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Retention of a Brightness Discrimination Task 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 1 minute. It is possible that paramecia can remember this task for longer than a second but shorter than the 1-minute interval that was used during test. It is also possible that remembering for more than a few seconds requires a nervous system, which paramecia do not have.

Previous investigations into the learning capabilities of the singled-celled organism *Paramecium caudatum* have been inconclusive at best. Although some researchers have found support for tube-escape behavior and discrimination learning, other studies have refuted these results. Day and Bentley (1911) studied the swimming behavior of paramecia in a restrictive capillary tube to determine if the paramecia would change their swimming behavior to avoid the possibly aversive sides of the tube. An increase in the frequency in reversal of the paramecia's position, paired with a decrease in time between reversals, suggested the paramecia were learning to avoid the sides of the capillary tubes. Although the researchers thought their findings lent support to learned behavior modification, Buytendijk (1919, as cited in French, 1940) suggested the change in behavior could be a result of increased "flexibility" of the paramecium. Buytendijk (above) suggested that the paramecia simply became more efficient at escaping the walls of the capillary tube due to some sort of sensitization or other mechanism, rather than a learned behavior.

French (1940) used capillary tubes that opened into a pool of medium, which was thought to be reinforcing, to study tube-escape behavior in paramecia. Over the course of successive trials he found that the time it took for a subject to escape the tube into the medium decreased. French thought this was a clear example of trial and error learning in paramecia, however, Applewhite and Gardner (1973) thought there could be an alternate explanation. French did not clean the capillary tube between trials, which lead Applewhite and Gardner to believe there was some sort of change in the medium inside the tube that was influencing the paramecia's ciliary action and swimming behavior. When they attempted to replicate French's findings with clean tubes before each trial they were unable to do so.

Gelber (1952, 1956, 1957, 1958) completed a series of investigations into paramecium behavior using bacteria as a food reinforcer. Multiple subjects in a pool of medium were trained to approach a platinum wire that was coated in bacteria. A non-reinforced control group of subjects was trained with a bare wire, and a second control group did not have any wire approach training. This procedure allowed Gelber to test for the attraction of the wire vs. food reinforcement. The wire was presented multiple times and, between each presentation the medium pool was gently 'swirled' to mix the liquid and redistribute the paramecia throughout the medium. During testing, each group of subjects was exposed to a bare wire, and counts of

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subjects in the immediate area were completed. Gelber found larger numbers of subjects near the wire in the experimental subject pools compared to either control group. Gelber suggested this research showed association learning between the wire and the bacteria reinforcement. Jensen (1957a, b) thought that Gelber's method of training introduced bacteria into the subject pool which were not present in the control pools. If bacteria were transferred to the medium pool and then not thoroughly mixed the experimental subjects might simply be gathering near a food source. Jensen completed Gelber's procedure in distilled water and found that bacteria were transferred from the wire into the medium pool. He then mixed the pool using Gelber's swirling technique and found that the bacteria were not adequately distributed across the medium and instead stayed near the point of origin. Jensen used this information to dispute Gelber's experiments as examples of learning in paramecia. Katz and Deterline (1958) completed a follow-up to the Gelber/Jensen debate in an attempt to clarify the contradictions. Katz and Deterline used an additional control group that was exposed to bacteria after the exposure to the bare wire was completed and found that the paramecia would gather near the food source without any learning or training experience. Although their experiment produced results similar to those of Gelber, the authors suggested that Jensen's assessment of the procedure and explanation of the data were more plausible based on observations of additional control subjects' behavior during their study.

Although multiple experiments were completed leading up to the 1960s, few reliable conclusions as to the learning capabilities of paramecia could be drawn. In the early 2000s a new series of investigations into paramecia behavior were completed by Armus and his associates. The first of these studies (Armus & Montgomery, 2001) found that if a weak shock, of approximately 6.5 V D.C., were delivered to a single subject located in a small glass trough of distilled water, the cathode area was attractive while the anode area was aversive to paramecia. Recently it has been suggested that the cathode shock is naturally attractive to paramecia because of a change in their membrane potentials. This change in the membrane causes the paramecia to reorient themselves and 'swim' towards the cathode due to changes in the beating of their cilia (Ogawa, Oku, Hashimoto, & Ishikawa, 2006). It is important to note that although the change in cilia may result in a natural motion towards the cathode, paramecia are capable of swimming away from the cathode which makes this a reasonable method of reinforcement.

