The time course of chromatic adaptation in human early visual cortex revealed by SSVEPs

Yuan Zhang

School of Psychology, Shanghai University of Sport, Shanghai, China ✉

Matteo Valsecchi

Dipartimento di Psicologia, Universitá di Bologna, Bologna, Italy 🏠 ✉

Karl R. Gegenfurtner

Abteilung Allgemeine Psychologie and Center for Mind, Brain & Behavior, Justus-Liebig-Universität Giessen, Giessen, Germany 🏠 ✉

Jing Chen (ORCID)

School of Psychology, Shanghai University of Sport, Shanghai, China ✉

Previous studies have identified at least two components of chromatic adaptation: a rapid component with a time scale between tens of milliseconds to a few seconds, and a slow component with a half-life of about 10 to 30 seconds. The basis of the rapid adaptation probably lies in receptor adaptation at the retina. The neural substrate for the slow adaptation remains unclear, although previous psychophysical results hint at the early visual cortex. A promising approach to investigate adaptation effects in the visual cortex is to analyze steady-state visual evoked potentials (SSVEPs) elicited by chromatic stimuli, which typically use long durations of stimulation. Here, we re-analyzed the data from two previous pattern-reversal SSVEP studies. In these experiments (N = 49 observers in total), SSVEPs were elicited by counter-phase flickering color- or luminance-defined grating stimuli for 150 seconds in each trial. By analyzing SSVEPs with short time windows, we found that chromatic SSVEP responses decreased with increasing stimulation duration and reached a lower asymptote within a minute of stimulation. The luminance SSVEPs did not show any systematic adaptation. The time course of chromatic SSVEPs can be well described by an exponential decay function with a half-life of about 20 seconds, which is very close to previous psychophysical reports. Despite the difference in stimuli between the current and previous studies, the coherent time course may indicate a more general adaptation mechanism in the early visual cortex. In addition, the current result also provides a guide for future color SSVEP studies in terms of either avoiding or exploiting this adaptation effect.

Introduction

Chromatic adaptation is a central characteristic of color vision, and a major contributory mechanism to color constancy (for review, see Smithson, 2005). Multiple neural mechanisms contribute to color adaptation along the neural processing pathway from the retina (Yeh, Lee, & Kremers, 1996), the lateral geniculate nucleus (LGN) (Chang, Hess, & Mullen, 2016) to the visual cortex (Engel, 2005; Engel & Furmanski, 2001; Mullen, Chang, & Hess, 2015). Color adaptation can also occur at multiple time scales. Previous studies have reported a rapid adaptation component with a time scale in milliseconds to seconds, and also a slow component with a time constant between 10 to 30 seconds (Fairchild & Lennie, 1992; Fairchild & Reniff, 1995; Rinner & Gegenfurtner, 2000; Werner, Sharpe, & Zrenner, 2000). The neural substrate of the rapid adaptation most likely lies in local receptor adaptation at the retina (Fairchild & Lennie, 1992; Kries, 1905; Rinner & Gegenfurtner, 2000; Werner, 2014). The neural basis of the slow adaptation, however, is poorly understood. Rinner & Gegenfurtner (2000) speculated that it may be at the subcortical or early cortical level, because slow adaptation occurs both for color discrimination and appearance. Werner et al. (2000) used dichoptic presentations to examine the contribution of subcortical and cortical mechanisms to chromatic adaptation. They observed a similar adaptation effect in the cross-eye adaptation condition (i.e., adapting one eye and testing the other eye), compared with the same-eye adaptation condition

(i.e., adapting and testing the same eye). Their result suggested a cortical contribution to chromatic adaptation (Werner et al., 2000). Based on these studies, the early visual cortex is a likely candidate for the neural basis of slow-phase chromatic adaptation.

To test whether slow chromatic adaptation occurs in the early visual cortex of humans, a promising approach is to analyze steady-state visually evoked potentials (SSVEPs) elicited by chromatic stimuli. SSVEPs are oscillatory brain responses to rhythmic visual stimulation, originating mainly from the early visual cortex, especially the primary visual cortex (for review, see Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015). Recently, chromatic SSVEP have been used to investigate a whole range of topics, including color and attention (Martinovic, Wuerger, Hillyard, Müller, & Andersen, 2018; Russo & Spinelli, 1999; Wang & Wade, 2011), higher-order color mechanisms (Chen & Gegenfurtner, 2021; Kaneko, Kuriki, & Andersen, 2020), eye movements and color (Chen, Valsecchi, & Gegenfurtner, 2017b), and the effect of color on higher-level visual perception (Or, Retter, & Rossion, 2019). A similar paradigm called cVEP (chromatic VEP) has also been widely used to investigate color processing (Duncan, Roth, Mizokami, McDermott, & Crognale, 2012; Highsmith & Crognale, 2010; Nunez, Shapley, & Gordon, 2017; Nunez, Shapley, & Gordon, 2018; Regan, 1970; Siegfried, Tepas, Sperling, & Hiss, 1965; Skiba, Duncan, & Crognale, 2014; Xing et al., 2015). The cVEP studies used the same periodic flickering stimulation, but usually presented the result in time domain rather than in frequency domain as SSVEP studies. For both cVEP and SSVEP studies, the stimulation duration is usually long, from tens of seconds to a few minutes. There is some evidence showing that slow adaptation occurs in such a setup. For example, Duncan et al. (2012) examined the effect of two-minute adaptation on the VEP responses to colors and indeed revealed reduced responses after adaptation. However, the time course of adaptation has not been investigated.

To address these questions, we re-analyzed the data from two previous pattern-reversal SSVEP studies (Chen, Valsecchi, & Gegenfurtner, 2017a; Chen et al., 2017b). Dataset 1 used luminance-defined gratings and equiluminant red-green gratings to elicit SSVEP responses. The aim of the original study was to examine the effect of smooth pursuit eye movements on chromatic SSVEPs; and the result showed that smooth pursuit enhances chromatic pattern-reversal SSVEPs (Chen et al., 2017b). Dataset 2 used multiple frequencies to tag neural responses at multiple locations. The aim of the original study was to examine attentional allocation during smooth pursuit; and the result showed that attention is allocated closely ahead of the tracking target (Chen et al., 2017a). Here, to investigate the potential adaptation effect during prolonged stimulation (150 seconds in both studies), we reanalyzed

only the control condition where no eye movements were executed in both datasets.

Unlike previous color adaptation studies which used a uniform adaptation field (e.g., Rinner & Gegenfurtner, 2000), the pattern-reversal SSVEPs here were elicited by red-green gratings with stable average color over time. Despite the difference, we observed a similar adaptation effect with the same half-life of about 20 seconds. The current result suggests that slow-phase chromatic adaptation might happen already in early visual cortex, as indicated by pattern-reversal SSVEP signals. Moreover, the result has implications for the design of future color SSVEP studies, which could either avoid or exploit the chromatic adaptation effect.

Methods

We re-analyzed data from two of our previous publications (Chen et al., 2017a; Chen et al., 2017b). The studies are briefly described here, and further details can be found in the original articles.

Dataset 1

Dataset 1 was from the previous study (Chen et al., 2017b), which is publicly available at https://zenodo.org/record/808197. The study had 25 observers (15 females and 10 males). In the experiment, the observer either fixated at the screen center or executed smooth pursuit eye movements to a moving target, against a full-screen background that was counter-phase flickering at a reversal rate of 7.5 Hz (7.5 reversals per second). The flickering background was a horizontal grating with a spatial frequency of 0.34 cycles/°, at a size of 61° × 38° on the whole screen. The grating could be modulated in either luminance or isoluminant red-green chromaticity (Figure 1A). Each trial lasted 150 seconds, and each observer underwent eight trials in total. Here for the purpose of investigating adaptation, we only re-analyzed the four trials in the fixation condition (two trials with luminance grating, and two trials with red-green color grating) to exclude any potential effect of eye movements on adaptation.

