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Adaptation effects on cortical activities for AM flickering lights

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For a sinusoidal flickering light amplitude modulated (AM) sinusoidally, flicker at a frequency corresponding to a periodicity of a temporal envelope of flickering light is detected although there is no frequency component at the flicker frequency. However, the mechanisms underlying the perception of the envelope are still unclear. Then, to consider where the processing of envelope extraction is carried out in the visual system, we investigated the effects of adaptation to temporal frequencies on the visual sensitivity and cortical activities for the envelope. It is known that there are two temporal channels with a lower and a higher peak frequency, respectively. Therefore, in this study, sinusoidal flickering lights with a low (2 Hz) and a high (16 Hz) temporal frequency were used as adapting stimuli. Following adaptation, the sinusoidal flickering lights of 2 and 16 Hz and an AM flickering light with a modulation frequency of 2 Hz and a carrier frequency of 16 Hz were presented as test stimuli. The results showed that the sensitivity and magnetoencephalographic (MEG) responses to the sinusoidal flicker were reduced more when the adapting and test stimuli had same frequency components than different ones. On the other hand, although the AM flickering light had a frequency component at the carrier frequency but not at the modulation frequency (envelope periodicity), the sensitivity and MEG responses to the envelope periodicity of AM flickering light were reduced more after adapting to the modulation frequency rather than the carrier frequency. Based on the present results, we discussed where the envelope component arises in the visual system.

Key words: Vision, Temporal processing, Flicker, AM, Adaptation

1. INTRODUCTION

Flickering lights generated by the addition of two sinusoidal flickering lights with different temporal frequencies produce flicker at the difference frequency. This phenomenon is referred to as temporal beat, and some studies have used such a flicker for investigating temporal visual processing [1-3]. In addition, flicker at a modulation frequency is perceived for amplitude modulated (AM) flickering light with a noise carrier [4] and sinusoidal carriers [5, 6]. Flicker detection for these flickering lights indicates that flicker at a frequency corresponding to the periodicity of the temporal envelope of luminance oscillation is detected, even though no frequency component is present at the flicker frequency.

However, the mechanism underlying the detection of flicker at the envelope periodicity is still unclear. Studies measured electroretinograms (ERG) for temporal beats suggested that the temporal beat were detected on the based on a distortion product due to a luminance non-linearity generated at an early stage (within retina) of visual processing [2, 3]. Moreover, a study recorded flicker ERG suggested that the nonlinearity is located before the convergence of signals from the different cone classes [7]. However, psychophysical measurements of masking and adaptation effects of the spatial and temporal beats suggested that beat detection in the spatial and temporal domains is not based purely on distortion products produced by a peripheral luminance non-linearity [1]. They also implied that the detection of temporal beats could rely on a cortical mechanism because it is shown that temporal beats are produced under dichoptic stimulation [8].

It is known that the contrast threshold for a high-contrast sinusoidal grating is elevated at the adapting and neighboring spatial frequency. However, the threshold elevation is small at the other nearby spatial frequencies [9]. This result indicates that, in the visual system, there are a relatively large number of channels which tuned to narrow spatial frequency ranges. On the other hand, for the temporal frequency, threshold elevation is observed at a broad frequency range [10, 11]. After adapting to a low temporal frequency, the detection threshold elevates broadly over the low frequency range. Also, after adapting to a high temporal frequency, the threshold elevation is observed broadly over the high frequency range. This result is probably explained by the finding that there are only two temporal channels in the visual system: one being low-pass with lower peak frequency and the other being band-pass with higher peak frequency [10, 12-14]

The purpose of this study was to discuss where the envelope component arises in the visual system by investigating the effects of two temporal channels on the envelope detection. An AM flickering light with a low modulation frequency (envelope periodicity) and a high carrier frequency was used as the test stimuli. The visual sensitivity and magnetoencephalographic (MEG) responses to the envelope periodicity of the AM flickering light were measured when the sensitivity of the temporal channel tuned for low or high frequency was reduced by adapting to low or high frequency, respectively. Under the same adaptation condition, the sensitivity and MEG responses to sinusoidal flickering lights were also measured to reconfirm whether the temporal channels were affected by the adaptation stimuli.

