Orientation-selective contrast adaptation measured with SSVEP

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Exposure to oriented luminance contrast patterns causes a reduction in visual sensitivity specifically for the adapter orientation. This orientation selectivity is probably the most studied aspect of contrast adaptation, but it has rarely been measured with steady-state visually evoked potentials (SSVEPs), despite their becoming one of the more popular methods of human neuroscience. Here, we measured orientation selective adaptation by presenting a plaid stimulus of which the horizontal and vertical grating reversed contrast at different temporal frequencies, while recording EEG signals from occipital visual areas. In three experiments, we compared SSVEP responses to the plaid before and after adaptation. All experiments showed a significant decrease in SSVEP response at the frequency of the adapter orientation, whereas such an effect was absent for the frequency of the orthogonal orientation. Adaptation also led to robust phase delays, selectively for the SSVEP frequency corresponding to the adapter orientation. These results demonstrate the efficiency of SSVEPs for measuring orientation selective adaptation; the method can measure changes in both amplitude and phase, simultaneously for two orientations.

Introduction

The visual system continuously adjusts its function in response to changes in the environment. These adjustments, referred to as visual adaptation, are sensitive to visual input statistics, potentially maximizing efficiency in the current environment. Whereas neural effects of adaptation occur throughout the visual hierarchy (e.g., Clifford et al., 2007), they have most frequently been studied in early visual cortex, where neurons show selectivity for motion, color and orientation. A classic finding is that prolonged exposure to a strong stimulus reduces neural response and perceptual sensitivity to the adapted feature (e.g., Blakemore, Muncey, & Ridley, 1973; Maffei, Fiorentini, & Bisti, 1973).

Steady-state visually evoked responses (SSVEPs) are an increasingly popular measure of neural activity. SSVEPs are generated by presenting the eyes with temporally periodic input, and appear as peak responses in the fast Fourier transform (FFT) of the EEG signal at the given frequency (and its harmonics; for a comprehensive review on SSVEPs see Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015). Past work using SSVEPs has measured adaptation to motion (e.g., Ales & Norcia, 2009; Hoffmann, Unsöld, & Bach, 2001), temporal frequency (Heinrich & Bach, 2002), and faces (e.g., Rossion & Boremanse, 2011; Rossion, Prieto, Boremanse, Kuefner, & Van Belle, 2012; Webster & MacLeod, 2011).

Here we measure effects of adaptation to luminance contrast. Perceptually, viewing a high contrast oriented pattern, for example a patch of sinusoidal grating, reduces the detectability and apparent contrast of similar patterns. Contrast adaptation is selective; patterns that differ from the adapter show smaller

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effects of adaptation (Graham, 1989). SSVEPs have measured selective effects of contrast adaptation for spatial frequency (Mecacci & Spinelli, 1976; Suter et al., 1991) and temporal frequency (Heinrich & Bach, 2002). However, orientation selectivity, the most studied aspect of contrast adaptation in behavioral (e.g., Blakemore et al., 1973; Blakemore & Nachmias, 1971; Gilinsky, 1968), single unit (e.g., Carandini, Anthony Movshon, & Ferster, 1998; Movshon & Lennie, 1979; Patterson, Wissig, & Kohn, 2013; Sclar, Lennie, & DePriest, 1989), and fMRI work (e.g., Boynton & Finney, 2003; Engel, 2005; Fang, Murray, Kersten, & He, 2005), has only been reported in a single, classic SSVEP study (Campbell & Maffei, 1970).

We measured orientation selective adaptation by presenting frequency-tagged gratings at two orthogonal orientations simultaneously. These gratings formed a plaid pattern, which is similar to stimuli used to determine the effect of one orientation on the other (pattern masking; Burr & Morrone, 1987). In the current study, presenting a plaid is a methodological advance that allows us to measure effects of adaptation on two orientations simultaneously and, hence, to use SSVEPs to study orientation selectivity of contrast adaptation. We expected adaptation to attenuate the SSVEP responses to the component at the same orientation as the adapter more than the other orientation.

Experiment 1

Methods

Participants

Eight volunteers (six males, two females; mean age: 25.2 years, *SD*: 6.1) participated in Experiment 1. All participants had normal or corrected-to-normal visual acuity, and gave written consent to participate under a protocol approved by the University of Minnesota IRB. The study was conducted in accordance with the Declaration of Helsinki.

Materials

Stimuli were generated on a laptop computer and fed into a head-mounted display (HMD; nVis Inc. nVisor SX60 with 37° field of view) running at a 60 Hz refresh rate using the Psychophysics Toolbox (Brainard, 1997). Display gamma curves were measured with a spectrophotometer (PhotoResearch, Inc), and linearized via a color look-up table. EEG signals were recorded using a dry electrode system (Wearable Sensing Inc., DSI-7-Flex) that was integrated into the display device using custom made mounts. The EEG system, recording at 300 samples/s, consisted of six electrodes: one ground electrode positioned frontally, one reference electrode, positioned near Cz, and three other occipitally placed electrodes (for details of positioning, see Supplementary Figure S1). The HMD was not critical for the present work; we used it here in order to facilitate future work on long-term adaptation.

Stimuli

The test stimulus was a circular plaid of 10.5° diameter, created by summing horizontal and vertical sinusoidal gratings of 2 cycles/deg and of 25% and 5% contrast, respectively. These gratings reversed their contrast at different temporal frequencies (6 and 15 Hz, the "frequency tags" for the horizontal and vertical gratings, respectively). The screen refresh rate of 60 Hz effectively limits the numbers of temporal frequencies to choose from, as an integer number of screen refreshes per stimulus is required to optimize the frequency tagging procedure. The 15 Hz stimulus updates once every 4 screen refreshes (60/15) whereas the 6 Hz stimulus updates once every 7 frames (60/8.57). Other possible frequencies could be problematic to use for different reasons. Lower frequencies have less cycles/trial, which can lead to low signal-to-noise, especially with the short trial durations that we are restricted to. 15 Hz is the 2nd harmonic of 7.5 Hz (60/8), making the two frequencies dependent of one another and 10 Hz (60/6) is more or less in the center of the alpha band where generally a strong resting state response is recorded that could suppress or disturb stimulus-driven activity. The adapting stimulus was a full contrast, circular, vertical, sinusoidal grating patch of 2 cycles/deg, reversing its contrast at 15 Hz.

