AMERICAN PSYCHOLOGICAL ASSOCIATION

Journal of Comparative Psychology

ISSN: 0735-7036

2026, Vol. 140, No. 3, 208–222
https://doi.org/10.1037/com0000436

Learning to Discriminate Between Shapes Generalizes to Novel Stimuli in North American River Otters (*Lontra canadensis*): A Preliminary Study on Perceptual Categorization

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Perceptual categorization is grouping objects based on similar physical features. Otters may use categorization to classify predators, prey, and conspecifics. This study was the first to examine whether North American river otters (*Lontra canadensis*) are capable of perceptual categorization. Previously, otters at the Seneca Park Zoo were trained to discriminate between a circle and an equilateral triangle in a two-alternative forced-choice task. In the present study, these otters were presented with novel geometric shapes (e.g., an oval and a right triangle) in Experiment 1 and novel drawings of real-world objects (e.g., a tomato and a tent) in Experiment 2 that could be classified into the circle or triangle category. Two otters performed significantly better than chance during Experiment 1 on subsets of the novel test stimuli. In Experiment 2, one otter was able to categorize drawings of real-world objects into two shape categories of circles and triangles, but only when the triangle-like stimuli were composed of straight lines, not when stimuli were composed of curved lines. The results from both experiments suggest that line type (straight vs. curved) and symmetry may have been salient features for the otters. It appears that otters have the ability to perceptually categorize two-dimensional shapes and line drawings, though further research with additional subjects and different stimuli is needed. Better understanding this ability in otters can expand our knowledge of categorization behavior in a variety of nonhuman animals.

Keywords: perceptual categorization, *Lontra canadensis*, otters, visual perception, stimulus features

Supplemental materials: https://doi.org/10.1037/com0000436.supp

Object categorization is a process where different objects are mentally grouped together into classes. Categorization is an essential ability in humans that allows us to reduce the complexity of the environment, identify and relate objects to each other, limits the need for constant learning, and helps to determine appropriate behaviors to objects (Reed, 2000). Visual object categorization is seen in human infants as young as 4 months old (Spriet et al., 2022). Categorization can also be used by nonhuman animals to

This article was published Online First November 13, 2025.
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Part of this work was presented at the 26th Annual International Conference on Comparative Cognition (Melbourne, Florida, United States). We have complied with American Psychological Association Ethical Standards in the treatment of our animal subjects. We thank the Seneca Park Zoo for allowing us to work with the otters for 3 years on this project, especially General Curator David Hamilton and Assistant Curator John Adamski. David Hamilton provided comments on this article. We thank Rochester Institute of Technology students Matt Altobelli, Tiffani Bragg, Kelsey Beers, Megan Cooper, Kaitlin Gunther, Kera Hampton, Rhiannon Jimenez, Ryan Krieger, Janessa Morelli, Evan Morrison, Trisha Rachfal, Hannah Sheldon, Beth Smith, and Grace Zdrojewski for their help in running research sessions. We also thank Jennifer Dami for producing the schematics showing the experimental setups and Hannah Sheldon for assistance in preparing the stimuli. This project was supported in part by grants to Jessica J. Wegman from the Rochester Institute of Technology College of Liberal Arts and the Department of Psychology. The authors of this study declare no conflicts of interest. This study was not preregistered. The code behind this analysis/simulation is available as the additional online materials on the Open Science Framework repository and can be accessed at https://osf.io/9rycf/.

Jessica J. Wegman contributed equally to conceptualization and served in a supporting role for data curation, funding acquisition, methodology, and visualization. Kenneth Tyler Wilcox served as lead for data curation, formal analysis, software, validation, and visualization and served in a supporting role for methodology, writing–original draft, and writing–review and editing. Caroline M. DeLong served as lead for conceptualization, methodology, project administration, resources, and supervision and served in a supporting role for formal analysis. Jessica J. Wegman and Catina Wright contributed equally to investigation. Jessica J. Wegman and Caroline M. DeLong contributed equally to writing–review and editing and writing–original draft.

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serve similar purposes as in humans. Categorization may increase an animal's fitness by aiding in identifying predators, prey, conspecifics, and determining if a novel object is dangerous (Schluessel & Duengen, 2015). To date, there has not been any research published investigating object categorization in North American river otters.

Pusch et al. (2023) provided different definitions of categories and concepts that are helpful for understanding the underlying cognitive processes. A perceptual category is formed when stimuli are grouped together based on similar physical features (Pusch et al., 2023). Concepts are formed when stimuli are grouped together even when they lack similar physical features. Grouped stimuli that signal the same consequence are called equivalence classes. Grouping stimuli into concepts demands more abstract cognitive processing than perceptual categorization and would require different mental representations of the stimuli.

In categorization research different types of categories can be studied. One type is a natural category, which forms through experience with the world. The specific categories can have variable definitions based on the individual's experiences that lead to the creation of the natural category (e.g., furniture). There are also artificial categories, which are defined by a specific set of rules, property, or criteria. Artificial categories are defined by humans and have clear definitions that are agreed upon by everyone (e.g., geometric shapes such as a triangle, which is a three-sided polygon that consists of three edges and three vertices). In the current study, we tested perceptual categorization using stimuli from artificial categories (geometric shapes). This was the first study to examine any form of categorization in North American river otters, and therefore we wanted to start with a perceptual categorization task using basic-level artificial categories that was less cognitively complex than a concept learning task and would include stimuli that have features that are easy to systematically manipulate (e.g., changing the lines from straight to curved).

While there has been no research investigating categorization in river otters, there have been many studies that found other nonhuman animals in both terrestrial and aquatic habitats are capable of some type of categorization. A wide variety of mammals have been investigated relating to their categorization abilities, including dogs (e.g., Autier-Dérian et al., 2013; Fugazza & Miklósi, 2020; Range et al., 2008), rats (e.g., Brooks et al., 2013; Vinken et al., 2014; Wasserman et al., 2012), goats (e.g., Meyer et al., 2012), baboons (e.g., Bovet & Vauclair, 1998, 2001; Medam et al., 2016), orangutans (e.g., Marsh & MacDonald, 2008), and monkeys (e.g., Fabre-Thorpe et al., 1998; Girard et al., 2008; Kawaguchi et al., 2019; Macé et al., 2010; Murai et al., 2004; Roberts & Mazmanian, 1988; Sigala et al., 2002; Smith et al., 2012; Spinozzi et al., 2004; Vogels, 1999). Birds have also been found to be able to categorize stimuli, with copious research on pigeons (e.g., Aust & Huber, 2010; Castro et al., 2020, 2021; Cook et al., 2013; Diaz et al., 2021; Güntürkün et al., 2018; Herbranson et al.,1999; Lazareva, 2021; Lazareva et al., 2004; Pusch et al., 2023; Roberts & Mazmanian, 1988; Soto & Wasserman, 2012) and a study on shrike (Němec et al., 2021). Fish have been found to categorize stimuli in two studies, namely, gray bamboo sharks (Schluessel & Duengen, 2015) and cichlids (Schluessel et al., 2012). Recently, insects such as bees have also been found to have categorization abilities (e.g., Howard et al., 2022; Xu & Plowright, 2022). These studies show that categorization abilities are widespread in different animal taxa, but categorization has not yet been investigated in any type of mustelid (e.g., otters, mink, ferrets, badgers, and weasels).

River otters are a good candidate for a test of perceptual categorization abilities because they use their visual perception to help them identify prey and prey locations (Carss, 1995). River otters have a varied diet that primarily includes fish, but also includes crustaceans and insects (Kruuk, 2006). Additionally, river otters may consume birds, smaller mammals, reptiles, and amphibians opportunistically, though not as a main staple of their diet. River otters preferentially choose prey based on prey size and speed that result in the greatest metabolic payoff (Crimmins et al., 2009). Thompson and Stelle (2014) found that captive river otters had a preference for brown trout, which the otters may have used their vision to identify. Although it is believed that river otters frequently use olfaction and touch to identify aspects in their environment such as prey, vision likely provides important complementary information. Green (1977) found that it can take European river otters (*Lutra lutra*) up to 4 times as long to find prey in turbid waters compared to clear waters, suggesting that river otters use their vision while foraging and supplement with tactile perception when necessary.

It is likely that vision is essential to many otter species both above and below water, especially when foraging. Otters may rely on more tactile perception while underwater than they do in the air because of poorer visual acuity when they are underwater (Kruuk, 2006). There has been very little research on visual perception in North American river otters, but there have been some studies done on visual acuity and color vision in other otter species. The visual acuity of sea otters is similar to that of some pinnipeds (e.g., California sea lion; 5.5 min of arc in air and underwater), while the visual acuity of Asian small-clawed otters is more similar to that of the mink when tested in the air (mink; 15 min of arc; Sinclair et al., 1974). Previous research has indicated that other species of otters such as sea otters (*Enhydra lutris*) and European river otters (*Lutra lutra*) possess dichromatic color vision (Levenson et al., 2006; Peichl et al., 2001). Sea otters (*Enhydra lutris*) and European river otters (*Lutra lutra*) possess two types of cones, S cones (green to red sensitive) and M/L cones (blue to ultraviolet sensitive; Levenson et al., 2006; Peichl et al., 2001). Svoke et al. (2014) found that one Asian small-clawed otter (*A. cineria*) was able to discriminate between gray and white, green, blue, and red (but not green vs. red). These studies suggest that North American river otters likely have dichromatic color vision and visual acuity between 6 and 15 min of arc if they are similar to other otter species.

