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EDITORIAL FOCUS

Not so early! Revisiting the question of visual pathway selectivity of saccadic suppression

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The execution of rapid saccadic eye movements is associated with a strong reduction in visual sensitivity to stimulus onsets, a phenomenon that may contribute to stabilizing our subjective visual experience in the face of continuous saccade-induced retinal image shifts. The perceptual consequences of saccadic suppression have been studied for many decades, and it has been suggested that the suppression is particularly selective for the magnocellular visual processing pathway, but not the parvocellular one (1). Now, a report by Zhang et al. (2) demonstrates that neural correlates of saccadic suppression in the human primary visual cortex are similar for both luminance and color contrasts, consistent with a generalized suppression in early visual system sensitivity (whether magnocellular or parvocellular) that is time-locked to rapid retinal image shifts caused by saccades.

The study by Zhang et al. (2) was motivated by a gap between psychophysical investigations of saccadic suppression in humans and neurophysiological experiments using nonhuman primates. Ideally, direct neural mechanisms would be investigated in humans simultaneously with their behavior. However, functional magnetic resonance imaging (fMRI) suffers from poor temporal resolution with respect to the relatively transient (on the order of 100 ms) changes in visual sensitivity that accompany saccades. To alleviate this problem, Zhang et al. (2) resorted to electroencephalography (EEG) over the occipital cortex, affording them a significantly higher temporal resolution than with fMRI. Using a stimulus continuously flickering at 7.5 Hz, they additionally exploited the fact that visual cortical activity entrains to the frequency of the flicker (7.5 Hz), in turn giving rise to a strong EEG harmonic with a dominant frequency tracking the stimulus transients. The advantage of this approach is that Zhang et al. (2) could now focus their analyses on very narrow frequency bands representing the so-called steady-state visually evoked potential (SSVEP) signal. This was critical because, besides brain signals, EEG electrodes can pick up other (generally broadband) artifactual signals, such as ones associated with eyeball rotations. By focusing on SSVEP amplitudes, Zhang et al. (2) could now measure how these amplitudes were altered when saccades occurred. More importantly, the authors could compare the saccade-related changes in SSVEP amplitudes when the stimulus flicker was caused by pure luminance contrasts or when it was caused by color contrasts selectively targeting the parvocellular visual processing pathway. In both cases (luminance or color contrasts), the background image itself (a grating of 1.03 cycles per deg) was oriented parallel to the vectors of the saccades, thus minimizing retinal spatiotemporal motion streaks (at least at the visual eccentricities that the authors focused on) caused by the eye movements themselves. Such motion streaks can be processed during saccades (3), and it was worthwhile to control them.

The participants in the study of Zhang et al. (2) performed their saccades at will while watching the flickering stimuli. Thus, even though saccade times can also entrain to stimulus flicker, at least to some extent, variability in saccade timing relative to the stimulus events was inevitable. This added yet another challenge, which Zhang et al. (2) cleverly solved. Specifically, if one were to align EEG signals exactly to saccade onset times, which is the most classic way of studying saccadic suppression, then variability in saccade times relative to stimulus onsets would also necessarily mean variable phases of the SSVEP signals relative to the saccade times. As a result, averaging across many saccade repetitions would strongly diminish the SSVEP signal amplitude even in the absence of any saccade-related suppression, and this would thus make it harder to assess the strength of the saccadic suppression effect itself (Fig. 1*A*, "Aligned to saccade time"). Instead, Zhang et al. (2) decided to favor signal-to-noise ratio (SNR) over exact saccade-related time courses. For every stimulus flicker cycle containing a saccade onset, they still aligned the SSVEP signal to the stimulus cycle rather than to the exact saccade onset time. This introduced some jitter in saccade onset times when they averaged across many repetitions. However, what it brought with it instead was a much higher SNR in the SSVEP signal (Fig. 1*A*, "Aligned to stimulus phase"). The net result was that the amplitude of the SSVEP signal before the saccade-related modulation was larger (due to better phase