Task and procedure

The experiment consisted of a Baseline session followed by an Adaptation session, each of which was comprised of six testing blocks. A Baseline block started with 30 s of passively viewing a mean gray screen with a central fixation cross. During each 1.5 s trial, a test plaid was presented, with its components reversing contrast as described above (Figure 1). Participants were instructed to attend the central fixation cross and count the number of times it changed color from black to white, which occurred either two, three, or four times per trial. Participants indicated with a key press how many color changes they perceived. Each trial was followed by 6.4 s of gray screen before the next trial was presented. A block consisted of 15 trials, after which participants received feedback on their task performance during a brief rest break. When ready to continue, they pressed a key to start the next block.

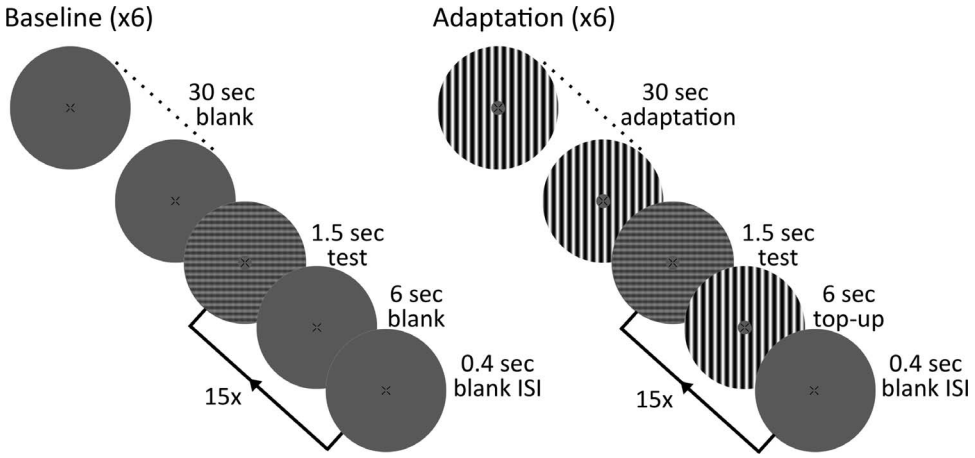

Figure 1. Trial sequence for Baseline and Adaptation blocks. Each block began with 30 s of mean field presentation (Baseline) or vertical contrast reversal (Adaptation), followed by the trial sequence, which consisted of a 1.5 s trial, a 6 s top-up or blank interval and 0.4 s intertrial interval. The trial sequence was repeated 15 times per block.

Adaptation blocks were similar to Baseline blocks with the following differences: Each block started with the adapting grating contrast reversing at 100% contrast for 30 s. Test trials were followed by 6 s of "top-up" adaptation, consisting of the adapting grating contrast reversing at full contrast. This was followed by a 0.4 s mean field presentation, and then the next test trial (see Figure 1).

Analyses

EEG analyses were performed in MATLAB using the EEGLAB toolbox (Delorme & Makeig, 2004) and custom MATLAB code. The EEG signal was band-pass filtered with a low cut-off frequency of 1 Hz and a high cut-off frequency of 45 Hz. Trials where an absolute voltage difference exceeded 50 μV between two neighboring sampling points and trials with a linear trend exceeding ±50 μV/630 samples were rejected as containing artifacts. On average 8.7 % of trials per observer were removed from the analysis. Fast Fourier Transformations (FFT) were computed on the epoch 400–1,500 ms from stimulus onset to avoid onset transients and allow analyses of frequency responses. FFTs were computed after applying a Hanning window to the first and last 67 ms (equal to one 15 Hz cycle) of each epoch. Analyses were performed on the mean FFTs of the three occipital electrodes, which were computed for each condition and participant, separately.

Results

Responses for the two component orientations in the test plaid were visible in the SSVEP amplitude spectrum (computed with an FFT) as peaks at the two temporal frequencies with which the components were tagged (Figure 2). To measure effects of adaptation, these SSVEP responses were compared between the Adaptation condition, in which presentation of the test plaids was preceded by presentation of high contrast "adapter" gratings, and the Baseline condition, where a gray, mean field preceded test plaids (Figure 1).

Contrast adaptation generally leads to a reduction in visual sensitivity. Therefore we predicted that the SSVEP signal generated by the test component at the orientation of the adapter (vertical) would decrease in magnitude after adaptation. This signal should arise at the temporal frequency of the adapter orientation's test component (15 Hz) and we term it "response to the adapter orientation." We term the SSVEP signal at the other tagged frequency (6 Hz, horizontal), "response to the orthogonal orientation," and we predicted that this response should be relatively unaffected by adaptation.

Adaptation produced selective effects, as indicated by a 2 × 2 ANOVA of frequency (15 vs. 6 Hz) × adaptation (Baseline vs. Adaptation). As predicted, this ANOVA revealed a statistically significant interaction between Frequency and Adaptation, $F(1, 7) = 7.61$, $p = 0.028$, indicating that adaptation reduces the FFT response to the adapter orientation relative to the orthogonal orientation. The main effects of frequency, $F(1, 7) = 5.22$, $p = 0.056$, and adaptation, $F(1, 7) = 2.44$, $p = 0.162$, were both not statistically significant.

Posthoc pairwise comparisons showed that the amplitude of the SSVEP response to the adapter orientation indeed decreased after adaptation, $t(7) = 3.23$, $p = 0.015$. Responses to the orthogonal orientation showed a small unreliable increase in amplitude after adaptation, $t(7) = 1.43$, $p = 0.196$.

