Studies on Squid Behavior in Relation to Fishing: III. On the optomotor response of squid, Todarodes pacificus Steenstrup, to various colors

Author(s)
FLORES, Efren Ed. C.; IGARASHI, Shuzo; MIKAMI, Takayoshi

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Studies on Squid Behavior in Relation to Fishing

III. On the optomotor response of squid, *Todarodes pacificus* Steenstrup, to various colors*

Efren Ed. C. FLORES**, Shuzo IGARASHI** and Takayoshi MIKAMI**

Abstract

The squid, *Todarodes pacificus* Steenstrup, was subjected to optomotor response (OMR) tests by using screens of various colors. Each screen had two colors matched with the least difference in value and chroma among available colors. Black and white, and gray screens were used as classic and control screens, respectively.

The OMR for the black and white screen was highly significant by comparison with that of the colored screens. The OMR on the colored screens must have been caused by a small amount of value or chroma differences within the sets of colors used instead of their hue differences. This was verified by running a similar test using goldfish with a known color vision. The OMR of the fish showed no significant difference between the black and white screen and the red and green screen. This shows that the fish OMR was caused by the marked hue difference on the red and green screen rather than by the small amount of value or chroma differences. These findings suggest that the squid can not discriminate color, and therefore with regards to the squid line fishing, the color of the jig is not important. What would be important is the contrast of the jig against the surrounding water.

Introduction

The optomotor response (OMR) is a visually induced locomotor response demonstrated by the movement of an animal after an object moves into its visual field. Messenger et al. made use of OMR in showing the absence of color vision in octopus (*O. vulgaris*). They used circular screens with pairs of matched colored stripes in compensation for brightness. Without color vision, these screens would appear as plain gray backgrounds, and therefore should cause no significant amount of OMR on the animal under test. Their results showed that the octopus exhibited no significant amount of OMR against the test screens. For this present study, the authors also applied the OMR test in the same manner as in the above on squid, *Todarodes pacificus* Steenstrup, to help settle the conflicting views on the color vision in squid.

Orlov and Byzov conducted studies on the color vision of the oceanic squid, *Ommastrephes sloani-pacifcus* (=*Todarodes pacificus*; see Voss) with

* An outline of this article was presented at the autumn meeting of the Japanese Society of Scientific Fisheries on October, 1977, Sendai.

** Laboratory of Mechanical Engineering for Fishing, Faculty of Fisheries, Hokkaido University
regards to its color perception using electroretinogram (ERG) technique. The squid retina when exposed to light undergoes a change in electrical potential lasting throughout the exposure. The change in electrical potential increases with the increase in light intensity. In their colorimetric experiment, they were able to match colors with respective intensities so that when applied to the isolated retina of the squid, produced the same change in electrical potential and thus giving the same ERG. In other words, the squid was not conscious of the change of the colors presented. An animal with color vision can still distinguish lights of different colors even when compensated for intensity.

On the other hand, Hara and Hara found a new photosensitive pigment in the squid retina with a different peak absorption (490 nm) as compared to rhodopsin (480 nm). This suggests that the squid retina could possess a system for detecting wavelength. Furthermore, Ito et al. in their study on the ERG of the squid retina, found that the electrical activity of the retina of freely swimming squid differed markedly from those of isolated preparation and of squid wrapped in a jacket with the gills aerated by passing seawater into the mantle.

The authors therefore found it necessary to investigate the color vision of the squid at a different level using live healthy specimen subjected to an optomotor stimulus. Whether the squid has color vision or not, is important not only for basic science but also for practical purposes such as squid line fishing where jigs of various colors are being used without reference to the behavior of the animal to color. The size and color of the jigs in use are mainly based on the experience of the fisherman which differs from one individual to another.

Recently, Yoza made studies on the respective effectiveness of jigs of various colors based on catch data. His results showed red and orange jigs to be the best, and green and fluorescent jigs to be the poorest. However, the available jigs used had significant value and chroma differences. So this leaves open the question whether the red jig after compensated for brightness would still be more efficient that the green jig. It is hoped that the present study would provide basic knowledge on the squid vision which for practical purposes could be applied to squid jig line fishing.

