Investigation of the Fraser-Wilcox illusion based on photoreceptor stimulations

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ABSTRACT

Fraser and Wilcox (1979) reported that observers perceive illusory motion in a stationary image, which consists of a repeated luminance gradient in a saw-tooth wave form. Although it is well known that visual attributes, i.e. luminance and color, play an important role in perception of the illusory motion, it is still not identified which physiological pathways/substrates convey the signal associated with the illusion. In this study, we used a four-primary stimulator that enables independent stimulation of photoreceptors, using a silent-substitution paradigm. We have investigated the Fraser-Wilcox illusion, based on stimulation of three types of cones and a recently discovered novel photoreceptor, melanopsin ganglion cell. We generated the following four test stimuli, melanopsin stimulus (Mel), cone stimulus (Cone), S-cone stimulus (S), and red-green isoluminant stimulus (|M-L|). It was found that observers perceived the strongest motion illusion from the isoluminant stimulus among the other three stimuli, indicating that an |M-L| cone-opponent pathway at a post-receptoral site contributed dominantly to the color-dependent Fraser-Wilcox illusion.

KEYWORDS: Fraser-Wilcox illusion, photoreceptor, illusory motion

INTRODUCTION

Fraser and Wilcox (1979) reported that observers perceive illusory motion in a stationary image that consists of a repeated luminance gradient in a saw-tooth wave form. Kitaoka and Ashida (2003) proposed an enhanced version of the Fraser-Wilcox illusion with a specific pattern of luminance gradient. The illusory motion in a stationary image was also observed with a specific pattern of colors (e.g. Kitaoka, 2014, 2017). Although it is well known that visual attributes, i.e. luminance and color, play an important role in perception of the illusory motion it is not clear which physiological pathways/substrates convey the signal associated with the illusion. The identification of physiological pathways is useful in the understanding of motion mechanism in the brain associated with the illusion. In this study, we focused on the photoreceptor stimulations caused by the static image that induces the Fraser-Wilcox illusion rather than on visual attributes, such as luminance and color.

There is the third class of photoreceptors in addition to cones and rods in primates, called intrinsically photosensitive retinal ganglion cells (ipRGCs). The ipRGCs containing photopigment melanopsin are known to support various non-image forming functions including circadian rhythm, pupillary light reflex, and some cognitive processes such as acute alerting (Lockley et al., 2006). There are four potential pathways that may contribute to the illusion: achromatic luminance pathway, red-green and blue-yellow color opponent pathways, rod pathway and ipRGC pathway. However, it is especially difficult to identify which pathway(s) contributes to the illusion since the perception was usually induced by a mixture of signals from all the pathways. We developed a multi-primary photostimulator that can modulate a target photoreceptor alone whereas the other photoreceptors were kept silent (Tsujimura et al. 2010, Brown et al., 2012). We used the following four test stimuli; cone stimulus (Cone), red-green isoluminant stimulus (|M-L|), blue-yellow isoluminant stimulus (S) and ipRGC stimulus (ipRGC), that correspond to luminance, red-green, blue-yellow and ipRGC pathways, respectively.

METHODS

Apparatus

The multi-primary photostimulator is a customized illumination system consisting of three projectors (NP-PA500X, NEC) and interference filters (Edmund Optics, USA) that enables independent stimulation of each photoreceptor class at retina (Figure 1). The peak wavelengths of the four primaries were 595 nm, 580 nm, 530 nm and 455 nm. The frame rate of the projector was 60 Hz. The characteristics of digit-luminance (i.e. Gamma correction) was carefully calibrated to achieve linearity of the light intensity. The light level was controlled by a 10-bit video-board (Quadro K5000, NVIDIA, USA) using customized software. The uniformity of the illumination was calibrated using the 2-dimensional colorimeter with XYZ filters (RTC-21, Ikegami, Japan).