Dataset 2

Dataset 2 was from the first and second experiments of the study (Chen et al., 2017a), which is publicly available at: https://zenodo.org/record/817545. In both experiments, the observers either fixated at the screen center or executed smooth pursuit eye movements to an array of flickering targets, which were moving across the screen back and forth. Here, we re-analyzed only the fixation trials. In experiment 1, observers (N = 12) underwent two fixation trials and each trial
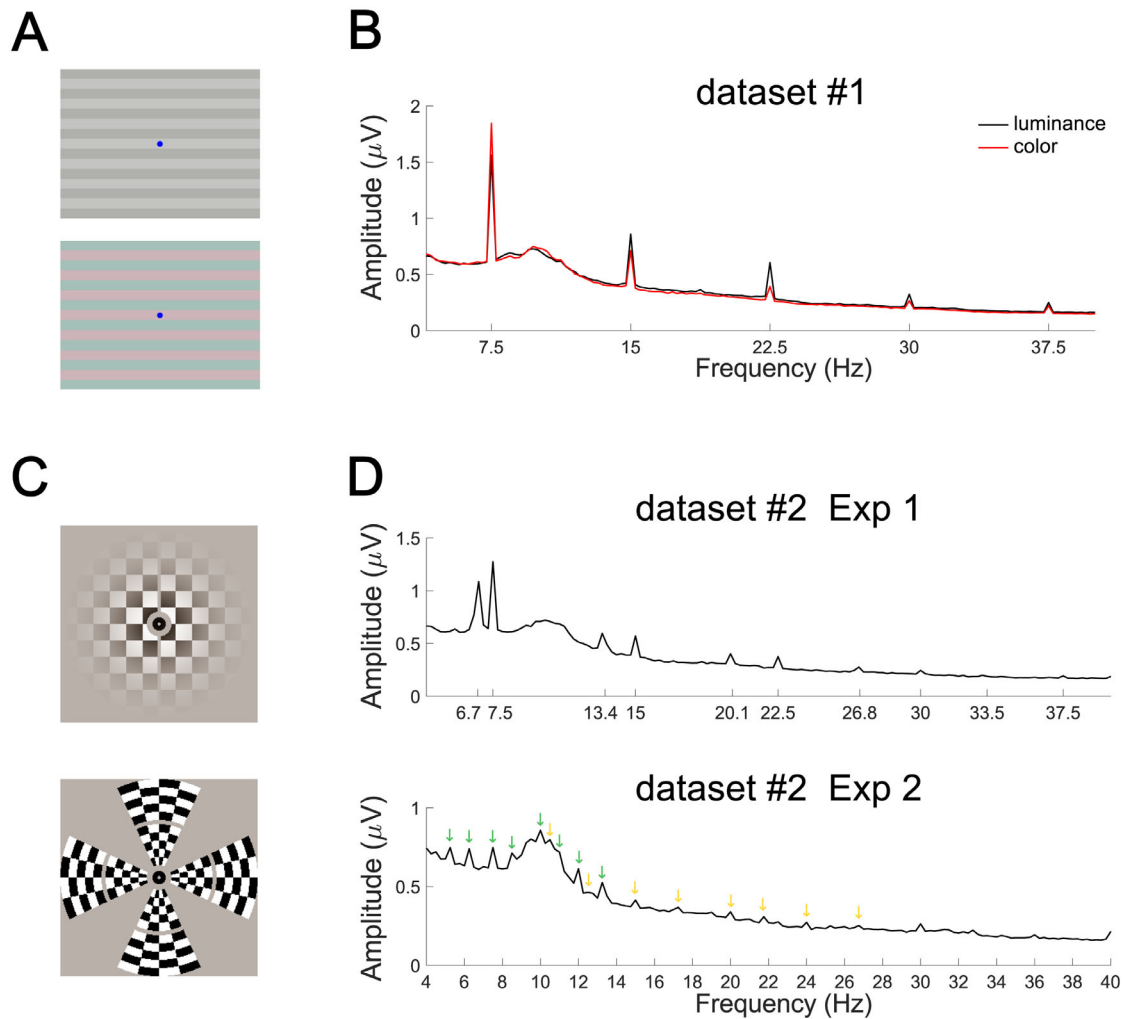
Figure 1. Stimuli and SSVEP responses. (**A**) Stimuli used in the dataset 1 (Chen et al., 2017b). (**B**) Grand-average amplitude spectrum over all observers (N = 25) for color and luminance stimuli. The response at 7.5 Hz and harmonics (e.g., 15, 22.5 Hz) is clearly visible. (**C**) Stimuli used in experiment 1 (top) and experiment 2 (bottom) in dataset 2 (Chen et al., 2017a). (**D**) Grand-average amplitude spectrums in dataset 2. For experiment 1, the responses are clear at 6.7 Hz and 7.5 Hz and their harmonics. For experiment 2, the response is visible at all eight stimulation frequencies (marked by green arrows at 5.2, 6.3, 7.5, 8.6, 10.0, 10.9, 12.0, and 13.3 Hz) and their second higher harmonics (marked by yellow arrows).

lasted 150 seconds. The stimuli were black-and-white checkerboard patterns extended 8.15° horizontally and 8.15° vertically, and were filtered through a 2D Gaussian window (SD = 1.46°). The checkerboards at the left and right sides were pattern-reversal flickering at either 6.7 Hz or 7.5 Hz. In experiment 2, observers (N = 12) underwent two fixation trials, each lasting 150 seconds. The stimuli were eight black-and-white checkerboard sectors centered along the four cardinal directions. Sectors were flickering at eight different frequencies separately (i.e., 5.2 Hz, 6.3 Hz, 7.5 Hz, 8.6 Hz, 10 Hz, 10.9 Hz, 12 Hz, and 13.3 Hz).

Data analysis

The analysis procedures were largely the same as in Chen et al. (2017a). The 32-channel electroencephalography (EEG) signals were first re-referenced to the average. In each trial, we discarded the first 1-second to remove the abrupt onset (e.g., Liu-Shuang, Torfs, & Rossion, 2016). Then the remaining signals were decomposed into 37 successive four-second epochs. Each epoch was detrended by removing the linear fit (Bach & Meigen, 1999). The amplitude spectrum of the epoch was obtained by fast-Fourier transformation (*fft*.m in Matlab). Response amplitude at a certain frequency was calculated by subtracting the baseline noise from the peak amplitude at the target frequency. In the analysis of dataset 1, we used the average amplitude of four bins near the target frequency as baseline. SSVEP amplitude for a certain condition was then calculated by taking the average of amplitudes over the fundamental frequency and two higher harmonics (i.e., 7.5, 15, and 22.5 Hz). We used these three frequencies because previous studies

have indicated that 10 to 20 Hz signals are the best to capture neural activities in the parvocellular pathway (Kremers, Aher, Popov, Mirsalehi, & Huchzermeyer, 2021; Regan, 1968a). In the analysis of dataset 2, we used the average amplitude of 2 bins near the target frequency as baseline (i.e., two immediately adjacent bins were not included to avoid frequency leakage). We first calculated the SNRs of SSVEP responses at all the flicker frequencies and their harmonics by dividing the baseline. According to the results of one-sample *t*-tests on SNRs, we only chose the harmonics where the SNRs were significant (SNRs > 1, $P < .05$) for further analyses. For experiment 1, the first to third harmonics of 7.5 and 6.7 Hz were used. For experiment 2, the first harmonics of all frequencies (i.e., 5.2, 6.3,

7.5, 8.6, 10.0, 10.9, 12.0, and 13.3 Hz) and second of 7.5, 8.6, 10, 12, 13.3 Hz were used. SSVEP amplitude was calculated by taking the average of amplitudes over these frequencies. In all the SSVEP analyses, only the O1, Oz, and O2 channels were used because they are the channels showing maximal responses (this is the case in our other studies with similar setups, Chen et al., 2017a; Chen et al., 2017b; Chen, McManus, Valsecchi, Harris, & Gegenfurtner, 2019; Chen & Gegenfurtner, 2021; and in similar studies from other groups, e.g., Martinovic et al., 2018; Nunez et al., 2017).

