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Enhanced brain responses to color during smooth pursuit eye movements

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Abstract

Eye movements alter visual perceptions in a number of ways. During smooth pursuit eye movements, previous studies reported decreased detection threshold for colored stimuli and for high-spatial-frequency luminance stimuli, suggesting a boost in the parvocellular system. The present study investigated the underlying neural mechanism using EEG in human participants. Participants followed a moving target with smooth pursuit eye movements while steady-state visually Evoked potentials (SSVEPs) were elicited by equiluminant red-green flickering gratings in the background. SSVEP responses to color gratings were 18.9% higher during smooth pursuit than during fixation. There was no enhancement of SSVEPs by smooth pursuit when the flickering grating was defined by luminance instead of color. This result provides physiological evidence that the chromatic response in the visual system is boosted by the execution of smooth pursuit eye movements in humans. Since the response improvement is thought to be due to an improved response in the parvocellular system, SSVEPs to equiluminant stimuli could provide a direct test of parvocellular signaling, especially in populations where an explicit behavioral response from the participant is not feasible.

New and Noteworthy

We constantly move our eyes when we explore the world. Eye movements alter visual perception in various ways. The smooth pursuit eye movements have been shown to boost color sensitivity. We recorded SSVEPs to equiluminant chromatic flickering stimuli, and observed increased SSVEPs when participants smoothly pursued a moving target compared to when they maintained fixation. This work provides direct neurophysiological evidence for the parvocellular boost by smooth pursuit eye movements in humans.

Introduction

We constantly move our eyes to bring objects of interest into the fovea for visual processing. Eye movements, however, present challenges to the visual system. For example, large saccadic eye movements create fast retinal motion that has to be discarded. This is thought to be achieved by a suppression of the magnocellular pathway at the time of saccades (Burr et al., 1994). Slow, smooth pursuit eye movements also alter visual performance. Object recognition is impaired during smooth pursuit compared to fixation, probably because of the larger instability in pursuit (Schütz, Braun & Gegenfurtner, 2009). Contrast sensitivity for moving stimuli and motion sensitivity opposite to pursuit direction is reduced (Schütz et al., 2007; Turano & Heidenreich, 1999). However, sensitivity to colored stimuli is enhanced rather than hampered by smooth pursuit (Schütz et al., 2008; Schütz, Braun & Gegenfurtner, 2009), and temporal resolution for color is improved (Terao et al, 2010). Since sensitivity is also increased for high spatial frequency luminance stimuli, it has been hypothesized that smooth pursuit eye movements selectively boost sensory gains in the parvocellular pathway (Schütz et al., 2008).

The present study aimed to measure neural responses in visual cortex directly, using EEG to isolate neural responses induced by the visual stimuli. We specifically measured steady-state visually evoked potentials (SSVEPs), an oscillatory brain response to periodic visual stimulation likely originating from primary visual cortex (see Norcia et al., 2015 for a review). Previous attempts have been made to measure SSVEPs to low and high contrast flickering stimuli in order to isolate the magnocellular and parvocellular pathways (Zemon & Gordon, 2006; Green et al., 2009). Using luminance contrast, however, is not generally accepted as an effective way to isolate the visual pathways (Skottun & Skoyles, 2011; Skottun, 2014). In our study, we used instead equiluminant stimuli with flickering chromaticity, in particular flickering between equiluminant red and green at 7.5 Hz. As magnocellular neurons do not tune to color, they would respond similarly to red and green color given equal luminance, despite of some residual responses (Gegenfurtner et al., 1994; Dobkins &

Albright, 1994). Instead, parvocellular neurons would respond much differently to red and green color, so that SSVEP responses to equiluminant flickering stimuli has to be generated mostly in the parvocellular pathway. Our results showed increased SSVEP responses to colored stimuli during smooth pursuit eye movements, providing neurophysiological support for an enhancement of the parvocellular system by smooth pursuit in humans.

Method

Participants

Twenty-five observers (15females and 10 males, age 19-45, average 26 years) participated in the experiment. They had normal or corrected-to-normal vision, and had no known neurological or oculomotor deficits. All signed written informed consent forms before taking part in the experiment. They were naïve to the purpose of the study before finishing the test. The experiment was approved by the local ethics committee (2013-0018) and was conducted in agreement with the Declaration of Helsinki.