Methods and Materials

Experimental animals were obtained from commercial squid fishing boats operating off Hakodate, Japan, and were transported to the laboratory in aerated plastic pails. The squid were maintained in large concrete tanks and fed daily with sardine fillet (see Flores et al. for detailed description on handling and maintenance procedures).

A total of 65 animals were collected between July and September, 1977 in four batches; 20 squid on July 12, and 15 squid each on July 25, August 15, September 6. Only healthy specimens were used for the OMR tests. The size of the squid ranged from 16.5 cm to 23 cm mantle length. The water temperature in the maintenance tanks ranged from 15° to 19°C (July), 18.5° to 22°C (August) and 18.5° to 21°C (September). The dates of OMR tests and corresponding seawater temperatures are shown in Table 1.
Table 1. Water temperature during optomotor response test.

<table>
<thead>
<tr>
<th>Screen</th>
<th>Date</th>
<th>Water temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gray</td>
<td>July 27</td>
<td>19.5</td>
</tr>
<tr>
<td>Black &amp; white</td>
<td>Aug. 22</td>
<td>21.0</td>
</tr>
<tr>
<td>Yellow-green &amp; compose blue</td>
<td>Aug. 17</td>
<td>22.0</td>
</tr>
<tr>
<td></td>
<td>Aug. 18</td>
<td>21.5</td>
</tr>
<tr>
<td></td>
<td>Aug. 25</td>
<td>20.5</td>
</tr>
<tr>
<td>Red &amp; green</td>
<td>Aug. 12</td>
<td>21.5</td>
</tr>
<tr>
<td></td>
<td>Aug. 18</td>
<td>21.5</td>
</tr>
<tr>
<td></td>
<td>Aug. 25</td>
<td>20.5</td>
</tr>
<tr>
<td>Light red &amp; dark red</td>
<td>Sept. 13</td>
<td>21.0</td>
</tr>
<tr>
<td></td>
<td>Sept. 16</td>
<td>18.0</td>
</tr>
</tbody>
</table>

Table 2. Characteristics of colors used.*

<table>
<thead>
<tr>
<th>Stripe</th>
<th>Value</th>
<th>Hue</th>
<th>Chroma</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Yellow-green</td>
<td>58.73</td>
<td>-28.97</td>
<td>32.80</td>
</tr>
<tr>
<td>Compose-blue</td>
<td>54.89</td>
<td>-25.55</td>
<td>-13.14</td>
</tr>
<tr>
<td>Green</td>
<td>38.06</td>
<td>-25.44</td>
<td>1.04</td>
</tr>
<tr>
<td>Red</td>
<td>35.25</td>
<td>49.38</td>
<td>17.17</td>
</tr>
<tr>
<td>Dark red</td>
<td>31.68</td>
<td>50.45</td>
<td>15.72</td>
</tr>
<tr>
<td>Light red</td>
<td>37.40</td>
<td>57.94</td>
<td>19.74</td>
</tr>
</tbody>
</table>

* data provided by Nakagawa Chemical based on CIE

The optomotor apparatus (Fig. 1) was composed of a circular tank enclosed in a revolving screen. The tank was made of transparent plastic, 2 mm thick, 535 mm diameter and 350 mm high with the water line maintained at 300 mm from the bottom. The white plastic screen, 1 mm thick, 570 mm diameter and 400 mm high was wrapped outside with a black illustration paper to prevent outside light from passing through.

The inner lining of the screen was made of adhesive plastic sheets (Nakagawa Chemical, Tokyo, Japan) cut into 50 mm wide stripes subtending an angle of approximately 10°. Five screens were made with their respective stripes; 1) black and white (BW) screen as shown in Fig. 2, 2) gray (G) screen, 3) red and green (RG) screen, 4) yellow-green and compose blue (YG-CB) screen, and 5) light red and dark red (LR-DR) screen. The properties of the colors used are shown in Table 2.

The screen was mounted on a carriage that could be revolved clockwise or counter-clockwise with six sets of rubber rollers one of which was connected to a variable speed gear box powered by an electric motor. For this experiment, the speed of the screen revolution was kept at 15 cm/sec (5RPM).
The OMR was observed by using a video camera mounted on top the hood placed just above the tank (see Fig. 1). The hood was made of the same material as that of the screen and also wrapped outside with a black illustration paper. A circular fluorescent lamp (30W) was fixed inside the hood to provide light in the test tank. During each test, the OMR was recorded on a video taperecorder (VTR). A playback therefore could provide repeated viewing of the test for better OMR analysis.

