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Visual Perception in a Bottlenose Dolphin (Tursiops truncatus): Successful Recognition of 2-D Objects Rotated in the Picture and Depth Planes

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Visual Perception in a Bottlenose Dolphin (*Tursiops truncatus*): Successful Recognition of 2-D Objects Rotated in the Picture and Depth Planes

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Aquatic species such as bottlenose dolphins can move in 3 dimensions and frequently view objects from different orientations. This study examined their ability to identify 2-D objects visually despite changes in orientation across 2 rotation planes. A dolphin performed a matching-to-sample task in which a sample was presented at a different orientation from its match in a 3-alternative choice array. Samples were presented at 6 aspect angles in the picture plane (0°, ±45°, ±135°, 180°) and 6 aspect angles in the depth plane (0°, −45°, ±90°, +135°, 180°). Alternatives were always presented at 0°. Performance was significantly better than chance for all aspect angles in both rotation plane tests. There was a significant linear decline in accuracy as the sample object was rotated from 0° toward 180° in the picture plane. Performance with familiar objects ($M = 97.1\%$) exceeded performance with novel objects ($M = 76.9\%$). In the depth plane rotation test, there was a significant quadratic trend in accuracy as the sample object was rotated from 0° toward 180°, in which performance was significantly lower at ±90° than at all other orientations. Performance in the picture plane where all object features were available irrespective of orientation was significantly better than performance in the depth plane where the availability of visible features were dependent upon orientation ($M = 81.2\%$ vs. $M = 63.0\%$). The dolphin's performance in this study shows evidence of both viewpoint-independent and viewpoint-dependent processes.

Keywords: bottlenose dolphin, mental rotation, object constancy, object discrimination, visual perception

Object constancy is the ability to recognize an object as having a stable shape despite changes in the shape of the retinal image resulting from viewing the object from different orientations. It is

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an essential property of human visual perception that allows us to recognize and interact with objects even if we view them from a novel position. This ability is also advantageous for nonhuman animals encountering objects from many aspect angles as they move though space. Bottlenose dolphins (*Tursiops truncatus*) live in an aquatic environment where they can view objects such as conspecifics, prey, predators, and objects in their habitat from many different orientations. Their ability to swim upright, sideways, and upside down as well as the independent movement of organisms near them means dolphins are frequently exposed to views of objects from all angles. The topic of the current study is the capability of dolphins to visually recognize objects independent of the viewing angle.

To date, there has been extensive research on object constancy focused on visual recognition of objects by humans (for a review see Graf, 2006; Jolicoeur & Humphrey, 1998). The results of these studies have led to competing theories of how people represent objects. One theory is that recognition performance is viewpoint-independent, and a single underlying 3-D representation is constructed of the object specifying structural relations between geons (Biederman & Gerhardstein, 1993; Marr, 1982). When shown novel views, performance accuracy is high and does not vary as a

function of aspect angle. In this view, object constancy is achieved because the same object representation is activated for any orientation of the object. Another theory is that recognition performance is viewpoint-dependent, and different 2-D object representations are formed with each different view (Tarr & Pinker, 1989). This explains why performance on novel viewpoints in a test tend to decline systematically with increasing distance from the viewpoint(s) presented to the participant during a training period (training can include one or several viewpoints). In this theory, the visual system stores several views of an object, and a given view is matched to the nearest stored representation. People's performance in different studies can appear consistent with both theories. The properties of the stimuli and differing experimental conditions can cause performance to be viewpoint-dependent or viewpoint-independent (Nielsen, Logothetis, & Rainer, 2008). For example, very differently shaped stimuli, small stimulus sets, extensive training, and the presence of distinctive features in stimuli that remain diagnostic despite changes in orientation can all lead to viewpoint-independent performance.

Another variable that can influence performance in an object constancy task is rotation plane. Objects can be rotated in the picture plane (also called a planar rotation) or rotated about the vertical or horizontal axis in the depth plane. When rotating objects in the picture plane, the same features are visible at every aspect angle, whereas when objects are rotated in the depth plane, one feature can disappear and another can appear at different aspect angles (Lawson, 1999). For example, turning a drawing of a front-facing bird upside down is the equivalent of a 180° picture plane rotation. The same object features (e.g., beak, eyes, throat, and feet) can be seen in both the 0° (upright) and 180° (inverted) orientations. Walking around a bird sitting on a tree branch would afford different views of the bird equivalent to a series of depth plane rotations about the vertical axis. In this case, different features of the bird would be dependent on aspect angle (the beak and throat would be visible from some angles, whereas the tail and back would be visible from other angles).

The ability to perceive visually objects rotated in the picture or depth planes has been investigated in a wide variety of nonhuman animals that live in terrestrial habitats (rats: Minini & Jeffery, 2006; Sutherland, 1969; ferrets: Pollard, Beale, Lysons, & Preston, 1967; sheep: Kendrick, Atkins, Hinton, Heavens, & Keverne, 1996; newborn chicks: Wood, 2013; dogs: Racca et al., 2010; and baboons: Hopkins, Fagot, & Vauclair, 1993), arboreal habitats (monkeys: Freedman, Riesenhuber, Poggio, & Miller, 2006; Köhler, Hoffmann, Dehnhardt, & Mauck, 2005; Logothetis, Pauls, Bülthoff, & Poggio, 1994; Nielsen et al., 2008; Parr, 2011; Parr & Heintz, 2008; lion-tailed macaques: Burmann, Dehnhardt, & Mauck, 2005; and chimpanzees: Parr, 2011), aerial habitats (pigeons: Cook & Katz, 1999; Delius & Hollard, 1995; Hamm, Matheson, & Honig, 1997; Hollard & Delius, 1982; Jitsumori & Ohkubo, 1996; Spetch, Friedman, & Reid, 2001; Wasserman et al., 1996; honeybees: Dyer & Vuong, 2008; Plowright et al., 2001), and aquatic habitats (sea lions: Mauck & Dehnhardt, 1997; Schusterman & Thomas, 1966; octopus: Sutherland, 1969; fish: Bowman & Sutherland, 1969; DeLong, Fobe, O'Leary, & Wilcox, 2018; Schluessel, Kraniotakes, & Bleckmann, 2014; Wang & Takeuchi, 2017). The results of such studies can vary based on stimulus type (simple or complex), task (match-to-sample, forced choice paradigm, go/no-go, same-different task), type of training

(one view vs. multiple views), and rotation plane. Different patterns of results showing viewpoint-independence or viewpoint-dependence have been obtained when testing the same species.