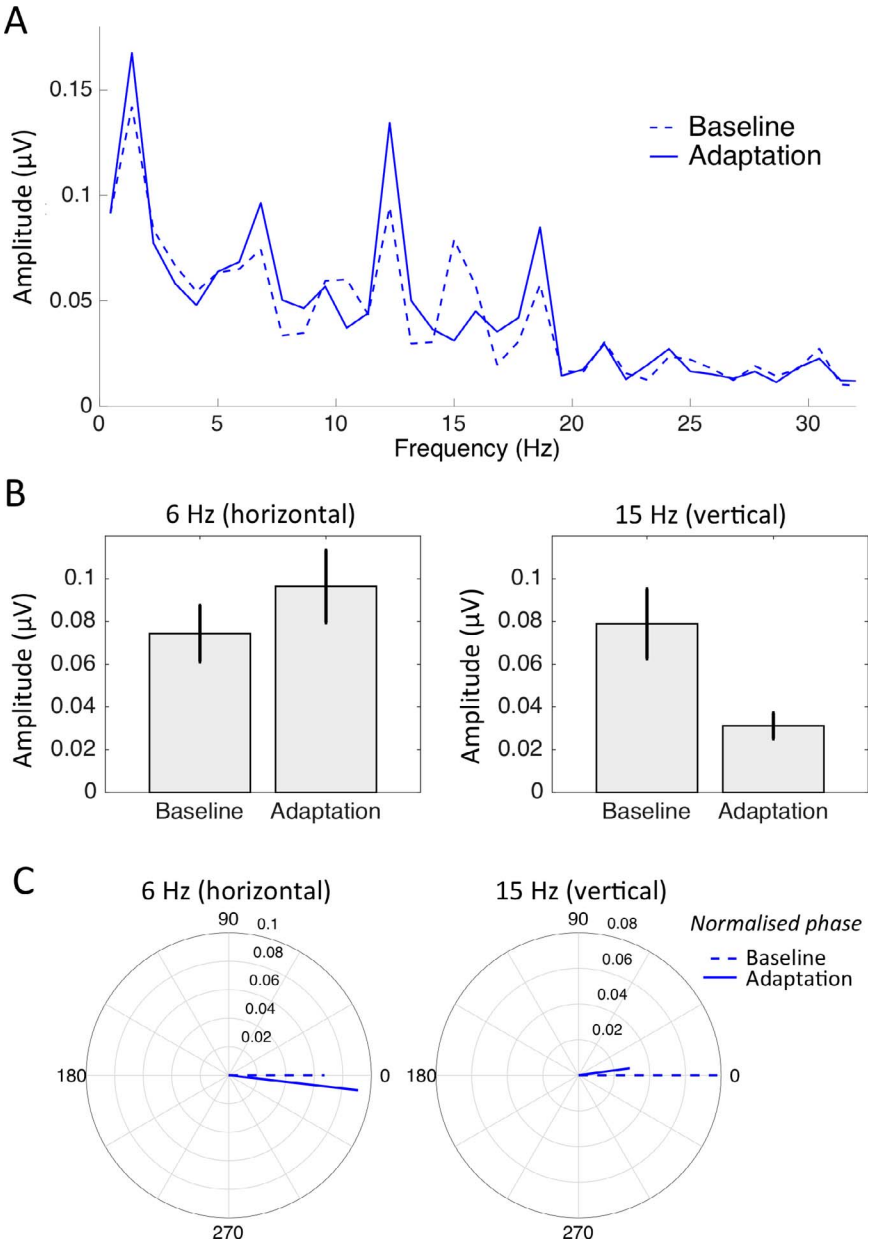

Figure 2. Experiment 1 Results: SSVEP signal amplitudes as a function of frequency. Panel A shows the frequency spectrum averaged across participants, for both the Baseline and the Adaptation conditions, with clear peak responses at the tagged frequencies (6 and 15 Hz), as well at the harmonics of 6 Hz (12 and 18 Hz). Panel B zooms in on the mean SSVEP response amplitudes for each condition, averaged across participants. Error bars represent the *SEM* computed across participants. Panel C shows the mean relative phase of the Adaptation condition, computed as difference from the phase in the Baseline condition.

The reduced SSVEP response to the vertical grating was consistent with the subjective experience during the experiment (only recorded for a few subjects): The difference in perceived contrast of the vertical and horizontal gratings was much larger in Adaptation than in Baseline trials, with the vertical grating appearing to lose contrast following Adaptation. The FFT amplitudes of all participants are plotted in Supplementary Figure S2.

We also examined the phases of the SSVEP responses at the different frequencies of interest, but no reliable differences between Baseline and Adaptation were found, neither at 6 Hz, $t(7) = 0.255$, $p = 0.81$, nor at 15 Hz, $t(7) = 0.\ 271$, $p = 0.79$. The FFT phases of all participants are plotted in Supplementary Figure S3.

Additionally, performance on the central fixation task during the EEG recordings did not differ between

Baseline (mean: 63% correct; *SD*: 7%) and Adaptation (mean: 65%; *SD*: 10%).

Discussion

The significant decrease in SSVEP amplitude for the adapter orientation shows that SSVEPs can provide a reliable measure of neural effects of contrast adaptation. The lack of such a decrease in SSVEP amplitude for the orthogonal orientation shows that adaptation was selective for the adapter orientation. This conclusion is supported by the significant decrease in relative response to vertical compared to horizontal after adaptation to vertical. In addition, the trend towards an increase in response to horizontal is consistent with models of divisive normalization (e.g., Heeger, 1992) and cross-orientation suppression (e.g., Priebe & Ferster, 2006): When adaptation reduces the gain and hence the effective contrast of one component of a plaid, response to the orthogonal component should increase.

Adaptation had no systematic effect on the phase of the SSVEP signal; this is unexpected since lower amplitude responses generated in visual cortex are generally delayed in time relative to higher amplitude ones (e.g., Burr & Morrone, 1987). The lack of a phase effect was likely due to adaptation (almost) completely suppressing the signal of the vertical test grating, as can be seen in the 15 Hz response in Figure 2A. The postadaptation response at this frequency is close to the floor response generated by noise, making systematic patterns in SSVEP phase difficult to measure. The lack of signal at 15 Hz after adaptation may have been due to the short trial length, which (a) did not allow time for the suppressed vertical response to recover above noise level, and (b) provided too little resolution in the frequency domain for the signal to be cleanly extracted from the SSVEP response.