Once it was established that cathode shock could be used as a positive reinforcer, Armus, Montgomery, and Jellison (2006) used it to condition paramecia in a brightness discrimination task. In this study experimental subjects were exposed to 50 ms 6.5 V D.C. shocks repeated every 0.5 s when they were in the appropriate location. The appropriate location consisted of a pairing of brightness (either light or dark) along with a side (left or right) but was always where the cathode was located. The time the subject spent in the appropriate location was compared to control subjects that did not receive any shock and also to a yoked-control group that received shock at the same time and of the same duration of their yoked experimental partners, regardless of their location in the trough. Experimental subjects stayed in the appropriate side of the trough significantly longer than their control group counterparts during test trials in which no shock was experienced. Although this seems to be strong evidence of learning, an alternate explanation for the findings was proposed based on the idea that the paramecia might have secreted something into the cathode side of the trough while they were shocked that kept them in the area once the shock was removed. To test this explanation the brightness levels of the trough were reversed (from right to left or left to right) during the no-shock testing trials; thus, subjects were trained to go to one side of the trough but tested on the opposite side. The experimental subjects changed location during testing to show a preference for the new 'cathode' location even though they had never been rewarded in that location previously. Control subjects did not show the same location

reversal. This experiment eliminated the possible "secretion" explanation and supported the notion that the paramecia learned the brightness discrimination task.

In a third study Armus, Montgomery and Gurney (2006) presented experimental subjects with shock when they were located in the 'incorrect' side of the trough which contained the anode, which had previously been shown to be aversive; control subjects did not receive any shock. Compared to control subjects, experimental subjects decreased the time they spent in the anode half of the trough during training and gradually increased the time in the anode half during extinction trials, during which no shock was delivered. This evidence of discrimination learning as well as extinction suggests that paramecia are capable of learning using either positive reinforcement or punishment.

Because the previously mentioned studies seem to clearly support the idea that paramecia are capable of learning, it seemed logical to further our knowledge of their learning capabilities by testing their retention capabilities. Gelber (1958) looked at retention in paramecia using the previously discussed procedure and found retention in paramecia to last three hours. 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, that is, increased motor efficiency, or increased, long-lasting, sensitization 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 sensitivity-based capability at swimming in the small space of the capillary tube rather than learning of the actions necessary for quick escape. Hennessey, Rucker, and McDiarmid (1979) carried out a classical conditioning study on paramecia using electric shock (US) and vibration (CS). They found that a CR could be reliably produced in experimental, but not control subjects. They further found that experimental subjects could remember the US/CS pairing and produce the CR 24 hours after exposure. However, their measure of retention involved complex computation of a savings score in a reconditioning phase, rather than pure retention. The current research is focused on pure retention, rather than relearning. As learning is inextricably tied to memory of the learned material or behavior, it seems important to investigate this phenomenon in those unicellular organisms (paramecia) in which learning has already been demonstrated.

Experiment 1
Method

Subjects

Subjects were paramecia (*P. caudatum*) from the laboratory-maintained colony, which was originally obtained from Ward's Natural Science Establishment, Rochester, NY 14692. 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 illumination was low, and the temperature varied from 70 - 74°F.

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. Additionally, the subject pool was 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 be looked at in subjects that did not learn the task in the first place. This resulted in a total of 111 subjects, 19 in each of the three control groups and 18 in each of the three experimental groups.

Apparatus

The apparatus was constructed from square cross-section quartz tubing that had one of the sides removed to create a trough approximately 10 mm long and 5 mm wide. 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 0.74 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 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.

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 randomly divided into one of three retention interval groups: 0-min retention (immediate testing), 6-min retention interval or 12-min retention interval. For each of the retention intervals there was a control group and 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 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 appropriate side 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); as in previous experiments shock was only delivered in the cathode side of the trough. Both location and illumination were counterbalanced across subjects and groups. A computer program recorded the total time of reinforcement each subject received during each trial; that is, the total time 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.

Results

The mean time spent in the 'correct' location, the cathode side of the trough, for each of the three retention levels was converted into percentages of total time and can be seen in Figures 1 through 3.