For example, pigeons tested with planar rotations of simple 2-D stimuli showed viewpoint-independent performance (Delius & Hollard, 1995; Hollard & Delius, 1982), whereas pigeons tested with planar rotations of stimuli consisting of line drawings or shaded images showed viewpoint-dependent performance (Hamm et al., 1997; Peissig, Young, Wasserman, & Biederman, 2005). Pigeons presented with depth-plane rotations of drawings of 3-D stimuli typically show generalization to novel views (e.g., above-chance performance), although their performance shows viewpoint-dependence because recognition accuracy decreases as stimuli are rotated away from their training view (Cook & Katz, 1999; Peissig, Young, Wasserman, & Biederman, 2000; Spetch et al., 2001; Wasserman et al., 1996).

Very few studies have explored object constancy in dolphins and previously only in the acoustic domain using echolocation tasks (Au & Turl, 1983; Helweg, Roitblat, Nachtigall, & Hautus, 1996; Nachtigall, Murchison, & Au, 1980). Dolphins echolocate by emitting a series of broadband clicks and listening to the returning echoes (Au, 1993). Dolphins extract information about objects from acoustic features of echoes (Harley & DeLong, 2008). Most of the objects dolphins encounter are aspect-dependent, meaning that the size and shape of the surfaces of the object will change as they are ensonified from different orientations. As with the retinal projections from visually inspected objects, the echoes from these types of objects can vary considerably depending on the angle from which they are inspected by the dolphin (Au, Branstetter, Benoit-Bird, & Kastelein, 2009; Helweg, Au, Roitblat, & Nachtigall, 1996). In fact, echoes from different orientations of a single object can vary more from each other than do echoes from different objects (DeLong, Au, Lemonds, Harley, & Roitblat, 2006). Echolocating dolphins face an analogous situation to organisms viewing objects—the object must be correctly identified despite large changes in the specific sensory information (the visual image or the auditory event) that result from changes in the object orientation.

The dolphin's success in recognizing objects at novel aspect angles using echolocation depends on the characteristics of the stimuli and the distance between the training aspect angle(s) and novel aspect angles. A dolphin trained to discriminate between cylinders made of coral rock and aluminum at 0°, 45°, and 90° showed nearly perfect transfer to novel aspect angles (15°, 30°, 60°, and 75°; Au & Turl, 1983). However, the cylinders were made of different materials, and the material of an object will provide an aspect-independent echoic cue, so the dolphin may not have used shape information at all in the task. A dolphin that learned to discriminate between an upright foam cylinder and a foam cube with its flat face forward showed poor performance at a novel angle when both objects were presented flat face forward (Nachtigall et al., 1980). Thus, a dolphin showed viewpoint-independent performance with objects made of different materials within 15° of a training aspect and viewpoint-dependent performance with objects made of the same material more than 15° away from a training aspect.

Dolphin and human performance is similar in tests of auditory object constancy using echoic stimuli. Human listeners presented with dolphin echoes from differently shaped objects made of

different materials were able to recognize the objects at all novel angles, and they reported using cues such as pitch, timbre, and loudness that were typically available at all aspect angles (DeLong, Heberle, Wisniewski, & Mercado, 2014). For example, the copper object usually had the highest pitched echoes regardless of aspect angle compared with the ceramic or wood objects. In contrast, human listeners showed viewpoint-dependent performance when presented with differently shaped objects made of the same material (DeLong, 2017). Participants reported that all three ceramic objects sounded similar in timbre and pitch at all aspect angles, so the task was very difficult. Therefore, both humans and dolphins showed viewpoint-independent performance when discriminating among objects differing in material, likely because they are relying on invariant auditory cues rather than identifying and representing the shape of the objects. A visual analogy would be a human subject's excelling at discriminating among a blue pyramid, red cube, and yellow cylinder presented at various aspect angles by using color alone.

Bottlenose dolphins are good candidates for a test of visual object constancy for several reasons. Dolphins have good vision in air and underwater (12.6 min of arc at 2.5 m), with higher acuity at nearer distances underwater (8 min of arc from 1 m) versus in air (17 min of arc from 1 m; Herman, Peacock, Yunker, & Madsen, 1975). They can visually discriminate 2-D objects (Tomonaga, Uwano, & Saito, 2014; von Fersen, Schall, & Güntürkün, 2000), 3-D objects (Harley, Roitblat, & Nachtigall, 1996), different quantities of objects (Jaakkola, Fellner, Erb, Rodriguez, & Guarino, 2005; Kilian, von Fersen, & Güntürkün, 2005), human gestural signs presented in person or displayed on a 2-D TV screen (Herman, Morrel-Samuels, & Pack, 1990; Herman, Richards, & Wolz, 1984), and their human trainers when they were wearing different outfits (Tomonaga et al., 2015). Using vision, dolphins have responded to human gestures to perform a variety of cognitively complex tasks (for a review, see Herman, 2010). However, to date, there have been no published studies of visual object constancy in dolphins.

The aim of the current study was to investigate a bottlenose dolphin's ability to recognize rotated 2-D objects in two rotation planes. We predicted that the dolphin would recognize objects visually across multiple orientations because dolphins have good visual acuity, have shown the ability to discriminate objects visually, and live in an environment where achieving object constancy would be advantageous (Herman et al., 1975; Tomonaga et al., 2014). In this matching-to-sample task, the dolphin viewed the sample object at multiple aspect angles, as it rotated in either the picture plane (using flat cutout shapes as stimuli) or the vertical-axis depth plane (using photos of rotated three-dimensional objects as stimuli). Alternative objects were always presented at 0° (upright in the picture plane or front face forward in the depth plane). Because the dolphin's head and body were unrestrained and there was no fixed viewing angle, it was possible to determine if he adopted a rotation-matching strategy by measuring his body position. When rotating objects in the picture plane, the same features are visible at every aspect angle, and the dolphin had the ability to rotate his body to match the orientation of the object. When objects are rotated in the depth plane, one feature can disappear and another can appear at different aspect angles (Lawson, 1999), and it is impossible for the dolphin to compensate for the object's varied viewpoint by adjusting his own body orientation. Therefore,

we predicted the dolphin's performance accuracy would be higher in the picture plane rotation test either because all features remain available or because he adjusted his own body orientation. In addition to rotation plane effects, familiarity can allow an individual to find unique rotation-invariant features or store more views of objects, which increases the likelihood of viewpoint-independent performance (Jolicoeur & Milliken, 1989). Therefore, we predicted the dolphin's performance would be higher with familiar object sets than with novel object sets.