Experiment 2

A second experiment was conducted to test the replicability of our findings, and to optimize the method's sensitivity to adaptation effects. The experimental paradigm was modified in several ways: The trial length was increased and also the contrast reversal frequency of the orthogonal, horizontal test grating was increased, with both changes aimed at increasing the signal of SSVEP amplitude and phase.

In an attempt to increase signal further, we also added an attention manipulation to the experiment. Whereas in Experiment 1 participants performed a fixation task, here we added a condition where participants performed a task on the test plaid, requiring them to attend to it. In Experiment 1 we were interested in measuring a basic effect of contrast adaptation. The fixation task helped control the foveal presentation of the stimuli. But, because participants attended the central fixation cross, the contrast-reversing test gratings were unattended. As previous research has shown that attention can boost SSVEP response, it could potentially increase sensitivity for measuring adaptation effects (for reviews on the effects of attention on SSVEPs see Andersen, Müller, & Hillyard, 2012; Norcia et al., 2015).

Methods

Participants

Eight volunteers (six males, two females; mean age: 26.5 years, *SD*: 5.5) participated in Experiment 2; five of them also participated in Experiment 1. All participants had normal or corrected-to-normal visual acuity, and gave written consent to participate according to a protocol approved by the University of Minnesota IRB.

Stimuli

Test plaids were as in Experiment 1, with the same size (except as noted below), spatial frequency, and contrast levels. However, the component gratings reversed contrast at 8.57 Hz and 15 Hz, for the horizontal and vertical grating, respectively. In addition, trials were increased in duration to 2.5 s.

We also added an attention task, in which the plaid area gradually and linearly increased in size from a perfect circle into an egg-shape, randomly in one out of four possible directions (up, left, down, or right). Half of the plaid envelope remained circular, while the other half was replaced by an oval with a matching minor axis, and gradually increasing major axis (Figure 3). By the end of a test trial, the major axis of the oval component increased by 1° of visual angle in the specified direction. During the size change, all other stimulus properties of the plaid (i.e., spatial frequency, contrast, and flickering frequencies) remained constant.

Task and procedure

The experiment consisted of two sessions that were run on separate days, with a protocol very similar to that of Experiment 1. Each session consisted of two conditions, Baseline followed by Adaptation, with each consisting of six blocks of 15 trials, as in Experiment 1 (Figure 1). In each block, fifteen 2.5 s

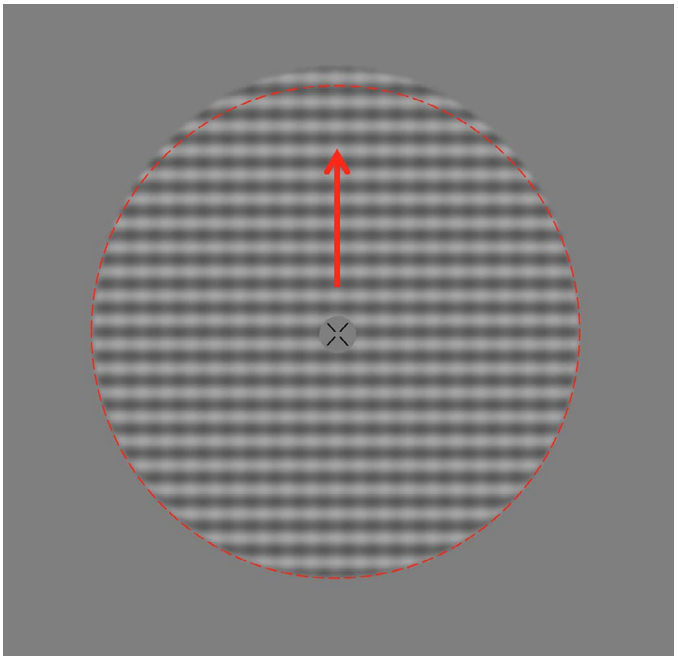

Figure 3. Example of the attentional manipulation in Experiment 2. The red dashed circle indicates the original circular shape of the plaid stimulus. In this example the plaid increased in size in the upward direction. This size increase occurred linearly from the beginning until the end of each trial. The red circle and arrow are presented for illustrational purpose and were not shown during the actual experiment.

trials alternated with 6 s top-up periods. As in Experiment 1, the block was preceded by an initial 30 s of passive viewing of a mean gray screen in the Baseline condition, and by 30 s of a full contrast vertical grating contrast reversing at 15 Hz in the Adaptation condition. The Baseline condition always preceded the Adaptation condition.

Participants performed different tasks during the two sessions. During one session (the Inattention condition) they performed the same task as in Experiment 1, counting the number of times the central fixation cross briefly changed color from dark to bright. In the other session (the Attention condition) the participants' task was to discriminate in which direction (up, right, down, or left) the plaid stimulus increased in size; response was again by a key press. Note that the tasks were performed during test presentations; no task was performed during the gray screen presentations in the Baseline blocks or during adapter presentations in the Adaptation blocks. In between blocks, participants received feedback on their performance and were given a short break. They pressed the spacebar to start the next block. For the first two participants, performance on this task was not recorded; hence, analyses were done on the performance of the final six participants.

Analyses

EEG preprocessing and analyses were performed as in Experiment 1. An average 14.2 % of trials per participant were removed from the analysis by the artifact rejection method. Because of the increased trial length, FFTs were now computed on the epoch 400–2,517 ms from stimulus onset. The resulting epoch length (2.117 s) allowed for an integer number of cycles for both tagging frequencies. As in Experiment 1, FFTs were computed after applying a Hanning window of 67 ms, equal to one 15 Hz cycle. To control for differences between participants in overall response delay, we normalized SSVEP phases by computing a phase shift by subtracting and unwrapping the difference between the phases of the FFT for the Inattention Baseline condition and each other condition. This normalization was done separately for each participant and frequency.

Results

As in Experiment 1, analysis focused on SSVEPs at the tagged frequencies of the horizontally and vertically orientated components. Responses to both components were clearly visible in the amplitude spectrum of the SSVEP (Figure 4A). We compared these responses between the Baseline and Adaptation conditions and the Inattention and Attention conditions.