There have been only two published studies investigating visual perception in North American river otters (DeLong et al., 2019; Slack, 1966). One behavioral study examined shape discrimination in two river otters (Slack, 1966). The otters were presented with two-dimensional (2D) stimuli, including black and white simple and complex shapes, symbols, and letters (e.g., circle, square, triangle, arrows, the letters E, S, V, F), in a two-alternative forced choice task. One otter was able to discriminate between different pairs of stimuli, but the other otter could only successfully discriminate between two pairs (Slack, 1966). This study did not look at the specific features used by the otters to make their decisions. A more recent study looked at two North American river otters' ability to discriminate between 2D stimuli using multiple visual features (DeLong et al., 2019). One otter was trained with a red circle as the rewarded positive stimuli (S+), and the other otter was trained with a blue triangle as the S+.

The otters were tested on their ability to discriminate between objects when one of two key features was eliminated (color or shape). During testing sessions, the otters were presented with novel shapes (e.g., blue hexagon vs. red hexagon), colors, (e.g., black circle vs. black triangle) or shape-color combinations (e.g., blue circle vs. blue triangle). Both otters could discriminate between stimuli varying both shape and color, and one of the otters could discriminate between novel test stimuli when either shape or color were removed as salient features. DeLong et al.'s (2019) study suggests that river otters can use shape as a feature to discriminate between different objects, so they could potentially categorize objects based on shape.

The current study investigated perceptual categorization in North American river otters using 2D stimuli that can be classified into two artificial categories: circle and triangle. A circle is defined as a closed two-dimensional figure in which the set of all the points in the plane is equidistant from a given point called the center. A triangle is defined as a three-sided polygon that consists of three edges and three vertices. Many categorization studies have used 2D stimuli (e.g., Marsh & MacDonald, 2008; Medam et al., 2016; Meyer et al., 2012; Schluessel & Duengen, 2015; Vogels, 1999). We used 2D stimuli because our otters were familiar with circle and triangle stimuli from our previous research (DeLong et al., 2019), and because the features of circles and triangles were easy to systematically manipulate. The test stimuli in both experiments were designed with the presence or absence of specific physical features that are shared with circles and triangles such as symmetry and line type (curved lines vs. straight lines). Presentation or removal of isolated category features is one approach to determining which features control categorical behavior (Lazareva, 2021).

The current study consisted of two experiments. Experiment 1 included novel geometric shapes (e.g., a right triangle and an oval) with some shared physical features as the equilateral triangle and circle used in training. We predicted that the otters would be able to correctly generalize their learning of the circle and triangle stimuli in our previous study (DeLong et al., 2019) to the novel stimuli in the current study, showing preliminary evidence of perceptual categorization. Experiment 2 included line drawings of real-world objects in which their overall shape matched a circle or triangle (e.g., a baseball and a watermelon slice). We chose these stimuli because they had some of the same physical features as the stimuli from Experiment 1 that would be easy to systematically manipulate, but they would add some visual complexity. We predicted otter performance would be lower in Experiment 2 relative to Experiment 1 because of the unfamiliar nature of the stimuli, but that the otters would still be able to perceptually categorize the stimuli.

Experiment 1

Method

Subjects

The subjects were three unrelated North American river otters, two females (Heather and Ashkii) and one male (Sailor), that resided at the Seneca Park Zoo in Rochester, New York, United States. Heather was 16 years of age and Sailor was 12 years of age at the start of this study in April 2019. Ashkii was 4 years old when she began the study in September 2020. Heather and Sailor were trained to perform the two-alternative forced choice task in a past study (DeLong et al., 2019). A veterinary exam in early 2019 revealed that Heather was developing cataracts, which had not been found during the previous study where she succeeded in discriminating among stimuli that varied in shape and color (DeLong et al., 2019). Heather's condition was monitored throughout the training phase in the study. It did not seem that Heather was having significant visual difficulties during the training phase given her behavior and performance, thus she advanced to the test phase once she reached the training criterion. Unfortunately, Heather died in August 2019 because of age-related health issues but successfully completed part of the test phase in Experiment 1 (seven out of 12 sessions). Veterinary exams did not reveal any evidence of eye disease in Sailor or Ashkii, so it was assumed they both had normal vision. Sailor completed both the training and test phase. Ashkii had never participated in a two-alternative forced choice task prior to this study. Ashkii participated in the training phase but did not progress to the test phase because of time constraints.

The otter habitat at the Seneca Park Zoo included two separate habitats, the on-exhibit habitat, which was viewable for guests, and a second off-exhibit habitat for zoo personnel only. The on-exhibit habitat (33.5 m × 18.5 m) was a naturalistic habitat composed of a large upper pool (9.1 m × 2.4 m × 1.8 m), a lower pool (9.1 m × 4.6 m × 1.5 m), and a waterfall connecting the two. The habitat contained dirt banks containing flowers, grass, shrubbery, felled conifer trees, and solid as well as hollowed out logs. Enrichment devices were also spread throughout this habitat including hollow plastic tubing, plastic rafts, buoys, hammocks, and beds filled with straw. Enrichments devices in the upper pool were removed from the central area prior to a session. The on-exhibit habitat also contained a large observation glass window that was split into three panes (central window = 3.5 m in length, side windows = 1.7 m in length), which provided an indoor space for guests to view both the underwater and above water portions of the habitat.

The off-exhibit habitat included two separate areas with a cement foundation and surrounded completely by chain-linked fencing with a metal roof covering the entire habitat. The areas were divided into separate stalls connected by gates that could be opened by the animal care staff to move the animals between stalls. Each pen contained dens (plastic dog houses filled with straw) and enrichment devices such as hammocks, blankets, hollow plastic tubing, buoys, plastic slides, and small plastic pools. Heather and Sailor were housed together, up until Heather's death, after which Sailor was housed with Ashkii. The otters had access to three adjacent stalls (each pen was approximately 2 m × 1.5 m). The Seneca Park Zoo was home to another otter in 2019, Sara, who was kept separated from Heather and Sailor. Sara had a separate pen off to the side of Heather and Sailor's adjacent stalls. She also was able to access the on-exhibit area, but not when Heather and Sailor were on the exhibit. Sara did not participate in the current study because of health issues.

The typical daily diet for the otters was determined by the animal care staff at the Seneca Park Zoo. It consisted of approximately 230 g of fish—capelin (*Mallotus villosus*), herring (*Clupea harengus*), and/or mackerel (*Scomber scombrus*)—in the morning, as well as one cup of dog chow mixed with 280 g of horse meat in the afternoon. During testing and training sessions, the otters were fed 75%–100% of their morning diet of fish or the same amount of their afternoon diet of meat as was done in a previous study with these otters (DeLong et al., 2019). Food was utilized as their primary form of reinforcement. The otters were always fed their entire daily diet regardless of their performance during training and test sessions.

This project was approved by the Seneca Park Zoo Institutional Care and Use Committee (Protocol 03302019), and the Rochester Institute of Technology Animal Care and Use Committee (Protocol 04162018 and Protocol 2020-2). This project was conducted according to Ethical Standards of the United States.

Stimuli

All stimuli were printed in the center of a black square outline (27 cm × 27 cm) on heavy matte paper squares (27.5 × 27.5 cm). A 5-cm loop of clear monofilament line was attached onto the back of the stimuli with heavy-duty tape. Zip ties were fastened in a 1-cm loop to the monofilament so the stimuli could be hung in the correct position. A 6-cm metal carabiner was attached to the monofilament of Sailor's stimuli so they could be hung on the wall of his habitat. Two flat square metal weights (4 cm × 4 cm) were placed on the back of Sailor's stimuli 1.25 cm from the bottom edges so that they were not visible from the front. These weights kept the stimuli from moving while they were being viewed. Sailor and Ashkii's stimuli were laminated to prevent deterioration since they were able to directly contact the stimuli (see the Procedure section).

Heather and Sailor's training and test stimuli were all black outlines of shapes with nearly equal surface areas (a maximum difference of 10 cm^2 among stimuli, see Table 1). An equilateral triangle and a circle were the training stimuli for Heather and Sailor (Figure 1A). Heather's S+ was the circle while Sailor's S+ was the triangle. This is consistent with their reinforced stimuli in a past experiment, although in the current study the stimuli were black outlines instead of a solid blue triangle and a solid red circle (DeLong et al., 2019, see Figure 1). Heather and Sailor had two sets of training stimuli. Training Set 1 (black outlines of a circle and equilateral triangle), used for the first 10 sessions and 17 sessions for Heather and Sailor, respectively, was of the same surface area of the circle and triangle used in a previous study (DeLong et al., 2019). At sessions 11 and 18 for Heather and Sailor, respectively, Training Set 2 (black outlines of a circle and equilateral triangle with equal surface areas) was introduced that approximately matched the areas of the test stimuli in the present study (see Table 1).

