3. RESULTS

All experiments were done in the following condition. A light bar moving in 12 directions was applied first to confirm a DSGC (Fig. 4A). Using the polar plot, the preferred-null axis was determined (Fig. 4C). Subsequently, a rotating vane surround with a moving-grating center stimulus was applied to characterize the motion-induced center-surround antagonism (Fig. 4B). In consistent with the previous finding (Chiao and Masland, 2003), a slow moving vane-surround gave a strong suppression to the center stimulation, but the cell response increased as the vane span faster (Fig. 4D). Afterwards, a series of moving background context stimuli (see Materials and Methods) were displayed for further investigation. Each stimulus was presented five times to average the cell's response (Fig. 5A). The trial-by-trial plot was used to compare the variations between trials (Fig. 5B), and the average response was also shown (Fig. 5C). Finally, a normalized plot, which normalized all other responses to the control response (the center alone one) and averaged across trials, was presented (Fig. 5D).

3.1 DSGCs have dynamic responses to motion background context

First we want to know how different spatial coverage percentages alter the cell response. Stimulus with various random dots densities was applied to the DSGC.

Surprisingly, DSGCs responded differently to the various stimuli. According to their responding curves, we can divide them into three distinct types. Type I DSGCs had an initial inhibition as the surround appeared, and gradually recovered as the surround spatial coverage gets higher (Fig. 6A). The same behavior was also found in the windmill experiment (Fig. 6D). This behavior is similar to the results of the windmill experiment (Chiao and Masland 2003), thus it is classified as a 'normal' type. In contrary, type II DSGCs had a sustained suppressive surround no matter what the coverage percentage of the surround is (Fig. 6B). This phenomenon also exhibited in the windmill experiment (Fig. 6E) and is classified as 'inhibitory' type. The last one, type III, had an inhibition as other two types in the low coverage percentage but had a relatively strong excitation as coverage percentage gets higher (Fig. 6C). They sometimes had twice the response of the control at high background coverage. The windmill experiment confirmed this property in which the cells had less inhibition as the vane spins faster (Fig. 6F). The greater response of static windmill surround than center alone may come from that windmill refers to a 50% coverage which could cause excitatory response compared to 0% coverage, i.e., center alone (Fig. 6C). Nearly one-third of the DSGCs have this 'surround facilitation' (Table 1). Type I cells percentage is higher than others and type II cells are about one quarter. Furthermore, among total of 16 cells, there is one cell that cannot be classified into any type. Although all three types can be separated manually, some errors may occur in distinguishing type I from type III. We therefore introduced a *Trend Index* to quantify the tendency of the response in higher background coverage (see Materials and Methods). In this definition, type III cells would have higher Trend Index and type I would have lower ones (Fig. 7). Type II cells do not need the Trend Index to separate them from others. The classification appears to be independent of DSI (see Materials and Methods). All three types DSGCs have DSI ranging between 0.56 and 0.68 and they are not significantly different (Table 1). In other words, these phenomena may not be involved in direction selective mechanism. For type III cells, we measured the critical point of coverage percentage where the cell starts to have excitatory response. As the background coverage exceeded 30%, surround was dominated by excitatory inputs (Table 1).

3.2 Neither the random stimulus sequence nor the same background context patterns alters the cell's response

In order to know whether a sequentially displayed stimulus, which increases mean luminance as the coverage percentage increases, would affect the response, a randomized sequence of stimulus presentation was applied. Figure 8 showed two types of cells in three different stimulus settings. A type I cell can be recognized in Fig. 8A, which was given a sequential stimulus. There was no obvious difference when a randomized sequence of stimulus was applied (Fig. 8E). The same result was also found in type III cell (Fig. 8B and 8F), indicates that a sequential displayed stimulus is appropriate throughout all experiments. Furthermore, DSGCs' responses to moving background context generally have a large variation among trials in all types of cells. There are two possible causes: one is from cell's intrinsic property to random dots, and another is from the randomness between different trials. To test these, we gave a stimulus in which the background context of specific coverage percentage is the same across repeats. The standard deviation did not decrease neither for a type I cell (Fig. 8C) nor for a type III cell (Fig. 8D). The result indicates that the variation does not come from the randomness across repeats and DSGCs cannot differentiate various background contexts with identical statistical properties, i.e., they only care about the global statistic, such as coverage percentage we used here. Besides, a previous study indicated that the directions of moving background context do not affect the center response (Chiao and Masland, 2003). Based on this finding, we used only the prefer direction of moving background context in this study.

3.3 Spatial scale can alter the response of DSGCs

We considered the stimulus of different spatial scales with the same coverage percentage on the response of DSGCs. In general, the cells had quite different response curves. For type I cells, although a typical response was exhibited when the random dots have 1/8 center diameter size, sustain inhibition was found when the square size increased to 1/4 or 1/2 center diameter (Fig. 9A). Type II cells were the most consistence ones. They had sustain inhibition responses regardless three difference size squares (Fig. 9B). Type III cells, like type I, had a large difference among different square diameters (Fig. 9C). The 1/4 and 1/2 center diameter size square almost had the same response throughout different spatial coverage percentages, but a typical type III cell response curve is different when the square size was 1/8 center diameter.

3.4 Surround excitation may come from the outer receptive field

The immediate surround extent experiment examined the spatial range that inhibition or excitation acts. To achieve this, we adjusted the width of black immediate surround such that the background area got further from the center as the width was set higher. For type I (Fig. 9A) and type II (Fig. 9B) cells, surround inhibition is reduced as the immediate surround annulus gets wider, thus the response curves tend to be flatter. For type III cells (Fig. 9C), although the inhibition in low background coverage is reduced, the excitation became more obvious when motion background displaying in only outer receptive field, as the coverage can induce facilitation to the center stimulation. This result indicates that excitation and inhibition both contribute to the surround effect but in an antagonistic fashion. In the low background coverage, excitation from the outer surround region is completely shunted by stronger inhibition from immediate surround region. When the background coverage is high, the outer surround induced excitation dominates the surround effect that leads to an excitation of overall response.

3.5 Motion coherence does not affect the center response

It has been shown that as long as about 10% of dots moving in coherence, human subjects can distinguish the motion direction. We varied the random dot coherence in this experiment. We found that modulation of the random dot coherence did not affect the cell response (Fig. 11).