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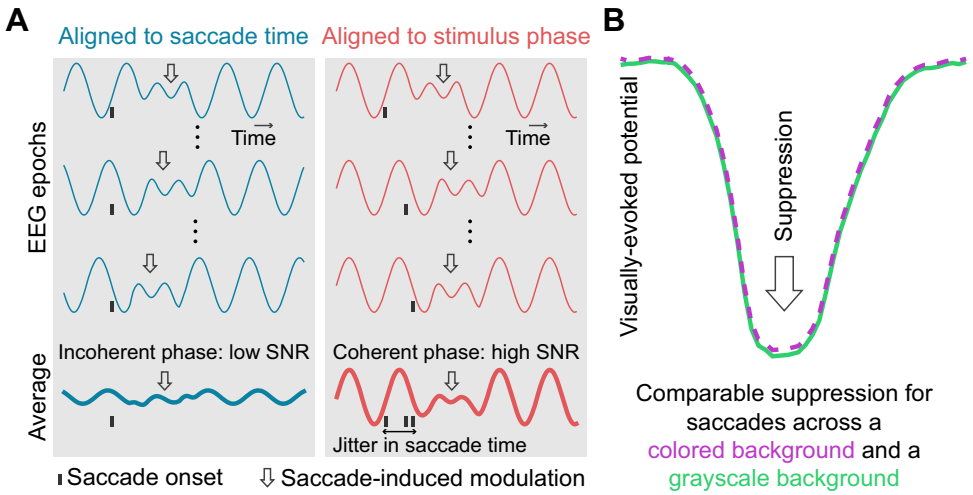

Figure 1. Probing saccadic suppression in the human visual cortex using steady-state visually evoked potentials (SSVEPs). *A*: for every analysis epoch of an EEG signal, aligning to saccade onset times can reduce the signal-to-noise ratio (SNR) in across-trial SSVEP averages (due to variability in saccade timing relative to the stimulus flicker events; *left*). Instead, in a novel analysis approach, Zhang et al. (2) accepted some jitter in saccade timing by still aligning all saccade-containing epochs of the EEG signal to the stimulus phase (*right*). As a result, across-trial SSVEP averages had much higher SNR (compare the thick average curves in the *bottom* of each column), and this is due to the fact that the SSVEP signal was phase-aligned with the stimulus events. *B*: using this approach, Zhang et al. (2) found that saccadic suppression in the human visual cortex was equally strong across either color- or luminance-defined contrasts, suggesting that saccadic suppression can still act on the parvocellular pathway of the primary visual cortex, and not just the magnocellular one. EEG, electroencephalography.

alignment across many trial repetitions). In turn, the saccadic suppression effect was also much clearer.

Armed with such a robust measure of visual sensitivity in the human visual cortex, Zhang et al. (2) then turned to their main goal of comparing saccadic suppression strengths with luminance versus color contrasts. Remarkably, they found very similar saccadic suppression strengths for both kinds of stimuli (Fig. 1*B*). That is, whether the participants were generating saccades across luminance- or color-defined flickering stimuli, there was clear saccadic suppression of SSVEP amplitude, and this suppression also reached similar levels for the two types of stimuli. Moreover, when they assessed suppression effects across different contrast levels, Zhang et al. (2) found that saccadic suppression in the human primary visual cortex acts as a response gain modulation of visual sensitivity, consistent with both perceptual results in humans (4) as well as neurophysiological evidence from nonhuman primates (5).

