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Temporal Feature of S-cone Pathway Described by Impulse Response Function

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1. Introduction

The impulse response function (IRF) is a temporal response of entire visual system to an extremely short flash, measured by a psychophysical method. In experiments with control of luminous and chromatic changes of the flash, it is possible to obtain the IRFs mainly determined by the achromatic or chromatic pathway.

I and my colleague, John S. Werner especially focused on IRFs of S-cone pathways. Because S-cone pathways are anatomically and physiologically different from achromatic pathway and chromatic pathways originated from L and M cones. Especially, in S-cone pathways, there are two different pathways for S-cone ON-response and S-cone OFF-response. In S-cone ON-response, excitatory (ON) signal from S-cones with inhibitory (OFF) L+M cones signal are going through small bistratified ganglion cells and connected to Konio-cellular pathway in LGN[1]. On the contrary, in S-cone OFF-response, excitatory signal from S-cones with inhibitory L+M cones signal are going through S-cone ON bipolar cell but they enter to a sign inversion connection of monostratified ganglion cells those are a few and large sparse cells[2].

By these differences in S-cone ON-pathway and OFF-pathway, it is expected that impulse responses of S-cone are different with the responses of L-cone and M-cone as previously expected[3]. Also, the responses of S-cone ON and S-cone OFF can be different each other. Thus, we measured the chromatic impulse response function of an isolated human S-cone pathway in double pulse method. About chromatic impulse response functions, mostly impulse responses were measured with red and green isoluminant pulses[4,5]. Chromatic (blue) impulse response functions have also been reported, but not with S-cone isolating stimuli[6]. Here, I measured the chromatic impulse response functions of an isolated human S-cone pathway. Additionally, I compared impulse response functions of putative ON- and OFF-pathways using chromatic increments and decrements.

As the results, the S-cone ON-IRF was slower than the luminous IRF but faster than the OFF-IRF. The difference between S-cone ON- and OFF-IRFs were statistically significant.

2. Method

2.1 Individual luminance and individual tritan line measured on CRT

Impulse response functions were derived from thresholds for a series of double-pulses in which the pulses were chromatically modulated on individual tritan lines at constant luminance.

First, we measured an individual luminance by obtaining minimum flicker points between

phosphors as our previous works[7,8]. Luminance of one phosphor (ex. blue phosphor) of the CRT was fixed at 6.9 cd/m^2 and presented stimulus consisting of the light only from that phosphor and the light only from the other phosphor (ex. red phosphor) in chromatic alternation flicker (18 Hz) of a temporal square wave. The stimulus was a 0.64-degree to 2.77-degree annulus surrounding a central fixation cross. Because ocular media transmission of the red phosphor is affected negligibly by lenticular senescence, and because the optical system produced an image of the stimulus in the plane of the pupil that was smaller (2.5 mm diameter) than that expected for observers spanning our age range[9], we expected that retinal illuminance was equated across observers.

In second, I measured individual tritan lines for each observer by color matching method with a strong adaptation to S-cones by the 420 nm light presented in a Maxwellian view. The observer was asked to find a match between two rectangular patches by adjusting the angle of the line around the white point and the intensity of one of the two test patches. All observers reported that they reached to the metameric match, which meant the match both in color appearance and brightness.

2.2 Apparatus and stimuli

Two-pulse thresholds were measured for stimuli that were modulated in chromaticity along a tritan line, changing from the white background (CIE (x, y)=(0.33, 0.33)) in 10 cd/m^2 (1.69 log Td) toward the short-wave spectrum locus (blue pulse) or the long-wave spectrum locus (yellow pulse). The two pulses were 6.7 ms each for blue pulses or 40 ms each for yellow pulses and separated by interstimulus intervals (ISI) ranging from 20–360 ms. A central fixation cross defined four positions of the test stimuli which were located 1.70 deg to one side or the other and 1.70 deg above or below the center of the fixation cross. The test stimulus was a Gaussian patch, 2.26 deg diameter at 1 SD, chosen as the test spatial profile to eliminate artifacts caused by spatial transients.

