Retention of brightness discrimination in Paramecia, P. caudatum

Catherine M. Mingee
The University of Toledo

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A Thesis

Entitled

Retention of Brightness Discrimination

in Paramecia, *P. caudatum*

by

Catherine M. Mingee

Submitted to the Graduate Faculty as partial fulfillment of the
requirements for the Master of Arts Degree in Psychology

Adviser: Dr. Harvard L. Armus

Committee Member: Dr. Stephen Christman

Committee Member: Dr. Henry Heffner

Dr. Patricia Komuniecki, Dean
College of Graduate Studies

The University of Toledo

December 2009
An Abstract of

Retention of Brightness Discrimination in Paramecia, *P. caudatum*

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Previous research into the possibility of learning in paramecia in this laboratory has shown that these organisms can learn to go to and remain in a specific location based on cathode shock reinforcement. The present experiment was designed to determine whether paramecia could retain (remember) the learned brightness discrimination task. The results indicate that the retention interval for this task in paramecia is shorter than six minutes. It is possible that paramecia can remember this task for longer than zero minutes but less than the interval of six minutes that was used during test. It is possible that remembering, for more than immediate testing, requires a central nervous system.
Acknowledgements

I would like to thank my committee members, Dr. Henry Heffner and Dr. Stephen Christman for their interest and suggestions on my work. I would also like to thank Dr. Gim Koay and Dr. Becky Gurney for their assistance with the computer program. A special thanks to my adviser, Dr. Harvard Armus, for his continued faith and support during the entire process.
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Chapter 1

Introduction

Paramecium behavior has been previously studied for learning capabilities, with some support for the learning of tube-escape behavior as well as discrimination learning. Tube-escape behavior allows the subject to enter a pool of medium after swimming through (escaping from) a small tube. Day and Bentley (1911) used capillary tubing that restricted the movement of paramecia in order to study swimming behavior. They counted reversals of the paramecia’s body position as well as time between reversals as a measure of behavior modification. An increase of reversals and decrease of time between reversals suggested the paramecia were altering their behavior to avoid the sides of the tubing, which were assumed to be aversive. These findings supported the idea of learned behavior modification in paramecia. However, “flexibility”, or the ability to change direction in a small space, could be an alternate explanation for the paramecium’s behavior, rather than the behavior modification through learning that was originally proposed as an explanation (Buylendijk, 1919 as cited in French, 1940). This is because the paramecia may have become better at the movements necessary to reverse their bodies in the tight space of the tube allowing them to move more quickly; that is the paramecia may not have learned anything, they may have simply become more effective
in escaping, possibly as a result of sensitization or some other mechanism. French (1940) used tubing that opened into a pool at the bottom to study escape behavior. He found a decrease in the time it took for paramecia to escape with successive trials, which he related to trial and error learning. Applewhite and Gardner (1973) suggested the liquid medium caused ions to collect in the tube interior, influencing the paramecia’s ciliary action and decreasing escape time. When the capillary tubes were cleaned before each subject, Applewhite and Gardner were not able to reproduce French’s findings.

Gelber completed a series of investigations into paramecium behavior (1952, 1956, 1957, 1958). Paramecia, which feed on bacteria, were shown to approach a bare but formerly bacteria-coated platinum wire after training with the bacteria–coated wire. Non-reinforced subjects were trained with a bare, rather than a bacteria-coated, wire while other control subjects did not have any prior wire exposure. Counts of paramecia on and around sterile test wires revealed significantly more paramecia in the reinforced group when compared to either control group. This research purported to show an association between the wire and food reinforcement, supporting learning in paramecia. However, Jensen (1957a, 1957b) suggested Gelber’s results were not supportive of learning in paramecia because the introduction of bacteria to the culture during reinforcement training and a lack of mixing of the culture between counts might have caused paramecia to be present in the test area for reasons other than learning. To explore these possibilities Jensen studied the effect of Gelber’s reinforcement procedure in distilled water and found that there was a transfer of bacteria to the culture pool from the wire. He then mixed the culture using Gelber’s swirling motion and found it be inadequate for distributing the bacteria throughout the culture. Jensen suggested that
Gelber’s results did not show learning in paramecia because the paramecia were simply accumulating in the bacteria-rich portions of the culture, rather than approaching the wire. In an effort to clarify the contradictions between Gelber and Jensen, a replication of Gelber’s work was attempted by Katz and Deterline (1958). Although results were similar to those of Gelber, the authors concluded that Jensen’s explanation of paramecia presence due to bacteria was more plausible due to the observed behavior of the subjects. Katz and Deterline used an additional group, which they exposed to food material at the end of the trials, and found the paramecia gathered there with no learning experience. They concluded that Gelber’s explanation of paramecia learning to move towards the wire could not be sufficient because groups with no learning exposure displayed similar behavior when bacteria were present. Although multiple studies had been completed to investigate learning in paramecia, the capabilities of the organism were still unclear as of the 1960s.