Method

Animal Subject

The subject was Ranier, an adult male bottlenose dolphin (*Tursiops truncatus*) in his early 30s residing at The Seas, Epcot, Walt Disney World Resort, Lake Buena Vista, FL. He had previous experience participating in a variety of cognitive research projects, including those utilizing matching-to-sample techniques (Harley, Fellner, & Stamper, 2010). He had multiple years of experience with visual matching tasks conducted at the underwater viewing windows. All training and testing sessions took place in the main environment—a 5.8-million gallon, mixed-species habitat—at two underwater viewing windows as part of a research demonstration for the public (Figure 1). The dolphin received a portion of his daily diet of herring, squid, and capelin for participating in the session.

All dolphins at The Seas, including Ranier, were cared for in a manner consistent with the Marine Mammal Protection Act (1972), and The Seas was authorized to house the animals by permit # 58-C-0076 issued by the U.S. Department of Agriculture Animal and Plant Health Inspection Service. All decisions regarding Ranier's diet, management, and care were made by husbandry and veterinary personnel, were independent of his participation or accuracy in research sessions, and were in accordance with the Animal Welfare Act (1966) and Association of Zoos and Aquariums (2014) accreditation guidelines. The Disney Animal Care and Welfare Committee approved this research.

Materials

The picture plane rotation test utilized six object sets, with each set containing three objects (Figures 2 and 3). The objects were constructed to be of equal surface area both within sets and between sets. They were made using a standard collection of small rectangles, circles, and triangles (Block Buddies, MindWare Inc., Roseville, Minnesota), assembling them into a variety of tangram-like shapes, then tracing and cutting the tangram shape from 0.32-cm thick, white foam-core board. The dolphin had viewed the three familiar object sets (F1, F2, and F3) for 24– to 36 trials during training sessions within a two-alternative visual discrimination task with all objects in the upright (0°) position. The other three novel object sets (N1, N2, and N3) had never been viewed by the dolphin or used in any other prior task. Affixed to the back of each object was a printed wheel that indicated to the trainer how far to rotate the sample object before presenting it for the dolphin to view. For example, if the object was to be presented at 180°, the trainer held the object such that the 180° marker on the wheel was on top.

The depth plane rotation test included nine object sets, with each set containing three objects (see Figure 4 for three object sets and Ap-
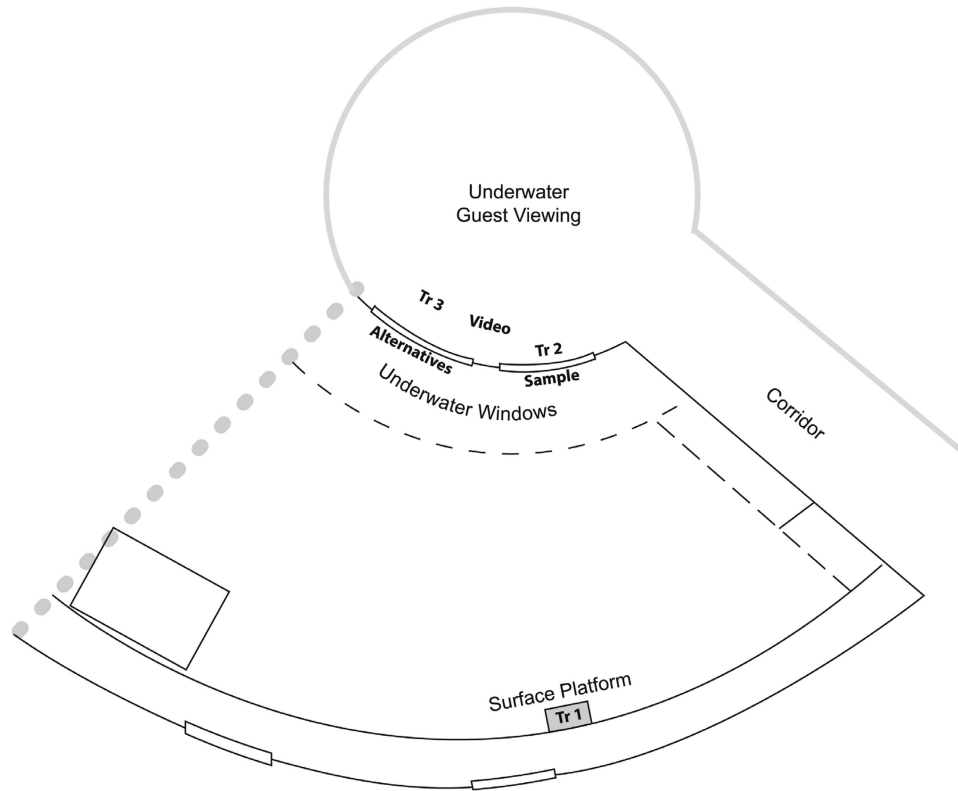
Figure 1. This figure shows the dolphin main display pool where experimental sessions took place. The dolphin started each trial at the surface platform with Trainer 1 (Tr 1). Trainer 2 (Tr 2) held the rotated sample on the sample window at arm's length and then indicated to Trainer 1 via portable radio that the trial could start. The dolphin traveled to the sample window and then to the alternatives window to make a selection. Trainer 3 (Tr 3), who was naïve to the identity of the sample, called out which object the dolphin chose. Trainer 2 blew a whistle to mark correct responses and then the dolphin returned to Trainer 1 at the surface platform and received fish. An assistant held a video camera (video) between the sample window and alternatives window and panned to follow the dolphin.

pendixes A and B for the other six object sets). Three-dimensional sculptures were constructed out of Lego Duplo building blocks (The LEGO Group, Billund, Denmark) and then photographed at six angles rotated around the vertical *y* axis in the depth plane. The photos were printed at actual size, affixed to 0.32-cm thick white foam-core board, and then the figure was traced with an X-Acto knife to cut the background away, leaving only a cutout of the photo of the Lego sculpture. All nine object sets (D1–D9) were novel to the dolphin.

In both rotation plane tests, alternative objects were presented at the 0° aspect angle and suspended with a 50-lb test monofilament line from 4.45-cm clear plastic suction cups affixed to the acrylic window. The alternative objects were spaced 1 m apart so that the dolphin could make a clear choice by stationing at only one object at a time (Figure 5). The sample and alternatives array were both centered within adjacent viewing windows, which resulted in a 4-m distance between the sample and the left-most alternative (Figure 1). Although the sample remained available in the left window when the dolphin swam to the alternatives, due to the curvature of the acrylic, a mirror-like reflection likely prevented the dolphin from continuing to view the sample while stationed at the alternatives. He could, however, likely have seen both the sample and the alternatives when approaching the testing area at the beginning of the trial.