The resulting time course of SSVEP responses to color flicker was fitted with an exponential decay function: $SSVEP = S_0 + A \times e^{-kt}$. For the fitting, we excluded the first data point in the time course, because
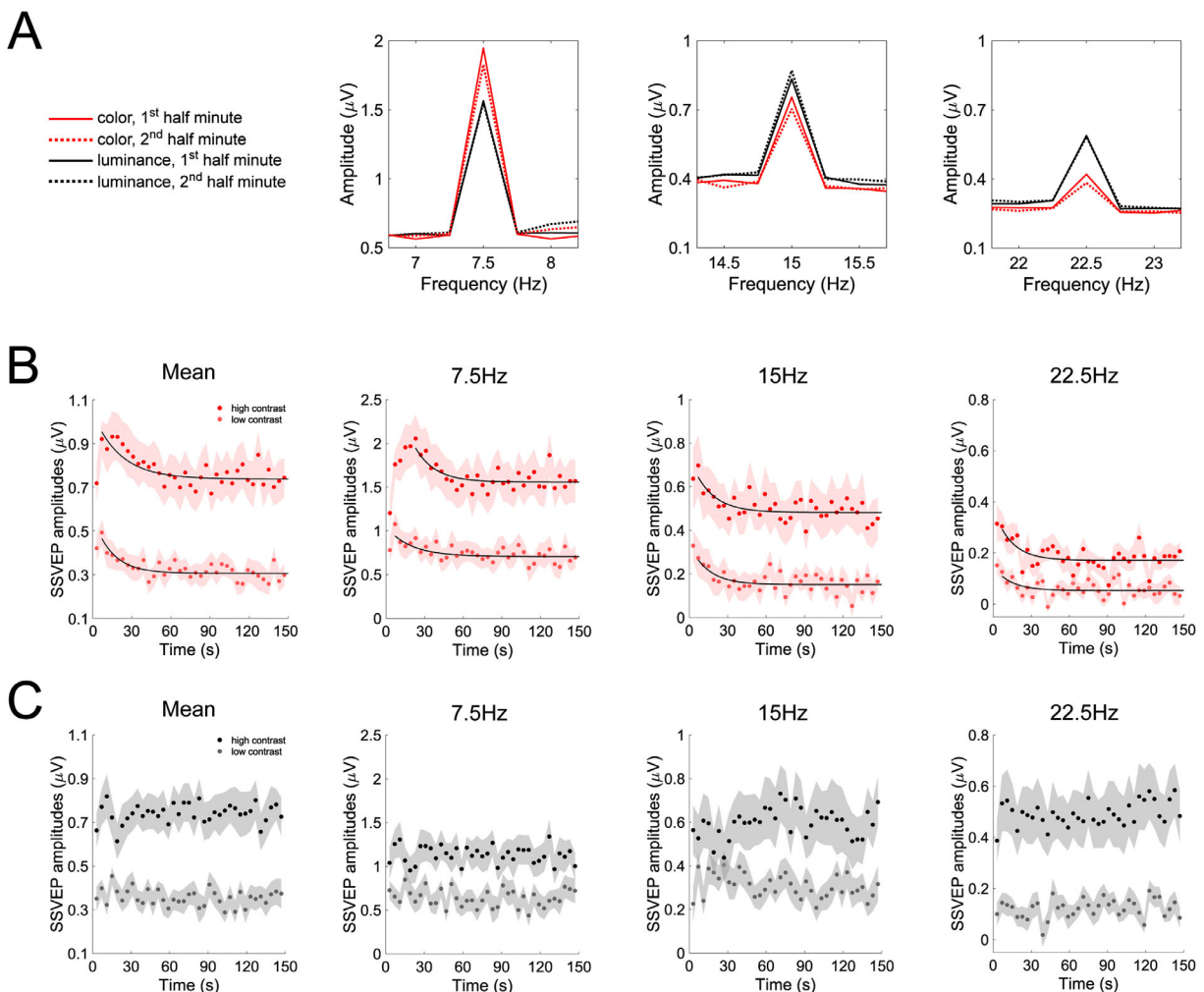

Figure 2. Time course of the adaptation effect in dataset 1. (A) Grand-average amplitude spectrum for color- and luminance-defined gratings during two intervals in each trial (i.e., first half versus second half-minute) at 7.5 Hz, 15 Hz, and 22.5 Hz. (B, C) Time course of SSVEP amplitudes elicited by color (B) and luminance (C) at low and high contrast. The first column is the mean SSVEP amplitudes of all three harmonics, and other columns are the amplitudes of individual harmonics (i.e., 7.5 Hz, 15 Hz, and 22.5 Hz). The black lines in B are the fit by an exponential decay function to the data. The half-life for mean SSVEP amplitudes is 17.1 seconds and 21.5 seconds for low and high contrast, respectively. Each dot shows the SSVEP amplitudes at every four-second epoch. Shaded areas indicate standard errors across observers.

the peak was typically given by the second time point (Figure 2B). The response at the first data point was smaller, probably because of contamination from the initial abrupt event-related response (which should have been minimized because we rejected the first second after stimulus onset) or because SSVEPs require some time to reach the steady-state entrainment (based on our visual inspections on waveforms, it takes about two seconds). Fitting was done on the average data, because EEG data of individual observers are noisy. To measure the half-life of the decay function, we calculated the time required for the decay function to drop to half of the amplitude (i.e., the peak minus the minimum).

Results

To estimate the adaptation effect in pattern-reversal SSVEPs elicited by chromatic and luminance flickers, we re-analyzed our previous datasets with short-term frequency analysis (4 seconds window). Figure 2 shows the result of dataset 1. Figure 2A plots the average spectrum at the reversal rate of 7.5 Hz, and its harmonics at 15 Hz and 22.5 Hz. One-sample t-tests on SNR values of all these peaks (SNR calculated by taking the peak amplitude divided by the average amplitude at nearby 4 bins) revealed that all the responses are
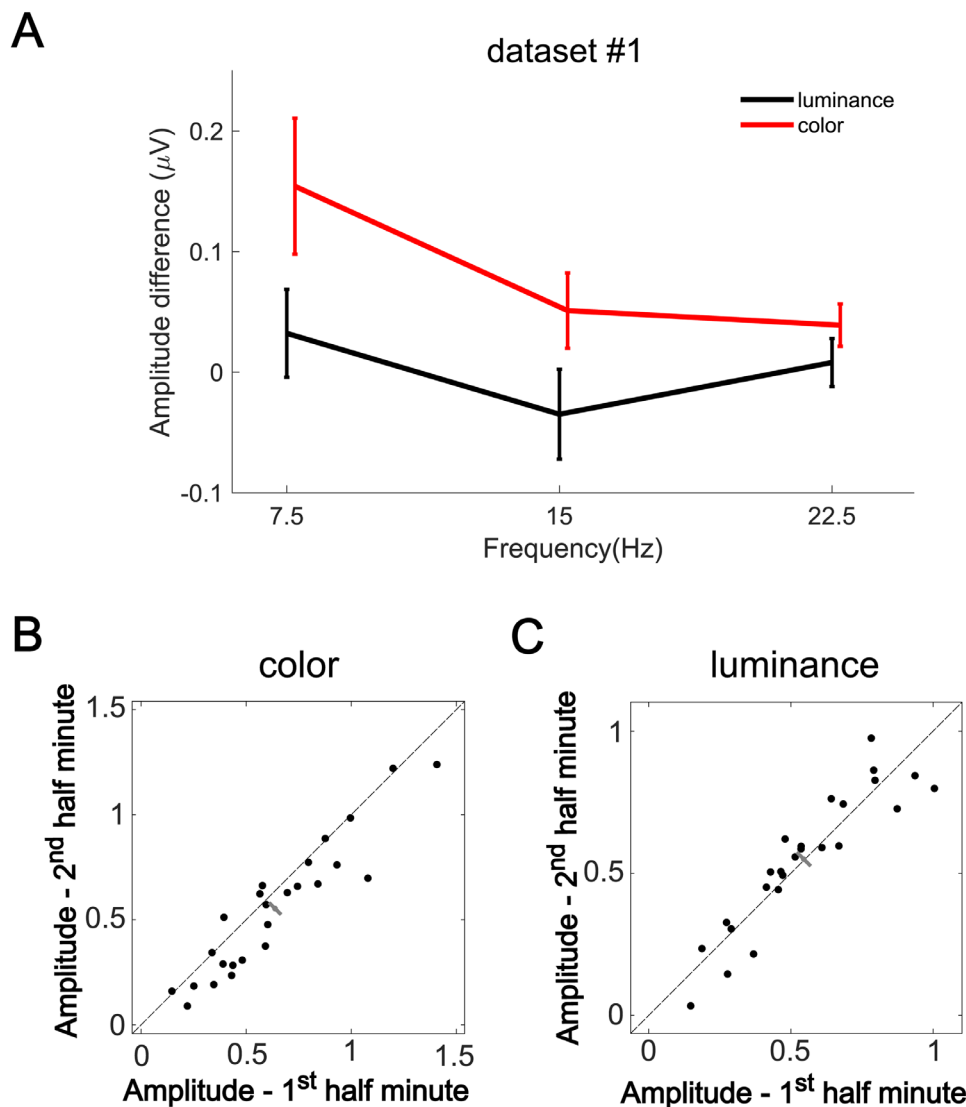