For each test, a healthy squid in the maintenance tank was captured by means of a scoop made of perforated plastic bag. A scooped squid was then transferred to a plastic bucket underwater and brought to the optomotor test tank. This
method prevented any possible water-air-water transfer. The optomotor apparatus was so constructed that the hood together with the mounted video camera could be lifted and then swung to either direction to allow the introduction of the squid into the test tank with the screen already set.

After its introduction into the test tank, the squid was allowed to get acclimatized for two minutes before the screen was rotated clockwise for 30 seconds. After this, a one-minute rest was allowed before the screen was rotated this time counter-clockwise for another 30 seconds. Then after a two-minute rest, the squid was taken to another maintenance tank prepared to receive the squid which had been subjected to the OMR test. This completed one OMR test. Since there was no aeration and filtration in the test tank, it was drained after every test and refilled with fresh seawater. The total rotation time of the screen was taken as the maximum optomotor response time. Ten successful tests were run for each screen.

A test was cancelled when the squid remained stationary at the bottom of the test tank for the entire duration of the test as shown in Fig. 3. This behavior was also displayed by some squid in the maintenance tanks that were either moribund or being sought after by other squid. A healthy squid settled to the bottom of the tank also when chased around in the maintenance tank by one of the authors. It seems that a squid that settled at the bottom of the tank was either in a state of shock or moribund. A similar behavior was also observed for Illex illecebrosus illecebrosus in maintenance tanks by Bradbury and Aldrich\textsuperscript{10}, and was described as in a “resting” state. Since the squid used in these tests were those that were healthy, then those that settled at the bottom of the test tank were taken to be in a state of shock and not “resting”. At this state, no OMR was observed even when using the black and white striped screen. A test was also cancelled when the squid upon introduction into the tank would commence swimming in circular pattern and not coming to a “hovering” position after a lapse of two minutes. A test can only proceed when the squid was found generally hovering in the test tank as shown in Fig. 4.

Usually, tests were done in the afternoon with feedings done in the morning. Tests were regularly done every other day for the same squid and when erratic feeding was observed, the squid was discarded. The OMR analysis was made after finishing one series of tests. Viewing the VTR playback on a black and white TV, the OMR time was measured by using a stop watch. At least three readings were made for each test and the average was taken.

To further augment the results of the squid OMR experiments, 25 goldfish, Carassius auratus (Linne) with known color vision\textsuperscript{11,12} were subjected to the same series of tests for comparison. The total length of the goldfish ranged from 60 to 80 mm.

Results and Discussions

Using first the classic stimulus (BW screen), the squid showed compensatory movements by swimming in the same direction as the stripes, which is a clear demonstration of an optomotor response. Three types of swimming patterns were clearly distinguished as OMR; (A) lateral swimming, (B) tail foremost
Fig. 2. Gray, and black and white screens.

Fig. 3. Squid stationary at the bottom of the test tank.

Fig. 4. Squid "hovering" in the test tank.
Fig. 5. Squid optomotor response; (A) lateral swimming, (B) tail foremost swimming, and (C) head foremost swimming; (S) direction of screen rotation.

Fig. 6. A typical sequence of lateral swimming; (I) initial position, (S) direction of screen rotation.

Fig. 7. A typical sequence of tail foremost swimming; (I) initial position, (S) direction of screen rotation.
swimming, and (C) head foremost swimming as shown in Fig. 5. Fig. 6 shows a typical sequence of a lateral swimming. This type of swimming was achieved by a combination of repeated forward and backward oblique movements (1→2→3→4). This may be followed by a fast turn (4→5→6) and then back to oblique swimming (6→7→8). A typical sequence of tail foremost swimming is shown in Fig. 7. Here from the initial position (I), the squid made a turn of approximately 260° making itself parallel to the wall and then proceeded swimming in this manner. With the head foremost swimming which was seldom observed, the squid when about the central area of the tank would swim head foremost towards the wall at an angle and then made itself parallel to the wall. From there, the squid continued swimming as shown in Fig. 5 O. These types of circular swimming patterns were clearly distinguished from random swimming.