2. DETECTION THRESHOLD

2.1 Adaptation effects for sinusoidal flicker

We used a steady light and sinusoidal flickering lights of 2 and 16 Hz as adaptation stimuli. The test stimuli were the sinusoidal flickering lights of 2 and 16 Hz. The luminance wave forms and their frequency spectra are shown in Fig. 1. After presenting the adaptation stimulus, the test stimulus was presented. At the onset of each experiment, subjects viewed adaptation stimulus for 90 s. Each test stimulus was presented for 2 s followed by 15 s "top-up" adoption. The detection thresholds for the test stimuli were estimated using the method of limits. Two ascending and 2 descending runs were conducted for each subject. The mean luminance of each stimulus was 20 cd/m^2. The stimuli were presented via a 5x5 array of green light emitting diodes (LEDs) that subtended 2.2° of the visual angle. Five healthy right-handed adults with normal or corrected-to-normal vision participated in the study.

Fig. 2 shows the averaged detection thresholds for test stimuli under the different adaptation conditions. Results showed that the detection threshold for the flickering light of 2 Hz elevated more after adapting to 2 Hz than after adapting to 16 Hz. Also, the detection threshold for the flickering light of 16 Hz elevated more after adapting to 16 Hz than after adapting to 2 Hz.

2.2 Adaptation effects for AM flicker

An AM flickering light with a carrier frequency of 16 Hz and a modulation frequency of 2 Hz was used as a test stimulus. The luminance waveform and its frequency spectrum were shown in Fig. 1. Frequency components were observed at the

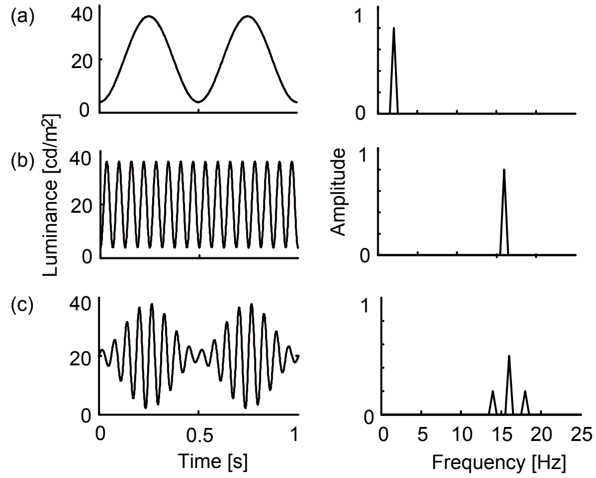

Fig. 1. Waveforms and frequency spectra of (a,b) the sinusoidal flickering lights of 2 and 16 Hz and (c) the AM flickering light.

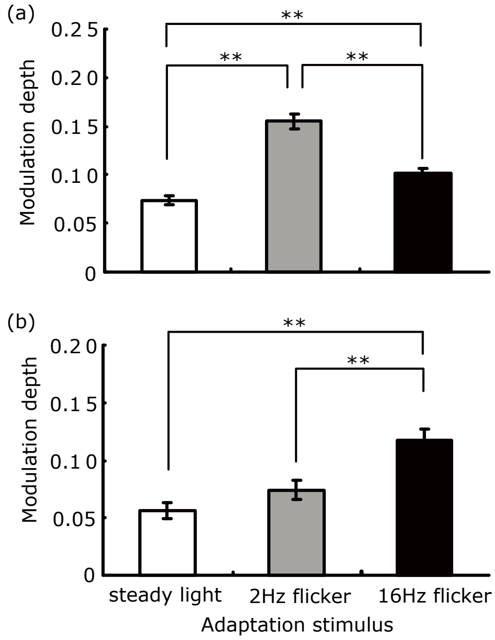

Fig. 2. Detection thresholds for the sinusoidal flickering light of (a) 2 Hz and (b) 16 Hz. Error bars indicate SEM (**p<0.01)

carrier frequencies and its sidebands, but not at the modulation frequencies (envelope periodicity). The adaptation stimuli and the procedures of threshold measurements were identical to those used in the detection threshold measurements of the sinusoidal flickering lights. The thresholds for detecting the flicker at the envelope periodicity of the AM flickering light after adapting to 2 or 16 Hz were estimated.