More recently, Armus and Montgomery (2001) found that cathode shock is attractive to paramecia and can be utilized as reward when conditioning paramecia; they also found that anode shock is aversive. It has been suggested that the attractive quality of the cathode shock is biologically driven by changes in the membrane potential of the paramecium. The changes in the membrane potential cause the paramecia to reorient in space and ‘swim’ towards the cathode stemming from a change in the direction of ciliary movement (Ogawa, Oku, Hashimoto & Ishikawa, 2006). By utilizing cathode shock Armus, Montgomery and Jellison (2006) found that paramecia are capable of brightness discrimination learning. In this study, as in more recent work by Armus and associates, experimental subjects were exposed to short but continuous bursts of 6.5 volt DC cathode
shock when they were in the designated brightness level and location. Time spent in the designated location was recorded and compared to a control group as well as to a paired shock group that received shock at the same times as the experimental subjects, regardless of their behavior. It was found that paramecia exposed to cathode shock stayed in the designated location significantly longer than the control groups did during test trials, when no shock was experienced. A possible alternate explanation for their findings was based on the possibility that paramecia might have exuded an attractive substance while experiencing the cathode shock, which continued to be present during the testing phase. To test this explanation the illumination level was reversed (from right to left or left to right) for the testing trials. The experimental group, which previously received cathode shock, changed side preference to the new ‘cathode’ location although no shock was received; control subjects did not exhibit this change in behavior. These results eliminated the possible secretion explanation. Armus, Montgomery and Gurney (2006) utilized the aversive anode shock and found evidence of discrimination learning as well as extinction. In this experiment the experimental group, which experienced anode shock, avoided the anode half of the trough during training trials but increased the time spent in it during the extinction trials, in which no aversive shock was experienced. This effect was not found in the non-shock control group. These studies suggest that paramecia are capable of learning based on both reinforcement and punishment.

The present study was designed to further knowledge of learning in single celled organisms. Since it has been established that paramecia are capable of learning, it seemed logical to test their retention capabilities. Gelber (1958) looked at retention in paramecia using the previously discussed procedure and found retention in paramecia to
last 3 h. Because of the previously mentioned potential flaws in the experimental design the ‘retention’ may not have been the result of a learned behavior. Huber, Rucker and McDiarmid (1974) looked at tube escape behavior and found retention in escape speed after as much as 150 min. Although this study found retention in escape speed, the initial findings could be explained as a practice effect rather than true learning. As in the training trials it is possible that the ‘retention’ of escape speed was due to the paramecia’s increased capability at swimming in the small space of the capillary tube rather than learning of the actions necessary for quick escape.
Chapter 2

Method

2.1 Subjects and Apparatus

Subjects were 306 paramecia (P. caudatum) from the laboratory-maintained colony, divided into six groups as described below. The colony was housed in a glass jar filled with Ward’s cereal culture medium, as directed by the supplier, and kept loosely covered. The colony was given two to three organic wheat grains each week to supply bacteria on which paramecia feed. The room temperature varied from 70 - 74°F. The colony was originally obtained from Ward’s Natural Science Establishment, Rochester, NY 14692.

The apparatus was constructed from square cross-section quartz tubing that had one side removed to create a trough. The tube ends were sealed with stainless steel blocks, and the entire trough was glued to a microscope slide using Goop brand adhesive, manufactured by Eclective Products, Inc. Electrical stimulation was provided by a Mallory recto power supply, model 12RS6D, set at 6.7 V DC at .74 mA with a duration of 60 ms and repeat frequency of 500 ms. Subjects were observed through a Leitz projection microscope, model 050222, under 22X magnification. The trough was divided into a light and dark side by a piece of gray transparent plastic filter that was placed under the appropriate side of the trough on the microscope stage. Twenty four paramecia
were run before the microscope light bulb exploded. It was replaced with an identical but unused bulb. However, it is possible that the illumination levels for these 24 subjects were lower than for the remaining 87 subjects. The illumination levels of the 250 w CSI lamp were 44132 lux without the filter and 12917 lux with the filter. These illumination levels provided contrast while still allowing the experimenter to see the paramecium in the dark side. Of the final 111 subjects used 24 were exposed to the old illumination levels; the other 87 subjects were exposed to the new light levels.

