



Influence of background size, luminance and eccentricity on different adaptation mechanisms



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ABSTRACT

Mechanisms of light adaptation have been traditionally explained with reference to psychophysical experimentation. However, the neural substrata involved in those mechanisms remain to be elucidated. Our study analyzed links between psychophysical measurements and retinal physiological evidence with consideration for the phenomena of rod-cone interactions, photon noise, and spatial summation. Threshold test luminances were obtained with steady background fields at mesopic and photopic light levels (i.e., 0.06–110 cd/m²) for retinal eccentricities from 0° to 15° using three combinations of background/test field sizes (i.e., 10°/2°, 10°/0.45°, and 1°/0.45°). A two-channel Maxwellian view optical system was employed to eliminate pupil effects on the measured thresholds. A model based on visual mechanisms that were described in the literature was optimized to fit the measured luminance thresholds in all experimental conditions. Our results can be described by a combination of visual mechanisms. We determined how spatial summation changed with eccentricity and how subtractive adaptation changed with eccentricity and background field size. According to our model, photon noise plays a significant role to explain contrast detection thresholds measured with the 1/0.45° background/test size combination at mesopic luminances and at off-axis eccentricities. In these conditions, our data reflect the presence of rod-cone interaction for eccentricities between 6° and 9° and luminances between 0.6 and 5 cd/m². In spite of the increasing noise effects with eccentricity, results also show that the visual system tends to maintain a constant signal-to-noise ratio in the off-axis detection task over the whole mesopic range.

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1. Introduction

Light adaptation allows visual detection in a large dynamic range of ambient light levels, which can span more than eight orders of magnitude (Hood & Finkelstein, 1986). Threshold versus intensity (*tvi*) functions have been traditionally used by psychophysicists to study adaptation to varying light levels (Barlow, 1965; Donner, 1992; Shapley & Enroth-Cugell, 1984). In these experiments, the effect of adapting backgrounds was quantified with a just-detectable probe flash superimposed on the background. The switching between rod and cone mediation is one adaptation mechanism that can be described with a *tvi* curve. Also, changes in spatial, temporal and spectral characteristics of the stimulation allowed determination of the laws of neural

adaptation based on these curves. Early studies typically ascribed behavioral findings to two main adaptation mechanisms: (1) Gain control mechanisms that establish a proportionality between the increments (or decrements) of impulse rate variation in retinal ganglion cells and increments (or decrements) in the retinal illumination (Shapley & Enroth-Cugell, 1984); and (2) Subtractive mechanisms partially eliminate the signal corresponding to steady luminance, reducing it to a lower effective value.

Based on psychophysical experiments, other adaptation mechanisms, such as contrast gain and non-linear processing stages (including saturation, noise and spatial summation) have been considered (Barrionuevo, Colombo, & Issolio, 2013; Cao & Pokorny, 2010; Murray & Plainis, 2003; Rieke & Rudd, 2009; Smith & Pokorny, 2003; Snippe, Poot, & van Hateren, 2000, 2004; Wilson, 1997). Saturation is understood as a non-linear process caused by the limited dynamic range of retinal neurons. Detection experiments are also thought to be affected by noise. The effect of

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noise was found to be significant at low light levels, especially with brief and small backgrounds in peripheral retina (Bauer, Frumkes, & Holstein, 1983; Bauer, Frumkes, & Nygaard, 1983). Spatial summation has also been traditionally studied using psychophysical approaches (Barlow, 1958; Redmond, Zlatkova, Vassilev, Garway-Heath, & Anderson, 2013) and its changes are explained by an increasing receptive field size with eccentricity. Modern physiology has also contributed to this type of study; e.g., functional magnetic resonance imaging methods estimated that the receptive field size increases with eccentricity in humans whereas other physiological studies provided a quantitative description of the spatial receptive fields in primates and rats (Croner & Kaplan, 1994; Dumoulin & Wandell, 2008; Heine & Passaglia, 2011).

Recent advances in understanding the underlying physiological mechanisms of adaptation processes have provided deeper insight into this field. Gain control mechanisms located at outer retina (photoreceptors) and inner retina (ganglion cell) levels have been characterized (Dunn et al., 2006; Dunn, Lankheet, & Rieke, 2007). Freeman, Graña, and Passaglia (2010) proposed a novel, fast and high-sensitivity luminance gain control mechanism whose changes followed Weber's law. This physiological mechanism was said to reside within the inner retinal network and not in the photoreceptors. In order to understand this mechanism, very recent works have focused on the interactions between photoreceptors, horizontal cells and bipolar cells (Joselevitch & Kamermans, 2013; Thoreson & Mangel, 2012). According to these authors, post-synaptic mechanisms at bipolar cell dendrites play a significantly important role by modulating the strength of their response to light. These mechanisms eventually extend the range of ambient luminances our visual system can be adapted. On the other hand, Tyler and Liu found that luminance variation of a small background pedestal does not affect the state of the gain control mechanism as much as it is affected by large background fields (Tyler & Liu, 1996). Concerning adaptation to contrast, Demb (2008) suggested that bipolar, amacrine and ganglion cells were involved in a complex process through synaptic and intrinsic mechanisms whose aim was to enhance contrast detection. The discussion concerning the physiological origin of luminance and background adaptation mechanisms is ongoing (Demb, 2008; Freeman et al., 2010) although the most recent studies have suggested that both mechanisms depend, in part, on a common synaptic process (Jarsky et al., 2011).