Ashkii had three sets of training stimuli because she had never participated in a two-alternative forced choice task. She proceeded through similar training sets as Heather and Sailor did in the previous study (DeLong et al., 2019). Training Set 1 included three-dimensional (3D) objects made of painted metal, a yellow square as the S+ and a blue triangle as the S−. The 3D stimuli had the same length and width as the 2D stimuli in Training Set 2 but were 0.3 cm thick and included 11.4 cm by 2.5 cm handles on the back. Training Set 2 included a 2D yellow square (S+) and blue triangle (S−) printed on paper (with the same approximate surface areas). Training Set 3 included 2D black outlines of a square (S+) and triangle (S−) to match Heather and Sailor's training stimuli.

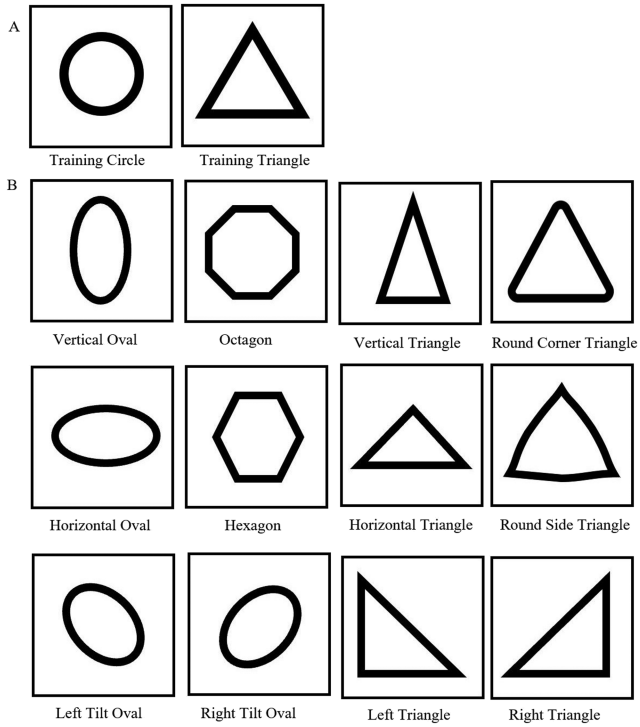
Only Heather and Sailor viewed test stimuli since Ashkii did not progress to the test phase. The test stimuli contained six stimuli to be categorized as circles and six stimuli to be categorized as triangles (see Figure 1B). The test stimuli were created by modifying different defining features of the training triangle and circle. The training triangle's defining features were sides with straight lines, equal length sides, three equivalent angles, and vertical symmetry (symmetry across the *y* axis). The training circle's defining features were horizontal symmetry (symmetry across the *x* axis), vertical symmetry, and curved lines. The features of symmetry and line type were altered for the novel test probes. For the triangle test probes, two stimuli retained both symmetry and straight lines (vertical and horizontal triangle), two stimuli eliminated straight lines or corners but retained symmetry (round side triangle and round corner triangle), two stimuli eliminated symmetry but retained straight lines (left and right triangle). For the circle test probes, two stimuli retained

Table 1
Stimulus Dimensions for Experiment 1

Triangle category stimuli	Area (cm^2)	Circle category stimuli	Area (cm^2)
Training triangle	**189.90**	Training circle	**181.46**
Vertical triangle	188.40	Vertical oval	182.45
Horizontal triangle	186.20	Horizontal oval	183.15
Right triangle	188.16	Right tilt oval	183.78
Left triangle	188.16	Left tilt oval	183.78
Round side triangle[a]	185.85	Hexagon	187.70
Round corner triangle[a]	180.42	Octagon	185.60

Note. All stimuli were within 180–190 cm^2. The training stimuli are shown in bold.
[a] Approximate area.

Figure 1
Stimuli Used for Training and Test Sessions in Experiment 1



Note. Refer to Table 1 for stimulus dimensions. Each square outline surrounding the shape was 27 × 27 cm. (A) Training stimuli that were used during the training phase as well as in the test sessions. Heather's S+ was the circle, and Sailor's S+ was the triangle. (B) Test probe stimuli along with their names. The names of the stimuli were not included on the stimuli that were presented to the otters.

symmetry and curved lines (vertical oval and horizontal oval), two stimuli eliminated vertical and horizontal symmetry but retained curved lines (right tilt oval and left tilt oval), and two stimuli eliminated curved lines but retained symmetry (hexagon and octagon).

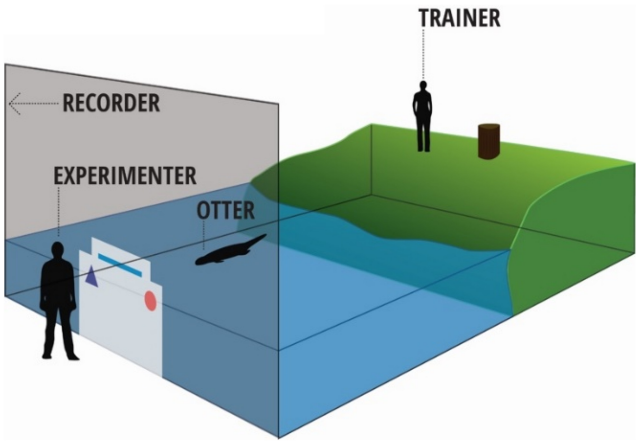
Experimental Setup

Two different experimental setups were used at the Seneca Park Zoo, one for Heather and one for Sailor and Ashkii (because of a protected contact protocol for Sailor and Ashkii). Both otters had to remain in their enclosure when interacting with zoo staff, rather than zoo staff having the ability to be in the habitat like in Heather's case. The same animal care staff served as the animal trainer for the entire study. Multiple research assistants served as the experimenter or recorder for each session.

Heather was trained and tested in the "Creatures from the River's Edge" building that houses the otter exhibit at the Seneca Park Zoo. Figure 2 shows the general experimental setup used in this building. Two 5-cm plastic suction cups with hooks were placed 30 cm apart on the glass window. The stimuli were hung from the hooks during training and testing sessions. A stimulus board made of 0.64 cm thick plywood and painted white (138 cm × 122 cm) was positioned against the window to shield the experimenter's body from the view of the otter, shield the stimuli from the otter when they were repositioned between trials, and provide a uniform background for the otter when she was viewing the stimuli (see the online supplemental materials). There was a narrow opening (5.7 cm × 59.4 cm) at the top of the board where the experimenter was able to look through and view Heather's choice. Two-way portable radios (Midland GXT 1000 series, Midland Radio Corporation) were used so the experimenter could communicate with the trainer when the otter made a choice, as well as to indicate when to start and end a trial and the session.

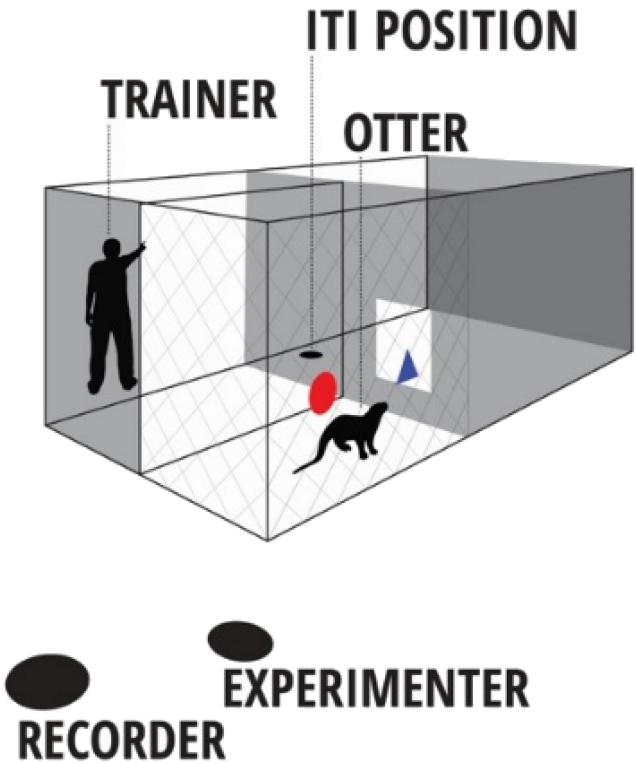
Sailor and Ashkii' sessions were conducted behind the Creatures From the River's Edge building inside the enclosure where they resided when they were in the off-exhibit area. Figure 3 shows the general experimental setup that was used in this area. Two 6 cm metal carabiners were hung on the mesh wall 76 cm apart and 40 cm from the top of the cement floor. The stimuli had a 3-cm monofilament loop to which 5.5 cm carabiners were attached. These small carabiners were then able to be connected to the larger carabiners, so the stimuli were able to hang against the mesh wall. The mesh wall consisted of wires creating a diamond shape with openings that were 3.8 × 3.8 cm. Since the experimenter was able to stand out of view of the otters with this setup a stimulus board was not used. The experimenter and recorder both stood about 3.5 m away from

Figure 2
Heather's Experimental Setup



Note. The blue (dark gray) triangle and red (light gray) circle pictured in the figure were used in a previous study (DeLong et al., 2019) and represent the placement of stimuli in the current study (although not used in the current study). The experimenter stood inside the building behind the stimulus board and hung the stimuli from suction cups on the glass window while the otter was on shore. The experimenter used a two-way radio to inform the trainer the trial could begin. The trainer then cued Heather to jump into the water, swim up to the stimulus board, and make her choice by touching her nose to the glass. The otter was positively reinforced with food for correct choices and called back to shore during the ITI. ITI = intertrial interval. The recorder stood inside the building out of view of the otter. See the online article for the color version of this figure.