Apparatus and Stimuli

Stimuli were displayed on a calibrated 120 Hz Samsung SyncMaster 2230R7 22-inch monitor (Samsung Group, Seoul, South Korea), which has a resolution of 1680×1050 pixels, extending 61º horizontally and 38º vertically at a viewing distance of 40 cm. Experiments were programmed using the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard & Pelli, 2007) in Matlab (MathWorks, Natick, MA, USA). Figure 1 shows the stimulus displays in the experiment. The blue spot (0.5º in radius) served as either the fixation spot or the pursuit target in different conditions. Horizontal gratings (spatial frequency = 0.34 c.p.d) in the background were counter-phase flickering at 7.5 Hz. In the fixation condition, the blue spot remained stationary in the center. In the pursuit condition, the blue spot moved horizontally back and forth between 18º to the left and 18º to the right. The trials lasted 150s each, resulting in 15 cycles of target motion. Each half-cycle of the movement consisted of an acceleration phase (0.83 second, speed growing from 0 to 8.77 deg/s), a steady phase (3.33 second, speed = 8.77 deg/s), and a deceleration phase (0.83 second, speed decreasing from 8.77 deg/s to 0). We chose to maximize the length of the epochs at a constant target speed, as the effect of smooth pursuit on color processing has been shown to vary with pursuit speed (Schütz et al., 2008).

=============[Please insert Figure 1 here] =============

Procedures

We adopted a single trial design, with one trial for each condition that lasted 150s (e.g., see Rossion & Boremanse, 2011, for a SSVEP study with a single trial design). Manipulations on eye movements (fixation vs. smooth pursuit), type of flickering stimulus (luminance defined vs. color defined stimuli), and contrast of stimulus (low vs. high contrast) resulted in 8 conditions, i.e., 8 trials. The sequence of the trials was randomized. The two levels of contrast, defined as the maximally possible modulation achievable in DKL color space on our monitor, were 6% and 24% for luminance-defined stimulus, and 12% and 48% for the color-defined stimulus. The contrasts were chosen such that the amplitude of SSVEPs induced by color stimuli was comparable to the SSVEP amplitude induced by luminance stimuli based on the results of a pilot study with both fixation and pursuit. Both modulations were centered at the white point of our monitor at CIE xyY = (0.33, 0.36, 108 cd/m^2). For the achromatic stimuli, the modulation was only in luminance, with the flickering grating bars ranging from 102 to 114 cd/m^2 at 6% contrast, and from 82 to 134 cd/m^2 at 24% contrast. For the red-green stimuli, luminance was fixed at 108 cd/m2, while color was modulated between CIE xy = (0.35, 0.34) and (0.31, 0.36) at 12% chromatic contrast, and between CIE xy = (0.40, 0.31) and (0.24, 0.40) at 48% contrast. We chose not to isolate each observer’s individual point of isoluminance, since potential luminance artifacts in our stimuli would show up as failures to find an effect, i.e. they would work against us.

Eye movement recordings and analyses

Eye movements from the right eye were recorded at 1000 Hz using an Eyelink 1000 table-mounted eye tracker (SR Research, Missisauga, ON, Canada). A chin rest was used to limit the head movements. We used an independent device (NI-6009; National Instruments, Austin, TX) to generate a digital trigger to feed into the eye tracker and the EEG system for synchronization.

EEG recordings and analyses

EEGs were recorded from 32 scalp sites according to the international 10-20 system (FP1, FP2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, Fz, Pz, Oz, FC1, FC2, CP1, CP2, FC5, FC6, CP5, CP6, TP9, TP10, HLeo, Veo, HReo). A BrainAmp amplifier (Brain Products GmbH, Munich, Germany) sampled signals at 1000 Hz. The ground electrode was placed at the AFz, and the on-line reference at the Cz. We kept electrode impedances below 5 kΩ.

EEGlab toolbox (Delorme & Makeig, 2004) and customized scripts in Matlab were used to analyze EEG data. Signals were first re-referenced to average reference. Each 150s trial was decomposed into 30 successive 5s epochs. In each epoch, we discarded the first 0.5s and the last 0.5s, as the smooth pursuit was just started or was about to stop. The remaining 4s epoch was de-trended by removing the linear fit (Bach & Meigen, 1999) and zero-padded to 10s to get a frequency resolution of 0.1 Hz. The amplitude spectrum was then obtained by fast Fourier transformation (*fft.m* in Matlab). To calculate SSVEP amplitude, we summed amplitudes at 5 harmonics (7.5, 15, 22.5, 30, 37.5 Hz). At each harmonic frequency (e.g., 7.5 Hz), we subtracted from the peak amplitude the average amplitude at nearby bins (e.g., 7.2, 7.3, 7.7, 7.8 Hz; two immediately adjacent bins were excluded). As a result, background noise was discounted from the computed SSVEP amplitude (e.g., Liu-Shuang, Torfs & Rossion, 2016). As SSVEP responses in the present study were exclusively located at O1, Oz, and O2 electrodes (Figure 3), we used the average value of these 3 electrodes for statistical testing.

