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The effect of motion aftereffect on optomotor response in larva and adult zebrafish

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HIGHLIGHTS

- Existence of motion aftereffect (MAE) was investigated in zebrafish.
- Simple gratings were shown to zebrafish in order to induce optomotor response.
- Adult zebrafish's behavior significantly was affected by the grating in test group.
- Further studies are required to establish or refute presence of MAE in larval zebrafish.

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ABSTRACT

Motion aftereffect (MAE) occurs after presenting a moving stimulus to fixed subjects, as an apparent MAE the subject moves in the opposite direction. This natural process provides an excellent tool to investigate visual motion perception. Zebrafish is an important animal model with an extensive molecular toolkit, but there is a lack of the comparative understanding of its perceptual processes. This study was designed to study the optomotor response (OMR), in which the fish swims in the same direction of a moving stimulus in both adult and larvae zebrafish. Simple square wave gratings moving in a specific horizontal direction (with a precise visual angle) were shown to a test group. After an adaptation phase, a static grating was shown for a short period during which the movement of the fish was recorded. In the control group, the same procedure was applied but the grating pattern was shown moving randomly back and forth followed by a static grating. Time spent swimming in either the same or the opposite direction of the adaptation grating was recorded as line index (LI) and non-line index (NI). The results indicate that NI was more than LI for the test group, while there was no significant difference between NI and LI in the control group. These results suggest that MAE occurs in zebrafish causing OMR.

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1. Introduction

All throughout life, inputs from a combination of senses are received and analyzed to better perceive and in turn react to the surrounding environment. Of all our senses, sight is of particular importance and yet many of its complexities remain unrevealed. Innumerable details of each scene are constantly received but how these details are interpreted is still an open question in visual perception. A fascinating area in vision sciences seeks to better understand how visual perception could arise from neurological processes. Many studies have been done to better understand how perceptual groupings could be originated from the interactions of different cells [10,17].

Visual illusions, misinterpretations of incoming sensory information by the brain, are often used to tackle the most interesting problems of perception. Another way of interpreting these illusions is to think of them as the manner, in which, the nervous system has evolved to handle specific stimuli that are common in the natural living environment of the animals. Thus, by studying different visual illusions, we can learn about different visual pathways and the processes that underlie these phenomena. Studies of visual illusions have made possible a better understanding of the neurobiology of vision and at the same time have paved the way to new experiments and possibilities for research in systems neuroscience [8,10,28].

Although the visual sensory system plays a vital role in making sense of the natural environment as a basic function for creating secondary behavior, the process of how the brain takes various inputs and generates meaningful outputs in such forms as locomotion, learning, and memory is still poorly understood. Various biological principles of perception have been extracted from studying different visual illusions in humans and other species. An example is the elegant study by Nieder and Wagnerin in which they

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determined that "owls can see illusory contours and they perceive this illusion in the same way which we do" [27].

Motion aftereffect (MAE) is a well-known and ancient visual illusion that has been well studied in visual perception literature. It occurs after viewing a moving stimulus as an apparent movement in the opposite direction. It was first reported by Aristotle and is considered to be caused by opponent processing, which explains these kinds of illusions according to the existence of competing neural populations in a balance of tonic activity. "According to this view, a subpopulation can be 'fatigued', and another subpopulation can dominate the push–pull competition and briefly control the perception" [10]. Neuroscience literatures has long established the effects of MAE in primates [1]. Also it has been reported in several studies that aftereffect adaptation occurs in different cortical sites of visual cortex, which only exists in primates and mammals [6,23]. MAE studies have had a central role in understanding and developing theories on motion perception and its neural circuits in the brain. Simple neural explanation of MAE was primarily advocated by Sutherland, who was inspired by Hubel and Wiesel's discovery of direction-selective cortical cells in cats. The direction of a moving object might depend on the ratio of firing in neural cells that are sensitive to different motion direction. After prolonged movement in one direction, presentation of a stationary image would produce a lower firing rate in cells that had just been stimulated, thus movement in the opposite direction would appear to occur [23,34].

The adaptation in the motion-selective cells in the primary visual cortex is the common view of MAE and has been verified in a variety of animals including cats [19], rabbits [34], macaques [20] and flies [26], specifying several visual cortical sites that are involved in the process of MAE. New studies have also revealed that MAE may operate at several levels of the motion detection pathways through mechanisms located pre-synaptic to motion-sensitive sites [23,26]. Besides, adaptation has been described as a form of gain of control that exploits the efficiency of the spread of information at multiple levels of the visual pathway [15,23,26]. Furthermore, MAE is tuned both by temporal and spatial frequencies [1,2,37]. For example, in the case of spatial frequency, "the strongest effect of the illusion is created when the adapting grating and the stationary test grating have the same spatial frequencies and for temporal frequency, the strongest effect has been reported in a specific frequency for each of the species studied" [32].