Figure 3. The adaptation effect in dataset 1. (A) The amplitude difference (i.e., the first half-minute minus the second half) at 7.5 Hz and its harmonics (15, 22.5 Hz) for color and luminance. The difference (i.e., adaptation effect) is more substantial for color than for luminance. Error bars represent standard errors across observers. (B, C) Adaptation effect in individual observers. Each data point denotes a single observer. For color-defined gratings (B), most data points fell below the diagonal line, revealing a significant adaptation effect. For luminance-defined gratings (C), there was no adaptation effect. Black bars denote 95% confidence intervals of the mean along the negative-slope diagonal line.

significant (all SNRs > 1, *P*s < .001). The plots show the spectra separately for the time window of the first half-minute of each trial (i.e., the 1st to 8th epochs, from 1 to 33 seconds) and the second half-minute (i.e., the nineth to sixteenth epochs, 33 to 65 seconds). Overall, the responses decrease across the two time intervals for color (i.e., showing adaptation effect), but not for luminance. Figures 2B and 2C show the mean (i.e., the mean of 7.5, 15, and 22.5 Hz) and the individual harmonics' SSVEP amplitudes as a function of time throughout the whole 150-second duration, for both high-contrast and low-contrast conditions. The overall pattern of SSVEPs to color looks remarkably similar to the color adaptation effect described previously with behavioral measurements (Figure 3 of Rinner & Gegenfurtner, 2000; Werner et al., 2000). A simple exponential decay model describes the data quite well (Figure 2B). The half-life of the exponential decay function for mean SSVEP amplitudes at low and high contrast is 17.1 and 21.5 seconds, which is also very

close to Rinner & Gegenfurtner's (2000) result (18.2 seconds for color discrimination and 19.6 seconds for color appearance). For luminance, the mean SSVEP amplitudes at both low- and high-contrast stimuli do not show any adaptation effect, neither do the individual harmonics (Figure 2C). Because the mean SSVEP amplitudes at low and high contrast have a similar effect, we combined the two levels of contrast in further analyses. A 2 (type of stimulus: luminance versus color) × 2 (time interval: first versus second half-minute) repeated-measure analysis of variance revealed an interaction, $F(1, 24) = 14.05$, $p < .001$, $\eta_{p2} = 0.369$, indicating different effects of time for luminance and color stimuli. We then proceeded to analyze SSVEP responses between the 1st half minute and 2nd half minute for color and luminance stimuli separately (Figures 3B, 3C), color response decreased significantly ($t(24) = 3.95$, $p < .001$) whereas luminance response did not ($t(24) = 0.10$, $p = 0.923$). There was no clear adaptation effect for luminance response.
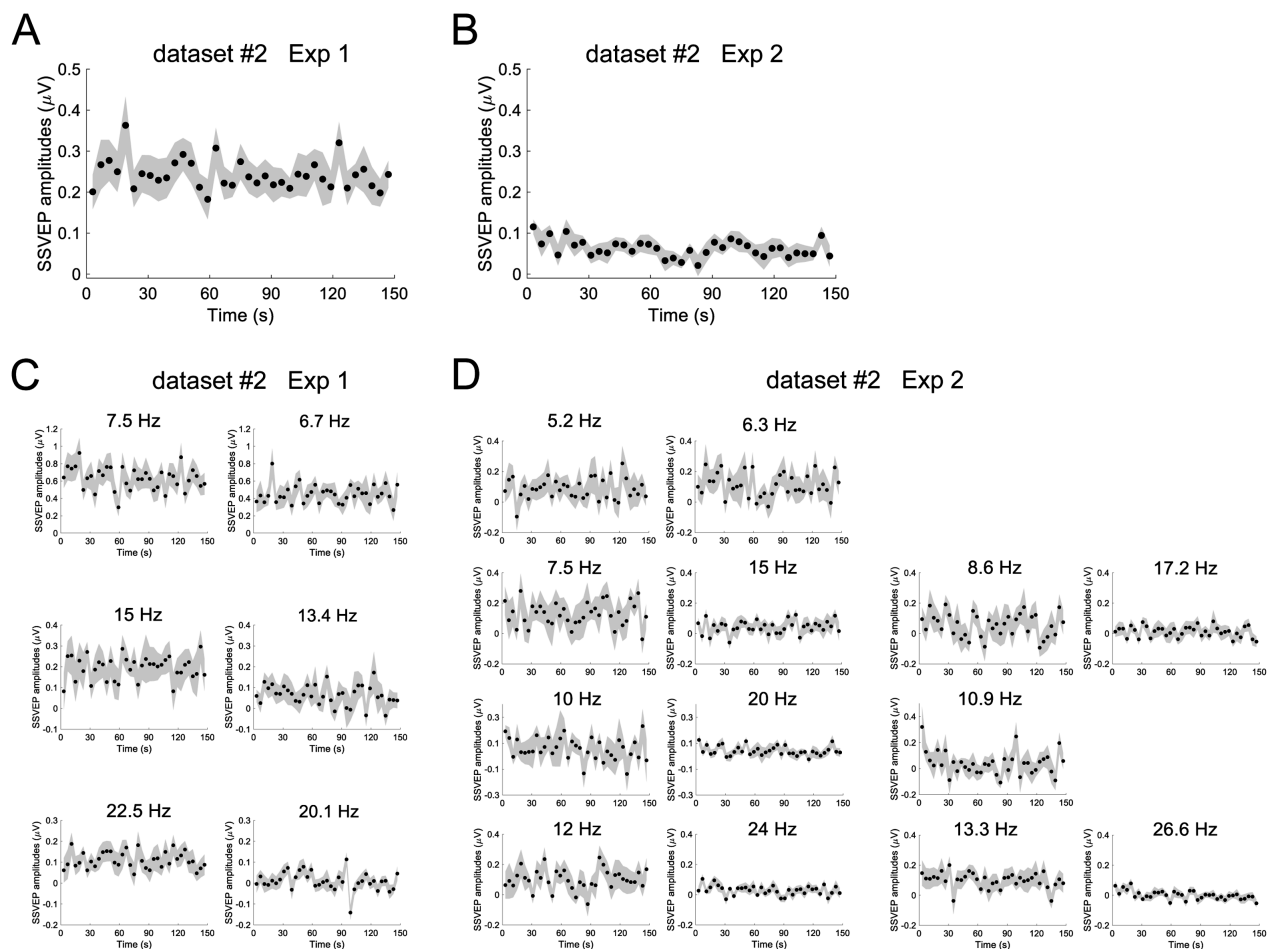

Figure 4. (A, B) The time course of the mean SSVEP amplitudes elicited by luminance-defined checkerboard patterns in two experiments of dataset 2. (C, D) The time course of SSVEP amplitudes of the individual harmonics in experiments 1 and 2, respectively. Each data point represents the SSVEP amplitudes at each four-second epoch. There is no clear sign of adaptation. Shaded areas indicate standard errors across observers.

Finally, we tested the adaptation effect separately at each harmonic frequency. For color stimuli, the SSVEP amplitudes at 7.5 Hz and 22.5 Hz showed significant adaptation effect (7.5 Hz: $t(24) = 4.60$, $p < 0.001$; 15 Hz: $t(24) = 1.64$, $p = 0.115$; 22.5 Hz: $t(24) = 2.22$, $p = 0.036$). For luminance stimuli, none of the harmonics showed significant effects (7.5 Hz: $t(24) = 0.87$, $p = 0.386$; 15 Hz: $t(24) = -0.94$, $p = 0.359$; 22.5 Hz: $t(24) = 0.40$, $p = 0.690$).