A subtractive mechanism was initially hypothesized as the result of feedback between cones and horizontal cells (Wilson, 1997). Wilson's assumptions and conjectures about this mechanism seem to have been corroborated by physiologists in the study of different fish species. For example, Klaassen, Fahrenfort, and Kamermans (2012) showed that gap junction proteins can also function as hemichannels that mediate a sign inverting inhibitory synaptic signal from horizontal cells to cones via an ephaptic mechanism. Furthermore, VanLeeuwen, Fahrenfort, Sjoerdsma, Numan, and Kamermans (2009) verified the existence of a lateral gain control mechanism in the horizontal cells of goldfish retinas that modulates the synaptic gain of cones and is finally visible in ganglion cell responses.

All these advances have renewed interest in relating psychophysical experiments with underlying physiological mechanisms. As an example, the work performed by Freeman et al. (2010) offers an explanation for the psychophysical evidence that low contrast stimuli can activate a local adaptation luminance mechanism in the mammalian retina, according to the authors. On the other hand, starting from psychophysics, Stockman, Petrova, and Henning (2014) proposed a physiologically relevant model of the chromatic and brightness pathways.

Concerning the background adaptation luminance, vision is mediated by cones at bright background light levels (photopic

vision), while rods alone are working at dim background light levels (scotopic vision). The mesopic light range covers four orders of magnitude, approximately, between the photopic and scotopic ranges. Under mesopic background light levels, both rods and cones are simultaneously activated (Buck, 2004, 2014; Zele & Cao, 2015). In addition to rod and cone spectral domains being relatively shifted, their density distributions across the retina are different (Curcio, Sloan, Kalina, & Hendrickson, 1990; Osterberg, 1935). Rod and cone temporal and spatial contrast sensitivity functions (Stockman & Sharpe, 2006), which are directly related to their receptive field characteristics, differ as well. Classic studies on *tvi* functions have shown that backgrounds of small size, designed to be detected by rods, affect contrast thresholds when the test is detected by cones, and stimuli designed to be detected by cones affect contrast thresholds when the test is detected by rods (Buck, Peeples, & Makous, 1979; Latch & Lennie, 1977; Temme & Frumkes, 1977). A conclusion from these studies is lateral involvement of rods is necessary for the increase in cone thresholds. Since this effect seems to happen only for small backgrounds, in mesopic conditions where rods and cones work together it is important to consider the effect of stimulus size. In conclusion, rod and cone signals interact and their light adaptation mechanisms change with intensity, eccentricity and stimuli sizes.

Furthermore, all types of photoreceptors, bipolar and ganglion cells change their densities and physiological properties in a significant way across the retina (e.g. Crook, Packer, Troy, & Dacey, 2014; Curcio et al., 1990; Garway-Heath, Caprioli, Fitzke, & Hitchings, 2000). Therefore, in order to reach a deeper insight into the retinal behavior, particularly in the whole perifoveal region, it is necessary to perform measurements at different retinal locations.

Psychophysical light adaptation measurements should reflect all of these physiological features. Because of the anatomical and physiological rod-cone differences, the study of mesopic vision is challenging. In this work, we report *tvi* measurements under several conditions, covering mesopic (0.06 cd/m²) to low photopic (110 cd/m²) adapting light levels, foveal (0°) to extrafoveal (15°) eccentricities, and three combinations of stimuli sizes, one of them including a 1° background field size. Traditional studies using large backgrounds, focused on overall retinal mechanisms. In this sense, it is particularly interesting to understand the adaptation-to-light mechanisms involved in a specific retinal position, a small background allowing for the study of this condition. Our study analyzed the following questions. (1) Is it possible to explain luminance thresholds under such diverse experimental conditions, particularly in off-axis retinal locations? (2) To what extent does a small stimulus size affect the adaptation process? (3) What links can be established between the psychophysical measurements and the underlying physiological mechanisms? The third question is probably the most important question. Despite the complexity that could arise from the wide span of our experimental conditions, we developed a physiological- and psychophysical-based model that successfully fitted our results. Our model was shown to be useful for analyzing the effects of light intensity, eccentricity and stimuli sizes on light adaptation mechanisms.

2. Methods

2.1. Experimental set-up

A two-channel Maxwellian view optical system was employed, which was previously described elsewhere (Matesanz et al., 2011). Briefly, two concentric beams reach the observer's pupil: a background beam (with luminance L_b) and a probe (with luminance ΔL). Henceforth, we will refer to the spatial region where both beams are combined ($L_b + \Delta L$) as the *test*. The angular size of the

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