2.2 Procedure

An eyedropper was used to place a small drop of medium from the main colony onto a microscope slide that was on the stage of a microscope. The blunted needle of a syringe was inserted into the droplet and a single paramecium was ‘scooped’ up and transferred to the mid-point of the prepared trough, which had been filled with approximately 0.15 ml of distilled water and had been placed on the stage of the projection microscope. If a single paramecium was not caught the procedure was repeated until successful, however, after three unsuccessful attempts were made the trough was emptied, cleaned and refilled to prevent an excess of medium in the trough. Subjects were divided into one of three retention interval groups: zero min retention (immediate testing), 6 min retention interval or 12 min retention interval. For each of the retention intervals there was a control group as well as an experimental group. Individual paramecia were observed in the trough for ten 90 s training trials with no intertrial interval. During these trials experimental subjects received reinforcing cathode shock for staying in an “appropriate” location as described below; control subjects did not receive shock. Subjects were then exposed to the neutral stimulus for the duration of the
retention interval before retention was tested. The neutral stimulus was the illumination level the subject was not conditioned to; light for those subjects conditioned to dark and dark for those subjects conditioned to light. Subjects were left on the microscope stage with the filter in the appropriate neutral setting for the entire retention interval. Retention procedure was similar to the training procedure, but no shock was used. The correct side of the trough was the cathode side which consisted of a combination of location (left or right) as well as illumination level (dark or light). Thus, there were four possible combinations (dark/right, dark/left, light/right, and light/left). Both location and illumination were counterbalanced. A computer program recorded the total time of reinforcement each subject received during each trial; that is, the total time (in .5 sec) per trial that each subject remained in the reinforced half of the trough. Time was signaled to the computer by the researcher using a toggle switch to indicate the paramecium’s location. Each paramecium was discarded at the completion of its session and the trough was thoroughly cleaned with distilled water.

Although 306 subjects were initially used, the following exclusion criteria were applied to limit the subject pool: each subject had to experience both brightness conditions within the ten training trials and each subject had to be visible at the end of the last testing trial. Applying these criteria reduced the subject pool to 146 paramecia. The subject pool was then further limited to include only the experimental subjects that had shown learning during the training trials. Subjects that spent more time in the reinforced location during the last two training trials, as determined by the mean, when compared to the mean of the first two training trials were said to have displayed learning. This was done because retention of the subjects was of interest and retention cannot logically be
looked at in subjects that did not learn the task in the first place. This resulted in 111 total subjects, 19 in each of the three control groups and 18 in each of the three experimental groups.
Chapter 3

Results

An independent samples t-test was completed to determine whether there was a preference for either the light or dark side of the trough. There was no significant difference in the times spent in either side for the experimental and control subjects combined or tested separately. The 111 control and experimental subjects that remained after application of the final exclusion criteria were compared using independent samples t-tests at two different times to determine if learning had taken place. The means of trials 1 and 2 combined were not significantly different between the control and experimental groups ($t_{109} = .22, p = .82$) while the means of trials 9 and 10 taken together were found to be significantly different ($t_{109} = 6.35, p < .05$). This pattern continued when the control and experimental subjects were broken down into the three retention intervals and retested. The means of training trials 1 and 2 taken together did not significantly differ from the control for any of the three retention intervals, 0, 6 and 12 minutes ($t_{35} = 1.00, p = .32, t_{35} = .43, p = .67$ and $t_{35} = .92, p = .37$), respectively. The means of training trials 9 and 10 taken together did significantly differ from the control for all three of the retention intervals (0: $t_{27} = 3.58, p < .05$, 6: $t_{28} = 3.68, p < .05$, 12: $t_{35} = 3.69, p < .05$). This suggests that learning did take place in all three groups of experimental subjects.
The means for these analyses can be seen in table 3.1.