Because we used three harmonics to calculate SSVEP amplitudes, we further tested whether the adaptation effect in color SSVEPs depends on the harmonics. Figure 3A shows the adaptation effect (i.e., amplitude difference between the first and second half minute), separately at 7.5, 15, and 22.5 Hz. A 2 (time interval: first vs. second half minute) × 3 (harmonic frequency: 7.5 versus 15 versus 22.5 Hz) repeated-measure analyses of variance on color SSVEPs revealed a main effect for time interval, $F(1, 24) = 14.99$, $p < 0.001$, $\eta_{p2} = 0.384$, indicating an adaptation effect, and a main effect for harmonic frequency, $F(2, 48) = 58.68$, $p < 0.001$, $\eta_{p2} = 0.710$, indicating smaller SSVEP amplitudes at higher harmonic frequencies. However, there was no interaction between harmonic frequency and time interval, $F(2, 48) = 1.12$, $p = 0.340$, $\eta_{p2} = 0.044$, which suggest that the adaptation effect in color SSVEPs does not depend on harmonics. For luminance pattern-reversal SSVEPs, there was a main effect for harmonic frequency, $F(2, 48) = 23.53$, $p < 0.001$, $\eta_{p2} = 0.495$, but no main effect for time interval, $F(1, 24) = 0.01$, $p = 0.930$, $\eta_{p2} = 0.0003$, and no interaction between harmonic frequency and time interval, $F(2,48) = 1.12$, $p = 0.340$, $\eta_{p2} = 0.044$. This suggests that there is no sign of adaptation effect for luminance SSVEPs, and the lack of adaptation is similar across the three harmonics.

To further confirm the lack of adaptation effect for luminance responses, we re-analyzed the pattern-reversal SSVEPs in two experiments of dataset 2. Figure 4 shows the SSVEP amplitudes as a function of time. Figures 4A and 4B show the mean SSVEP amplitudes of all harmonics in experiments 1 and 2, respectively; and Figures 4C and 4D show the SSVEP amplitudes at individual harmonics with significant responses (SNRs > 1, $ps < 0.05$). Consistent with the result of dataset 1, we did not observe any clear sign of adaptation for pattern-reversal SSVEPs elicited by luminance-defined stimuli. Comparing the overall SSVEP responses between the first half-minute and second half-minute intervals in both experiments (Figures 4A, 4B), neither showed any significant difference (Exp 1: $t(11) = 0.50$, $p = 0.630$; Exp 2: $t(11) = 1.39$, $p = 0.193$). We also tested the adaptation effect (i.e., SSVEP amplitudes decrease at the second half-minute compared with the first half-minute of each trial) at each harmonic (Figures 4C, 4D). In experiment 1, the effect at 7.5Hz was significant if no multiple comparison correction was applied ($t(11) = 2.61$, $p = 0.024$), but it did not hold after multiple comparison correction. Except for that, none of the harmonics in experiments 1 and 2 showed any significant adaptation (all $ps > 0.05$).

Discussion

By re-analyzing data from previous studies, we found chromatic pattern-reversal SSVEPs decreased with increasing stimulating duration. This is likely to reflect activity changes in the early visual cortex. The time course can be well fitted by an exponential decay function with a half-life of about 20 seconds and reached a lower asymptote within a minute. The 20-second half-life in SSVEPs is consistent with previous psychophysical reports, where the perceptual performance declined to half at around 10 to 30 seconds during chromatic adaptation (Gupta, Gross, Pastilha, & Hurlbert, 2020; Rinner & Gegenfurtner, 2000; Werner et al., 2000). The current result suggests that slow-phase chromatic adaptation happens already in the early visual cortex, which confirms previous speculations (Rinner & Gegenfurtner, 2000; Werner et al., 2000).

To our knowledge, such slow phase of color adaptation has not been identified in animal physiological studies. A few previous studies recorded single-neuron activities to prolonged stimulations in animals and reported slow phase adaptation effect. The time constant of adaptation to luminance gratings in the visual cortex of cat is around 6 seconds (Albrecht, Farrar, & Hamilton, 1984; Ohzawa, Sclar, & Freeman, 1985; Vautin & Berkley, 1977). Sclar, Lennie, and DePriest (1989) also reported that activities of simple cells in monkey visual cortex declined for the initial 10 to 20 seconds during adaptation. These studies did not use color stimuli, but their time course is consistent with our current finding.

One may question whether the pattern-reversal SSVEP signals in the current study could capture chromatic processing, since the reversal rate of 7.5Hz is relatively high. Previously, Regan has suggested that the SSVEP amplitude at 10-20 Hz was mainly generated by the parvocellular pathway, while signals above 30 Hz were mostly due to the magnocellular pathway (Regan, 1968a; Regan, 1968b; Regan, 1970; Regan, 2009). Similarly, Kremers and colleagues have shown that electroretinographic (ERG) responses at 12Hz reflects L-/M-cone opponency, and responses at 36Hz reflect luminance signals (Kremers, Rodrigues, de Lima Silveira, & da Silva Filho, 2010; Kremers et al. 2021). Therefore the frequencies we used (i.e., 7.5, 15, and 22.5 Hz) should be able to capture chromatic processing. A further issue is whether these responses (7.5Hz-22.5Hz) reflect activity of only one of the multiple chromatic

processing channels. Indeed, previous studies have generally found that color is processed through multiple temporal channels (Cass, Clifford, Alais, & Spehar, 2009; Cropper, 1994; Fylan, Holliday, Singh, Anderson, & Harding, 1997; Gegenfurtner & Hawken, 1996; Metha & Mullen, 1996; Morrone, Fiorentini, & Burr, 1996; Muthukumaraswamy & Singh, 2008; Sun et al., 2007), with at least a slower channel (∼2Hz) and a fast channel (∼8Hz). The adaptation effect reported here is probably a property of the fast channel, and further studies are required to test whether a similar adaptation effect is also present for the slow channel.

Note that there is a key difference between the stimuli we used to elicit pattern-reversal SSVEPs and the stimuli used in previous psychophysical studies (Gupta et al., 2020; Rinner & Gegenfurtner, 2000; Werner et al., 2000). Previous experiments used the DC offsets of color, changing the average color in the scene. Here the pattern-reversal SSVEP experiment used counter-phase flickering red-green gratings with the same average color over time (i.e., the average color never changed). As a result, what we revealed in SSVEP is an adaptation effect to color contrast, and this does not necessarily correspond to the adaptation effect studied in previous psychophysical experiments. However, they might at least in part share similar mechanism, given that the time courses are strikingly similar. Besides, their neural loci are most likely both at the cortical level (Albrecht et al., 1984; Engel & Furmanski, 2001; Gardner et al., 2005; Goddard, Chang, D. H. F., Hess, R. F., & Mullen, 2019; Goddard, Shooner, & Mullen 2022; Maffei, Fiorentini, & Bisti, 1973; Mullen et al., 2015; Ohzawa, Sclar, & Freeman, 1982; Saul & Cynader, 1989; Sclar et al., 1989; Solomon, Peirce, Dhruv, & Lennie, 2004; Webster & Mollon, 1994). We speculate that the adaptation effect we found might share a similar cortical mechanism with the adaptation effects in previous psychophysical experiments.

A few previous studies investigated the effect of chromatic adaptation in SSVEPs (Regan, 1968a) and VEPs (Duncan et al., 2012; Rabin, Switkes, Crognale, Schneck, & Adams, 1994). Regan (1968a) and Rabin et al. (1994) found that there is an instant adaptation effect of a color field on cortical responses to another color. The instant adaptation effect also varied with flickering frequency (Regan, 1968a) and color similarity between the adapting and testing color (Rabin et al., 1994). They, however, did not test the slow phase of adaptation. Duncan et al. (2012) examined the effect of adapting one color for two minutes on the VEP responses to other colors. They found that two minutes of adaptation reduces amplitude to colors in neighboring angles in color space but has minimal effect on amplitude to colors at orthogonal angles. Their results provided evidence for higher-order chromatic mechanisms, similar to psychophysical results (Bouet &

Knoblauch, 2004; Gegenfurtner & Kiper, 1992; Hansen & Gegenfurtner, 2013; Krauskopf & Gegenfurtner, 1992; Webster & Mollon, 1991) and also a recent SSVEPs study (Chen & Gegenfurtner, 2021). However, Duncan et al. (2012) did not investigate the time course of adaptation within these two minutes. Our results show that adaptation is largely complete within one minute, such that an adaptation period of one minute is sufficient to elicit adaptation in color SSVEPs in future studies.