Figure 3
Sailor and Ashkii's Experimental Setup



Note. The blue (dark gray) triangle and red (light gray) circle, pictured in the figure, were not used in this study but represent the placement of stimuli in the current study. The otter began each trial in the ITI position, which is separated from the experimental area with a wall and a gate. The recorder began the session after the experimenter hung the stimuli from the mesh wall on the enclosure and was out of the otter's view. Sailor was then cued to enter the experimental area through the gate and make his choice by standing on his hind-paws and touching his nose to a stimulus. The recorder announced to the trainer if the otter was correct or wrong. The trainer positively reinforced the otter with food for correct choices in the ITI position. ITI = intertrial interval. See the online article for the color version of this figure.

the enclosure and positioned behind the otter to stay out of view during their choice. Two-way radios were not used since the trainer was within hearing range of the experimenter and recorder in this setup.

Procedure

The procedure followed the one previously used in a similar study conducted with these otters (DeLong et al., 2019). Training and testing for Heather and Sailor occurred 3 days per week at the zoo starting at 8:45 a.m. for morning sessions or at 4:00 p.m. for afternoon sessions from April 2019 through November 2019. Ashkii was always trained in the mornings starting at 8:45 a.m. from September 2020 through November 2020, and March 2021 through July 2021. During morning and afternoon sessions efforts were made to minimize distractions from zoo guests. Morning sessions took place before the zoo was open to guests and afternoon sessions took place right before the zoo closed for the day (when the building was empty or nearly empty). The otters were trained and tested in dry as well as light rain conditions, so long as they were willing to participate. If an otter left the testing area during a session and did not return after 15 min of attempting to regain their participation, the session ended. If the otter did not make contact with any stimulus during a trial, it was considered no choice. In this case, the trial was repeated until the otter made a clear choice. The otters were not trained or tested during strong winds, heavy rains, or heavy snow. A modified pseudorandom Gellerman series was used to determine the side the S+ was placed on for each trial in both training and testing sessions (Gellermann, 1933). The S+ was never shown on the same side more than twice in a row to prevent potential side biases, as these otters were prone to side biases in previous research (DeLong et al., 2019).

Training Phase

All otters used only the training stimuli during this phase (Figure 1a shows Heather's and Sailor's stimuli). At the start of a session for Heather, all otters were removed from the upper and lower pools in the exhibit by the trainer while two research assistants began the setup for the session. The suction cups were placed in the correct positions on the glass and the stimulus board was placed against the glass wall (see Figure 2 for a schematic of Heather's experimental setup). The experimenter radioed the trainer to begin trial one once all the materials were setup. The trainer opened the gate for the otter to enter the testing area and then cued the otter to move to the start position on a tree stump at the edge of the pool. The stimuli were hung from the hooks on the suction cups in their correct position, at which time the experimenter called "ready" over the radio to the trainer. The trainer then cued the otter to approach the stimuli by pointing at the glass window and saying "target." The trainer faced away from the stimuli to not inadvertently cue the otter to a certain side. Heather dove into the water and swam towards the stimuli, making her choice by pressing her nose against the glass in front of a stimulus. The experimenter viewed Heather's choice and radioed the trainer to report if she was correct or wrong. If the otter made a correct choice, the trainer bridged the otter with a clicker and threw a piece of the food reward into the pool directly next to Heather for her to eat. The trainer then cued the otter (by pointing and saying "land") to return to the start position for the next trial. If the otter made a wrong choice the trainer only cued the otter back to the start position for the next trial without giving a click or a food reward. When the otter made any choice, the experimenter immediately removed the stimuli from the hooks and placed them behind the board. The start and end time, date, weather, and any potential distractions were recorded for each session, as well as the otter's choice for each trial, and any other notable behaviors or conditions that occurred during each trial.

Before beginning Sailor and Ashkii's sessions, the trainer removed all enrichment items from the experimental area and also sprayed down the floor to remove any odor cues or physical distractions. The otters were kept in a different area of the enclosure away from the experimental area while the two research assistants prepared for the start of a trial. The experimenter would hang the first pair of stimuli from the carabiners and move out of view of the otter. The recorder called "ready" to begin the first trial and the trainer then opened the gate to let the otter into the experimental area. The trainer cued the otter to approach the stimuli by pointing, and to make a choice by saying "target." This process occurred while the trainer looked away from the two choice stimuli to not inadvertently cue the otter. The otters indicated their choice by standing up on their hind paws and placing their nose near the stimulus. The recorder viewed the otter's choice and said correct or wrong for the benefit of the trainer. If the otter made the correct choice, the trainer bridged the otter with a clicker and gave the food reward back in the intertrial interval (ITI) position. If the otter made the wrong choice, the trainer cued the otter back to the ITI position and would not give any food reward or use the clicker. The experimenter immediately removed the stimuli and set up for the next trial while the otter was still in the ITI position. The recorder noted which stimulus was selected and wrote down any behavioral comments for each trial, along with the start and end time, date, weather, and potential distractions were recorded for each session.

The training phase for Heather and Sailor occurred from April 2019 through June 2019. Both otters typically completed 20 trials per session but ranged from 15–25 trials per session (depending on the otters' motivation levels and/or the animal care staff's time constraints). The training criterion was set at an accuracy of 80% or greater for two sessions in a row, after completing a minimum of eight sessions using Training Set 2. Heather completed 10 total sessions with Training Set 1 (186 trials; $M = 85.2\%$, $SE = 4.4\%$) and met the training criterion after the minimum of eight sessions with Training Set 2 (145 trials; $M = 79.8\%$, $SE = 3.7\%$). Sailor completed 17 total sessions with Training Set 1 (349 trials; $M = 83.7\%$, $SE = 3.0\%$) and met the criterion after 10 sessions with Training Set 2 ($M = 76.2\%$, $SE = 4.1\%$). During the training phase, both Heather and Sailor's performance was better than chance both when the S+ was on the right (summed binomial, $p < .001$) and when the S+ was on the left (summed binomial, $p < .001$). Sailor did not exhibit a side bias; he showed no significant difference in performance when the S+ was on the right ($M = 83.4\%$, $SE = 3.4\%$) versus when the S+ was on the left ($M = 78.3\%$, $SE = 4.5\%$, $Z = 0.9$, $p = .182$). However, Heather was significantly more accurate when the S+ was on the right ($M = 96.6\%$, $SE = 1.7\%$) than when the S+ was on the left ($M = 69.9\%$, $SE = 5.6\%$, $Z = 4.5$, $p < .001$).

The training phase for Ashkii occurred from September 2020 through November 2020 (limited sessions because of the pandemic), and the end of March 2021 through July 2021 (there was a break in training for the winter months because of the animal care staff's availability). Ashkii completed six sessions with Training Set 1 (202 trials, $M = 69.1\%$, $SE = 8.6\%$), 25 sessions with Training Set 2 (739 trials, $M = 80.0\%$, $SE = 2.0\%$), and then 42 sessions with

Training Set 3 (1,023 trials, $M = 71.9\%$, $SE = 2.0\%$). Ashkii did not meet the training criterion, and she did not show a side bias (accuracy when S+ on right: $M = 71.2\%$, $SE = 3.1\%$, accuracy when S+ on left: $M = 72.5\%$, $SE = 3.4\%$, $Z = -0.6$, $p = .287$).

Test Phase

The procedure for the test phase was the same as the procedure for the training phase. Test sessions contained both training stimuli and the novel test probes. There were 14 trials in each test session: Eight were training stimuli trials and six were test probe trials. The first two trials always contained the training stimuli (one with the S+ on the left and one with the S+ on the right, with an equal number of left-start and right-start sessions), and the last 12 trials contained six training stimuli trials and six test probe trials presented in a random order.

Test sessions for Heather occurred in July 2019 during which she was only able to complete seven of 12 test sessions (see Subject section above). Heather was having motivational issues during sessions six and seven for which she only completed part of a session each day and finished the remaining trials on the following day. Two training trials (one on the right and one on the left) were always presented prior to resuming these partially completed test sessions. Test sessions for Sailor occurred from July 2019–August 2019 during which he completed all 12 sessions (each of his sessions was completed in a single day).

