP modulations. I had a total of 198 sessions containing saccade-related activity for these analyses (95 upper visual field electrode tracks and 103 lower visual field electrode tracks).

For the memory-guided saccades, their saccade-related activity was not previously described, either in terms of firing rates or LFP modulations. I thus analyzed them here, motivated by the peri-saccadic LFP results of the visually-guided saccades. The database had a total of 131 sessions possessing saccade-related activity in memory-guided saccades (49 upper visual field electrode tracks and 82 lower visual field electrode tracks). Visually-dependent saccade-related neurons[17-21,51] were excluded because we were interested in genuine motor bursts at the time of memory-guided saccades.

Data analysis

First, I plotted peri-saccadic LFP modulations in the delayed, visually-guided saccade task. For each electrode track, I found the interval from -200 ms to +200 ms from saccade onset. The saccade was always towards the RF hotspot location of the neuron(s) recorded in the session[14]. Then, I averaged the LFP signals across all trial repetitions of the same saccade type. In the figures, I plotted the mean peri-saccadic LFP signal around saccade onset from across all sessions of a given analysis, and I surrounded the mean traces with SEM bounds. For example, in Fig. 1D, I collected the average peri-saccadic LFP signal of each session in which the electrode was in the upper visual field representation of the SC. Then, I plotted the average of all such curves across all sessions in which the electrode track was in the upper visual field representation. This gave the blue curve in Fig. 1D. The error bars represented SEM across the sessions. A similar procedure was applied to obtain the red curve and error bars of Fig. 1D.

For some plots (like Fig. 1E in Results), I binned the electrode tracks according to the direction from horizontal represented by the encountered neurons. For example, if the SC site represented an eccentricity of 5 deg and direction from horizontal of +10 deg, then this session's data was included in the direction bin of 0-20 deg from the horizon, in the upper visual field. This is a similar direction binning of the SC sites to what we performed earlier in the original publication with the stimulus-evoked LFP responses[14].

To summarize the dependence of peri-saccadic LFP modulations on the visual field location, and particularly to demonstrate a step-like change as a function of direction from the horizon (e.g. Fig. 1F in Results), I measured the magnitude of the LFP signal in the interval 0-50 ms after saccade onset. In each session, I averaged the LFP values in this interval. Knowing the preferred direction of the recorded SC site of the session meant that I now had an LFP measurement (y-axis value) and a preferred direction (x-axis value) per session. Across sessions, I then binned all sessions according to their RF's direction from the horizontal meridian (20 deg bins, in steps of 10 deg; minimum of 10 samples per angular direction bin), and I averaged the LFP magnitudes obtained from all sessions within each direction bin. This resulted in figures like Fig. 1F, with error bars denoting SEM across the sessions. The approach described here is identical to what we did earlier for visual burst epochs[14]. In other analyses, such as in Fig. S1, I performed the same analysis but this time measuring the pre-saccadic LFP value. In this case, my measurement interval was from -50 ms to 0 ms relative to saccade onset.

To test that there was a statistically significant effect of upper/lower visual field location in the above analyses, I used two approaches. First, I collected all measurements (e.g. during the interval 0 ms to 50 ms after saccade onset in Fig. 1D, F, or during the interval -50 ms to 0 ms from saccade onset in Fig. S1), and I classified them as being in either the upper or lower visual field group. Then, I applied a two-way t-test to check whether there was a statistically significant difference between the upper and lower visual field electrode track groups. I also ran a one-way ANOVA across all angular direction bins in analyses like those of Fig. 1E, to test whether direction from the horizontal indeed mattered for peri-saccadic LFP's. I used a similar approach when analyzing spiking effects (e.g. Fig. S4).

I also binned sessions according to both eccentricity and direction bins, such as in the example analyses of Fig. 2. Here, I grouped the sessions into their appropriate bins using a similar approach as above, but now taking into account both the preferred eccentricity of the recorded SC site as well as its direction from the horizontal meridian. Again, this is the same approach that we used earlier for visual response epochs[14]. The bin ranges, which are shown in the figures in Results were sometimes not having any sufficient number of sessions within them. In this case, I did not plot the corresponding bar in the bar plots (e.g. Fig. 3E for the eccentricity bin <2 deg and upper visual field). If this happened, the bin of concern was also not included in the statistical tests because there was no data available from one of the visual field groups (e.g. the upper visual field group in the example of Fig. 3E's eccentricity bin of <2 deg). I also applied the same approach for the firing rates in Figs. 2A, 2B, 4C, 4D, S2A, S2B.