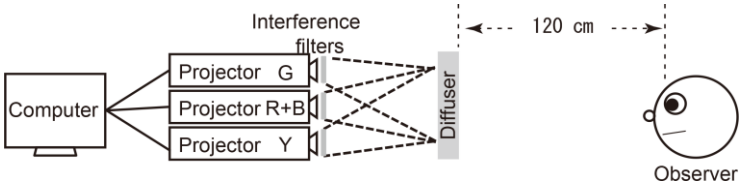

Figure 1: Four-primary photostimulator

A personal computer controlled the stimulation system and the stimuli were displayed on a diffuser. The viewing distance was 120 cm. The background luminance was 139 cd/m^2 and the color was (0.43, 0.36) in CIE *xy* color coordinate. Each observer focused on the fixation presented at the center of the diffuser in a dark room under binocular viewing condition.

Stimuli

We used an optimized Fraser-Wilcox illusion Type IIa image designed by Kitaoka (2014) (http://www.psy.ritsumei.ac.jp/~akitaoka/rotate-colordependentFW.html). Each disk was presented at peripheral visual field at eccentricities of 3.5° and 7.3° in visual angle. The diameter of each disk was 3.9°. Each disk is composed of micropatterns, each of which consists of 4 regions: light purple (region A), pink, red (region B) and dark purple (Figure 2). When colors of region A and B were switched a direction illusory motion was reversed, suggesting a strong contribution in two regions' color to the illusory motion. We then varied stimulations of these regions.

We had 4 stimulus conditions to vary in these regions. Figure 2 showed a schematic of the experimental conditions in terms of stimulations of photoreceptors at retina. In luminance condition, there was a difference in luminance between the regions while keeping color and melanopsin stimulation constant. In red-green and blue-yellow opponent color conditions there was a color difference while keeping luminance and melanopsin stimulation constant. In ipRGC condition there was a difference in stimulation of ipRGC while keeping color and

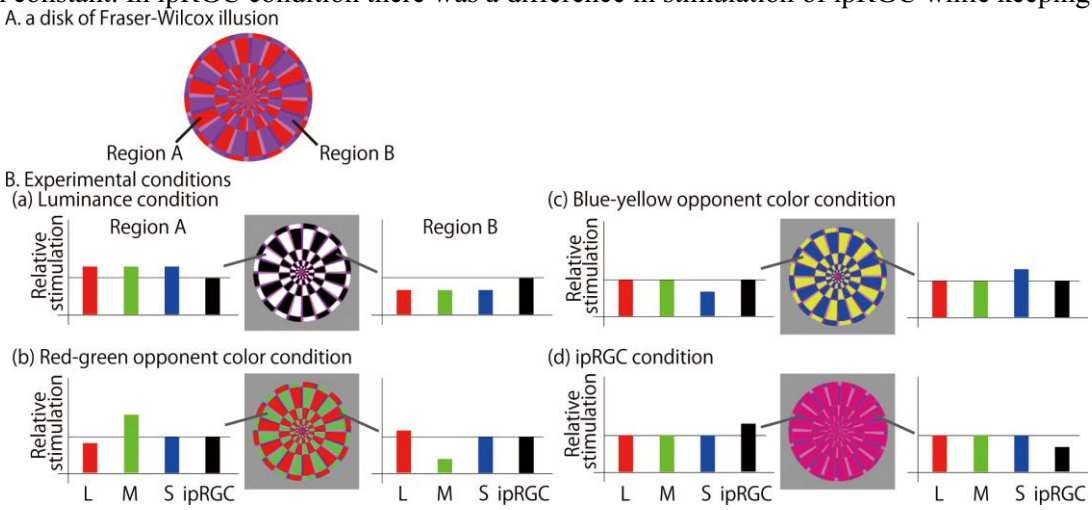

Figure 2: A schematic of the experimental conditions

luminance constant. The luminance condition differs only luminance of the two regions, which varied L-, M- and S-cone stimulations without changing color and ipRGCs stimulation (a). The red-green opponent color conditions varied L- and M-cone stimuli without changing in luminance and ipRGCs stimulation (b). The blue-yellow opponent color condition varied S-cone stimulation without changing luminance and ipRGCs stimulation (c). The ipRGC condition varied ipRGC stimulation without changing luminance and color (d). All modulations between the regions were based on an average between the regions of A and B, called reference (the horizontal bar in a panel). Stimulations of the photoreceptors varied 1.27 times based on cone contrast. The average luminance of region A and B was 464 cd/m^2 and the color was (0.48, 0.32) in CIE *xy* color coordinate. The contrast for the isoluminant color conditions was calculated in cone contrast. The contrast in luminance condition was calculated in cone contrast for direct comparison between chromatic and achromatic sensitivities based on the assumption that L- and M-cone contribute to the luminance pathway.

