

1. INTRODUCTION

1.1 Classical receptive field

Kuffler's attempt in characterizing the receptive field of retinal ganglion cells (RGCs) in 1953 laid a foundation for anyone who wants to study neurophysiology of the mammalian retina (Kuffler, 1953). Following Hartline's (1940) initial concept of spatially limited responsive area for a given RGC in frog, he used a spot mapping technique to examine the RGCs of cats, and indicated that the discharge rate of each ganglion cell is affected by the luminance change in a restricted area of visual field. Furthermore, he also found that there is a subregion where light stimulation produces the opposite response on the discharge rate of the cell. This finding was supported by another study in the same year (Barlow, 1953), in which increasing the area of light stimulus leads to a decrease in the discharge rate of the ganglion cell in frog retina such that only an optimal sized spot can effectively evoke the maximal response in the center region. The *receptive field* of a ganglion cell is a region of space in which the presentation or withdrawal of light stimulus can alter the firing rate of that cell (Hartline, 1940; Barlow, 1953; Kuffler, 1953; Chalupa and Werner, 2004). Additionally, it has been shown that light falling outside the receptive field center has an inhibitory effect to the center stimulation (Barlow, 1953; Enroth-Cugell and Robson, 1966). This

center-surround interaction was further formulated by Wiesel in 1959 that the excitatory and inhibitory area can be stimulated selectively, and the center response is reduced when light stimulates both of the center and surround areas (Wiesel, 1959). Given the fact that the ganglion cell draws antagonistic input from concentrically organized regions to form a center-surround organization, it has been theorized that a simple difference-of-Gaussians (DOG) model could describe this center-surround interaction (Rodieck and Stone, 1965). In this model, center and surround mechanism are represented by two Gaussians with different contrast sensitivity and space constant, and this classical surround exhibits an extensive region across and beyond the center (Enroth-Cugell and Robson, 1966). Therefore, a ganglion cell's classical receptive field can be modeled by a linear subtraction of two Gaussians to form a "sombbrero" (Mexican hat) like property. This center-surround antagonism was also found in the lateral geniculate nucleus cells in the thalamus (Hubel and Wiesel, 1961).

1.2 Motion surround inhibition

Aside from the steady surround inhibition, a moving object spreaded outside the receptive field of a cell will also lower its center response (Barlow and Levick, 1965). One classical experiment to demonstrate this moving surround inhibition is the "spinning windmill patterns" first proposed by Werblin (1972), in which a sectorized disk ('windmill')

was rotated in an annulus region while the center was stimulated by a test flash. In this experimental paradigm, the cell response was reduced depending on the windmill intensity, area, and velocity, and was closely correlated with the increasing activity of the amacrine cells (Werblin, 1972; Thibos and Werblin, 1978; Enroth-Cugell and Jakiela, 1980; Chiao and Masland, 2003). Since the windmill surround causes local changes in illumination throughout the periphery but keeps constant mean luminance for all the areas, thus the suppression of the center response is induced by the local illumination change. Because the response of horizontal cells is sustained in nature, the suppression caused by lateral interaction must be driven by the amacrine cells in the inner plexiform layer (IPL) of the retina (Werblin, 1972). Furthermore, Chiao and Masland (2003) showed a more complicated suppressive surround effect depending on diverse background contexts such that difference in spatial phase, spatial frequency, or temporal frequency between the center and the annulus surround can relieve inhibition from the suppressive surround during the global motion (Shapley and Victor, 1979; Enroth-Cugell and Jakiela, 1980; Solomon et al., 2006).

1.3 Beyond the classical – peripheral effect

As early as 1960s, McIlwain (1964) demonstrated that the discharge patterns of retinal ganglion cells are influenced by a light stimulus presented in the outside region of

the classical receptive field defined by Kuffler's work in 1953. He noticed that moving stimuli in the periphery of the classical receptive field lower the threshold for the center response (peripheral effect) and cause a slow increase of the maintained discharge, and thus increase the responsiveness of the cell (McIlwain, 1964). Subsequently, Ikeda and Wright (1972) introduced the idea of a disinhibitory surround in which the responses of both the center and surround have the same polarity when stimulated. Transient bursts of spikes were also observed when a sudden motion is applied to the nonclassical receptive field (Barlow et al., 1977). However, the general concept of surround inhibition and suppression are largely supported (Werblin, 1972; Werblin and Copenhagen, 1974; Thibos and Werblin, 1978; Shapley and Victor, 1979; Enroth-Cugell and Jakiela, 1980). Passaglia et al. (2001) end this enigma by showing that the increase or decrease of mean firing rate depends on the spatiotemporal characteristics of remote stimulus patterns. This finding provides a dual effect for the non-classical receptive field area.

1.4 Direction selective ganglion cell

Different surround contexts can modulate the center response, but how different features affect the center response? Among various types of ganglion cells responded to novel trigger features (Levick, 1967) the *direction selective ganglion cells* (DSGCs) were

the most famous ones. The DSGCs were first characterized in the rabbit retina (Barlow et al., 1964). The 'direction selective' means that this type of cell can distinguish the motion direction of an object. In the electrophysiological experiment, the DSGC shows vigorous spiking activity when an object moves in its 'preferred' direction through the receptive field center, and gives little or no response when an object moves in the opposite way, the 'null' direction (Barlow and Hill, 1963). Among the two distinct types of DSGCs, the ON-OFF DSGCs are probably the most well studied ganglion cells in the rabbit retina. It has been suggested that the ON-OFF DSGCs are specialized for signaling local motion rather than global motion (Vaney et al., 2001; Chiao and Masland, 2003). While the mechanism underlying direction selectivity have been debated for a long time (Barlow and Levick, 1965; Wyatt and Daw, 1975; Borg-Graham and Grzywacz, 1992; Vaney et al., 2001; Chiao and Masland, 2002; Fried et al., 2002; Vaney and Taylor, 2002; Taylor and Vaney, 2003; Fried et al., 2005; Lee and Zhou, 2006), the DSGCs also show the surround modulation to the center response and this interaction is correlated to the ability of recognizing moving objects against the moving background (Chiao and Masland, 2003).

1.5 What the eye tells the brain

The ganglion cells are sending different visual information to our brain in a parallel

fashion (Wassle, 2004). The processing starts as early as the first synapse in the retina. In addition, the center-surround antagonism is not only a passive property, but is used for cells to segregate the object and background motion in the retina, even multiple objects in the same background (Olveczky et al., 2003). A recent study even indicates that the retina can detect and predict the miss in periodic patterns (Schwartz et al., 2007). Such an impressive ability of ganglion cells inspires us to study how the background modulates the behavior of the DSGCs, and what information the DSGCs tell the brain.

1.6 Questions and brief summary

The DSGC can signal the motion of the object, and a center – surround interaction can enhance edge detecting, further separating the object and the background, etc.

However, the information of the outside world changes all the time , and the separation of object and background is an important task for helping to position ourselves in the space.

The various responses to surround stimuli imply adaptation to the complexity of various environments. This study is to ask how the motion background contexts, given different spatial and temporal properties to mimic variable natural environments, modulate the DSGC response in multiple ways.