In this study, zebrafish was used as an animal model to investigate the effect of MAE. Zebrafish has been an effective animal model in different fields of biological sciences throughout the years. Among other animal models, they have been a suitable choice in developmental neuroscience investigations. One of the most important reasons that has made this organism a valuable model in vision science is the similarity of its visual system to that of other vertebrates. There are some other important characteristics of zebrafish to be mentioned. Firstly, they breed in abundant numbers and eggs are laid regularly. Secondly, their developmental processes are rapid and they get to maturity within 3 months [4–2]. In addition, as an emphasis on visual analysis, zebrafish is the ideal animal model for its visual system develops rapidly during the larval stage. This might be due to the fact that vision is required in both avoiding predators and capturing food. Zebrafish show signs of visual behavior and capture prey at 5 days post fertilization (dpf) [14]. "The adult zebrafish brain is only about 4.5 mm long and between 0.4 and 2 mm thick and the larval brain at 5 dpf is less than 500 mm thick and 1.5 mm long; making virtually all neurons accessible to multi photon microscopy in vivo" [14,15].

Optomotor response (OMR), a commonly studied visual behavior in zebrafish, is observed as swimming in the direction of moving visual stimuli. It is probably a way to reduce any 'slippage' of the visual surroundings on the retina and could be induced by a moving repetitive stimulus pattern in the environment. This behavior is a valuable paradigm that is mostly used for studying visual system functions. In most studies this pattern consists of vertical stripes, which may be in black and white, different gray contrasts or in color. In general, the accessory optic area (AOS), the pre-tectal complex (PTC), and the tectum opticum (TO) appear to interact with motor areas of the fish. This behavior is also considered to be mediated by red and green cones [22,26,31]. In order to evoke OMR in larvae, computer animated grating is usually presented underneath or beside the chamber where zebrafish are placed and it is observed that they swim in the direction of moving stripes. This behavior is commonly observed at 7 dpf and can also be applied in adult zebrafish [14,17,26].

Zebrafish show a strong OMR that may be stimulated mechanically. OMR can potentially be used to investigate complex visual phenomena such as motion perception in zebrafish. Zebrafish have been providing clues into better understanding the formation and function of visual sensory circuits in an organism [18,25,26]. However, there is not much information available on MAE in zebrafish in the literature and the present study was designed to investigate such behavior in this animal.

2. Materials and methods

2.1. Adults

120 six-month-old male and female adult zebrafish were used in this experiment. The fish were purchased from a local pet store. In order to start conditioning procedures in a new environment, they were accommodated in an aquarium housing system two weeks prior to the test sessions. All subjects were approximately the same size [29,21,30,35]. The fish were housed in two separate 300-mm long plexiglass tanks, each containing 60 adults, one maintaining the test subjects and the other as the control group. The water temperature was kept between 28 and 30 °C, a pH range between 6.8 and 7.0 was maintained and a light cycle of 14 h on and 10 h off was provided [29,12,24]. Fish were fed twice daily with flake fish food containing frozen and live brine shrimp [5,6,4]. All experiments described here were carried out between 1 pm and 6 pm. The fish were housed individually for at least 30 min in order to get naturally schooling fish accustomed to being alone and to provide a means of identifying each fish. The fish were able to swim back and forth in the test tanks, 10–20 mm away from the screen [4,35].

2.2. Larvae

Larvae were bred from crosses of the wild type adult zebrafish. They were raised on a 14:10 h light–dark cycle and the lights were on at 8 am daily. Behavioral testing always took place between 1 pm and 6 pm on day 7 of post fertilization. For each experiment, a shallow 300 mm long plexiglass tank containing approximately 50 larvae was placed in front of the monitor screen and adaptation index (AI) was then measured [23,38] (Fig. 1).

2.3. Movie design and presentation

Movies were created using MATLAB and Psychophysics Toolbox Version 3 (PTB-3 Mario Kleiner, David Brainard 2007). Movies were displayed using a flat LCD monitor located behind the test tank [29,11,30]. Each movie contained two phases. The first phase was a 2-min adaptation phase containing rightward or leftward simple gratings with 30 horizontal degrees, temporal frequency of 0.93 Hz and spatial frequency of 0.08 cycle/degree. During the adaptation phase fish were swimming in the direction of the

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