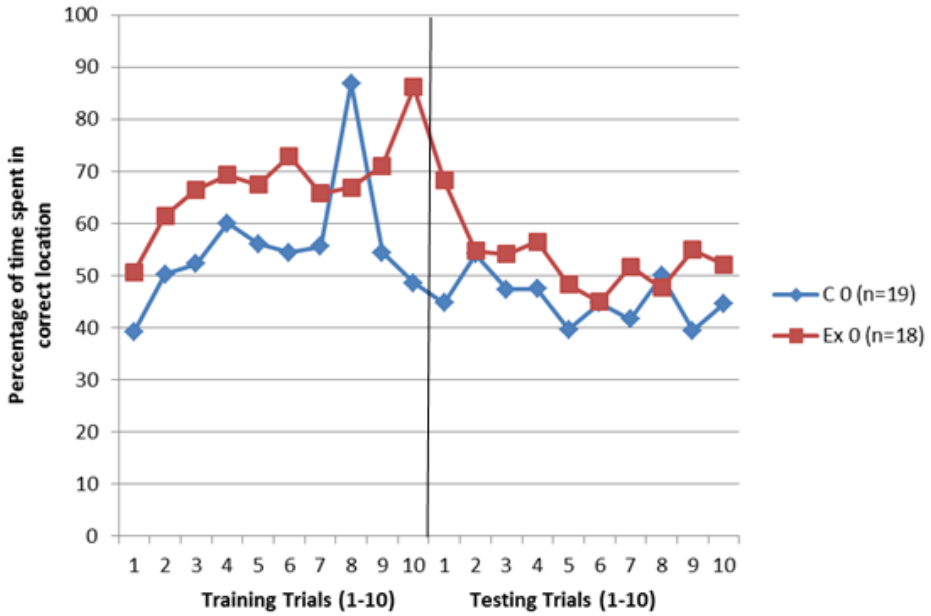

Figure 1. Mean percentage of time spent in 'correct' location by Control (n = 19) and Experimental (n = 18) subjects tested after a 0-min retention interval.

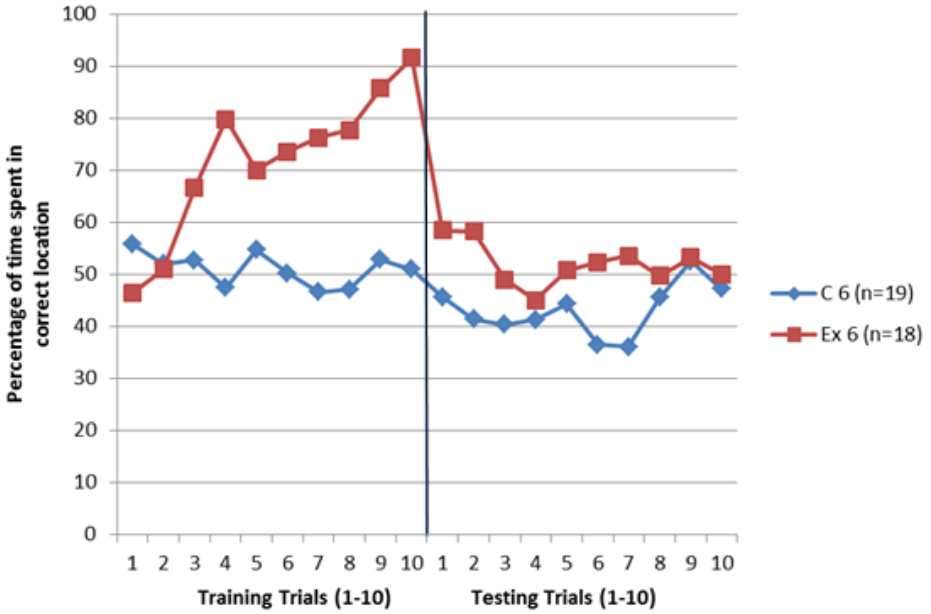

Figure 2. Mean percentage of time spent in 'correct' location by Control (n = 19) and Experimental (n = 18) subjects tested after a 6-min retention interval.