The question of whether saccadic suppression is selective for the magnocellular pathway is almost as old as the modern field of saccadic suppression research itself. Behaviorally, a popular psychophysical study demonstrated selective suppression of low (but not high) spatial frequencies, as well as no suppression for equiluminant color stimuli (1). However, these observations alone do not directly imply a lack of suppression in the parvocellular subsystem of the early visual pathways. For example, selective suppression of low spatial frequencies can also occur in the complete absence of saccades, when rapid image shifts are introduced on the retina (6). More importantly, even with saccades, perceptual suppression can become completely unselective for low spatial frequencies if the surrounding visual context is slightly altered (6). Thus, whether with or without saccades, selective suppression of low spatial frequencies may or may not occur (6), tempering an impregnable interpretation of psychophysical suppression of low spatial frequencies as being direct evidence of selective magnocellular pathway saccadic suppression. Moreover, in the superior colliculus of non-human primates, one class of visually responsive neurons shows stronger saccadic suppression for low spatial frequencies, consistent with perceptual and behavioral evidence (1, 7), whereas another class shows equal saccadic suppression across all tested spatial frequencies (7). Finally, in even more direct neurophysiological investigations of the lateral geniculate nucleus (8) and primary visual cortex (9) of nonhuman primates, evidence for clear saccadic suppression could be observed in both magnocellular and parvocellular neurons. Therefore, the results of Zhang et al. (2) add to increasing evidence that the early visual system, as early as in the retina itself (6), may be generally suppressed in the temporal vicinity of saccades (and not just the magnocellular subsystem).

Perceptually, there is also convincing evidence that saccadic suppression does indeed still take place for equiluminant chromatic stimuli (10). Thus, together with the novel results of Zhang et al. (2), this suggests that more nuanced questions about saccadic suppression should be asked than the one on the selectivity for magnocellular pathway suppression. For example, it would be interesting to consider the numbers of parvocellular versus magnocellular neurons that are present in a given brain area at the different retinotopic eccentricities typically used in experiments. One could then quantitatively relate these numbers to the observed differences in the strengths of chromatic versus achromatic saccadic suppression during perceptual investigations. This could help clarify, for example, why a significantly smaller fraction of parvocellular than magnocellular neurons are individually suppressed by saccades in the lateral geniculate nucleus (8), even though the differences in perceptual effects between chromatic and achromatic conditions are smaller in magnitude

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(10) than what these relative fractions indicate. More importantly, such an approach could potentially also reconcile the observation that global measures like those obtained in the SSVEP signals of Zhang et al. (2) could be similar in the primary visual cortex for chromatic and achromatic stimuli (Fig. 1*B*), even when different fractions of individual magnocellular versus parvocellular neurons may be significantly modulated by saccades. The results of Zhang et al. (2) certainly place us in a position to consider these questions, and others, further.

Other interesting topics that emerge out of the work of Zhang et al. (2) could relate to the time courses of saccadic suppression under different conditions. In the study of Zhang et al. (2), exact timing relative to saccade onset was sacrificed (to some extent) in favor of SNR (Fig. 1*A*). Nonetheless, it would still be valuable if one could investigate primary visual cortical modulations with finer time resolution than performed by Zhang et al., and perhaps consider the issue of presaccadic modulations of visual sensitivity. For example, in the superior colliculus and frontal eye fields of nonhuman primates, premovement enhancement rather than suppression can be observed (5). However, these sensory-motor areas likely have very different patterns of lateral interactions than the primary visual cortex, and it would be valuable to know whether cortical areas in general might exhibit premovement enhancement, and under what conditions.

Finally, saccadic suppression clearly involves an interaction between visual consequences of rapid retinal image shifts and saccade generation commands. Anatomical pathways do exist, which would allow the primary visual cortex to be potentially influenced by corollary discharge signals associated with motor commands (e.g., from the superior colliculus). It would thus be interesting to investigate the differential contributions of such signals (both in cortex and subcortically) to the global perceptual phenomenon of saccadic suppression, and to other active vision phenomena, such as the processing of retinal motion streaks during saccades (3). Neural mechanisms of masking by either pre- or postsaccadic stable images must also be elucidated.

In all, the results of Zhang et al. (2) are an important addition to the field of active perception, and they promise to spur numerous additional future experiments spanning perception, computation, and neurophysiology.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Z.M.H., S.I., and M.P.B. prepared figures; Z.M.H., S.I., and M.P.B. drafted manuscript; Z.M.H., S.I., and M.P.B. edited and revised manuscript; Z.M.H., S.I., and M.P.B. approved final version of manuscript.

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