One remarkable aspect of our data is that pattern-reversal SSVEPs elicited by luminance-defined stimuli did not show any systematic adaptation at all. To our knowledge, few studies have investigated slow adaptation effects in SSVEP elicited by grating stimuli similar to ours. One early study reported some preliminary observations (Blakemore & Campbell, 1969). They showed that after viewing a high-contrast grating for 30 or 60 seconds, the VEPs to a low-contrast grating were reduced. This result, however, was based on a single observer. Also, they used high spatial frequency stimuli (12 c/deg), whereas the current study used stimuli with low spatial frequency (0.34 c/deg). It will therefore be interesting to test whether spatial frequency is a determining factor for the presence of an adaptation effect in SSVEPs to luminance gratings. A later study found that neural responses to achromatic gratings are attenuated after adapting to a mask at certain contrast (Robson & Kulikowski, 2012). However, they did not examine the slow adaptation effect and the time course. For SSVEPs elicited by motion stimuli, Heinrich & Bach (2003) found an absence of adaptation after exposure to motion reversals (flickering between motion expansion and contraction). When the adaptation stimuli were moving only in a single direction, instead of moving back and forth, adaptation did occur (Ales & Norcia, 2009; Heinrich & Bach, 2003). For example, Ales & Norcia (2009) presented an adaptor moving in a single direction for 25 seconds and then tested SSVEPs to moving stimuli oscillating left and right. They found that responses in the adapted direction were reduced but not in the un-adapted direction, and this induced an asymmetry in the population responses. Therefore, in the domain of motion SSVEPs, direction-specific motion adaptation has been observed, whereas non-direction-specific adaptation may not occur in the early visual cortex as indicated by SSVEPs. At this stage, we don't know exactly why luminance-gratings did not induce an adaptation effect in the current result. Based on motion SSVEP, we speculate that adaptation might be revealed with "uni-direction" adaptation (i.e., adapting to a black or white field).

The lack of adaptation effect for luminance response may also be related to the transient and sustained response in visual processing. It is well known that neural processing of luminance is relatively transient, whereas the processing of color tends to be sustained

(Kulikowski & Walsh, 1993; Robson & Kulikowski, 2012; Schiller & Malpeli, 1978; Schwartz & Loop, 1982; Shapley, Kaplan, & Soodak, 1981; Valberg & Lee, 1991). The lack of slow adaptation for luminance response might be due to the transient nature of the response. In addition, SSVEPs in the current study were produced by pattern-reversal stimuli, which have been shown to elicit transient responses more than on-off stimuli (Strasburger, Murray, & Remky, 1993). It is thus possible that luminance SSVEPs with on-off stimulation may show a slow adaptation effect.

Although we believe our results show that adaptation affects luminance and color mechanisms differentially, one might also come to the conclusion that it is habituation that causes these differences. In our opinion, the difference between adaptation and habituation is difficult to resolve, and both terms have been used interchangeably in large parts of the literature (e.g., Krauskopf, Williams, & Heeley, 1982, versus Webster & Mollon, 1991). In the EEG or SSVEP literature, there is also no well-defined and accepted way to distinguish habituation from adaptation. Although most studies investigating habituation with SSVEPs did not consider the potential role of adaptation (Abdulhussein, An, Alsakaa, & Ming, 2022; Cao et al., 2020; Labecki, Nowicka, & Suffczynski, 2019; Shibata, Yamane, Otuka, & Iwata, 2008; Shibata, Yamane, Nishimura, Kondo, & Otuka, 2011), one study discussed this issue and explicitly said that their results can be explained by habituation as well as adaptation (Omland, Nilsen, & Sand, 2011). There was only one SSVEP study, as far as we know, that tried to manipulate habituation and adaptation in the experiment design (Dong, Du, & Bao, 2020). In their study, the change in visual sensitivity observed after exposure to the stimulus within a testing session (190 trials) was defined as "adaptation effect." In addition, their participants were tested every day for 11 days in a row. The change in visual sensitivity observed due to such long-term exposure (across a few days) was defined as "habituation effect." Based on their definition, what we reported in the current study should be "adaptation" rather than "habituation." However, because there is no well-accepted definition to distinguish the two, we think that further work is need to determine the contribution of habituation and adaptation to the present result.

The current result has important implications for designing color SSVEP studies in the future. First, SSVEP studies usually use long stimulation durations. Most previous color SSVEP studies employed a duration in the range of 20 to 150 seconds (Chen et al., 2017b; Chen & Gegenfurtner, 2021; Highsmith & Crognale, 2010; Kaneko et al., 2020; Nunez et al., 2017; Nunez et al., 2018; Or et al., 2019; Regan, 1968a; Xing et al., 2015), with a few in shorter duration from three to 12 seconds (Martinovic et al., 2018; Rabin et al., 1994; Skiba et al., 2014; Wang & Wade, 2011).

Based on the current result, it seems optimal to use a relatively short duration of no more than 20 seconds if avoiding adaptation is preferred. Second, adaptation has been a widely used technique to investigate color processing in both psychophysical studies, as well as functional magnetic resonance imaging studies. In SSVEP studies, it is much less used. Our result suggests that an adaptation duration of 30 to 60 seconds should be sufficient. Third, caution should be taken if future studies want to directly compare color and luminance SSVEPs, because their adaptation time courses are different.

References

Abdulhussein, M. A., An, X., Alsakaa, A. A., & Ming, D. (2022). Lack of habituation in migraine patients and evoked potential types: Analysis study from EEG signals. *Journal of Information and Optimization Sciences, 43*(4), 855–891, https://doi.org/10.1080/02522667.2022.2095958.

Albrecht, D. G., Farrar, S. B., & Hamilton, D. B. (1984). Spatial contrast adaptation characteristics of neurones recorded in the cat's visual cortex. *Journal of Physiology, 347*(1), 713–739, https://doi.org/10.1113/jphysiol.1984.sp015092.

Ales, J. M., & Norcia, A. M. (2009). Assessing direction-specific adaptation using the steady-state visual evoked potential: Results from EEG source imaging. *Journal of Vision, 9*(7), 8–8, https://doi.org/10.1167/9.7.8.

Bach, M., & Meigen, T. (1999). Do's and don'ts in Fourier analysis of steady-state potentials. *Documenta Ophthalmologica, 99*(1), 69–82, https://doi.org/10.1023/A:1002648202420.

Blakemore, C., & Campbell, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology, 203*(1), 237–260, https://doi.org/10.1113/jphysiol.1969.sp008862.

Bouet, R., & Knoblauch, K. (2004). Perceptual classification of chromatic modulation. *Visual Neuroscience, 21*(3), 283–289, https://doi.org/10.1017/S0952523804213141.

Cao, Z., Ding, W., Wang, Y.-K., Hussain, F. K., Al-Jumaily, A., & Lin, C.-T. (2020). Effects of repetitive SSVEPs on EEG complexity using multiscale inherent fuzzy entropy. *Neurocomputing, 389*, 198–206, https://doi.org/10.1016/j.neucom.2018.08.091.

Cass, J., Clifford, C. W. G., Alais, D., & Spehar, B. (2009). Temporal structure of chromatic channels revealed through masking. *Journal of Vision, 9*(5), 17–17, https://doi.org/10.1167/9.5.17.

Chang, D. H. F., Hess, R. F., & Mullen, K. T. (2016). Color responses and their adaptation in human superior colliculus and lateral geniculate nucleus. *NeuroImage, 138*, 211–220, https://doi.org/10.1016/j.neuroimage.2016.04.067.

Chen, J., & Gegenfurtner, K. R. (2021). Electro-physiological evidence for higher-level chromatic mechanisms in humans. *Journal of Vision, 21*(8), 12, https://doi.org/10.1167/jov.21.8.12.

Chen, J., McManus, M., Valsecchi, M., Harris, L. R., & Gegenfurtner, K. R. (2019). Steady-state visually evoked potentials reveal partial size constancy in early visual cortex. *Journal of Vision, 19*(6), 8, https://doi.org/10.1167/19.6.8.

Chen, J., Valsecchi, M., & Gegenfurtner, K. R. (2017a). Attention is allocated closely ahead of the target during smooth pursuit eye movements: Evidence from EEG frequency tagging. *Neuropsychologia, 102*, 206–216, https://doi.org/10.1016/j.neuropsychologia.2017.06.024.

Chen, J., Valsecchi, M., & Gegenfurtner, K. R. (2017b). Enhanced brain responses to color during smooth-pursuit eye movements. *Journal of Neurophysiology, 118*(2), 749–754, https://doi.org/10.1152/jn.00208.2017.

Cropper, S. J. (1994). Velocity discrimination in chromatic gratings and beats. *Vision Research, 34*(1), 41–48, https://doi.org/10.1016/0042-6989(94)90255-0.