Fig. 3 shows the averaged threshold for detecting flicker at the envelope periodicity of the AM flickering light. The results showed that the detection threshold for the flicker at the envelope periodicity elevated more after adapting to the 2 Hz (envelope periodicity) than after adapting to 16 Hz (carrier frequency).

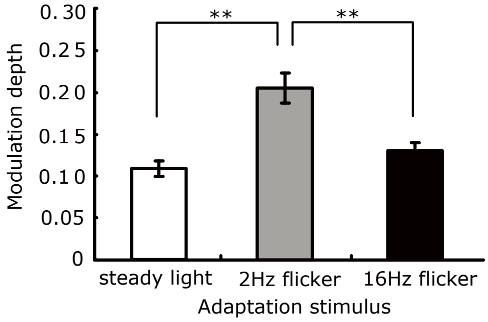

Fig. 3. Detection thresholds for flicker at the envelope periodicity of the AM flickering light. Error bars indicate SEM ($^{**}p$<0.01)

3. MEG RESPONSES

3.1 Adaptation effects for sinusoidal flicker

The adaptation stimuli used for the detection threshold measurements were also used for the MEG measurements. The test stimuli were sinusoidal flickering lights of 2 and 16 Hz with the modulation depth of 0.8. There were an initial adaptation period of 120 s and 30 s top-up adaptation periods. Following the adaptation period, subjects viewed the test stimulus for 4 s. Each test stimulus was presented 5 times. The cortical responses during the test periods were measured by using a whole-head MEG system (Neuromag-122^{TM}, Neuromag Ltd.), which has 122 planar gradiometers placed at 61 measurement sites. The signals were recorded with a pass band of 0.03-100 Hz and digitized with a sampling rate of 400 Hz. The recordings were performed in a dimly lit, magnetically shielded room. MEG responses obtained from 16 sensors located over the occipital area (which included the primary visual cortex) were used for the analysis. Power spectra were calculated by fast Fourier transform (FFT) for the data obtained from each sensor. Prominent peak components were observed at the test stimulus frequency. Therefore, the strengths of MEG responses at the frequency of the test stimulus (2 or 16 Hz) were analyzed.

Fig. 4 shows the power of MEG signals for the test stimuli under the different adaptation conditions. The results showed that the strength of the MEG responses for the flickering light of 2 Hz decreased more after adapting to the 2 Hz than after adapting to 16 Hz. Also, the strength of the MEG responses for the flickering light of 16 Hz decreased more after adapting to 16 Hz than after adapting to 2 Hz.

3.2 Adaptation effects for AM flicker

An AM flickering light with a modulation frequency of 2 Hz and a carrier frequency of 16 Hz was used as the test stimuli.

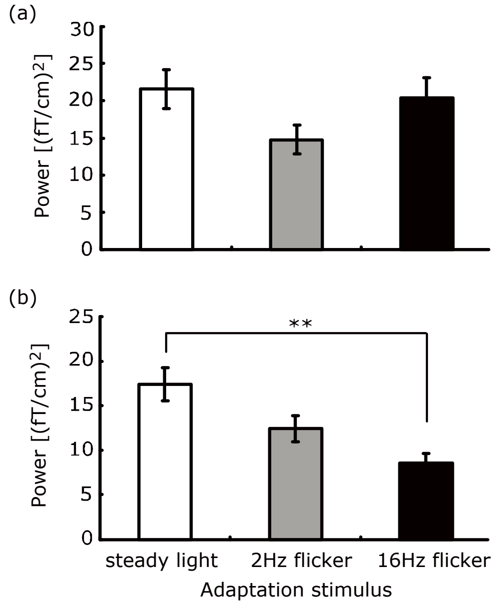

Fig. 4. Strength of MEG responses to sinusoidal flickering light of (a) 2 Hz and (b) 16 Hz. Error bars indicate SEM ($^{**}p$<0.01)