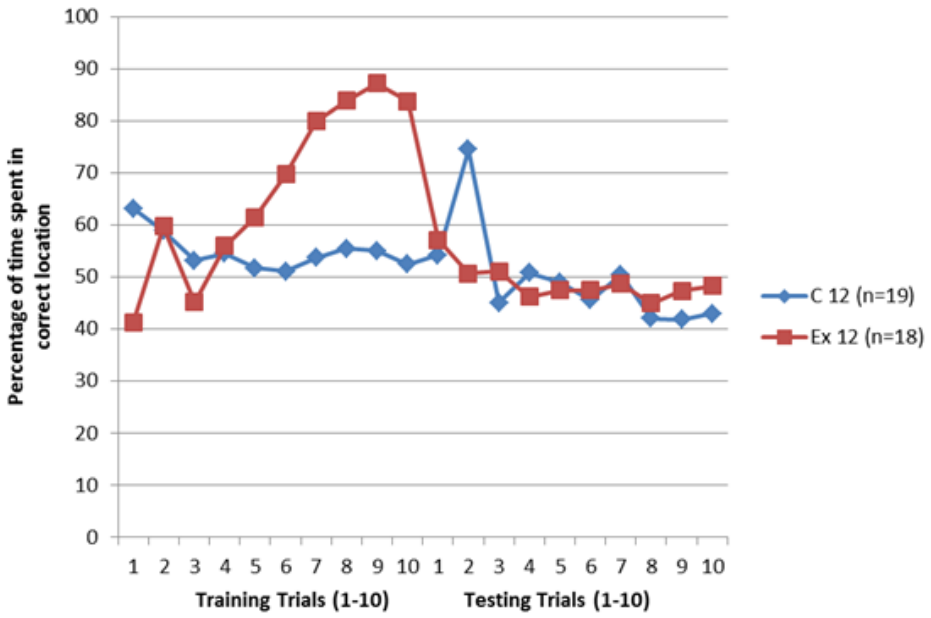

Figure 3. Mean percentage of time spent in 'correct' location by Control (n = 19) and Experimental (n = 18) subjects tested after a 12-min retention interval.

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. As in the exclusion criteria, learning was defined as having a higher mean time in the cathode location during the last two training trials as compared to the first two training trials. The means of trials 1 and 2 together were not significantly different between the control and experimental groups ($t_{109} = 0.22$, $p = 0.82$) while the means of trials 9 and 10 taken together were found to be significantly different ($t_{109} = 6.35$, $p < 0.05$), with the experimental subjects spending a greater amount of time in the cathode area than the control group. This pattern continued when the control and experimental subjects were broken down into the three retention intervals and retested. There was no significant difference between the experimental and the control groups training trials 1 and 2 taken together for each of the three retention intervals, 0, 6 and 12 min ($t_{35} = 1.00$, $p = 0.32$, $t_{35} = 0.43$, $p = 0.67$ and $t_{35} = 0.92$, $p = 0.37$), respectively. The means of the experimental groups for training trials 9 and 10 taken together did significantly differ from the control for all three of the retention intervals (0: $t_{27} = 3.58$, $p < 0.05$, 6: $t_{28} = 3.68$, $p < 0.05$, 12: $t_{35} = 3.69$, $p < 0.05$). This suggests that learning did take place in all three groups of experimental subjects. The means for these analyses can be seen in Table 1.

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 paramecium's initial location choice. When all three levels of retention were grouped as either control or experimental subjects there was a significant difference found in time spent in the 'correct' location, $t_{93} = 2.26$, $p < 0.05$. The zero min retention interval data shows that the experimental subjects stayed in the 'correct' location for more time than the control subjects, $t_{28} = 2.42$, $p < 0.05$. The control and experimental subjects in the 6- and 12-min retention interval

groups did not perform at significantly different levels from their controls, $t_{31} = 1.22$, $p = 0.23$ and $t_{30} = 0.29$, $p = 0.78$ 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, $t_{101} = 1.38$, $p = 0.17$. The mean of all ten testing trials was also looked at for the control and experimental subjects in their respective retention time groups. None of these comparisons was found to be significant, means can be seen in Table 2: 0-min $t_{25} = 1.22$, $p = 0.24$; 6-min $t_{35} = 1.44$, $p = 0.16$; 12-min $t_{35} = 0.09$, $p = 0.93$.

The results of Experiment 1 replicate the findings of Armus et al. (2006) which demonstrated brightness discrimination learning in *Paramecia caudatum*. Additionally, Experiment 1 shows that paramecia have a retention interval that could be as high as 6 minutes but it does not clearly demonstrate what the upper limit of retention in this task is.