To test for overall patterns of effects across conditions, we performed an initial $2 \times 2 \times 2$ ANOVA (frequency $\times$ adaptation $\times$ attention). There was no reliable three-way interaction between the three factors, $F(1, 7) = 2.09$, $p = 0.191$, suggesting that attention did not alter effects of orientation selective adaptation. To test for orientation selective adaptation, we examined the interaction between frequency and adaptation, which was statistically marginally significant, $F(1, 7) = 4.45$, $p = 0.073$, reflecting a decrease in FFT response after adaptation for the frequency of the adapter orientation, relative to the frequency of the orthogonal orientation. The marginal reliability of this effect is probably due to the relatively large variance in the response to the unadapted orientation.

The interaction between attention and frequency was also reliable, $F(1, 7) = 12.31$, $p = 0.01$, reflecting a lower response for the lower contrast vertical grating when the pattern was attended, relative to the response for the higher contrast horizontal grating. This result suggests that contrast masking, or normalization, may be greater under conditions of attention. In addition, the ANOVA revealed a significant main effect of frequency, $F(1, 7) = 18.36$, $p = 0.004$, whereas adaptation, $F(1, 7) = 1.93$, $p = 0.207$, and attention, $F(1, 7) = 3.29$, $p = 0.113$, did not show reliable main effects.

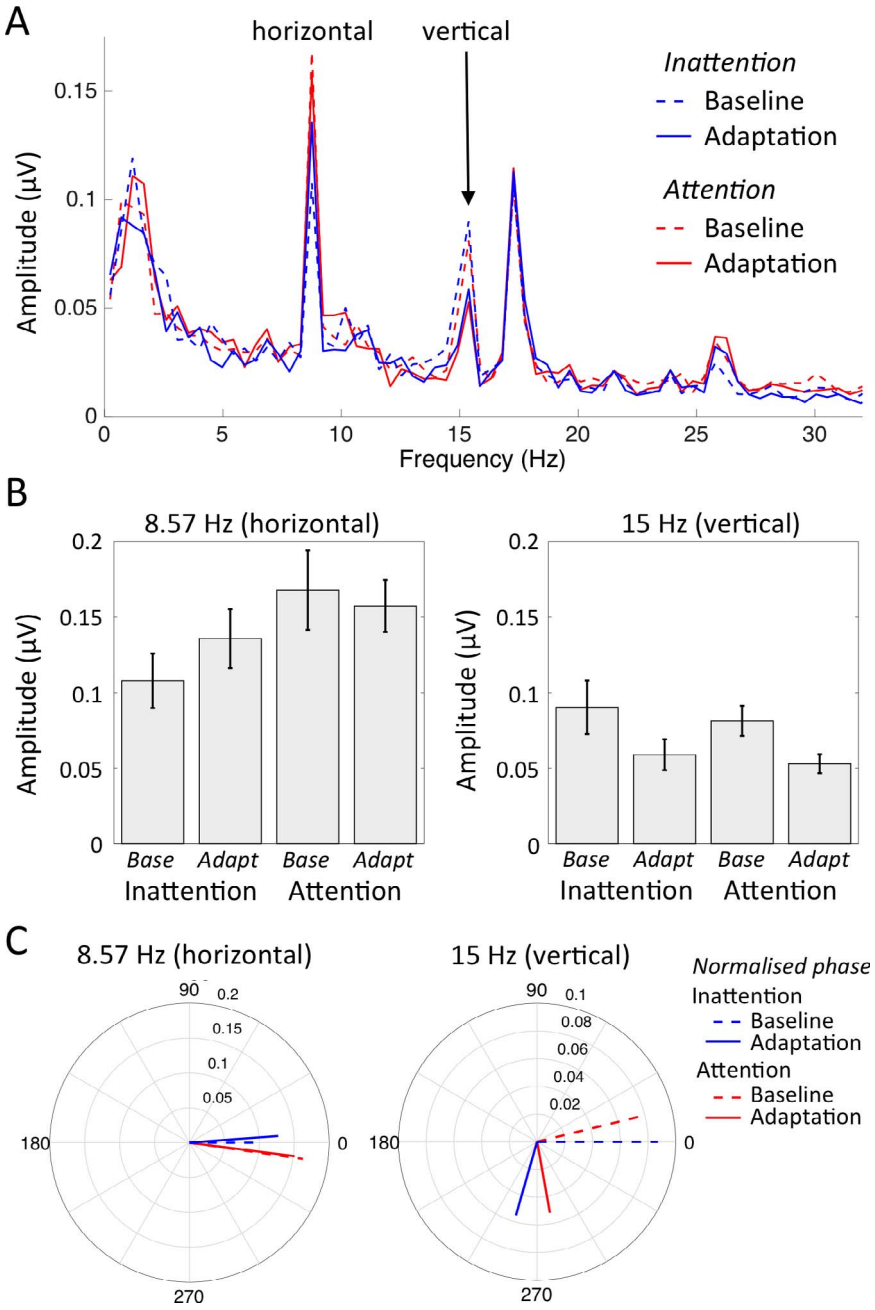

Figure 4. Experiment 2 Results: SSVEP signals as a function of frequency. Panel A shows the FFT amplitude spectrum averaged across participants, for Baseline and Adaptation condition blocks in the Attention and Inattention conditions. Clear peak responses can be observed at the tagged frequencies (8.57 Hz and 15 Hz), as well as at the second harmonic of 8.57 Hz (17.1 Hz). Panel B displays mean SSVEP amplitudes for each tagged frequency, averaged across participants (Note that the mean amplitudes presented here are identical to the peak responses at these frequencies that can be observed in panel A). Error bars represent the *SEM*. Panel C shows the mean relative phase of each condition, computed as difference from the phase in the Inattention Baseline condition. Adaptation delayed the phase of the response; hence, the inferred direction of phase shift at 15 Hz in panel C is counterclockwise.

The FFT amplitudes of all participants are plotted in Supplementary Figure S4.