Angles of rotation were chosen differently for the two rotation planes tested. Balancing a three-alternative session for sample identity and location within the choice array requires an 18-trial session with six presentations of each sample object. Dividing a circle into 45° increments yields eight unique angles. Therefore, to maintain a balanced session, two angles in each rotation phase were not tested. In the picture plane rotation test, because all object features were available at every rotation, there was no a priori reason to predict that orthogonal (±90°) orientations would be different from other angles, so we selected the diagonal angles that were mirror images of each other (±45° and ±135°) as well as the upright angle (0°) and the opposite, upside-down angle (180°). In the depth plane rotation test, the orthogonal presentations were maximally different from the front side orientation (0°), and therefore, two diagonal orientations were eliminated from testing leaving one diagonal adjacent to 0° (−45°) and the other adjacent to 180° (+135°; see Figure 6 for angles tested in each plane).

Procedure

The dolphin performed a three-alternative matching-to-sample task, shown in Figures 1 and 5. For each trial, the dolphin swam
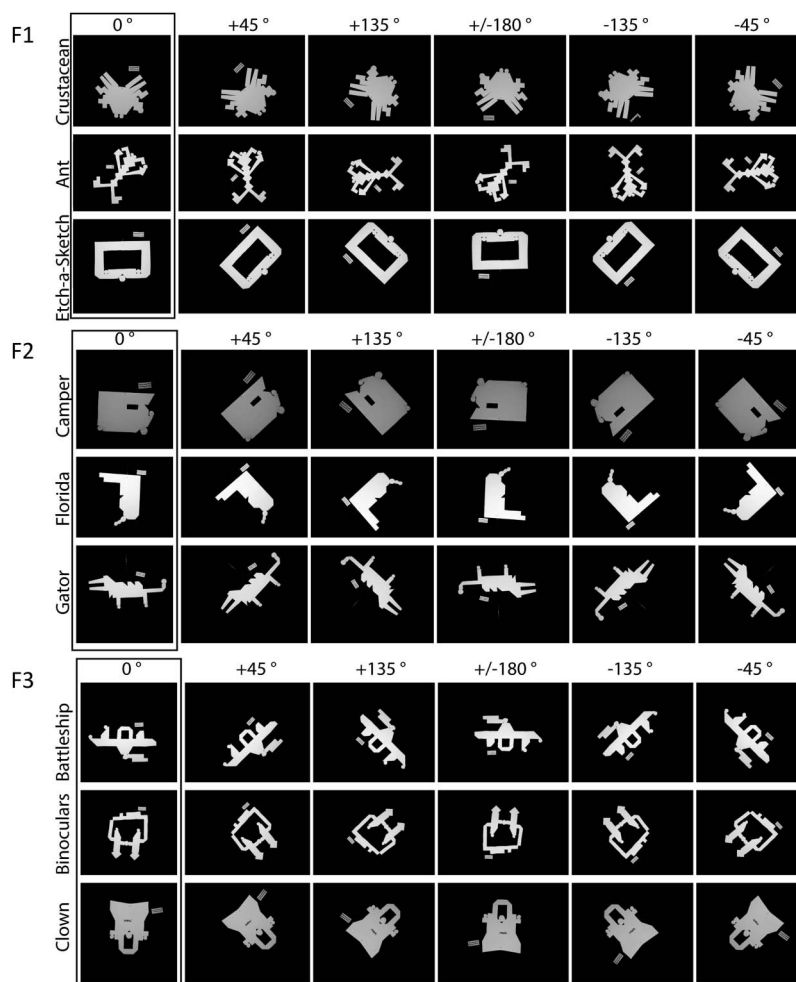
Figure 2. The three object sets that were familiar to the dolphin used for the picture plane rotation test (Sets F1, F2, and F3). The small rectangle near the object in each photo is a paper ruler that is 5-cm long.

from Trainer 1 at the surface platform (Tr1) to an underwater viewing window (Tr2) to view the rotated sample object held by Trainer 2 at one arm's length away from her body up against the window. The dolphin then traveled to the adjacent window where Trainer 3 was stationed (Tr3) to make his selection from the three 0° alternatives by stopping in front of one alternative and emitting bubbles from his blowhole. Trainer 3, who was naïve to the identity of the sample, called out which object the dolphin had selected. If the dolphin was correct, Trainer 2 blew a whistle and directed the dolphin to return to Trainer 1, who provided a fish reward at the surface platform. If the dolphin was incorrect, he received no response from the trainer and could choose to repeat the trial (recorded as a "correction trial" and not included in the performance accuracy data) by returning to Trainer 2 and viewing the sample again or returning to Trainer 1 in preparation for the next trial. The intertrial interval was approximately 1 min. The dolphin's performance accuracy was recorded by Trainer 3. Video recordings were made of 100% of the sessions. The video camera was held by an assistant who sat between the two windows and panned to follow the dolphin (see Figure 1).

All test sessions included 18 trials in pseudorandom order in which the identity of the sample and its location within the choice array were balanced across trials. Each session included six trials of each of the three objects within a three-object set as the sample rotated to one of six angles. For picture plane rotation test sessions, the dolphin completed five sessions for the three familiar object sets and 15 sessions for the three novel object sets: five sessions in which the sample was rotated, followed by five "practice" sessions in which the samples remained upright (0°), and then an additional five sessions in which the sample was rotated. The picture plane object sets were presented in the following order: F1, F2, F3, N1, N2, N3. The picture plane rotation test sessions were conducted 5 to 7 days per week across a 2.5-month period.