Dong, X., Du, X., & Bao, M. (2020). Repeated contrast adaptation does not cause habituation of the adapter. *Frontiers in Human Neuroscience, 14*, 589634, https://doi.org/10.3389/fnhum.2020.589634.

Duncan, C. S., Roth, E. J., Mizokami, Y., McDermott, K. C., & Crognale, M. A. (2012). Contrast adaptation reveals increased organizational complexity of chromatic processing in the visual evoked potential. *Journal of the Optical Society of America A, 29*(2), A152, https://doi.org/10.1364/JOSAA.29.00A152.

Engel, S. A. (2005). Adaptation of oriented and unoriented color-selective neurons in human visual areas. *Neuron, 45*(4), 613–623, https://doi.org/10.1016/j.neuron.2005.01.014.

Engel, S. A., & Furmanski, C. S. (2001). Selective adaptation to color contrast in human primary visual cortex. *Journal of Neuroscience, 21*(11), 3949–3954, https://doi.org/10.1523/JNEUROSCI.21-11-03949.2001.

Fairchild, M. D., & Lennie, P. (1992). Chromatic adaptation to natural and incandescent illuminants. *Vision Research, 32*(11), 2077–2085, https://doi.org/10.1016/0042-6989(92)90069-U.

Fairchild, M. D., & Reniff, L. (1995). Time course of chromatic adaptation for color-appearance judgments. *Journal of the Optical Society of America A, 12*(5), 824, https://doi.org/10.1364/JOSAA.12.000824.

Fylan, F., Holliday, I. E., Singh, K. D., Anderson, S. J., & Harding, G. F. A. (1997). Magnetoencephalographic investigation of human cortical area V1 using color stimuli. *NeuroImage, 6*(1), 47–57, https://doi.org/10.1006/nimg.1997.0273.

Gardner, J. L., Sun, P., Waggoner, R. A., Ueno, K., Tanaka, K., & Cheng, K. (2005). Contrast adaptation and representation in human early visual cortex. *Neuron, 47*(4), 607–620, https://doi.org/10.1016/j.neuron.2005.07.016.

Gegenfurtner, K. R., & Hawken, M. J. (1996). Interaction of motion and color in the visual pathways. *Trends in Neurosciences, 19*(9), 394–401, https://doi.org/10.1016/S0166-2236(96)10036-9.

Gegenfurtner, K. R., & Kiper, D. C. (1992). Contrast detection in luminance and chromatic noise. *Journal of the Optical Society of America A, 9*(11), 1880, https://doi.org/10.1364/JOSAA.9.001880.

Goddard, E., Chang, D. H. F., Hess, R. F., & Mullen, K. T. (2019). Color contrast adaptation: FMRI fails to predict behavioral adaptation. *NeuroImage, 201*, 116032, https://doi.org/10.1016/j.neuroimage.2019.116032.

Goddard, E., Shooner, C., & Mullen, K. T. (2022). Magnetoencephalography contrast adaptation reflects perceptual adaptation. *Journal of Vision, 22*(10), 16, https://doi.org/10.1167/jov.22.10.16.

Gupta, G., Gross, N., Pastilha, R., & Hurlbert, A. (2020). The time course of chromatic

adaptation under immersive illumination [Preprint]. *Neuroscience,* https://doi.org/10.1101/2020.03.10.984567.

Hansen, T., & Gegenfurtner, K. R. (2013). Higher order color mechanisms: Evidence from noise-masking experiments in cone contrast space. *Journal of Vision, 13*(1), 26–26, https://doi.org/10.1167/13.1.26.

Heinrich, S. P., & Bach, M. (2003). Adaptation characteristics of steady-state motion visual evoked potentials. *Clinical Neurophysiology, 114*(7), 1359–1366, https://doi.org/10.1016/S1388-2457(03)00088-9.

Highsmith, J., & Crognale, M. A. (2010). Attentional shifts have little effect on the waveform of the chromatic onset VEP: Attentional effects on chromatic VEP. *Ophthalmic and Physiological Optics, 30*(5), 525–533, https://doi.org/10.1111/j.1475-1313.2010.00747.x.

Kaneko, S., Kuriki, I., & Andersen, S. K. (2020). Steady-state visual evoked potentials elicited from early visual cortex reflect both perceptual color space and cone-opponent mechanisms. *Cerebral Cortex Communications, 1*(1), tgaa059, https://doi.org/10.1093/texcom/tgaa059.

Krauskopf, J., & Gegenfurtner, K. (1992). Color discrimination and adaptation. *Vision Research, 32*(11), 2165–2175, https://doi.org/10.1016/0042-6989(92)90077-V.

Krauskopf, J., Williams, D. R., & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research, 22*(9), 1123–1131, https://doi.org/10.1016/0042-6989(82)90077-3.

Kremers, J., Aher, A. J., Popov, Y., Mirsalehi, M., & Huchzermeyer, C. (2021). The influence of temporal frequency and stimulus size on the relative contribution of luminance and L-/M-cone opponent mechanisms in heterochromatic flicker ERGs. *Documenta Ophthalmologica, 143*(2), 207–220, https://doi.org/10.1007/s10633-021-09837-9.

Kremers, J., Rodrigues, A. R., de Lima Silveira, L. C., & da Silva Filho, M. (2010). Flicker ERGs representing chromaticity and luminance signals. *Investigative Ophthalmology & Visual Science, 51*(1), 577, https://doi.org/10.1167/iovs.09-3899.

Kries, J. (1905). Die gesichtsempfindungen. *Nagel's Handbuch Der Physiologie Des Menschen, 3*, 109–282.

Kulikowski, J. J., & Walsh, V. (1993). Colour vision: Isolating mechanisms in overlapping streams. *Progress in Brain Research, 95*, 417–426, https://doi.org/10.1016/s0079-6123(08)60385-4.

Labecki, M., Nowicka, M. M., & Suffczynski, P. (2019). Temporal modulation of steady-state visual evoked potentials. *International Journal of Neural Systems, 29*(03), 1850050, https://doi.org/10.1142/S0129065718500508.

Liu-Shuang, J., Torfs, K., & Rossion, B. (2016). An objective electrophysiological marker of face individualisation impairment in acquired prosopagnosia with fast periodic visual stimulation. *Neuropsychologia, 83*, 100–113, https://doi.org/10.1016/j.neuropsychologia.2015.08.023.

Maffei, L., Fiorentini, A., & Bisti, S. (1973). Neural correlate of perceptual adaptation to gratings. *Science, 182*(4116), 1036–1038, https://doi.org/10.1126/science.182.4116.1036.

Martinovic, J., Wuerger, S. M., Hillyard, S. A., Müller, M. M., & Andersen, S. K. (2018). Neural mechanisms of divided feature-selective attention to colour. *NeuroImage, 181*, 670–682, https://doi.org/10.1016/j.neuroimage.2018.07.033.

Metha, A. B., & Mullen, K. T. (1996). Temporal mechanisms underlying flicker detection and identification for red–green and achromatic stimuli. *Journal of the Optical Society of America A, 13*(10), 1969, https://doi.org/10.1364/JOSAA.13.001969.

Morrone, M. C., Fiorentini, A., & Burr, D. C. (1996). Development of the temporal properties of visual evoked potentials to luminance and colour contrast in infants. *Vision Research, 36*(19), 3141–3155, https://doi.org/10.1016/0042-6989(96)00050-8.

Mullen, K. T., Chang, D. H. F., & Hess, R. F. (2015). The selectivity of responses to red-green colour and achromatic contrast in the human visual cortex: An fMRI adaptation study. *European Journal of Neuroscience, 42*(11), 2923–2933, https://doi.org/10.1111/ejn.13090.

Muthukumaraswamy, S. D., & Singh, K. D. (2008). Spatiotemporal frequency tuning of BOLD and gamma band MEG responses compared in primary visual cortex. *NeuroImage, 40*(4), 1552–1560, https://doi.org/10.1016/j.neuroimage.2008.01.052.

Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottereau, B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: A review. *Journal of Vision, 15*(6), 4, https://doi.org/10.1167/15.6.4.

Nunez, V., Shapley, R. M., & Gordon, J. (2017). Nonlinear dynamics of cortical responses to color in the human cVEP. *Journal of Vision, 17*(11), 9, https://doi.org/10.1167/17.11.9.

Nunez, V., Shapley, R. M., & Gordon, J. (2018). Cortical double-opponent cells in color perception: Perceptual scaling and chromatic visual evoked potentials. *I-Perception, 9*(1), 204166951775271, https://doi.org/10.1177/2041669517752715.