Since the speed of the screen revolution was not taken as a parameter in this present study, only pilot tests were conducted to find a speed that was enough to produce an OMR with the test screens having 50 mm wide stripes. Using the black and white striped screen, at 5 RPM, the squid swimming at a more or less regular speed made clear OMR. At 10 RPM, the squid moved fast using jet propulsion (abrupt blowing of water through the funnel); a similar behavior observed when the squid jets away when disturbed. This would then cause more strain on the animal than in running the screen at lower speed. So it was decided to run the tests at 5 RPM for this present study. A future study will be made using various patterned screens run at a number of speeds.

To check whether outside noise would have some effect on the animal under test, a control screen (G screen) made of gray stripes pasted together to form a uniform gray background was used. No OMR was observed for this screen. Generally throughout the test, the squid made itself perpendicular to the wall with the head towards the center and making slight forward and backward movements. The BW screen produced maximum OMR among the screens used. On the average, it takes about four seconds before OMR starts and continued until the end of the 30-second screen revolution time. For the colored screens, the OMR observed were not continuous for most tests. There were interruptions in between with movements across the tank or a pause. This made OMR measurements difficult, and so repeated readings were made necessary.

The mean OMR of ten squid per screen plotted as a histogram, is shown in Fig. 8. The mean OMR for the BW screen was 50.2 seconds which showed a highly significant difference between that of RG screen at 11.1 seconds (F=111.64; d.f.=1/18; P<0.01) and that of the YG-CB screen at 19.1 seconds (F=79.67; d.f.=1/18; P<0.01). On the other hand, the OMR of both colored screens compared showed no significant difference (F=2.3; d.f.=1/18; P>0.05).

With reference to the squid retina, the YG-CB screen compared with the RG screen, has lesser spectral sensitivity difference (see Orlov and Byzov², and Ito et al.⁹) for the spectral sensitivity curve of T. pacificus). However, on the value difference, the RG screen had lesser difference (2.81) than that of the YG-CB screen (3.84). This compensating relationship may be a factor in inducing OMR on the squid for the above screens with no significant difference.

The small amount of OMR recorded for these colored screens must have been
caused by slight differences in value or chroma of the respective pairs of color used as shown in Table 2 rather than the hue difference. A fifth screen, made of colors of the same hue (LR-DR screen) showed the same OMR performance compared with the RG screen ($F=0.18$; d.f.$=1/17$; $P>0.05$). It is clear that the OMR in this case was caused by small value and chroma differences. The spectral sensitivity of the squid is weakest in the red part of the spectrum.\(^5\)

The problem caused by the presence of slight value and chroma differences between the matched colors used, was further resolved by running a similar test on goldfish which has good color vision. The results of the OMR tests on the goldfish are also plotted in Fig. 8. The diagram shows that there is no significant difference between the BW screen against the RG screen ($F=0.74$; d.f.$=1/18$; $P>0.05$), in contrast to the low performance of the squid on the RG screen. However, against the YG-CB screen, there is a slight significant difference ($F=7.76$; d.f.$=1/18$; $P<0.05$) which may be caused by the poor contrast of this screen with reference to the BW screen. Comparing the colored screens, the YG-CB screen against the RG screen showed no significant difference ($F=2.29$; d.f.$=1/18$; $P>0.05$). For the RG screen versus the LR-DR screen, the fish showed a slight significant difference in OMR ($F=6.06$; d.f.$=1/18$; $P<0.05$). The latter screen had poorer contrast than the former.

The above discussion shows that the goldfish which has good color vision had its OMR induced by the hue differences of the stripes in the colored screens rather than by the value or chroma differences. In contrast, the squid had its OMR with
the colored screens induced by the value and chroma differences rather than by the hue differences. This strongly suggests the absence of color vision in squid. Taking this as a fact, the use of different colored jigs for squid line fishing is not important. What would be important is the contrast of the jig against the surrounding water. The degree of contrast necessary to induce an attack by the squid on the jig would be a good topic for future studies on squid behavior.

The authors wish to acknowledge sincerely the kind cooperation of Dr. Ryogo Yuuki, Director, Hokkaido Hakodate Fisheries Experimental Station for the continued use of the experimental tanks.

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