Table 1
Mean time spent in 'correct' location during training trials

Experimental Groups	Mean of Trials 1 & 2	Mean of Trials 9 & 10
l Control subjects	87.3	85.9
All Experimental subjects	84.8	138.1
0-min retention Control	73.3	84.4
0-min retention Experimental	91.8	128.9
6-min retention Control	88.4	85.1
6-min retention Experimental	79.8	145.3
12-min retention Control	100.1	88.1
12-min retention Experimental	82.8	140.1

Table 2
Mean time spent in 'correct' location during testing trials

Experimental Groups	Mean of Trial 1	Mean of Trials 1 – 10
All Control subjects	79.0	75.5
All Experimental subjects	100.5	84.3
0-min retention Control	73.3	74.3
0-min retention Experimental	111.8	87.4
6-min retention Control	74.8	70.7
6-min retention Experimental	95.9	85.3
12-min retention Control	88.9	81.3
12-min retention Experimental	93.7	80.2

Experiment 2

Because the results of Experiment 1 suggest the retention interval in paramecia is between 0 and 6 min, a second study was completed with shorter retention intervals. The general methods of the second study were the same as the first, however retention intervals were shortened to 0, 1 and 3 min and a different microscope was used. The microscope used in the second experiment was a direct view binocular microscope with one eye piece removed so it was monocular. Subjects were viewed under 15x magnification. The unfiltered 'bright' condition was approximately 516.7 lux and the filtered 'dark' condition was approximately 269.1 lux.

Results

The mean time spent in the 'correct' location for each of the three retention levels was converted into percentages of total time and can be seen in Figures 4 through 6.

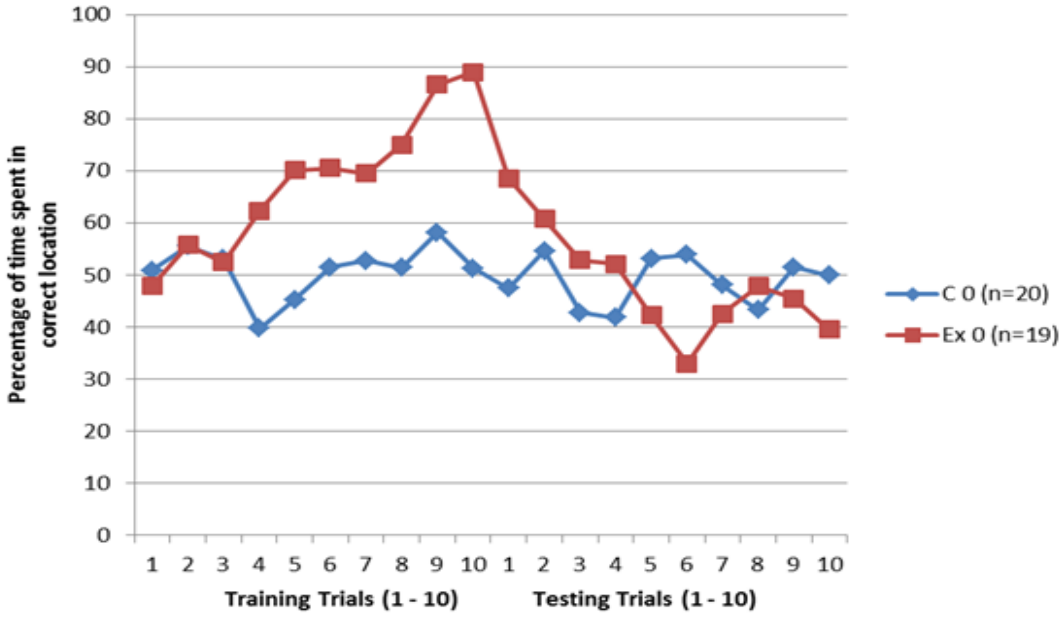

Figure 4. Mean percentage of time spent in 'correct' location by Control (n = 20) and Experimental (n = 19) subjects tested after a 0-min retention interval.