A 2×2 ANOVA on the 15 Hz phase results showed a reliable main effect of adaptation, $F(1, 7) = 21.34$, $p = 0.002$, and a marginally significant effect of attention, $F(1, 7) = 5.46$, $p = 0.052$, and no reliable interaction between adaptation and attention, $F(1, 7) = 0.57$, $p = 0.47$. A similar 2×2 ANOVA on the 8.57 Hz phase results did not show reliable main effects, neither for adaptation, $F(1, 7) = 0.02$, $p = 0.89$, nor for attention,

$F(1, 7) = 2.77$, $p = 0.140$. Also the interaction between adaptation and attention was not reliable, $F(1, 7) = 0.04$, $p = 0.85$. We next performed posthoc comparisons to focus in on the orientation selective adaptation and attention effects.

Adaptation

SSVEP amplitudes: As expected for orientation selective adaptation, the amplitude of response at the adapter orientation (15 Hz) decreased after Adaptation compared to Baseline (Figure 4). This difference was significant in the Inattention condition, $t(7) = 2.9$, $p = 0.023$, as well as in the Attention condition, $t(7) = 4.58$, $p = 0.003$. No reliable effects of adaptation were found at the orthogonal orientation (8.57 Hz), neither for the Inattention condition, $t(7) = 1.85$, $p = 0.107$, nor for the Attention condition, $t(7) = 0.42$, $p = 0.687$.

SSVEP phases: Adaptation delayed the response for the adapter orientation. Figure 4C shows the normalized response phases for both orientations, averaged across participants. The length of the vectors corresponds to the SSVEP amplitude for that response. For the adapter orientation there were robust phase shifts in the Adaptation condition, as compared to Baseline, corresponding to a temporal delay of 19.6 ms in the Inattention task, $t(7) = 3.745$, $p = 0.007$, 95% CI [7.2, 32.0], and 17.3 ms delay in the Attention task, $t(7) = 5.728$, $p = 0.0007$, 95% CI [10.2, 24.5]. No systematic effects of adaptation were found for the orthogonal orientation. The FFT phases of all participants are plotted in Supplementary Figure S5.

Attention

SSVEP amplitudes: To examine effects of attention, we tested whether SSVEP amplitudes were greater, and phases less delayed, in the Attention condition as compared to the Inattention condition. No significant difference in SSVEP response amplitude was found for the adapter orientation, neither for the Baseline, $t(7) = 0.748$, $p = 0.48$, nor for the Adaptation condition, $t(7) = 0.640$, $p = 0.54$. For the orthogonal orientation, pairwise comparisons indicated that attention reliably increased amplitudes for the Baseline conditions, $t(7) = 2.763$, $p = 0.03$, but not for the Adaptation conditions, $t(7) = 1.33$, $p = 0.23$.

SSVEP phases: For the adapter frequency, no reliable difference in SSVEP phase was found as a function of attention for the Baseline, $t(7) = 1.156$, $p = 0.28$, whereas a marginally significant effect difference was found for the Adaptation conditions, $t(7) = 2.232$, $p = 0.06$. For the frequency of the orthogonal orientation, no reliable phase differences were found for Baseline, $t(7) = 0.603$, $p = 0.57$, and Adaptation, $t(7) = 1.667$, $p = 0.14$.

Behavioral performance

As in Experiment 1, performance on the central fixation task (in the Inattention condition) was unaffected by adaptation, being roughly equal for Baseline (mean: 85%; *SD*: 3%) and Adaptation blocks (mean: 84%; *SD*: 10%). However, adaptation did affect performance in the Attention condition, where participants had to detect a shape change of the plaid pattern: Whereas in Baseline blocks performance was similar for detecting a size increase in the vertical (mean: 65%; *SD*: 12%) and horizontal directions (mean: 67%; $SD = 9\%$), after adaptation participants were much worse in detecting vertical changes (mean: 57%; *SD*: 12%) than in detecting horizontal changes (mean: 70%; *SD*: 12%). This pattern suggests that participants used the vertical grating, which was affected by adaptation, to detect vertical changes, and the horizontal grating to detect changes in the horizontal direction. In a 2×2 ANOVA (orientation $\times$ adaptation) this effect of adaptation on task performance was evident as a significant interaction, $F(1, 5) = 13.65$, $p = 0.01$. There were no significant main effects of orientation, $F(1, 5) = 1.59$, $p = 0.26$, and of adaptation, $F(1, 5) = 0.54$, $p = 0.49$. These behavioral results are consistent with the SSVEP results, providing additional support for a selective reduction in sensitivity to vertical following adaptation.

Discussion

Contrast adaptation again led to decreased SSVEP amplitude for the adapter orientation, relative to the amplitude change for the orthogonal orientation. The results of Experiment 2 also showed a relative phase delay after adaptation. This finding is consistent with reduced neural sensitivity after adaptation, as previous research has shown that SSVEP phase is delayed for weaker responses, as generated by manipulating stimulus contrast (e.g., Burr & Morrone, 1987).

Attention has previously been shown to boost SSVEP amplitude (e.g., Di Russo, Spinelli, & Morrone, 2001) and advance its phase (e.g., Di Russo & Spinelli, 1999). Based on these findings, we expected SSVEP amplitude to increase and SSVEP phase to advance when participants were attending the stimulus compared to when they were not. These predictions were only partially confirmed by our data; for the orthogonal orientation we found an overall increase in SSVEP amplitude in the Attention condition, but no changes in SSVEP phase. We also found no effect for the adapter orientation in either condition.

We can speculate why attention showed a differential effect on the two component gratings. The attention task required participants to analyze the exact shape of the plaid patch. It seems plausible that it caused participants to selectively attend the unadapted grating,

since this component had higher contrast, and so provided the strongest signal for detecting the plaid's boundaries.

Experiment 3

In the previous two experiments the adapting vertical grating always was always contrast reversing at the same temporal frequency as the test vertical grating. We conducted a third experiment to test whether the adaptation effects of the previous experiments could be (partially) due to temporal frequency selective adaptation, or whether they indeed reflected orientation selective adaptation.

Methods

Participants

Eight volunteers (six males, two females; mean age: 30.7 years, *SD*: 10.3) participated in Experiment 3; Four of them also participated in Experiment 1, and five in Experiment 2. All participants had normal or corrected-to-normal visual acuity, and gave written consent to participate according to a protocol approved by the University of Minnesota IRB.