The picture plane rotation test sessions were conducted first, followed by depth plane rotation test sessions. After the picture plane test sessions and before the depth plane test sessions, the Lego stimuli were gradually introduced to the dolphin by systematically replacing one foam-core object at a time with one real Lego sculpture (not photos) within training sessions. Once the three-object set was composed of all Lego objects, we replaced the
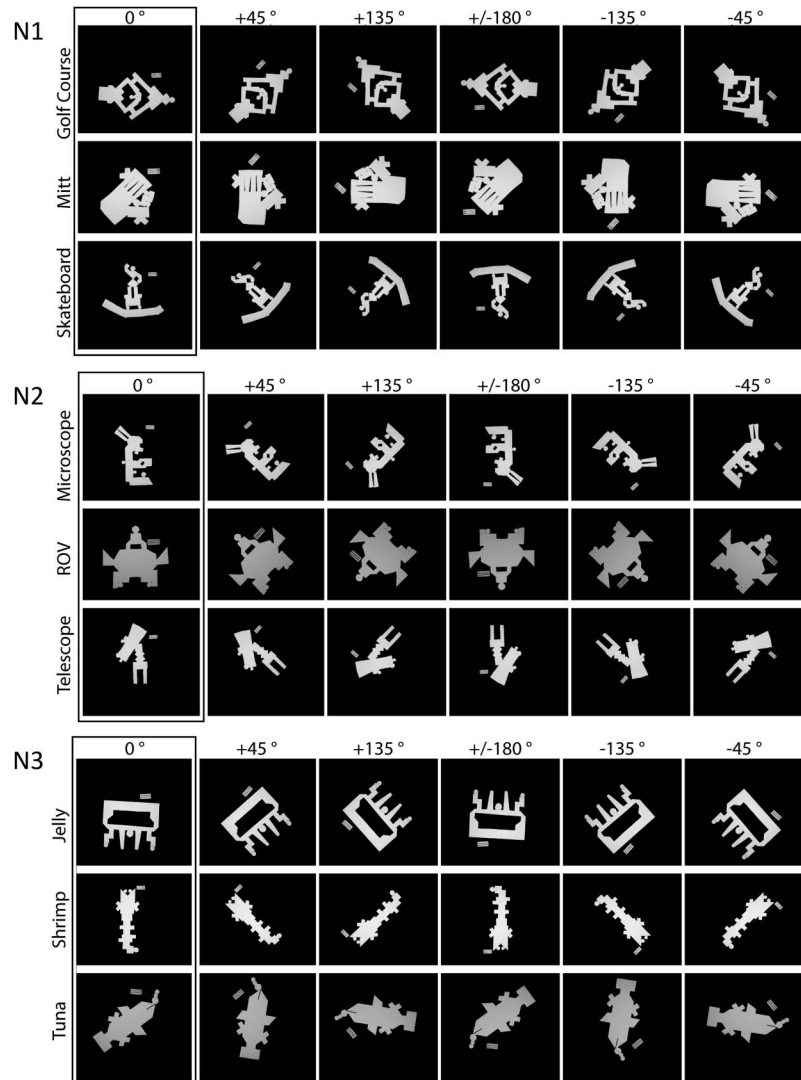
Figure 3. The three object sets that were novel to the dolphin used for the picture plane rotation test (Sets N1, N2, N3). The small rectangle near the object in each photo is a paper ruler that is 5-cm long.

real Lego sculptures with their photo cutout counterparts and then presented photos of the same Lego objects rotated. The choice alternatives were always presented at 0° of rotation. The training stimuli were no longer novel by this stage, and the dolphin's performance on this training set was not included in the data for analysis. Once this training phase was completed, the dolphin completed 10 depth plane rotation test sessions for each of the nine object sets. All stimuli in analyzed sessions were cut-out photographs of the Lego objects. The depth plane object sets were presented in the following order: D1, D2, D3, D4, D5, D6, D7, D8, D9. The depth plane rotation test sessions were typically conducted 4 to 5 days per week across a 7.5 month period.

Data Analyses

Statistical analyses of overall accuracy were performed using R v3.5.2 (R Core Team, 2018). An experimental Type I error level of $\alpha = .05$ was used. To control the experimental error level at $\alpha = .05$, p values were adjusted using Holm's (1979) method. Tukey's (1949) honest significant difference was used for multiple comparison Type I error control for pairwise comparisons where appropriate. Multilevel models were used to account for dependence among trials from the same subject. This allowed for modeling of variability among samples and experimental variables that were manipulated at the trial level and experimental variables that were manipulated at the session level.

To determine whether the dolphin adopted a strategy of rotating his body to match the orientation of the rotated object in the picture plane (this option was precluded in the depth plane, where the dolphin could not use this strategy), we analyzed his body positioning in a subset of the sessions. Using Adobe Premiere Pro, 2017 applied to video recordings, we extracted five still images per second of the dolphin's sample approach from one randomly
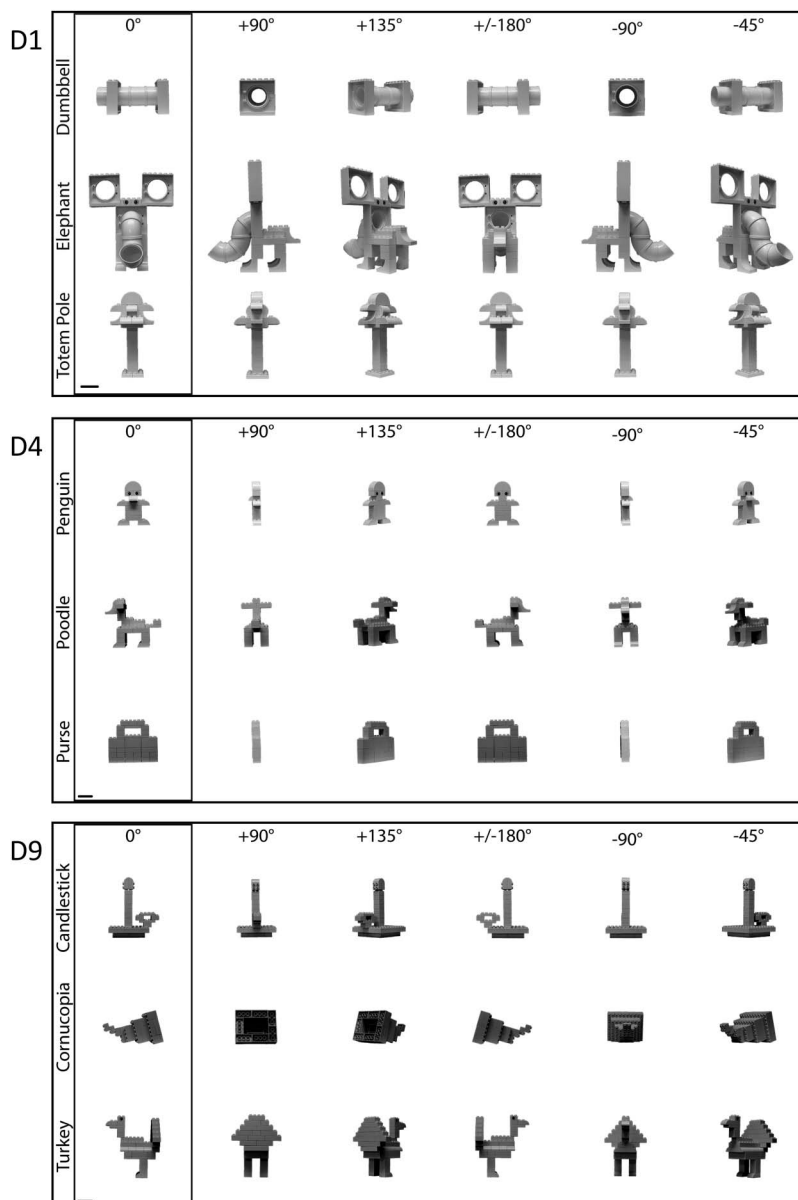
Figure 4. Three of the nine object sets used for the depth plane rotation test (Sets D1, D4, D9). The small rectangle in the bottom left corner of each object set is a 5-cm scale bar (near the 0° view of the totem pole, purse, and turkey). The other six object sets can be found in Appendixes A and B.