Transparency and Openness

We report how we determined our sample size, all manipulations, and all measures in the study, and we follow APA Style Journal Article Reporting Standards (Kazak, 2018). All data and analysis code are available at https://osf.io/9rycf/ (Wilcox et al., 2025). Data were analyzed using the emmeans R package (Lenth, 2024). This study's design and its analysis were not preregistered.

Data Analysis

Otter performance in the test phase as measured by a correct (chose the S+) or incorrect (chose the S−) choice in each trial was modeled using logistic regression. Logistic regression models the probability of a correct choice (i.e., performance ranging from 0% to 100%) and allowed us to test for differences in performance of each otter among target shape categories and S+ locations while controlling for potential change over time. Differences between the two otters were modeled as a main effect while otter-specific performance differences among target shape categories were modeled as nested factors (within otters). Based on the experimental design, a target shape category by otter interaction was estimated, but a target shape category main effect was not, allowing for the assessment of overall differences between otters and differences among the otter-specific target shape categories. Change in performance over time for each otter was modeled by including linear effects of change across sessions and change across trials as well as their interaction with otter. Finally, we tested for potential differences between S+ locations (left, right) by including a S+ location main effect and a S+ location by otter interaction. Post hoc contrasts of marginal means (EMM) and risk ratios (RR)—the probability of a correct choice divided by the probability of an incorrect choice—were computed using the emmeans R package (Lenth, 2024). Tukey's (1949) honestly significantly different procedure was used to correct for multiple pairwise comparisons.

Results

Overall performance for both otters was significantly better than chance during the test phase (50%), EMM = 78.2%, 95% confidence interval (CI) = [69.5%, 85.0%]. There were statistically significant differences in performance between otters, $\chi^2(1) = 4.78$, $p = .029$, but none of the other main effects and interactions were significant, all $p > .150$. These nonsignificant effects include S+ side, $\chi^2(1) = 0.09$, $p = .76$; session, $\chi^2(1) = 0.08$, $p = .77$; trial, $\chi^2(1) = 0.78$, $p = .38$; S+ side × otter, $\chi^2(1) = 1.93$, $p = .17$; target shape (otter), $\chi^2(6) = 2.84$, $p = 2.84$, $p = .83$; session (otter), $\chi^2(1) = .26$, $p = .61$; and trial (otter), $\chi^2(1) = 0.45$, $p = .50$. While both otters performed significantly better than chance, Heather (EMM = 85.7%, 95% CI = [72.6%, 93.1%]) performed significantly better than Sailor (EMM = 68.4%, 95% CI = [58.8%, 76.6%]), RR = 1.25 ($SE = 0.11$), 95% CI = [1.05, 1.49], $Z = 2.52$, $p = .012$.

Although there were no statistically significant differences in performance among target stimuli for either otter, $\chi^2(6) = 2.84$, $p = .83$, average performance for each otter and target shape category is shown in Figure 4. Both otters performed statistically significantly better than chance on their respective training target shapes, both $p < .001$. In addition, Heather performed statistically significantly better than chance when the target shape was curved with symmetric lines (vertical oval, horizontal oval), EMM = 90.1%, 95% CI = [65.5%, 97.8%], $p = .006$, or was composed of straight lines (hexagon, octagon), EMM = 90.7%, 95% CI = [54.3%, 98.8%], $p = .034$. Sailor performed statistically significantly better than chance when the target shape was composed of straight nonsymmetric lines (left triangle, right triangle), EMM = 74.1%, 95% CI = [52.6%, 88.0%], $p = .029$.

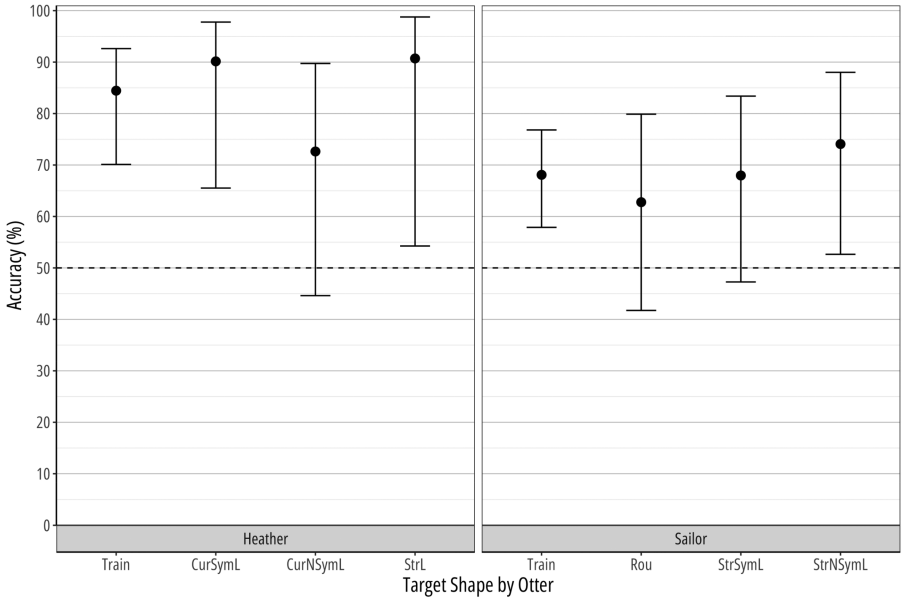
Discussion

Two of three otters successfully learned to discriminate between black outlines of two geometric shapes. Both otters were able to generalize that discrimination to novel geometric shapes into two perceptual categories in the test phase. However, each otter was successful on a subset of the novel test stimuli, indicating that certain stimulus features may have been more salient than others. Heather performed significantly better than chance when the novel stimuli had symmetry and were composed of either straight or curved lines but she did not succeed when the stimuli lacked symmetry. These results suggest that for Heather, a stimulus could belong to the circle category if both horizontal and vertical symmetry were present, but it did not matter if the stimuli were composed of curved or straight lines. Sailor performed significantly better than chance on test stimuli only when the novel stimuli had straight lines but lacked symmetry, but Sailor failed when the stimuli had a rounded aspect (round sides or corners) or both straight lines and symmetry. Perhaps symmetry was less salient for Sailor than for Heather in creating a perceptual category representation. However, these results should be interpreted with caution as they also could be influenced by a lack of statistical power and their performance could have improved with further trials (see Experiment 2).

There were individual differences between the otters. Heather performed significantly better than Sailor overall and on more novel test stimuli. Prior to the current study, both otters participated in research involving a two-alternative forced-choice task (DeLong et al., 2019).

Figure 4

Experiment 1 Otter Performance Across Target Shape Categories



Note. Model-estimated marginal means and 95% CIs are shown. Note that performance was not significantly different from chance (50%) for target shape categories where CIs include 50%. CurSymL = curved symmetric lines (vertical oval, horizontal oval); CurNSymL = curved nonsymmetric lines (left tilt oval, right tilt oval); StrL = straight lines (hexagon, octagon); Rou = rounded (round side triangle, round corner triangle); StrSymL = straight symmetric lines (vertical triangle, horizontal triangle); StrNSymL = straight nonsymmetric lines (left triangle, right triangle); CI = confidence interval.

Heather had additional experience with research including 3 years of experience training for a match-to-sample task (but she did not meet the training criterion). Heather's red circle was used as her target in demonstrations where her targeting behaviors were displayed for zoo guests during summer programming (e.g., a guest would hold up the red circle against the exhibit glass and Heather would swim to it from the other side of the glass). The red circle had been her target for at least 8 years prior to the current study. This extensive history of training on two types of tasks and targeting behavior to the red circle may explain why Heather performed better than Sailor.

Other individual differences between Heather and Sailor may have also played a role. It is possible that Heather may have performed better than Sailor because of her age or sex, but the small sample size makes this impossible to ascertain. Additionally, Heather was found to have cataracts prior to this study and had other age-related ailments which did not seem to have a negative impact on her results, but this may mean we have a conservative estimate of her performance. She may have performed even better if we had tested her a few years prior. Zoo policy dictated that we test Heather and Sailor using different experimental setups, which may have influenced their visual perspective of the stimuli—but both otters were accustomed to their experimental setups from a previous study (DeLong et al., 2019). Heather viewed the stimuli underwater and through glass, (which may have had a glare at times) which could have impacted her ability to see the stimuli depending on weather or her approach. In contrast, Sailor viewed the stimuli through chain-link fencing which may have partially obscured small parts of the stimuli. Heather also swam straight towards the stimuli, and Sailor walked to the stimuli from the right side of his enclosure and climbed through a gate to reach them. This means that Heather approached both stimuli straight on while Sailor encountered the stimulus placed on the right first, and also first observed the stimuli from an angle. An experimental setup in which the animal approaches one stimulus before the other can have an impact on results (DeLong, et al., 2020). The benefit of using these two different experimental setups is that we determined that the otters were able to categorize geometric shape stimuli when observing stimuli in the water (Heather) as well as in the air (Sailor).