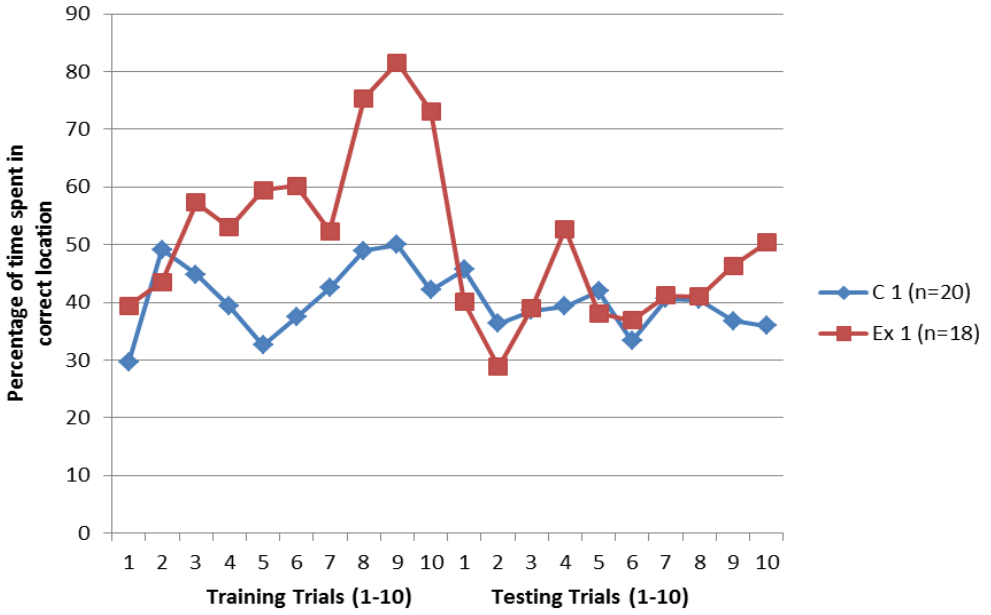

Figure 5. Mean percentage of time spent in 'correct' location by Control (n = 20) and Experimental (n = 18) subjects tested after a 1-min retention interval.

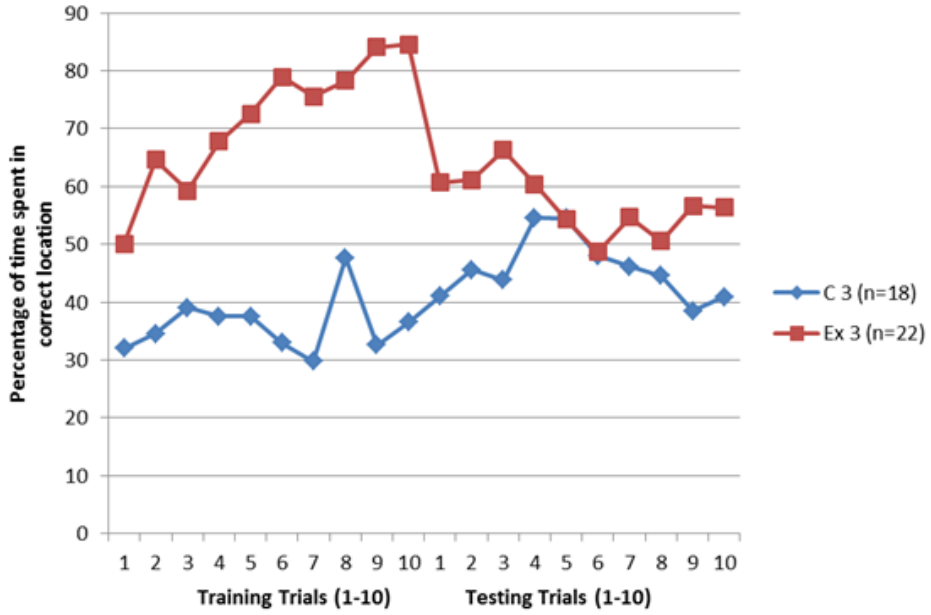

Figure 6. Mean percentage of time spent in 'correct' location by Control (n = 18) and Experimental (n = 22) subjects tested after a 3-min retention interval.