selected session from the first, middle, and last sets tested (Sets F1, N1, and N3). Using the ruler tool in Adobe Photoshop, 2017, we measured the angle of a line drawn from the tip of the dolphin's rostrum to the center of his blowhole. Because Photoshop's measuring tool describes a horizontal line drawn from left to right as having 0° of angle and our objects were aligned such that 0° was described as vertical, measured values were corrected by −90° so that if the dolphin aligned himself with the object, their angles of orientation would be the same. The dolphin's body orientation measurements were then compared with those of the sample presentations graphically.

Results

Picture Plane Rotation Test

Performance accuracy. The overall accuracy after controlling for location of the correct choice, object set, and sample object orientation using a multilevel mixed-effects logistic regression model was significantly better than chance (i.e., 33.3%) in the picture plane ($M = 81.2\%$, $SE = 4.2\%$, $Z = 8.14$, $p < .0001$, 95% confidence interval [CI] [72.8%, 89.2%]). From the intercepts-only model where accuracy was allowed to vary among samples, the intraclass correlation (ICC) was large in the picture plane
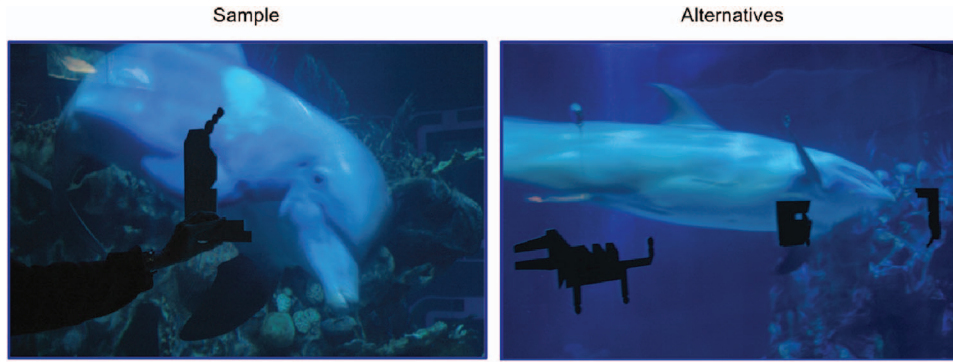
Figure 5. The matching-to-sample task. The dolphin inspects the sample object (presented here at 180°). The trainer uses the compass on the back of the object to orient the sample at the correct aspect angle. The dolphin then inspects the alternative objects, which are always presented at 0°. The sample was 4 m from the closest alternative, and alternatives were 1 m apart (Figure 1). Objects pictured here are from the picture plane rotation test. Objects were made from white foam board, but appear black here because they are backlit. Alternative objects appear distorted in size due to the camera angle (see Figure 2 for an undistorted view of this object set). See the online article for the color version of this figure.

(ICC = 0.51; Wu, Crespi, & Wong, 2012). There was a strong correlation between performance and sample identity that we can account for in a multilevel model (i.e., trial accuracies were more similar for trials with the same sample object than for trials with different sample objects). Therefore, we fit a multilevel logistic regression model, which was a significantly better predictor of performance than an intercepts-only model based on a likelihood ratio test of model goodness-of-fit for the picture plane rotation test, $\chi^2(12) = 86.17$, $p < .0001$.

A sequential analysis of deviance using likelihood ratio tests was performed to test the statistical significance of main effects of

Figure 6. The aspect angles used for sample object presentations in both the picture plane rotation test (P) and the depth plane rotation test (D).

object set, sample object orientation, correct object location (left, middle, right), session number, trainer, and rotation phase for novel object sets (Phase A = S + rotated; upright = S + not rotated; Phase B = S + rotated). These predictors reduced the ICC from 0.51 to 0.28, which suggests that these main effects explained roughly 62% of the variability in accuracy between samples. Adjusting all p values using Holm's method (1979), there was no statistically significant change over time, $\chi^2(1) = 2.12$, $p = .1456$, and there was no significant difference in the dolphin's performance among trainers, $\chi^2(2) = 1.73$, $p = .4218$.

There were several significant main effects. First, there was a significant main effect of sample object orientation, $\chi^2(5) = 20.44$, $p = .0010$. In post hoc analyses, we compared performance among 0°, ±45°, ±135°, and 180° orientations and found that there was a significant linear decline in accuracy as the sample was rotated from 0° toward 180°, $Z = -3.36$, $p = .0102$. Performance was significantly better at 0° than 180°, $Z = 2.93$, $p = .0180$, but no other pairwise comparisons were significantly different, all $p > .05$. Performance was significantly better than chance for all sample object orientations as shown in Figure 7A.