Stimuli

Test plaids were as in Experiment 1, with the same size, spatial frequency and contrasts. The component gratings reversed contrast at 8.57 Hz and 15 Hz, for the horizontal and vertical grating, respectively, as in Experiment 2. Trial duration was 2.5 s, also similar to that of Experiment 2. Critically, whereas the vertical full-contrast adapting grating in the previous two experiments contrast reversed at the frequency of the vertical test grating (15 Hz), it now contrast reversed at the frequency of the horizontal test grating (8.57 Hz).

Task and procedure

The experiment again consisted of a Baseline session followed by an Adaptation session, each of which was comprised of 90 trials. The Baseline session started with 30 s of passively viewing a mean gray screen with a central fixation cross. Participants performed the same fixation task as in Experiment 1, counting the number of times the fixation cross-flashed during each trial. Each trial was followed by 6.4 s of gray screen before the next trial was presented.

The Adaptation session was similar to the Baseline session with the following differences: The session started with the adapting grating contrast reversing at 100% contrast at 8.57 Hz for 30 s. Test trials (containing 15 Hz vertical and 8.57 Hz horizontal components) were followed by 6 s of "top-up" adaptation, consisting of the adapting grating contrast reversing at full contrast. This was followed by a 0.4 s mean field presentation, and then the next test trial. Contrary to previous experiments, in this experiment there were no breaks within each session.

Analyses

EEG preprocessing and analyses were performed as in Experiment 1 and 2. An average 16.7 % of trials per participant were removed from the analysis by the artifact rejection method. As in Experiment 2, FFTs were computed on the epoch 400–2,517 ms from stimulus onset. As in the previous experiments, FFTs were computed after applying a Hanning window to the first and last 67 ms (equal to one 15 Hz cycle) of each epoch SSVEP phases were normalized in a similar way as in the previous experiments.

Results

As in the previous experiments, responses for the two component orientations in the test plaid were visible in the SSVEP amplitude spectrum as peaks at the two temporal frequencies with which the components were tagged (Figure 5). To measure effects of adaptation, SSVEP response amplitudes were compared between the Baseline and Adaptation condition.

We again found orientation selective effects of adaptation. A 2×2 ANOVA of frequency (15 vs. 8.57 Hz) $\times$ adaptation (Baseline vs. Adaptation) revealed a reliable interaction between Frequency and Adaptation, $F(1, 7) = 16.54$, $p = 0.005$, indicating that adaptation reduced the response to the adapter orientation relative to the orthogonal orientation. There was also a reliable main effect of frequency, $F(1, 7) = 10.19$, $p = 0.015$, and the main effect of adaptation, $F(1, 7) = 2.44$, $p = 0.162$, was not statistically significant. The response amplitudes of all participants are plotted in Supplementary Figure S6.

Posthoc pairwise comparisons show that the amplitude of the SSVEP response to the adapter orientation indeed decreased after adaptation, $t(7) = 3.34$, $p = 0.012$. Responses to the orthogonal orientation showed a marginally significant increase in amplitude after adaptation, $t(7) = 2.18$, $p = 0.066$.

Analysis of the SSVEP phases showed no reliable differences between Baseline and Adaptation at 8.57 Hz, $t(7) = 0.667$, $p = 0.53$, but, as in Experiment 2, at 15 Hz a reliable phase delay was observed after adaptation, $t(7) = 4.703$, $p = 0.002$. The FFT phases of all participants are plotted in Supplementary Figure S7.