Results

We first analyzed the eye movement data. Figure 2A shows horizontal eye/target traces in an example epoch. As the flickering stimuli were horizontal gratings (Figure 1), horizontal pursuit does not induce any retinal image motion. However, some residual vertical eye movements still occur during pursuit and during fixation. As shown in Figure 2B, residual vertical eye movement velocities were not different between conditions (all *Ps* > .32). This excludes the possibility that retinal image motion can explain the enhancement of the SSVEP responses during pursuit. We further compared horizontal pursuit velocity between the luminance stimulus condition and the color stimulus condition, calculated by differentiating position data after excluding saccades. In the central 4 seconds of each epoch (where we analyzed SSVEPs), the average pursuit velocity was 7.3 deg/s (SD =0.77) in the luminance flicker condition, and 7.2 deg/s (SD = 0.68) in the color flicker condition, t (24) = 0.57, P = .57. Since there is no significant difference in the eye movements between luminance and color, the difference in SSVEPs cannot be explained by pursuit behavior or the corresponding retinal image motion.

=============[Please insert Figure 2 here] =============

Figure 3A and 3B are the topographic plots of SSVEP amplitudes for luminance flickers and color flickers, showing a typical SSVEP response confined at O1, Oz, and O2 electrodes. Figure 3C shows the amplitude spectrum. The amplitude at the stimulation frequency (7.5 Hz) for color flickering stimuli is higher during pursuit than during fixation.

=============[Please insert Figure 3 here] =============

We computed SSVEP amplitude by subtracting background noise and summing all harmonics. The same pattern of results holds for both rightward and leftward pursuit, we thus collapsed both directions in the following analyses. The result is shown in Figure 4. A 2 (eye movements: fix vs. pursuit) × 2 (type of stimulus: luminance vs. color) × 2 (contrast level: low vs. high) repeated- measure ANOVA revealed a main effect of contrast, F (1, 24) = 135.57, P < .001, η_p^2 = 0.85, indicating a higher SSVEP response for the high contrast stimulus than for the low contrast stimulus, and an interaction between eye movements and type of stimulus, F (1, 24) = 7.83, P = .01, η_p^2 = 0.25, indicating different effects of eye movements for luminance and color stimuli. We then proceeded to analyze the luminance and color stimuli separately. The two contrast levels were aggregated, as contrast did not interact with eye movements or types of stimuli. For luminance stimuli, there was not any significant difference between fixation and pursuit, t (24) = 1.15, P = .26 (Figure 4B). For colored stimuli, the SSVEP amplitude during pursuit was significantly higher than that during fixation, t (24) = 4.16, P < .001 (Figure 4C). The average increase in percentage was 18.8% across 25 observers (95% confidence interval 7.8%-29.9%). This result confirms our hypothesis that smooth pursuit eye movements enhance brain responses to color stimuli, but not to luminance stimuli.

=============[Please insert Figure 4 here] =============

Discussion

Our results show that SSVEP responses induced by equiluminant colored flickering stimulus are enhanced during smooth pursuit. As equiluminant red-green stimuli mainly drive the parvocellular pathway, this result supports the idea that smooth pursuit eye movements boost the parvocellular visual system. This constitutes a confirmation and clarification of earlier results showing a perceptual improvement of color processing during pursuit. Schütz et al (2008) reported that smooth pursuit eye movements decrease the detection threshold for chromatic stimuli, coherent with our finding of increased SSVEP amplitude. Schütz et al. (2008) also reported a small decrease in the sensitivity of achromatic luminance stimulus during smooth pursuit, whereas we did not find any decrease in SSVEP amplitude. Most likely this discrepancy is because their participants were required to attend to peripheral locations in order to report the presence of the probe stimulus. The decrease of sensitivity to luminance was most likely due to the fact that at least some attentional resources had to be withdrawn from the periphery and allocated to the area around the pursuit target (Khurana & Kowler, 1987; Kerzel & Ziegler, 2005). This problem does not apply to our study as the observers did not have to attend to the periphery to report the probe stimulus and the flickering stimulus was presented throughout the display. This exemplifies one of the major advantages of the SSVEP technique, the fact that it allows to measure brain responses in the absence of an overt task, thereby reducing the impact of such attentional confounds. Terao et al (2010) reported that smooth pursuit reduces the fusion of sliding stimuli with opposite colors presented in a retinotopic spatial framework. Their results suggest that this increased temporal resolution is due to deblurring of the pursuit-related retinal slip, as evidenced by the fact that sensitivity was not increased if the stimuli were flickering rather than sliding.