The 117 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. As in Experiment 1, the means of trials 1 and 2 taken together were not significantly different between the control and experimental groups ($t_{116} = 1.65$, $p = 0.10$) while the means of trials 9 and 10 taken together were found to be significantly different ($t_{116} = 8.91$, $p < 0.05$). The means of training trials 1 and 2 taken together compared to control were not significantly different in the 0- or 1- min retention interval groups (0: $t_{37} = 0.16$, $p = 0.86$, 1: $t_{36} = 0.23$, $p = 0.82$). The means of training trials 1 and 2 together were significantly different from the control for the 3-min retention interval ($t_{39} = 2.74$, $p < 0.05$) with the control group spending less time in the 'correct' side of the trough than the experimental group. The means of training trials 9 and 10 taken together did significantly differ from the control for all three retention intervals (0: $t_{37} = 5.46$, $p < 0.05$, 1: $t_{36} = 3.66$, $p < 0.05$, 3: $t_{39} = 7.22$, $p < 0.05$). This suggests that learning occurred in the first two groups of experimental subjects. By looking at the statistics along with the graph for the third group it is reasonable to say learning took place, however, there were some initial differences between the control and experimental subjects. The control subjects in the 3-min retention group performed substantially under chance during training. The means for these analyses can be seen in Table 3.

Retention was again tested by looking at the time the subject spent in the 'correct' location during the first testing trial. When all three levels of retention were grouped as either control or experimental subjects there was a significant difference found in time spent in the 'correct' location, $t_{102} = 2.10$, $p < 0.05$. The zero retention interval replicated the findings of Experiment 1 by showing experimental subjects stayed in the 'correct' location for more time than the control subjects, $t_{37} = 2.10$, $p < 0.05$. The control and experimental subjects in the 1-min retention interval groups did not perform at significantly different levels, $t_{27} = 0.58$, $p = 0.57$. The difference for the 3-min retention interval group was just at significance, $t_{38} = 2.01$, $p = 0.05$. It is

possible that this difference is a result of the control group performing below chance during testing; during testing trial 1 the control subjects spent approximately 41% of their time in the cathode side of the trough. When the experimental subjects were compared to chance the significant difference in cathode location and brightness preference was eliminated, $t_{22} = 1.29$, $p = 0.21$. Retention over all ten testing trials was once again considered; an independent samples *t*-test was completed on the mean of the ten testing trials, grouping all control and experimental subjects, $t_{110} = 1.40$, $p = 0.16$. The mean of all ten testing trials was also looked at based on retention groups. None of these comparisons was found to be significant: 0-min $t_{37} = 0.02$, $p = 0.98$; 1-min $t_{36} = 0.40$, $p = 0.70$; 3-min $t_{38} = 1.84$, $p = 0.07$. The means for these analyses can be seen in Table 4.

As in Experiment 1 the experimental subjects showed learning of the brightness discrimination task. The exact duration of the retention interval is still unclear, but the data from Experiment 2 suggest that paramecia are capable of remembering for only a brief period, less than 1 min.

Table 3
Mean time spent in 'correct' location during training trials

Experimental Groups	Mean of Trials 1 & 2	Mean of Trials 9 & 10
All Control subjects	67.6	72.8
All Experimental subjects	81.3	133.3
0-min retention Control	85.1	87.5
0-min retention Experimental	82.9	140.4
1-min retention Control	63.0	73.7
1-min retention Experimental	66.4	123.8
3-min retention Control	53.3	55.3
3-min retention Experimental	91.8	134.9

Table 4
Mean time spent in 'correct' location during testing trials

Experimental Groups	Mean of Trial 1	Mean of Trials 1 - 10
All Control subjects	71.7	71.0
All Experimental subjects	91.2	79.4
0-min retention Control	75.8	77.8
0-min retention Experimental	109.7	77.6
1-min retention Control	73.1	62.2
1-min retention Experimental	64.1	66.3
3-min retention Control	65.6	73.2
3-min retention Experimental	97.0	91.1

Discussion

Based on the previous research into paramecia's retention capabilities completed by Gelber (1958), Huber et al. (1974), and Hennessey et al. (1979) 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 1 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. When exposed to a 1-min retention interval, there was no noticeable difference in performance of experimental and control subjects. A visual 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. This difference is also seen in the 3-min retention group; the difference is statistically just at the level of significance and may be attributed to pre-existing differences between control and experimental subjects. After a 12-min retention interval there are once again no noticeable differences in performance between control and experimental subjects during testing trial one. This suggests that extinction or forgetting had already taken place for subjects exposed to 1 min or more 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 one minute 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 nervous system, which is absent in paramecia.

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