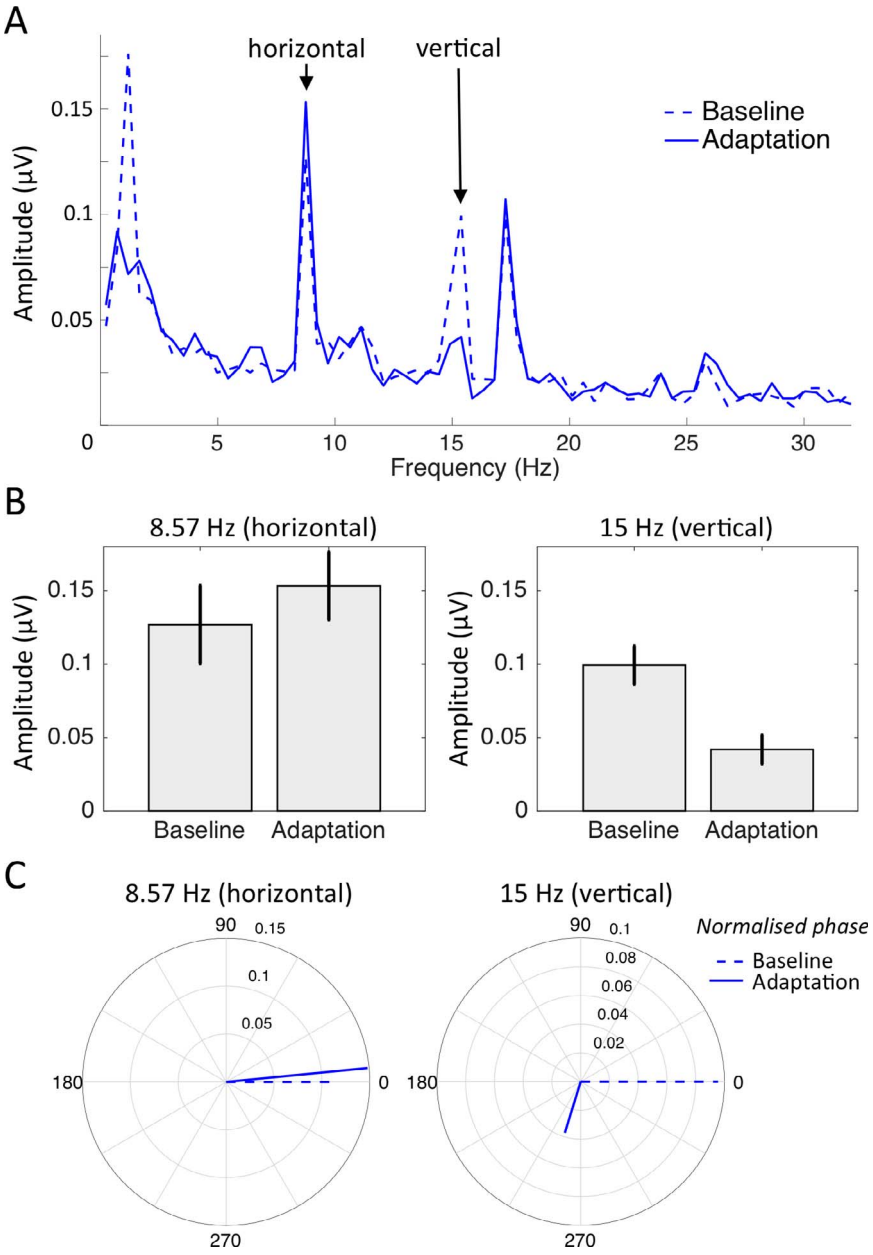

Figure 5. Experiment 3 Results: SSVEP signal amplitudes and phases as a function of frequency. Panel A shows the frequency spectrum averaged across participants, for both the Baseline and the Adaptation conditions, with clear peak responses at the tagged frequencies (8.57 and 15 Hz). Panel B zooms in on the mean SSVEP response amplitudes for each condition, averaged across participants. Error bars represent the *SEM* computed across participants. Panel C shows the mean relative phase of the Adaptation condition, computed as difference from the phase in the Baseline condition.

Discussion

Experiments 1 and 2 could not distinguish between orientation selective adaptation and frequency selective adaptation, because, the temporal frequency (15 Hz) and orientation (vertical) of the adapter were both identical to that of the vertical test grating. In Experiment 3, the temporal frequency of the vertical adapter was changed to the temporal frequency of the *horizontal* test grating (8.57 Hz). The results showed almost identical effects of contrast adaptation on SSVEP amplitudes as in the previous experiments. This pattern strongly supports the conclusion that the observed effects of adaptation are indeed orientation selective. Because the effects were so similar across experiments, regardless of the temporal frequency of the adapter (compare Figures 2B and 5B), our experiment provides little to no evidence for temporal frequency selective adaptation.

General discussion

Our results provide convincing SSVEP evidence of orientation selectivity in contrast adaptation. In three experiments, SSVEP responses to horizontal and vertical components' contrast reversal were measured with and without adaptation to vertical. All experiments showed that contrast adaptation reduces SSVEP amplitude at the frequency of the adapted orientation, while not significantly affecting the orthogonal orientation. In addition, this study is the first to show robust orientation selective effects of contrast adaptation on SSVEP phase (in Experiment 2 and 3).

A number of previous SSVEP studies of contrast adaptation focused on changes in responses to the adapted feature. This has led to inconsistent findings. Heinrich and Bach (2001a), for example, presented checkerboard patterns that contrast reversed at 8.3 Hz over extended durations Their results showed a continuous decline in occipital SSVEP amplitude over time, indicating a (partial) desensitization to the adapted pattern due to adaptation. Other studies showed the opposite pattern, however (Bach, Greenlee, & Buhler, 1988; Heinrich & Bach, 2001b), with the former finding this pattern to be orientation-selective. Heinrich and Bach (2002) resolved inconsistencies in this literature by demonstrating that contrast adaptation produced response decreases when the adapter and the test stimulus shared the same temporal frequency, which suggests that the adapting mechanisms are tuned in the temporal domain. In addition, Rebaï and Bonnet (1989), found that contrast adaptation initially leads to a strong decrease in contrast sensitivity, compared to a preadaptation baseline, for a target stimulus with the same orientation and spatial frequency as the adapter, while sensitivity subsequently gradually increased again over time.

One previous VEP study measured orientation-selective adaptation effects, by varying the orientation of an adapting grating (Campbell & Maffei, 1970). VEP amplitude was suppressed when the adapter and test gratings differed less than 20° with suppression being strongest when both orientations were the same. A more recent study, however, alternated stimulation between high and low contrast every 8 s, and found no support for orientation selectivity of contrast adaptation: When contrast changed, similar SSVEP amplitude changes occurred when grating orientation was changed by 90° compared to when orientation remained the same (Xin, Seiple, Holopigian, & Kupersmith, 1994).

Feature-selective effects of adaptation have also been shown with SSVEPs for motion (Ales & Norcia, 2009) and spatial frequency (Mecacci & Spinelli, 1976; Suter et al., 1991). In Suter et al., for example, adaptation to an oriented grating led to decreased SSVEP amplitude in response to spatial frequencies near the adapted spatial frequency, while a small amplitude enhancement was found 1.0–2.0 octaves below the adapting spatial frequency.

Weaker neural responses in early visual cortex generally begin later in time (e.g., Albrecht, 1995). Accordingly, previous SSVEP studies have shown phase shifts as a function of stimulus contrast (e.g., Burr & Morrone, 1987), as well as following contrast adaptation (Peachey, Demarco, Ubilluz, & Yee, 1994). In the latter study, however, no consistent effects of contrast adaptation on SSVEP amplitude were found. In Experiment 2, the SSVEP phase delays due to adaptation appear to be at least as consistent across participants as the reduction in amplitude. Phase should therefore be considered a valuable metric for measuring adaptation's effects. In Experiment 1, the short trial durations likely limited our ability to measure similarly reliable SSVEP phase responses.

Neither SSVEP phase nor amplitude showed effects of attention for the adapter orientation. This could be due to our methods not being sensitive enough to pick up such effects, or other factors that compromised the magnitude of our attention manipulation. As mentioned above, participants may have selectively attended the higher contrast grating, which corresponded to the orthogonal orientation.

Conclusions

Our results show that orientation-selectivity, a key feature of contrast adaptation, can be measured with a single test stimulus that presents both adapter and orthogonal orientations simultaneously. Effects of adaptation were visible in both the amplitude and the phase of the SSVEPs, but only at the adapter orientation. Future work should be able to use this methodology to measure orientation-selective effects for many different adaptation paradigms.

Keywords: contrast sensitivity, visual adaptation, SSVEP, EEG, visual cortex

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