Statistically, for either the eccentricity dimension (e.g. Fig. 2C) or the direction dimension (e.g. Fig. 2D), I applied a two-way ANOVA on all sessions, after grouping them according to the two main factors of the ANOVA: (1) upper/lower visual field location; and (2) eccentricity or direction bin. I then reported the p-values for each main factor.

For the memory-guided saccades, I used similar analyses as above. To assess peri-saccadic LFP modulations despite the influence of working memory on pre-saccadic LFP values (e.g. Fig. 3A), I applied a baseline shift to the LFP's. In particular, for each session, I obtained the average of the LFP signal during the interval from -300 ms to -200 ms relative to saccade onset. I then subtracted this baseline level from all LFP measurements in the peri-saccadic interval (-200 ms to +200 ms from saccade onset). This way, all baseline-shifted LFP curves had a value very close to zero well before saccade onset, and, therefore, well before the peri-saccadic modulations in LFP's were expected to kick in (Fig. 3A-D).

Supplemental information

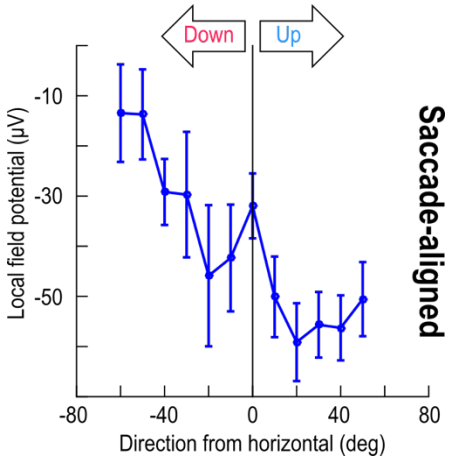

Figure S1 Stronger pre-saccadic local field potential (LFP) negativity in the upper visual field representation of the primate superior colliculus (SC). This figure shows an analysis similar to that of Fig. 1F, except that I now measured the LFP in the final 50 ms before saccade onset, instead of peri-saccadically (Methods). There was still a stronger negativity in the upper visual field representation of the SC. Error bars denote SEM. Statistically, I grouped all upper visual field electrode tracks into one group and all lower visual field electrode tracks into another, and I then performed a t-test during the pre-saccadic interval. The result revealed a significant effect ($p=0.0014$), and that upper visual field pre-saccadic LFP negativity was ~1.8 times larger than lower visual field LFP negativity (in absolute value). In addition, a one-way ANOVA across the shown angular direction bins revealed a significant effect of direction from the horizontal meridian ($p=0.0055$). Thus, the results of Fig. 1D-F also held in the pre-saccadic interval when the peri-saccadic LFP modulation was still just building up.

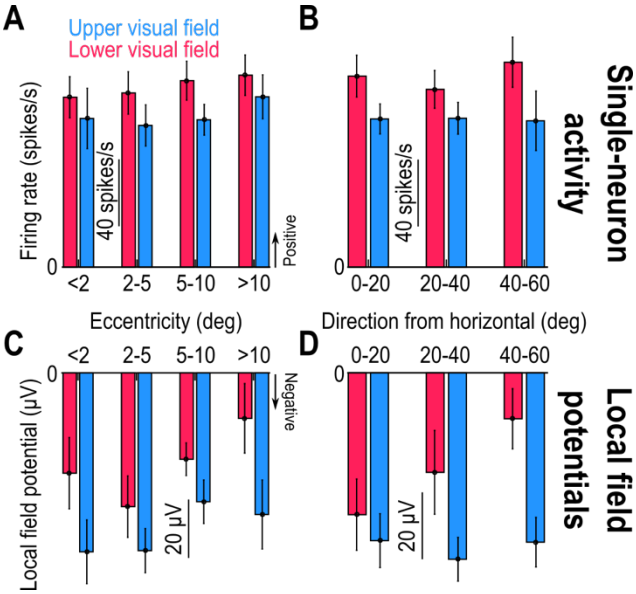

Figure S2 Consistency of the results of Fig. 2 in the pre-saccadic interval. I repeated the analyses of Fig. 2, but now taking measurements during the final 50 ms before saccade onset. There were similar results to those seen in Fig. 2. Note how the LFP asymmetry was generally stronger than the spiking asymmetry. Statistically, I compared the LFP measurements in **C** using a two-way ANOVA with the two main factors of the ANOVA being visual field location (upper or lower visual field) and eccentricity represented by the electrode track location penetrating the SC. I obtained a significant main effect for upper/lower visual field location (p=0.0083) but not for eccentricity (p=0.1675). Similarly, for **D**, I performed a two-way ANOVA with the main factors of the ANOVA being upper/lower visual field location and direction from the horizon. Again, there was a significant main effect of upper/lower visual field location (p=0.005) but not direction (p=0.4015). For the spiking activity, there was a marginal main effect of upper/lower visual field location (p=0.0993) but not eccentricity (p=0.7285) in **A**; in **B**, there was a significant main effect of upper/lower visual field location (p=0.0114) but not direction (p=0.8558). Thus, in both the spiking and LFP's, there were consistent asymmetries between the upper and lower visual field electrode track locations during pre-saccadic epochs. Error bars denote SEM.