This experiment was the first to show that North American river otters were able to perceptually categorize novel geometric shapes into two artificial categories (triangles and circles) and suggests that otters could be using features such as symmetry and line type (straight vs. curved) to form those categories. The focus of Experiment 2 was on investigating whether otters are capable of categorizing drawings of real-world objects into circle and triangle categories (e.g., a tomato in the circle category and a tent in the triangle category). These types of stimuli were completely novel for the otters and allowed us to continue to investigate which stimulus features may be controlling category membership.

Experiment 2

Method

Subject

The male otter, Sailor, participated in Experiment 2. Sailor was the only otter at the zoo available to participate who had successfully met the training criterion. Sailor was 12 years old at the

start of this experiment. Training and test sessions were only run in the morning. Sailor was fed 75%–100% of his morning fish diet as his primary reinforcement. He received his entire daily diet regardless of his performance during training and test sessions. Sailor was housed in the same enclosure at the Seneca Park Zoo described in Experiment 1.

Stimuli

All stimuli used were black and white drawings of everyday objects (see Table 2 and Figure 5), and the printing and attachment methods for these stimuli were the same as in Experiment 1. We used the exact same training stimuli from Training Set 2 presented to Sailor in Experiment 1 (circle and triangle). Additional training stimuli were added after the first phase of testing, and included black and white drawings of everyday objects (Figure 6). Sailor had never seen the drawings of objects depicted in the novel test stimuli set or additional training stimuli set prior to this study.

Different stimulus features were varied within the novel test set. The triangle category included drawings of an ice cream cone, flag, tent, sandwich, watermelon slice, and a hat. The circle category included drawings of a baseball, cloud, orange, apple, beach ball, and a tomato. Within each category, stimuli could include curved or straight lines. For example, in the triangle category the watermelon, hat, ice cream cone included a curved line on the top or bottom whereas the tent, sandwich, and flag had straight lines. Within each category, there were two stimuli with more lines, dots, or other details in the center of the stimulus (seeds in the watermelon, a door in the tent, stitches in the baseball, and lines on the beach ball). The additional training stimuli all included details in the center of the stimulus, since this was one of the key differences between Experiment 1 stimuli and Experiment 2 stimuli and we wanted to give Sailor more exposure to these types of objects (Figure 6).

Experimental Setup

Sailor was tested using the same setup as in Experiment 1.

Procedure

Training Phase 1

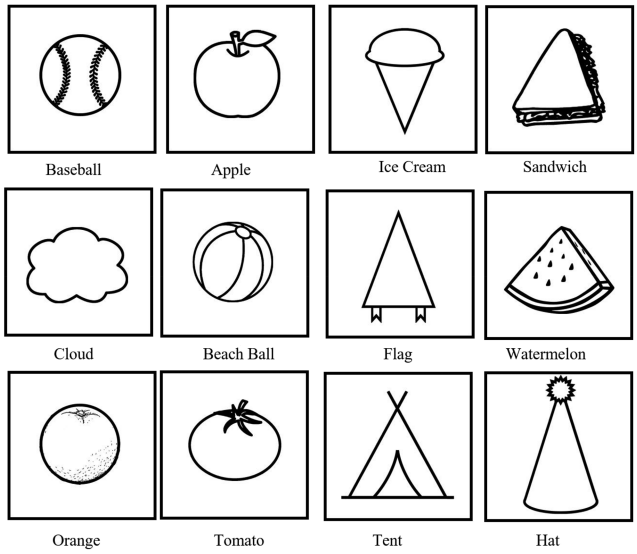
This training phase began 3 days after the completion of the test phase of Experiment 1. Sailor completed two training sessions, then after Heather's death, a 3-week break was taken to allow Sailor time to adjust to his new housing situation before training sessions resumed (he had been housed with Heather). Due to Sailor's lack of motivation and slower trial times over the next few weeks, we instituted a correction trial procedure in which Sailor repeated trials he got wrong. In the first correction trial, the two choice stimuli were presented exactly the same as in the original trial. If Sailor chose incorrectly again, the S− was taken away and the S+ remained on the same side as it had been presented on in the previous trial (only the correct choice remained). Sailor continued in the training phase until he reached the same training criterion as in Experiment 1 (two sessions in a row with accuracy of 80% or better, which was only assessed for noncorrection trials) and completed his session within 10–12 min (his typical speed in Experiment 1). Sailor reached the training criterion after 23 sessions (426 trials, $M = 74.7\%$, $SE = 2.0\%$), where his last six sessions showed typical session times. Sailor did show a side bias overall during this training phase, where he was significantly more accurate when the S+ was on the right, $M = 80.6\%$, $SE = 3.6\%$, than on the left, $M = 68.8\%$, $SE = 3.8\%$, $Z = 2.2$, $p = .015$.

Table 2
Stimulus Dimensions for Experiment 2 Test

Shape	Area (cm^2)	Shape	Area (cm^2)
Flag	154.13	Apple	155.55
Watermelon	155.00	Cloud	157.08
Ice cream	155.95	Baseball	159.49
Hat	159.85	Tomato	163.20
Sandwich	160.13	Orange	164.00
Tent	163.63	Beach ball	164.00

Note. All stimuli have approximate areas because of there not being a specific area formula for these exact shapes. All stimuli were within 154–164 cm^2. Training stimuli used were the same as used in Experiment 1. See Table 1 for areas of training stimuli.

Figure 5
Stimuli Used for Test Sessions in Experiment 2



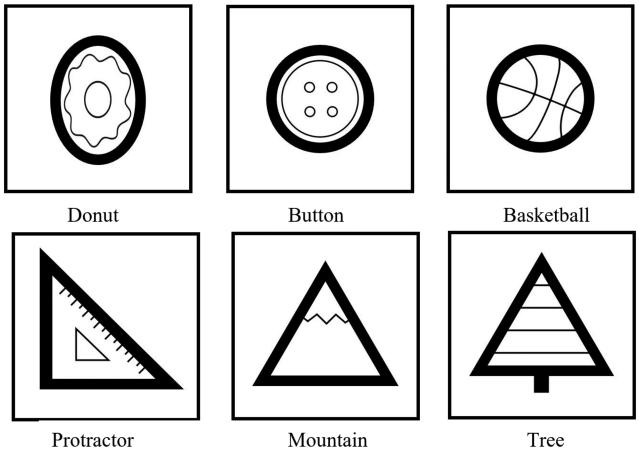
Note. Refer to Table 2 for stimulus dimensions. Each square outline surrounding the shape was 27 × 27 cm. The stimuli were all black and white line drawings, shown here with their assigned names. These names were not included on the stimuli that were presented to the otters. During Experiment 2 Training Phase 1, the same training stimuli were used from Experiment 1 and are shown in Figure 1A. During Experiment 2 Training Phase 2, additional training stimuli were added and are shown in Figure 6. All the circle stimuli are on the left, and all the triangle stimuli are on the right.

Test Phase 1

The procedure for the test phase was the same as described in Experiment 1. Like Experiment 1, test sessions contained both training stimuli and the novel test probes. There were 14 trials in each test session: Eight were training trials and six were test probe trials. The first two trials always contained the training stimuli (one with the S+ on the left and one with the S+ on the right), and the last 12 trials

Figure 6

Stimuli Used in Experiment 2 Training Phase 2



Note. Each square outline surrounding the shape was 27 × 27 cm. The stimuli were all black and white complex line drawings, shown here with their assigned names. These names were not included on the stimuli that were presented to the otters. These were all novel stimuli and not included in any test phase. The two original training shapes (circle and triangle) that are shown in Figure 1a were also used with this training set. The top three stimuli should be classified as circles, and the bottom three stimuli should be classified as triangles.

contained six training trials and six test trials presented in a random order. Correction trials were not used during the test phase. Testing began 1 day after the Training Phase 1 was completed. All 12 sessions were completed in the morning with one session per day.

Training Phase 2

Because Sailor's performance on novel test stimuli in Test Phase 1 was at chance ($M = 50\%$), we conducted an additional training phase with new training stimuli added (Figure 6). These new training stimuli allowed Sailor more experience with drawings of real-world objects like those in the test phase. In fall of 2020 we had limited access because of the pandemic, but we were able to conduct 15 sessions using Training Set 2 from Experiment 1 (black outlines of a circle and equilateral triangle, $M = 78.1\%$ $SE = 2.1\%$) and 10 sessions with the new training stimuli ($M = 69.7\%$, $SE = 3.9\%$). Training resumed in March 2021 and lasted 2 months. Sailor completed his first five sessions using Training Set 2 from Experiment 1 ($M = 83.5\%$, $SE = 5.6\%$). Sailor then completed 18 sessions with both Training Set 2 from Experiment 1 and the new training stimuli (six trials of Training Set 2, 10 trials of the new stimuli (one triangle category stimulus and one circle category stimulus), then 10 trials of Training Set 2. Sailor saw all pairs of the six new training stimuli an equal number of times. His overall performance on the new training stimuli ($M = 81.1\%$, $SE = 2.7\%$) was similar to his overall performance on Training Set 2 ($M = 78.5\%$, $SE = 3.2\%$). Sailor did not show a side bias with either the new training stimuli (right, $M = 81.1\%$, $SE = 4.2\%$ left, $M = 81.1\%$, $SE = 3.9\%$, $Z = -0.5$, $p = .29$) or Training Set 2 (right $M = 76.4\%$, $SE = 4.0\%$, left, $M = 80.6\%$, $SE = 3.3\%$, $Z = -0.7$, $p = .24$) during this set of training.