Table 3.1: Mean Time (in .5 sec) Spent in Correct Location during Training Trials

<table>
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<th>Mean of Trials 1 &amp; 2</th>
<th>Mean of Trials 9 &amp; 10</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Control subjects</td>
<td>87.3</td>
<td>85.9</td>
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<tr>
<td>All Experimental subjects</td>
<td>84.8</td>
<td>138.1</td>
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<tr>
<td>Zero retention Control</td>
<td>73.3</td>
<td>84.4</td>
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<tr>
<td>Zero retention Experimental</td>
<td>91.8</td>
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<td>6 min retention Control</td>
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<td>6 min retention Experimental</td>
<td>79.8</td>
<td>145.3</td>
</tr>
<tr>
<td>12 min retention Control</td>
<td>100.1</td>
<td>88.1</td>
</tr>
<tr>
<td>12 min retention Experimental</td>
<td>82.8</td>
<td>140.1</td>
</tr>
</tbody>
</table>

Retention was tested by looking at the time the subject spent in the correct location during the first testing trial. It was possible that extinction or forgetting would take place quickly; therefore, the first testing trial was of considerable interest as it would represent the paramecia’s initial location choice. When all three levels of retention were grouped as either control or experimental subjects it was found that experimental subjects spent a significantly longer time in the correct location, $t_{93} = 2.26$, $p < .05$. The zero retention interval shows that the experimental subjects stayed in the correct location for more time than the control subjects, $t_{28} = 2.42$, $p < .05$. The control and experimental subjects in the 6 and 12 minute retention interval groups did not perform at significantly different levels from their controls, $t_{31} = 1.22$, $p = .23$ and $t_{30} = .29$, $p = .78$ respectively. Retention over all ten testing trials was also considered, however it was of less interest as extinction or forgetting was anticipated. An independent samples t-test was completed on the mean of the ten testing trials, grouping all control and experimental subjects, $t_{101} = 1.38$, $p = .17$. The mean of all ten testing trials was also looked at for the control and experimental subjects in their retention time groups. None of these comparisons was
found to be significant; zero min $t_{25} = 1.22$, $p = .24$, 6 min $t_{35} = 1.44$, $p = .16$, 12 min $t_{35} = .09$, $p = .93$. The means for these analyses can be seen in table 3.2.

Table 3.2: Mean Time (in .5 sec) Spent in Correct Location during Testing Trials

<table>
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<th>Mean of Trial 1</th>
<th>Mean of Trials 1 - 10</th>
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</thead>
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<td>All Control subjects</td>
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<td>All Experimental subjects</td>
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<td>84.3</td>
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<td>Zero retention Control</td>
<td>73.3</td>
<td>74.3</td>
</tr>
<tr>
<td>Zero retention Experimental</td>
<td>111.8</td>
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<td>6 min retention Control</td>
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<tr>
<td>6 min retention Experimental</td>
<td>95.9</td>
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<td>12 min retention Control</td>
<td>88.9</td>
<td>81.3</td>
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<tr>
<td>12 min retention Experimental</td>
<td>93.7</td>
<td>80.2</td>
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</table>

The percentage of time spent in the correct location for each of the three retention levels can be seen in Figures 3.1 through 3.3.

Figure 3.1: Percentage of time spent in correct location by Control (n=19) and Experimental (n=18) subjects exposed to zero retention interval
Figure 3.2: Percentage of time spent in correct location by Control (n=19) and Experimental (n=18) subjects exposed to a six minute retention interval
Figure 3.3: Percentage of time spent in correct location by Control (n=19) and Experimental (n=18) subjects exposed to a twelve minute retention interval.
Chapter 4

Discussion

Based on the previous research into paramecia’s retention capabilities completed by Gelber (1958) and Huber et al. (1974) it was expected that paramecia would remember a learned task for a retention interval of several minutes. However, analysis of the data suggests that if a retention interval exists in paramecium it is less than 6 min long. Experimental subjects were able to learn the brightness discrimination task, however, only those that were immediately tested out-performed their control group counterparts in the first testing trial. A difference in time spent in the reinforced location by experimental and control subjects during the first testing trial of the 6 min retention groups can be seen, but the difference is not significant. At the 12 min retention level there is not a noticeable difference in performance during testing trial one. This suggests that extinction or forgetting had already taken place for subjects exposed to 12 min of a neutral stimulus.

Future work to investigate possible procedural parameters can be completed. For example, it is possible that the neutral stimulus, the non-reinforced brightness condition, was not actually neutral for all subjects. To test for this, a different neutral stimulus would need to be provided during the retention interval; however, it is not clear what an
acceptable alternate neutral stimulus could be. It is possible that paramecia are capable of remembering over shorter retention intervals. If so, work utilizing retention intervals ranging from a few seconds to multiple minutes should be looked at before a conclusion as to the retention capabilities of paramecia is drawn. It is also possible that retention, other than immediate retention, requires a central nervous system.
References


Appendix A

Time (in .5 sec) Spent in Correct Side of Trough during Training

<table>
<thead>
<tr>
<th>Brightness</th>
<th>Side</th>
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<th>3</th>
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