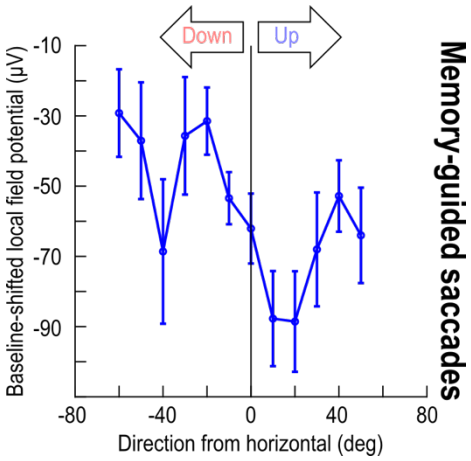

Figure S3 Analysis of the memory-guided saccade data of Fig. 3 as a function of direction from the horizontal meridian of the recorded SC sites. This figure bins all electrode tracks as a function of the direction from horizontal represented by the recorded SC neurons. For baseline-shifted peri-saccadic LFP measurements (during the interval of 0-50 ms from saccade onset), there was a stronger LFP negativity in the upper visual field representation of the SC than in the lower visual field representation. This was confirmed statistically when I grouped all upper visual field electrode tracks into one group and all lower visual field electrode tracks into another (p=0.0021; t-test). Similarly, a one-way ANOVA across the shown angular direction bins revealed a significant effect of direction from the horizontal meridian (p=0.0057). Error bars denote SEM.

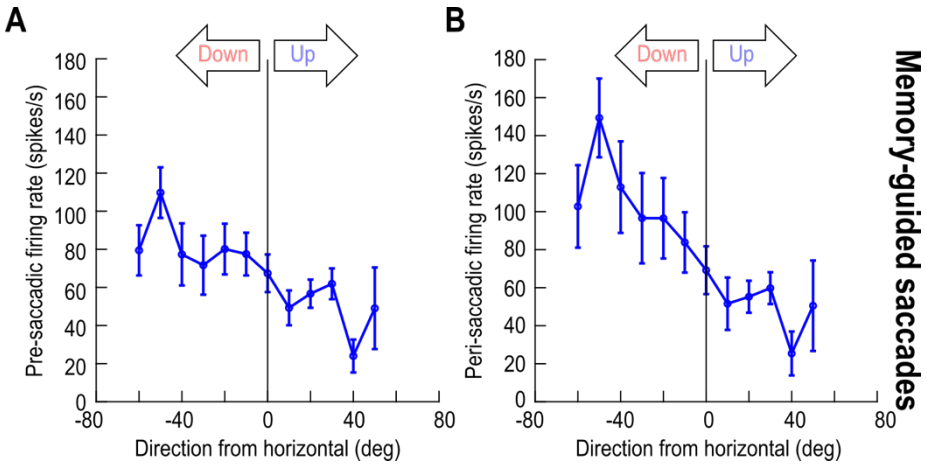

Figure S4 Weaker upper visual field SC motor bursts for memory-guided saccades. (A) An analysis similar to that in Fig. S1, except that I now measured firing rates in the final 50 ms before saccade onset. Pre-saccadic firing rates were weaker in the upper than in the lower visual field representation of the SC, and this happened even with saccades towards a blank (memory-guided saccades). I confirmed this with a t-test comparing all upper visual field neurons in the database in one group to all lower visual field neurons in the other (p=0.0044). I also performed a one-way ANOVA across all shown angular direction bins, again with a significant effect (p=0.0347). **(B)** Same as **A** but now for the measurement interval 0-50 ms from saccade onset. Again, peri-saccadic firing rates were weaker in the upper visual field for memory-guided saccades (p=0.0043; one-way ANOVA across all shown angular direction bins). Note that the overall firing rates were generally higher than in **A** (same y-axis ranges in the two panels), which is expected because motor bursts are known to peak peak firing rates some time peri-saccadically rather than pre-saccadically[3,33].