Test Phase 2

Testing was completed in the same manner as in Test Phase 1 in Experiment 2. Sailor began this test phase 7 days after the completion of Training Phase 2. and completed two blocks of 12-trial sessions (with 1 day in between the two sets).

Data Analysis

As in Experiment 1, otter performance across trials was modeled using logistic regression. Only Sailor participated in Experiment 2, so differences among otters were not included in the model: Performance differences among target shape categories were modeled as a main effect. Change in performance over time was modeled by including linear effects of change across sessions and change across trials. We tested for potential differences between S+ locations (left, right) by including a S+ location main effect. Finally, test block-specific differences in performance among target shape categories were assessed by including the interaction between test block and target shape category. Similarly, test block-specific differences in S+ location effects were modeled by including the interaction between test block and S+ location.

Results

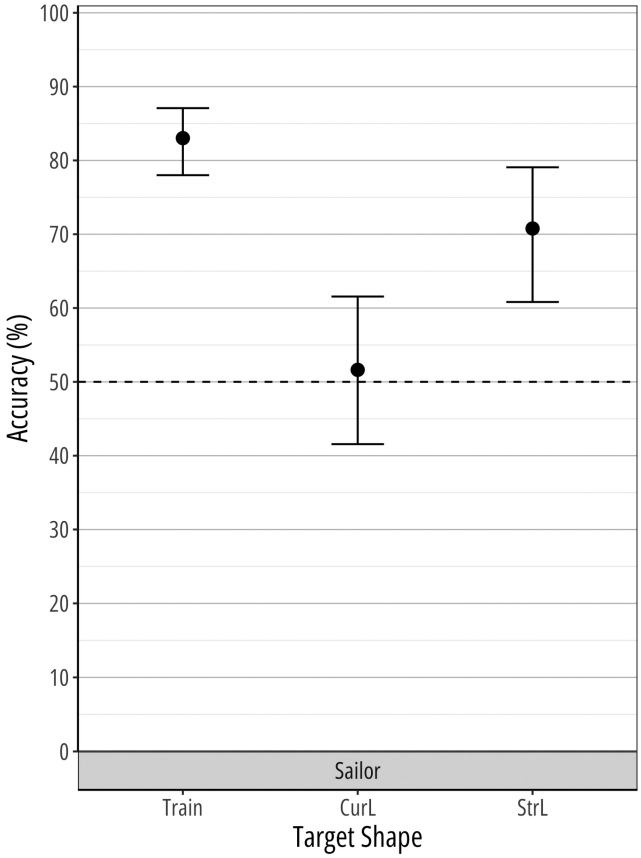
Sailor's overall performance across all three test blocks was significantly better than chance (50%), EMM = 73.7%, 95% CI = [69.2%, 77.8%]. There were statistically significant differences in performance among target shape categories, $\chi^2(2) = 62.82$, $p < .001$. Average performance for Sailor on each target shape category is shown in Figure 7. Performance was statistically significantly better than chance on the training stimuli, EMM = 83.0%, 95% CI = [78.0%, 87.1%]. In addition, Sailor performed statistically significantly better than chance when the test stimuli were composed of straight lines (tent, sandwich, flag), EMM = 70.8%, 95% CI = [60.8%, 79.1%], but not significantly different from chance when the test stimuli were composed of curved lines (watermelon, hat, ice cream cone), EMM = 51.6%, 95% CI = [41.6%, 61.6%]. Of the three target shape categories, performance was significantly worse on curved line test stimuli compared to training stimuli, RR = 0.62 ($SE = 0.06$), 95% CI = [0.49, 0.79], $Z = -4.57$, $p < .001$, and compared to straight line test stimuli, RR = 0.73 ($SE = 0.09$), 95% CI = [0.55, 0.97], $Z = -2.62$, $p = .024$. There was no statistically significant difference in performance between training and straight-line test stimuli, RR = 1.17 ($SE = 0.08$), 95% CI = [0.99, 1.38], $Z = 2.25$, $p = .063$.

Comparison of performance between S+ locations (left, right) indicated that Sailor performed significantly better when the S+ was on the right, EMM = 84.5%, 95% CI = [79.2%, 88.7%], than on the left, EMM = 59.0%, 95% CI = [52.3%, 65.4%], RR = 1.43 ($SE = 0.09$), $\chi^2(1) = 32.32$, $p < .001$, but this did not vary across test blocks, $\chi^2(2) = 3.15$, $p = .21$. None of the other main effects were significant, including session, $\chi^2(1) = 0.12$, $p = .73$, and trial, $\chi^2(1) = 0.02$, $p = .88$.

Comparing performance on test trials only across the three test blocks (Test Phase 1 included Test Block 1, and Test Phase 2 included Test Blocks 2 and 3), there were no statistically significant differences in performance among Test Blocks 1 (46.4%), 2 (63.7%), and 3 (73.2%), $\chi^2(2) = 2.07$, $p = .35$. When Test Blocks 2 and 3 were pooled together, performance was not significantly

Figure 7

Experiment 2 Otter Performance Across Target Shape Categories



Note. Model-estimated marginal means and 95% CIs are shown. Note that performance was not significantly different from chance (50%) for target shape categories where CIs include 50%. CurL = curved lines (watermelon, hat, ice cream cone); StrL = straight lines (tent, sandwich, flag); CI = confidence interval.

different on novel test trials in Test Block 1 (46.4%) than in the combined Test Blocks 2 and 3 (68.6%), $Z = -1.44$, $p = .15$. When trials with training stimuli were also included along with test trials in each test block, there were no statistically significant differences in performance among the three test blocks, $\chi^2(2) = 1.01$, $p = .60$. This suggests that although the target shape interaction was statistically significant, $\chi^2(2) = 10.30$, $p = .006$, this interaction did not reflect differences across test blocks on test trials only or on average when considering both training and test trials.

Discussion

Sailor was able to generalize his discrimination of circle versus triangle to novel drawings of real-world objects, but only when the triangle-like stimuli were composed of straight lines (tent, sandwich, and flag), not when the triangle-like stimuli were composed of curved lines (watermelon, hat, and ice cream cone). This suggests that line type (straight vs. curved) was a salient feature of the triangle category. Line type seems to have been more important than symmetry because the tent, flag, hat, and ice cream cone were all symmetrical, but he did not perform well on the hat ($M = 50\%$) or ice cream cone ($M = 58\%$). It is likely that multiple features contribute to perceptual category membership for otters, as has been found for pigeons (Lazareva, 2021). These results showing successful perceptual categorization are in agreement with some other studies that have found animals to be capable of categorizing 2D line drawings of real objects including sharks (Schluessel & Duengen, 2015) and cichlids (Schluessel et al., 2012). Schluessel and Duengen's (2015) study as well as Schluessel et al.'s (2012) study both used drawings of fish and snails, which the sharks and cichlids were able to categorize. Other animals have also been found to categorize 2D pictures of real-world objects such as baboons (Bovet & Vauclair, 1998). The baboons were trained with 3D objects that were food (such as an apple) and nonfood (such as a key). The baboons were then able to categorize an array of 2D pictures of the objects into these trained categories. However, when the picture had a background, only one of two baboons could categorize the stimuli. Specific features of the stimuli such as symmetry or line type were not explored.

Sailor's performance on the test stimuli did increase with each block of testing—Test Blocks 1 ($M = 46.4\%$), 2 ($M = 63.7\%$), and 3 ($M = 73.2\%$)—though not significantly. Some studies showed that nonhuman animal subjects required additional training trials beyond the planned training phase (Bovet & Vauclair, 1998; Cook & Smith, 2006; Roberts & Mazmanian, 1988; Smith et al., 2012) while other nonhuman animal subjects were able to succeed with the initial training provided (24–156 trials in Autier-Dérian et al., 2013; an average of 198 trials in Spinozzi et al., 2004; less than 100 trials in Schluessel & Duengen, 2015). Due to Sailor's poor performance in Test Block 1, training trials with additional novel stimuli were conducted to provide him with more experience with these new stimuli (line drawings of objects). However, it appears that Sailor's performance did not significantly increase because of such additional training. It is possible that additional training could have led to better overall performance in a fourth test block.