Second, there was a significant main effect of object set, $\chi^2(5) = 20.21$, $p = .0011$. Post hoc analyses of the object sets compared performance on the familiar (i.e., F1, F2, and F3) and novel (i.e., N1, N2, and N3) sets. Performance was significantly better for the familiar object sets ($M = 97.1\%$, 95% CI [90.9%, 99.1%]) than the novel object sets ($M = 76.9\%$, 95% CI [60.1%, 88.0%]), $Z = 3.18$, $p = .0015$, although performance was significantly better than chance on both the familiar sets overall as a group and the novel sets overall as a group (Figure 8). The dolphin's performance was better than chance on two of three object sets within both groups. Note that the dolphin's higher performance on familiar object sets was due primarily to his near ceiling performance on Set F1 ($M = 98.6\%$) and Set F2 ($M = 99.0\%$). The dolphin received only five sessions with the familiar sets, but he received 15 sessions with the novel sets (five sessions in Phase A = sample object rotated; five upright practice sessions = sample object not rotated; five sessions in Phase B =
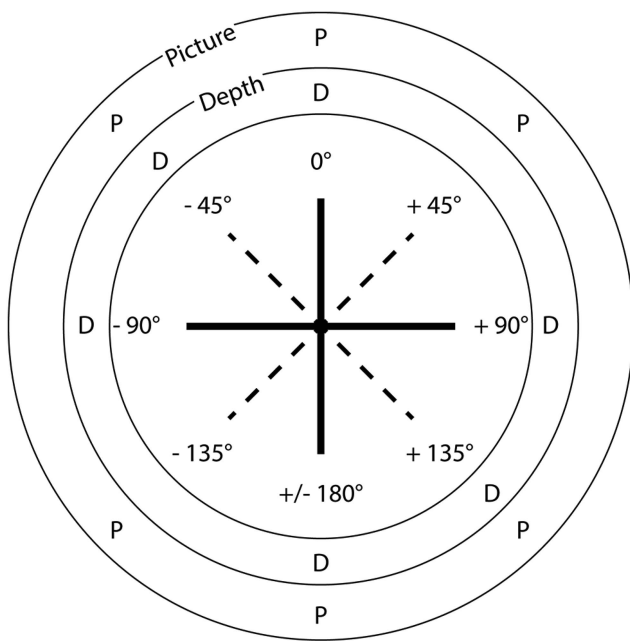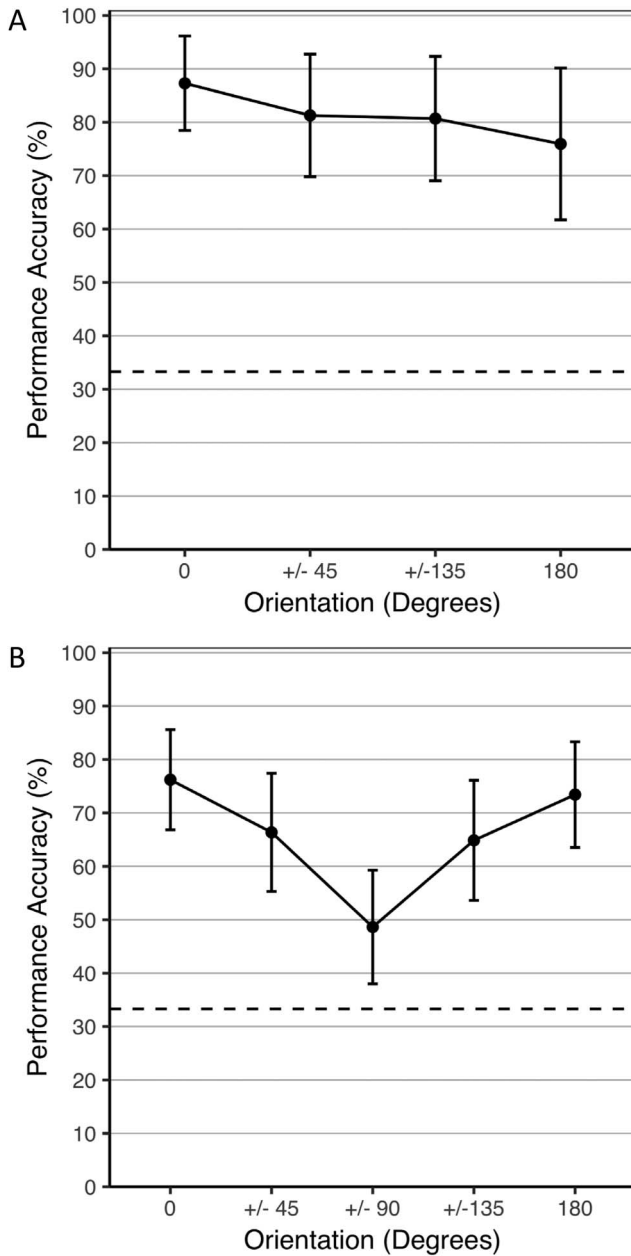
Figure 7. The performance accuracy of the dolphin for each orientation of the sample object shown for the picture plane rotation test (A) and the depth plane rotation test (B). Accuracies are shown along with 95% simultaneous Tukey-adjusted confidence intervals. Chance performance of 33.3% is shown as a dashed line.

sample object rotated). There was no significant difference in performance among the three rotation phases, $\chi^2(2) = 0.45$, $p = .7968$, meaning the five upright practice sessions did not improve his performance with rotated samples in Phase B (see Figure 9).

Third, there was a statistically significant main effect of the correct choice location within the array of three alternative objects, $\chi^2(2) = 42.80$, $p < .0001$. The dolphin was more accurate when the correct object was on the left (closest to the sample) than in the middle, $Z = 2.89$, $p = .0108$, and on the right (at the far end of the

array), $Z = 5.20$, $p < .0001$, and more accurate when the correct object was in the middle than on the right, $Z = 3.21$, $p = .0038$ (i.e., he had a side bias). Figure 10A shows the dolphin's performance when the correct choice was on the left, middle, and right positions.

Dolphin's body position. Although we controlled the orientation of the sample object, the dolphin was unrestricted in his approach toward the sample and could have rotated his own body to match the rotation of the sample object when we tested the picture plane. The video analysis of the dolphin's approach to the sample revealed that he maintained approximately the same body orientation for every trial and did not change his positioning in relation to the object's presentation. Although he changed his orientation while inspecting the sample, the changes were stereotypic; the dolphin engaged in a consistent set of inspection behaviors regardless of the orientation of the sample stimulus (Figure 11). Note that the dolphin's body orientation was irrelevant for tests in the depth plane because these were inherently controlled within the stimulus presentation.

Depth Plane Rotation Test

The overall accuracy after controlling for location of the correct choice, object set, and sample object orientation using a multilevel mixed-effects logistic regression model was significantly better than chance (i.e., 33.3%) in the depth plane ($M = 63.0\%$, $SE = 3.3\%$, $Z = 8.35$, $p < .0001$, 95% CI [56.6%, 69.5%]). From the intercepts-only model where accuracy was allowed to vary among samples, the ICC was moderate in the depth plane (ICC $= 0.12$). There was a moderate correlation between performance and sample identity that we can account for in a multilevel model (i.e., trial accuracies were more similar for trials with the same sample object than for trials with different sample objects). Therefore, we fit a multilevel mixed-effects logistic regression model, which was a significantly better predictor of performance than an intercepts-
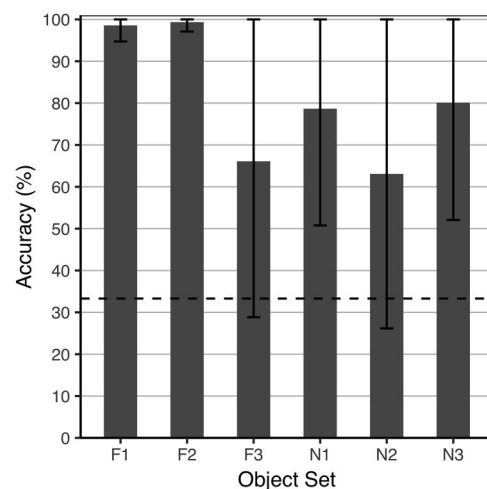