Note that image motion cannot account for the SSVEP difference between fixation and pursuit, and between color and luminance condition. We circumvent horizontal retinal image motion by using horizontal gratings. There were, of course, residual vertical eye movements, but these were of comparable magnitude in all four conditions (Figure 2B).

What is the functional role of an enhancement in parvocellular signaling during pursuit? It has been argued elsewhere (Schütz et al, 2008; Gegenfurtner, 2016) that the increase in color sensitivity could be an efficient way to reduce the effects of blur, as blur mainly occurs for colored and high spatial frequency stimuli (Kelly, 1983). Another hypothesis is that the sensitivity increase underlies the oculomotor response (Gegenfurtner, 2016). To sustain pursuit, the eyes have to detect small changes in stimulus speed. There is ample evidence that there are two channels for motion perception, a slow motion channel and a fast motion channel (Gegenfurtner & Hawken, 1996, Kulikowski & Tolhurst, 1973; Thompson, 1983; van der Smagt, Verstratee, & van de Grind, 1999). A boost in the slow motion channel – likely to be mediated by the parvocellular system – could increase sensitivity to slow speed changes and thus enhance pursuit. This way, the enhanced color processing might just be a side effect. Either way, the underlying effect has been proven to be very robust and linked to goal-directed pursuit movements (Schütz, Braun & Gegenfurtner, 2009a, 2009b).

It is believed that the SSVEPs are generated in the primary visual cortex (Müller et al., 1997; Di Russo et al., 2007). SSVEPs have been widely used in accessing low-level visual functions and attention. Previous studies reported modulation effects on SSVEP responses by adaptation (Ales & Norcia, 2009), binocular rivalry (Brown & Norcia, 1997; Zhang et al., 2011), spatial attention (Morgan, Hansen & Hillyard, 1996; Müller et al, 1998) and feature-based attention (Müller et al., 2006). Our study shows that the SSVEPs can also be modulated by the execution of eye movements.

Our results are also relevant to the question as to what is the best method to assess magnocellular and parvocellular signaling in SSVEPs. Previous studies have proposed different levels of luminance-defined contrast as a tool to measure magnocellular and parvocellular functions in Schizophrenia (Zemon & Gordon, 2006; Green et al., 2009). There is however some controversy on its effectiveness to isolate the two visual pathways (Skottun & Skoyles, 2011; Skottun, 2014). A more established dissociation between magnocellular neurons and parvocellular neurons is in color processing, since magnocellular neurons are not tuned color-opponent, while parvocellular neurons are (De Valois et al., 1966; Lee et al., 1988; Derrington, Krauskopf & Lennie, 1984). Our finding that SSVEPs to color- and luminance-modulated stimuli are selectively modulated by smooth pursuit eye movements suggest that using colored stimuli during pursuit is a suitable way to assess the parvocellular and magnocellular visual pathways and could constitute a useful tool both in vision research and clinic applications, as long as smooth pursuit is not impaired in patients.

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Figure captions:

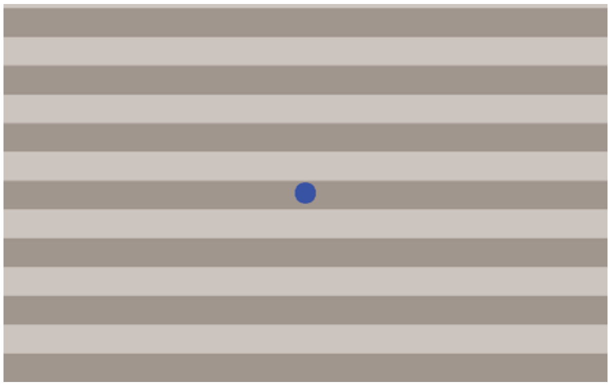
Figure 1. Stimuli used in two experiments. The blue spot remained in the center to serve as the fixation spot in the fixation condition, or was moving back and forth horizontally as the pursuit target in the pursuit condition. The achromatic black and white grating (***A***) or the equiluminant red-green grating (***B***) in the background was pattern-reverse flickering at 7.5 Hz to elicit SSVEP responses.