During testing, Sailor also showed a pervasive right-side bias. Sailor likely defaulted to a side bias for the curved line test stimuli since he was not able to categorize them and may have been unsure which stimulus to choose. This side bias may have been due in part because of limitations imposed by the experimental setup. Sailor viewed the stimulus placed on the right first because of the location of the door where he entered the experimental area. He showed a right-side bias in the test phase of a previous study, although he showed a left side bias in the training phase (DeLong et al., 2019). Interestingly, he did not show a side bias during training or testing in Experiment 1, so a side bias is not inevitable in this setup. Another factor for Sailor's setup was that he viewed the stimuli through mesh wire. This mesh wire did not seem to impact his performance in Experiment 1 nor in previous studies when he viewed geometric shapes (DeLong et al., 2019). However, in Experiment 2 the stimuli contained finer details (e.g., leaves, stems, seeds, stitches; see Figure 5) perhaps more occluded by the mesh, but those details were not necessary for perceptual categorization. The overall outlines of the objects should have been visually accessible and likely provided the basis for perceptual categorization of the stimuli. A major limitation of this experiment was that we had a single otter subject. Thus, the results showing successful perceptual categorization with these particular stimuli should be interpreted with caution. Sailor's personality (e.g., curiosity, boldness, sociability; Skinner & Miller, 2020), age, and sex may have played a role in

his performance here and in other studies (DeLong et al., 2019; Wegman & DeLong, 2023). Clearly, this study should be repeated with more otters and using a variety of stimuli to better pinpoint the salient features that permit categorization in otters.

General Discussion

In Experiment 1 two otters were able to successfully generalize their discrimination of a circle and triangle to novel stimuli, showing preliminary evidence of perceptual categorization. In Experiment 2, one otter was able to perceptually categorize novel drawings of real-world objects into two categories. In both experiments, the otters succeeded with a subset of stimuli that suggest potentially important physical stimulus features such as line type (straight vs. curved) and symmetry were driving perceptual categorization performance. These results are broadly consistent with previous literature that has shown animals including baboons (Bovet & Vauclair, 1998), goats (Meyer et al., 2012), and bamboo sharks (Schluessel & Duengen, 2015) were all able to form perceptual categories or concepts for trained stimuli and then use that knowledge to categorize novel stimuli. The baboons in Bovet and Vauclair's (1998) study were able to categorize 2D pictures of real objects after being trained with 3D objects from the same categories (food vs. nonfood objects such as an apple vs. a key). Meyer et al. (2012) used similar stimuli as presented in the current study in that they were black and white, 2D, and artificial objects. Instead of categorizing based on shape, as conducted in the present study, the goats had to create a category for either an open-centered object or a completely filled object. Schluessel and Duengen (2015) used similar methods as in the present study, first presenting sharks with 2D training stimuli in which they had to make single-pair discriminations with three pairs (fish vs. snails). The sharks were then presented with an array of stimuli that belonged to the same categories (fish and snail) from training, but there were differences such as the addition of color in the real images, as well as outlined cartoon images. The results from the present study build on findings of categorization abilities in other types of nonhuman animals, adding that river otters display perceptual categorization abilities.

The results of the study were influenced by the stimuli we used: 2D circles and triangles, other geometric shapes, and simple line drawings. All the stimuli in the current study were not ecologically valid, novel (except for the training circle and triangle), and unlikely to be important for survival to the otters. They were developed based on Heather's and Sailor's recent experience with the circle and triangle (DeLong et al., 2019). The stimuli themselves also had limitations considering that there was slight variation in the areas (a maximum difference of 10 cm^2). The otters could have used small size differences instead of shape differences to make their decisions, but it is unlikely. The chief advantage of these stimuli was that they had physical features that could be systematically manipulated, and we were able to learn something about which features were salient to the otters (e.g., symmetry, line type). Future studies could further manipulate physical features to better understand what the otters learned about these type of stimuli. For example, would three detached vertices in a triangular configuration or three lines without vertices be classified as triangles? This could help us better understand how exactly the otters were representing the stimuli—as a collection of low-level visual features or a coherent whole object.

Future categorization studies could utilize different stimuli such as pictures containing color, surface features, and shading (as opposed to black and white line drawings), or photos of real-world objects that are ecologically valid for otters. There is evidence that animals perform better on tests of object recognition or object constancy when stimuli have color and/or shading and surface features (e.g., DeLong et al., 2025; Peissig et al., 2005; Wood & Wood, 2024). If testing otters' ability to categorize real-world objects, photographs could be used; however, it is important to keep in mind that picture-object recognition has not yet been tested in otters. Thus, we do not know if they recognize the correspondence between a picture/photo of an object and the actual object.

The current study investigated perceptual categorization and not concept learning, which would require grouping objects that do not share physical features. Research with pigeons (Lazareva et al., 2004) investigated categorization at the basic-level and at the superordinate level using natural stimuli. The stimuli within each basic-level category (cars, chairs, flowers, and people) shared physical features but the stimuli within superordinate categories (natural: flowers and people vs. artificial: cars and chairs) did not. The pigeons were able to successfully classify the objects at both levels. Sea lions were able to categorize objects into equivalence classes with zero physical similarities, showing true concept learning (Schusterman & Kastak, 1993). The pigeons and sea lions in the above studies were using more complex cognitive processing than what we have shown in the current study. Future studies could explore concept learning in otters using ecologically relevant stimuli that could be classified into basic-level categories like fish versus birds (both river otter prey items) and superordinate categories like predators (alligators, bobcats, coyotes, mountain lions, and wolves) versus prey items (fish, insects, crayfish, frogs, and birds). If otters can classify items into superordinate categories where the stimuli within the category share few or no physical features (e.g., a bird and a fish in the prey category), then it would show concept learning.

A constraint in interpreting the results of the present study is that we did not establish whether the subjects could discriminate among the stimuli within the categories (e.g., discriminate between an equilateral triangle and a horizontal triangle). A strong demonstration of perceptual categorization would entail showing that the subjects viewed each stimulus as a distinctive entity, a unique exemplar that can be placed within a perceptual category (Lazareva, 2021). It is possible that the subjects did not notice the differences between some stimuli within a category, so they were placed in the same category because of failures of visual perception or a failure to attend to stimulus properties.

The limitation of low sample size in the present study is a common one when working with otters housed at zoos. Otters need a large amount of space to thrive in their environment because of their size and behaviors and need for both land and water habitats. These large spaces produce high costs to build, maintain, and staff, so even when there are zoos that house a greater number of otters, they are not always easily available for research purposes as zoos have other important priorities. These costly requirements for quality care of otters may be why there are many published otter studies with a low number of subjects, usually ranging from one to three individuals (Balliet & Schusterman, 1971; DeLong et al., 2019; Gentry & Peterson, 1967; Ghoul & Reichmuth, 2014; Slack, 1966; Svoke et al., 2014; Wegman & DeLong, 2023) or at most five to 12 individuals (Frick et al., 2016; Ladds et al., 2017; Perdue et al., 2013;

Saliveros et al., 2020; Schmelz et al., 2017). A way to try and increase the number of subjects when researching otters is to replicate the same study across several facilities, which is the big team science approach that has been successful with other nonhuman animal research (ManyBirds—Lambert et al., 2022; ManyDogs—Alberghina et al., 2023; ManyPrimates—Aguenounon et al., 2020). This collaborative approach is now being applied to otter research (ManyOtters et al., 2024). An advantage of this method is that a large number of diverse individuals of different species, ages, sexes, behavioral traits, and research experience levels can participate. The otters Heather and Sailor in the current study were both considered old, and we do not yet know the effects of old age on perceptual and cognitive abilities in North American river otters.

There are a few applications for categorization research (and investigations of other cognitive abilities) in any species of otters. This research helps to enrich the environment of individuals residing under human care and contributes to conservation efforts for otters. Enrichment of captive animals is typically a priority for zoos and aquariums, so it is directly beneficial to the individuals participating in our studies, as well as other animals in different facilities. Knowing more about an animal's visual perception can help us to create better enrichment items or habitats that are more stimulating for the specific animal species. It is important to study visual perception in otters because it will add to the limited knowledge we have about them, and lead to improved conservation efforts for these species. If we are more aware of how otters view the world, we can figure out what specific issues they face and how we can help to solve those in the most effective way. North American river otters reside in a variety of habitats such as rivers, lakes, marshes, swamps, and estuaries (Yoxon & Yoxon, 2014). These otters live throughout Canada as well as the United States, particularly along the Atlantic and Pacific coasts. River otters were once extinct in some areas of the country and had very low numbers in others because of over hunting, loss of habitat, and water pollution up through the 1950s. Through reintroduction programs and improved water quality, river otters have increased in number once again and are now present in 48 out of 50 states in the United States (Yoxon & Yoxon, 2014).

In conclusion, this was the first study to investigate perceptual categorization abilities in North American river otters. Two otters were able to successfully generalize their discrimination of a circle and triangle to novel geometric shape stimuli, showing preliminary evidence of perceptual categorization. One otter was able to perceptually categorize novel drawings of real-world objects into two categories. The otters' performances suggested that certain physical features such as symmetry and the presence of straight or curved lines may have been salient. Future research should continue to investigate otters' abilities to form categories and concepts so that we are able to better understand the visual and cognitive abilities of these animals.

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Received February 6, 2025
Revision received October 1, 2025
Accepted October 3, 2025 ■