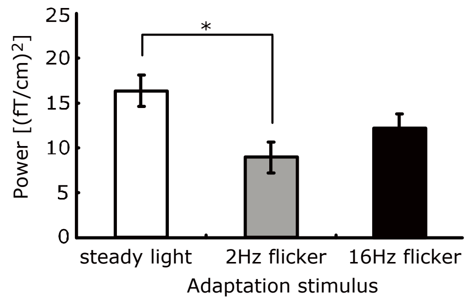

Fig. 5. Strength of MEG responses to flicker at the envelope periodicity of the AM flickering light. Error bars indicate SEM ($^{*}p$<0.05)

The modulation depth of the AM flickering light was 0.8. The adaptation stimuli and the MEG recording procedures were identical to those for the sinusoidal flickering lights. Prominent peak components were observed at the modulation frequency (envelope periodicity) of the AM flickering light as well as at the carrier frequency. Therefore, the strengths of MEG responses at the modulation frequency of the AM flickering light frequency (2 Hz) were analyzed.

Fig. 5 shows the power of MEG signals for the AM flickering light under the different adaptation conditions. The results showed that the strength of the MEG responses at the envelope periodicity of the AM flickering light decreased more after adapting to 2 Hz (envelope periodicity) than after adapting to 16 Hz (carrier frequency).

4. DISCUSSION

As the previous studies suggested [10, 11], for the sinusoidal flickering light, the adaptation effect for flicker at the low temporal frequency (2 Hz) was greater when the subjects adapted to the low temporal frequency (2 Hz) than when they adapted to the high temporal frequency (16 Hz). Also, the adaptation effect for flicker at the high temporal frequency (16 Hz) was greater after adapting to the high temporal frequency (16 Hz) than after adapting to the low temporal frequency (2 Hz). This is due to the reduction of sensitivity of the low- or high-frequency channel by adapting to the low or high frequency, respectively.

For the AM flickering light, the adaptation effect for the flicker at the envelope periodicity of the AM flickering light was greater after adapting to the modulation frequency than after adapting to the carrier frequency of the AM flickering light. These results indicated that the sensitivity to the flicker at the envelope periodicity was reduced more when the sensitivity to the frequency corresponding to the envelope periodicity was reduced than when that to the carrier frequency was reduced, although the AM flickering light has a frequency component at the carrier frequency but not at the frequency corresponding to the envelope periodicity. The present results suggested that the envelope component of AM flickering light was affected by the temporal channel responsible for a low temporal frequency. Therefore, this interpretation suggests the possibility that the envelope component of AM flickering light arises before the AM flickering signal passes the low-frequency channel.

Regarding to the two temporal channels in the visual system, it is suggested that the first stage involves low-pass filtering by photoreceptors, while the second involves high-pass filtering associated with neural transmission, mainly due to lateral antagonism in the retina but also potentially in the brain [15]. If we adopt their suggestion, the present results show the possibility that the envelope component arises before the two temporal channels. However, the previous study suggested that the envelope component arises after the AM flickering light passes the low-frequency channel because the sensitivity to flicker at the envelope periodicity is reduced when the carrier frequency of AM flickering light is high [6]. Also, it is suggested that the there is a low-frequency channel before the envelope component arises [2]. These suggestions are not consistent with the present suggestion. However, the configuration of the two temporal channels is not yet clear. For example, the recent study proposed that there is a high-frequency channel before a low-frequency channel [14]. Therefore, we need a further consideration of the stage in the visual system where the envelope extraction is careered out, taking some proposals for a configuration of the temporal channels into consideration.

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