A paired comparison was used to estimate an amount of illusory motion. The distances among conditions were evaluated from pairwise comparisons with Bradley-Terry (1952). Disks were presented at right and left visual fields under the 4 stimulus conditions. For example, the disks at right field were in ipRGC condition and at the left in luminance condition. Each observer was asked to answer which disks cause larger illusion motion.

Observers

Six observers (aged 18-40 years) joined the experiments they had normal or corrected-to-normal visual acuity. All observers had normal color vision according to the Ishihara color blindness test and gave written informed consent. The study was approved by the local research ethics committee.

RESULTS AND DISCUSSION

Table 1 showed the amount of illusory motion in each condition from typical 2 observers, and Table 2 showed that summed from all observers. The results showed that the illusory motion was strongest in a red-green opponent color condition consistently for all observers. Figure 3 showed a relative difference summed from all observers calculated with a Bradley and Terry model (1952).

Table 1. The amount of illusory motion

No illusory motion

Illusory motion

A

	Luminance	Red-green opponent color	Blue-yellow opponent color	ipRGC
Luminance		0	10	6
Red-green opponent color	10		10	10
Blue-yellow opponent color	0	0		6
ipRGC	4	0	4	

B

	Luminance	Red-green opponent color	Blue-yellow opponent color	ipRGC
Luminance		3	10	10
Red-green opponent color	7		8	8
Blue-yellow opponent color	0	2		7
ipRGC	0	2	3	

Results showed that the amount of the illusory motion were significantly different among all conditions ($X^2 = 41.385$, df = 3, $p<.00001$).

It was found that the red-green color plays an important role in perception of the illusory motion that is consistent with the previous study (Kitaoka, 2014). Furthermore, we focused on the photoreceptor stimulations of

Table 2. Summary of the amount of illusory motion for all observers

No illusory motion

Illusory motion

	Luminance	Red-green opponent color	Blue-yellow opponent color	ipRGC
Luminance		15	63	49
Red-green opponent color	65		73	71
Blue-yellow opponent color	17	7		44
ipRGC	31	9	36	

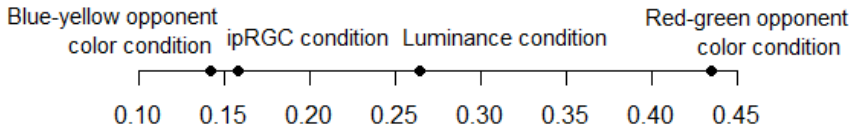

Figure 3: Score from Bradley-Terry model with summation of each observer's evaluation

the static image that induces the Fraser-Wilcox illusion. Since photoreceptor stimulation is strongly associated with physiological pathway it is useful in the understanding of motion mechanism in the brain. We found that the modulation of L- and M-cone stimulation in the opposite phase (i.e. |M-L|) in red-green opponent color condition, in contributing to the illusory motion. In physiology since the |M-L| signals at retina were conveyed through parvo-cellular pathway to the brain it seems that the parvocellular pathway contributes to the illusory motion. This is surprising since in physiology the magno-cellular pathway has been proposed as the physiological substrates for the luminance and motion pathways (e.g. Livingstone & Hubel, 1988; Merigan & Maunsell, 1990). On the other hand, Smith et al. (1992) have shown that magno-cellular ganglion cells in monkey retina, receive |M-L| opponent signals. Whether the magno− and parvo- schemata exist in illusory motion pathway, or whether further physiological schemata are necessary, must be a matter for future research.

From a purely psychological perspective this phenomenon could add to our understanding of several behavioral patterns that don't now have acknowledged stimuli.

CONCLUSION

Observers perceived the strongest motion illusion to the isoluminant stimulus, indicating that an |M-L| cone-opponent pathway at a post-receptoral site contributed dominantly to the color-dependent Fraser-Wilcox illusion.

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