Figure 2. ***A***, eye and target traces in an example epoch of 10 seconds. Shaded periods are the central 4 seconds in each one-way pursuit, where we analyzed SSVEPs. Each trial consists of 15 such epochs. ***B***, absolute vertical eye movement velocity. No significant differences were observed between conditions. ***C***, pursuit velocities in the two pursuit conditions. There was no difference between the luminance- and color-pursuit conditions. Error bars show the mean ± between-observer SD.

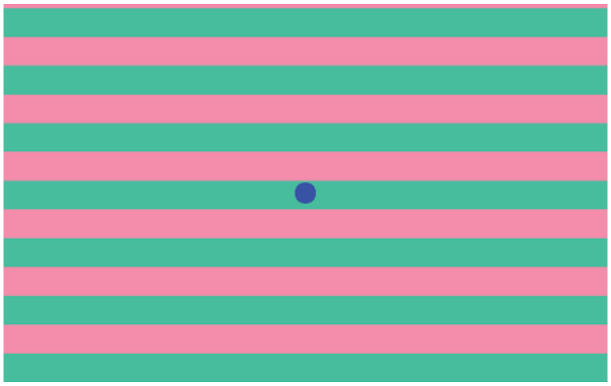
Figure 3. Topographic plots of SSVEP amplitudes (calculated by summing five harmonics) for luminance flickers (***A***) and color flickers (***B***). ***C***, grand-average amplitude spectrum for all 4 conditions at the fundamental pattern-reversal frequency (7.5 Hz).

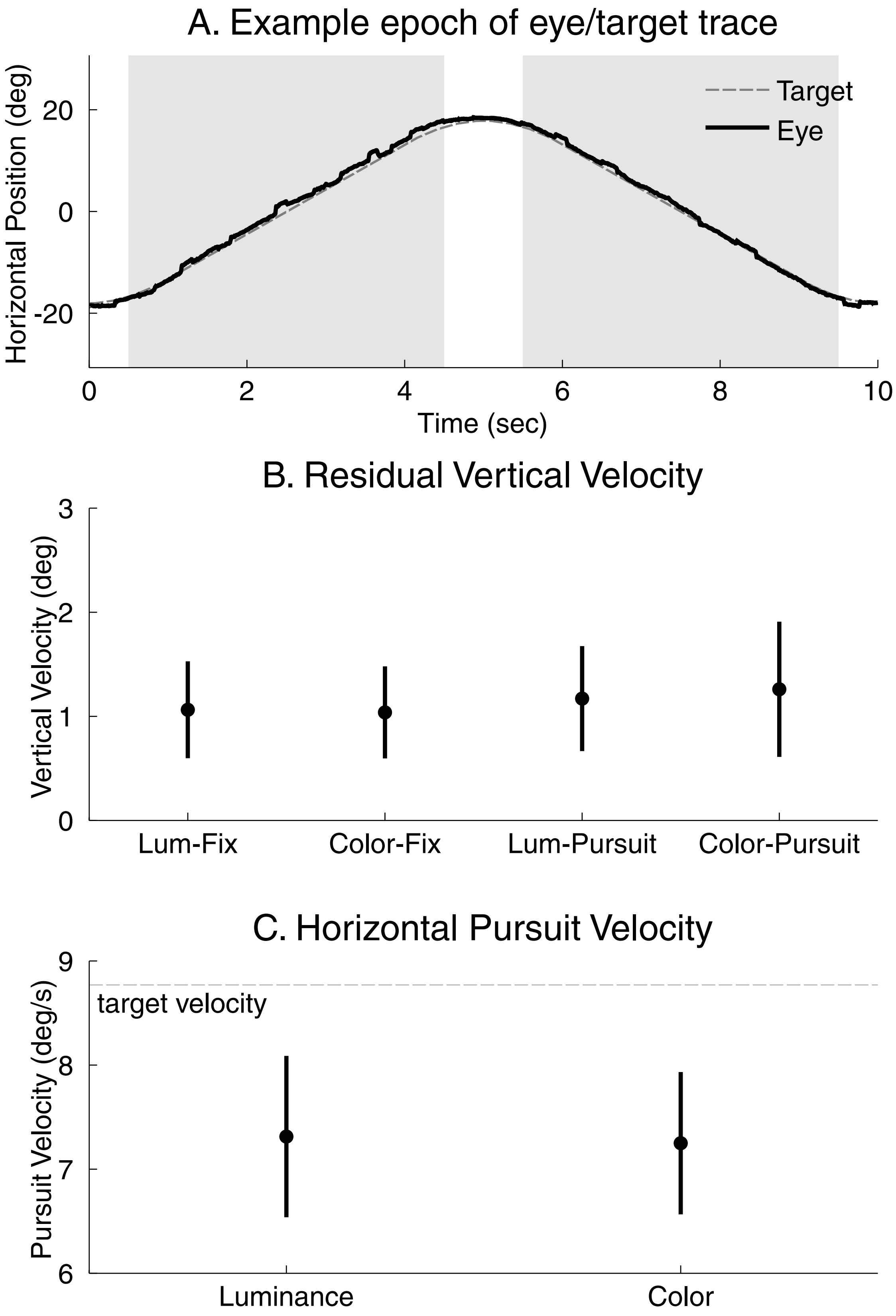
Figure 4. ***A***, SSVEP amplitudes in the 4 conditions, plotted as a function of stimulus contrast. Higher contrast stimuli induce larger SSVEPs. For color stimuli, SSVEPs were higher during the execution of pursuit eye movements compared to fixation. Error bars represent within-participant 95% confidence intervals (Cousineau, 2005). ***B*** and ***C*** show individual observer SSVEP amplitudes after aggregating the contrast conditions. ***B***, for luminance gratings, no difference emerges between fixation and pursuit. ***C***, for color gratings, most data points are above the diagonal line, corresponding to higher SSVEP amplitude for pursuit than fixation. Black bars show bootstrap (N = 5000) 95% confidence intervals of the mean along the negative-slope diagonal line.