These stimuli were presented on a CRT display (Sony GDM-200 PS) operating at a 150 Hz frame rate that was controlled by a video board with 15-bit resolution (Cambridge Research Systems, VSG 2/4). An aperture was placed before the telescope objective and the focused image of the CRT and adapting field were 1.5 mm in the plane of the eye pupil. Observer position was maintained with a dental-impression bite-bar.

2.3 Procedure

We tested four normal observers (3 males and 1 female), ranging in age from 21.3 to 40.1 years.

Each session began after 5 min dark adaptation and 5 min adaptation to a 10-cd/m^2 equal-energy white background. Two pulses were presented on the screen, preceded by a high-pitched tone and followed by a low-pitched tone. The observer's task was to indicate in which of four quadrants the stimulus was detected by pressing one of four correspondingly arranged buttons. The stimulus was a chromaticity change in one Gaussian patch from equal-energy white along the individually determined tritan line.

In S-cone ON impulse response function measurement, only two blue pulses were presented in one session. The change was a double pulse (6.7 ms with interstimulus intervals from 20 to 360 ms) in which the two flashes were modulated equally in chromaticity at constant luminance toward blue, resulting in increased S-cone excitation. This 4-alternative forced-choice task was combined with a two-down, one-up staircase in which staircases for each ISI were interleaved. Thresholds for each

ISI were based on the last four of six reversals corresponding to a 70.7% probability of detection. This was repeated in at least 4-6 sessions per observer.

In the case of S-cone OFF impulse response function measurement, the procedure was basically the same except only two yellow pulses were presented in one session, and 6 frames instead of one frame were used for each yellow pulse, because of insufficient chromatic change to yellow in a single frame.

The double pulse method is the method to derive a shape of an IRF with some hypothesis by measuring the change of thresholds of flashes when an inter-stimulus interval of two flashes is changed. From the threshold change as a function of inter-stimulus interval, the shape of the IRF can be estimated precisely in some degree. We employed the model of the IRF by Burr and Morrone[5] as described in our previous works[7,8].

3. Results

Fig. 1 shows results of threshold as a function of ISI measurement by S-cone ON flashes (top panels) and S-cone OFF flashes (bottom panels). Not like luminous IRFs, both S-cone IRFs are mono-phasic and the durations protracted compared to the bi-phasic and tri-phasic IRFs that characterize response to an achromatic double pulse[7]. On this observer, the time to the peak are 64 ms for S-cone increment IRF and 145 ms for S-cone decrement IRF, compared with 21.3 ms with luminance modulation (shown in Ref. 7, Fig.7). With luminance modulation, the first excitatory phase is followed by an inhibitory phase making the excitatory duration easy to define. For the S-cone IRF, the duration of the excitatory phase will be operationally defined as the value on the descending slope corresponding to 5% of the peak amplitude.