Ohzawa, I., Sclar, G., & Freeman, R. D. (1982). Contrast gain control in the cat visual cortex. *Nature, 298*(5871), 266–268, https://doi.org/10.1038/298266a0.

Ohzawa, I., Sclar, G., & Freeman, R. D. (1985). Contrast gain control in the cat's visual system. *Journal of Neurophysiology, 54*(3), 651–667, https://doi.org/10.1152/jn.1985.54.3.651.

Omland, P. M., Nilsen, K. B., & Sand, T. (2011). Habituation measured by pattern reversal visual evoked potentials depends more on check size than reversal rate. *Clinical Neurophysiology, 122*(9), 1846–1853, https://doi.org/10.1016/j.clinph.2011.02.025.

Or, C. C.-F., Retter, T. L., & Rossion, B. (2019). The contribution of color information to rapid face categorization in natural scenes. *Journal of Vision, 19*(5), 20, https://doi.org/10.1167/19.5.20.

Rabin, J., Switkes, E., Crognale, M., Schneck, M. E., & Adams, A. J. (1994). Visual evoked potentials in three-dimensional color space: Correlates of spatio-chromatic processing. *Vision Research, 34*(20), 2657–2671, https://doi.org/10.1016/0042-6989(94)90222-4.

Regan, D. (1968a). Chromatic adaptation and steady-state evoked potentials. *Vision Research, 8*(2), 149–158, https://doi.org/10.1016/0042-6989(68)90003-5.

Regan, D. (1968b). A high frequency mechanism which underlies visual evoked potentials. *Electroencephalography and Clinical Neurophysiology, 25*(3), 231–237, https://doi.org/10.1016/0013-4694(68)90020-5.

Regan, D. (1970). Objective method of measuring the relative spectral-luminosity curve in man. *Journal of the Optical Society of America, 60*(6), 856, https://doi.org/10.1364/JOSA.60.000856.

Regan, D. (2009). Some early uses of evoked brain responses in investigations of human visual function. *Vision Research, 49*(9), 882–897, https://doi.org/10.1016/j.visres.2008.01.017.

Rinner, O., & Gegenfurtner, K. R. (2000). Time course of chromatic adaptation for color appearance and discrimination. *Vision Research, 40*(14), 1813–1826, https://doi.org/10.1016/S0042-6989(00)00050-X.

Robson, A. G., & Kulikowski, J. J. (2012). Objective assessment of chromatic and achromatic pattern adaptation reveals the temporal response properties of different visual pathways. *Visual Neuroscience, 29*(6), 301–313, https://doi.org/10.1017/S0952523812000351.

Russo, F. D., & Spinelli, D. (1999). Spatial attention has different effects on the magno- and parvocellular pathways: *NeuroReport, 10*(13), 2755–2762, https://doi.org/10.1097/00001756-199909090-00011.

Saul, A. B., & Cynader, M. S. (1989). Adaptation in single units in visual cortex: The tuning of aftereffects in the spatial domain. *Visual Neuroscience, 2*(6), 593–607, https://doi.org/10.1017/S0952523800003527.

Schiller, P. H., & Malpeli, J. G. (1978). Functional specificity of lateral geniculate nucleus laminae of the rhesus monkey. *Journal of Neurophysiology, 41*(3), 788–797, https://doi.org/10.1152/jn.1978.41.3.788.

Schwartz, S. H., & Loop, M. S. (1982). Evidence for transient luminance and quasi-sustained color mechanisms. *Vision Research, 22*(4), 445–447, https://doi.org/10.1016/0042-6989(82)90192-4.

Sclar, G., Lennie, P., & DePriest, D. D. (1989). Contrast adaptation in striate cortex of macaque. *Vision Research, 29*(7), 747–755, https://doi.org/10.1016/0042-6989(89)90087-4.

Shapley, R., Kaplan, E., & Soodak, R. (1981). Spatial summation and contrast sensitivity of X and Y cells in the lateral geniculate nucleus of the macaque. *Nature, 292*(5823), 543–545, https://doi.org/10.1038/292543a0.

Shibata, K., Yamane, K., Nishimura, Y., Kondo, H., & Otuka, K. (2011). Spatial frequency differentially affects habituation in migraineurs: A steady-state visual-evoked potential study. *Documenta Ophthalmologica, 123*(2), 65–73, https://doi.org/10.1007/s10633-011-9281-2.

Shibata, K., Yamane, K., Otuka, K., & Iwata, M. (2008). Abnormal visual processing in migraine with aura: A study of steady-state visual evoked potentials. *Journal of the Neurological Sciences, 271*(1–2), 119–126, https://doi.org/10.1016/j.jns.2008.04.004.

Siegfried, J. B., Tepas, D. I., Sperling, H. G., & Hiss, R. H. (1965). Evoked brain potential correlates of psychophysical responses: Heterochromatic flicker photometry. *Science, 149*(3681), 321–323, https://doi.org/10.1126/science.149.3681.321.

Skiba, R. M., Duncan, C. S., & Crognale, M. A. (2014). The effects of luminance contribution from large fields to chromatic visual evoked potentials. *Vision Research, 95*, 68–74, https://doi.org/10.1016/j.visres.2013.12.011.

Smithson, H. E. (2005). Sensory, computational and cognitive components of human colour constancy. *Philosophical Transactions of the Royal Society B: Biological Sciences, 360*(1458), 1329–1346, https://doi.org/10.1098/rstb.2005.1633.

Solomon, S. G., Peirce, J. W., Dhruv, N. T., & Lennie, P. (2004). Profound contrast adaptation early in the visual pathway. *Neuron, 42*(1), 155–162, https://doi.org/10.1016/S0896-6273(04)00178-3.

Strasburger, H., Murray, I., & Remky, A. (1993). Sustained and transient mechanisms in the steady-state visual evoked potential: Onset presentation compared to pattern reversal. *Clinical Vision Sciences, 8*, 211–211.

Sun, P., Ueno, K., Waggoner, R. A., Gardner, J. L., Tanaka, K., & Cheng, K. (2007). A temporal frequency–dependent functional architecture in human V1 revealed by high-resolution fMRI. *Nature Neuroscience, 10*(11), 1404–1406, https://doi.org/10.1038/nn1983.

A. Valberg, & B. B. Lee (Eds.). (1991). *From Pigments to Perception: Advances in Understanding Visual Processes*. New York: Springer US, https://doi.org/10.1007/978-1-4615-3718-2.

Vautin, R. G., & Berkley, M. A. (1977). Responses of single cells in cat visual cortex to prolonged stimulus movement: Neural correlates of visual aftereffects. *Journal of Neurophysiology, 40*(5), 1051–1065, https://doi.org/10.1152/jn.1977.40.5.1051.

Wang, J., & Wade, A. R. (2011). Differential attentional modulation of cortical responses to S-cone and luminance stimuli. *Journal of Vision, 11*(6), 1–1, https://doi.org/10.1167/11.6.1.

Webster, M. A., & Mollon, J. D. (1991). Changes in colour appearance following post-receptoral adaptation. *Nature, 349*(6306), 235–238, https://doi.org/10.1038/349235a0.

Webster, M. A., & Mollon, J. D. (1994). The influence of contrast adaptation on color appearance. *Vision Research, 34*(15), 1993–2020, https://doi.org/10.1016/0042-6989(94)90028-0.

Werner, A. (2014). Spatial and temporal aspects of chromatic adaptation and their functional significance for colour constancy. *Vision Research, 104*, 80–89, https://doi.org/10.1016/j.visres.2014.10.005.

Werner, A., Sharpe, L. T., & Zrenner, E. (2000). Asymmetries in the time-course of chromatic adaptation and the significance of contrast. *Vision Research, 40*(9), 1101–1113, https://doi.org/10.1016/S0042-6989(00)00012-2.

Xing, D., Ouni, A., Chen, S., Sahmoud, H., Gordon, J., & Shapley, R. (2015). Brightness-color interactions in human early visual cortex. *Journal of Neuroscience, 35*(5), 2226–2232, https://doi.org/10.1523/JNEUROSCI.3740-14.2015.

Yeh, T., Lee, B. B., & Kremers, J. (1996). The time course of adaptation in macaque retinal ganglion cells. *Vision Research, 36*(7), 913–931, https://doi.org/10.1016/0042-6989(95)00332-0.