A



B

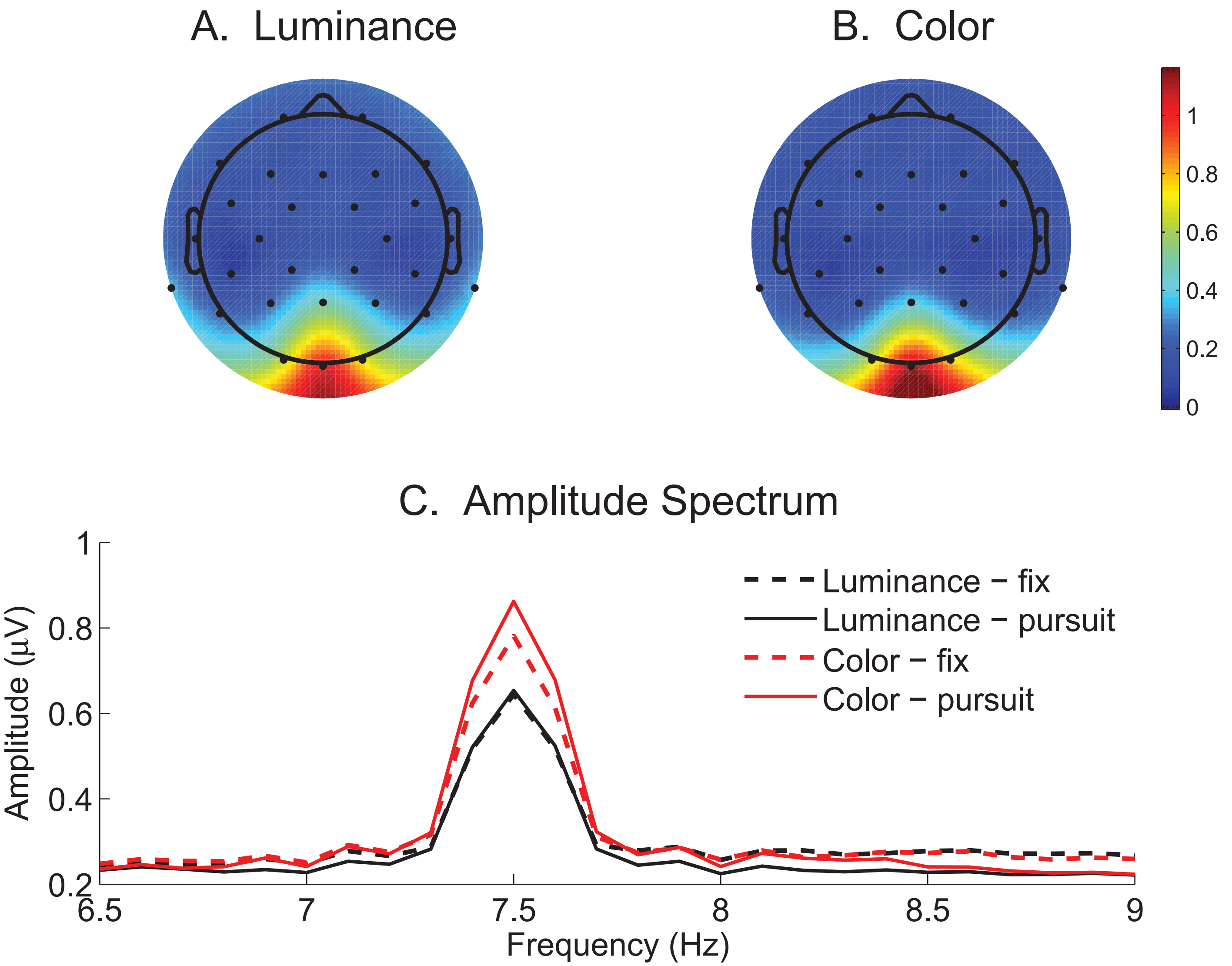


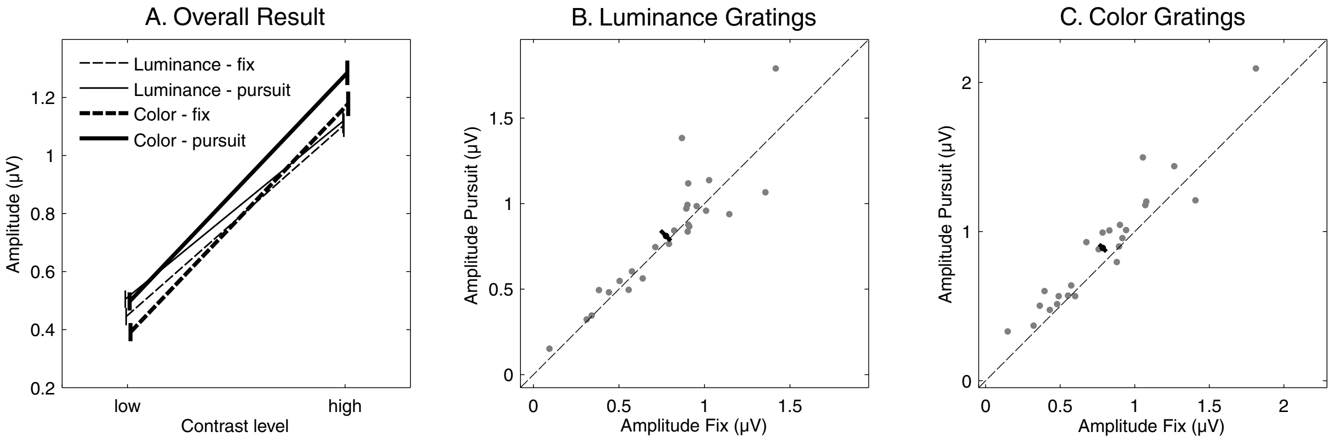


A. Example epoch of eye/target trace

B. Residual Vertical Velocity

C. Horizontal Pursuit Velocity


A. Luminance
B. Color
1
0.8
0.6
0.4
0.2
0
C. Amplitude Spectrum
Amplitude (µV)
1
0.8
0.6
0.4
0.2
6.5
7
7.5
8
8.5
9
Frequency (Hz)
Luminance − fix
Luminance − pursuit
Color − fix
Color − pursuit


A. Overall Result
Luminance - fix
Luminance - pursuit
Color - fix
Color - pursuit
Amplitude (μV)
0.2
0.4
0.6
0.8
1
1.2
low
high
Contrast level
B. Luminance Gratings
Amplitude Pursuit (μV)
0
0.5
1
1.5
Amplitude Fix (μV)
0
0.5
1
1.5
C. Color Gratings
Amplitude Pursuit (μV)
0
1
2
Amplitude Fix (μV)
0
0.5
1
1.5
2