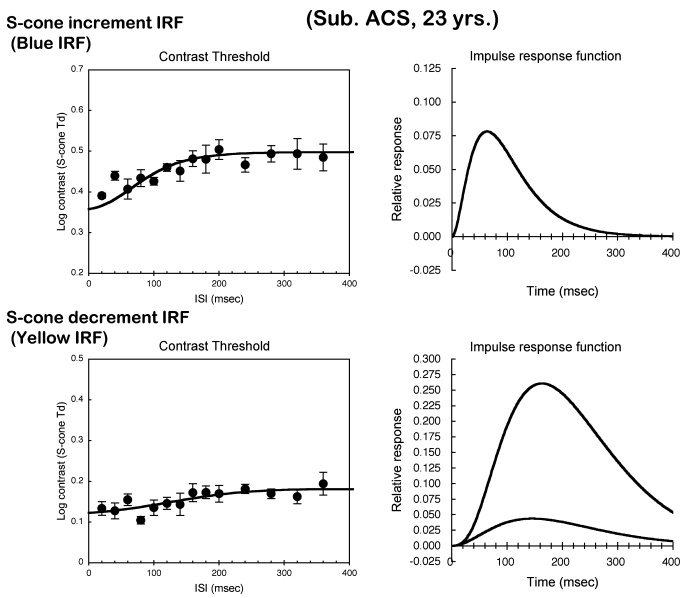

Fig. 1. Threshold data with the model fit and impulse response functions (IRFs) calculated by the model for one observer (Observer ACS, 23 years old). Top panels are for S-cone increment IRF and bottom panes are for S-cone decrement IRF, respectively. In the case of S-cone decrement IRF, because one pulse consisted of 6 frames, linear summation of 6 response functions with 6.67 ms delay each was used to calculate the expected threshold curve from the shape of IRF (denote by black curve in the threshold data panel).

In the experiment, it was not possible to obtain sufficient S-cone modulation in a double-pulse defined by single frames because of the luminance limit of the CRT phosphors. However, because the S-cone IRF is slow, it was possible to use multiple frames (typically 6 frames) to define each pulse without affecting the shape of the IRF. In this case, I defined each pulse as one series of successive frames of the IRF calculated as the summation of S-cone IRFs with time delay by each frame (6.67 ms frame rate). In Fig. 1, this IRF is shown by the smaller curve in which each pulse was defined by six frames for S-cone decrement IRF measurement. This method of measurement and calculation assuming linear summation is justified because the double-pulse method itself has to employ this assumption to obtain the IRFs.

4. Discussion

In order to confirm the difference between S-cone increment and decrement IRFs, two characteristics of IRFs were compared on each observer in a statistical significance. **Fig. 2** and **3** show the difference between S-cone increment and decrement IRFs in terms of relative peak amplitude and peak time, respectively. Differences in all characteristics are statistically significant in 5% significance level when the data were paired on each observer.

There are, however, some individual differences between observers. For observer BFA, the difference is not so large, although for observer KS the difference is critical. I expect that this individual variation is caused by a usage of these S-cone increment and decrement pathways. In other words, these S-cone pathways are regularly not used to process visual stimulation concerning to temporal information. Thus, it is possible that these S-cone pathways are not well controlled in terms of temporal characteristics but only controlled in terms of chromatic characteristics. This hypothesis can be supported by the fact that S-cones are sparse and do not exist at the central fovea. Also, as described at the first part of this paper, S-cone pathways are quite different with L-cones and M-cones pathways.

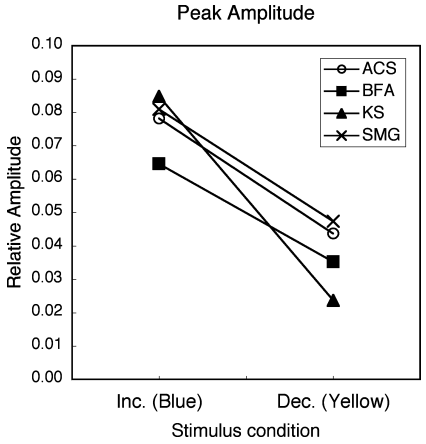

Fig. 2. Relative peak amplitude in S-cone increment and decrement IRFs compared on each observer.

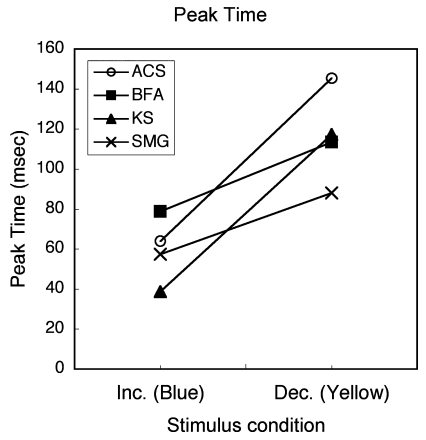

Fig. 3. Peak time in S-cone increment and decrement IRFs compared on each observer.

Acknowledgments

Main part of the presentation and this summary has already been described in ref.10.

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