Figure 8. The performance accuracy of the dolphin for all six object sets used for the picture plane rotations. The familiar object sets are F1, F2, and F3, and the novel object sets are N1, N2, and N3. Accuracies are shown along with 95% simultaneous Tukey-adjusted confidence intervals. Chance performance of 33.3% is shown as a dashed line.
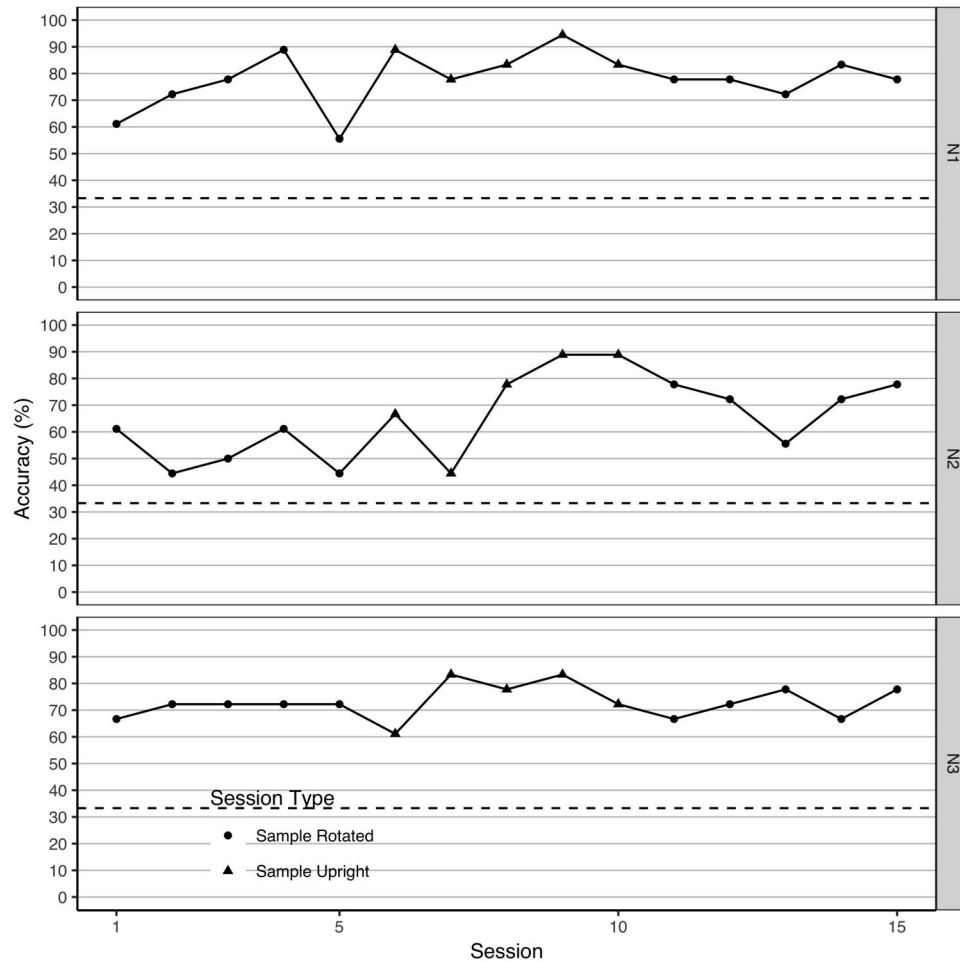
Figure 9. The performance accuracy of the dolphin for only the novel object sets used for the picture plane rotations. The dolphin received 15 sessions with the novel sets (five sessions with sample rotated; five sessions with sample upright; another five sessions with the sample rotated). Chance performance of 33.3% is shown as a dashed line.

only model based on a likelihood ratio test of model goodness-of-fit, $\chi^2(7) = 104.84$, $p < .0001$. The accuracy of the dolphin for the depth plane rotation test was significantly lower than for the picture plane rotation test ($Z = -4.43$, $p < .0001$, 95% CI for log-odds difference $[-2.58, -1.00]$).

A sequential analysis of deviance using likelihood ratio tests was performed to test the statistical significance of main effects of object set, sample object orientation, correct choice location (left, middle, right), session number, and trainer. These predictors did not change the ICC. Adjusting all p values using Holm's method (1979), there was no statistically significant change over time, $\chi^2(1) = 3.51$, $p = .1825$, no significant differences among trainers, $\chi^2(2) = 3.75$, $p = .3060$, and, unlike the results for the picture plane rotation test, there was no significant main effect of object set for the depth plane rotation test, $\chi^2(8) = 5.76$, $p = .6738$.

There were two significant main effects. First, there was a significant main effect of sample object orientation, $\chi^2(5) = 73.32$, $p < .0001$. In post hoc analyses, we compared performance among $0°$, $-45°$, $\pm90°$, $135°$, and $180°$ orientations and found that there was a significant quadratic trend in accuracy as the sample was

rotated from $0°$ toward $180°$, $Z = 6.62$, $p < .0001$, but no linear trend, $Z = -0.82$, $p = .9550$. Performance was highest at $0°$, declined through $-45°$ rotations to its minimum at $\pm90°$ rotations, and then increased through $135°$ and $180°$ rotations with accuracy nearly equal at $-45°$ and $+135°$ rotations and $0°$ and $180°$ rotations, respectively. Performance was significantly lower at $\pm90°$ than at all other orientations, all $p < .001$, and performance was significantly lower at $135°$ than at $0°$, $Z = 2.81$, $p = .0394$. No other pairwise comparisons were significantly different, $p > .05$. Performance was significantly better than chance for all orientations (Figure 7B).

Second, there was a statistically significant main effect of the correct object location within the array of three alternative objects, $\chi^2(2) = 14.82$, $p = .0024$. The dolphin was more accurate when the correct object was on the left (closer to the sample) than in the middle, $Z = 3.46$, $p = .0016$, and on the right (at the far end of the array), $Z = 3.28$, $p = .0029$, but equally accurate when the correct object was in the middle and on the right, $Z = 0.13$, $p = .9902$ (i.e., he had a side bias). Figure 10B shows the dolphin's performance when the correct choice was on the left, middle, and right positions.
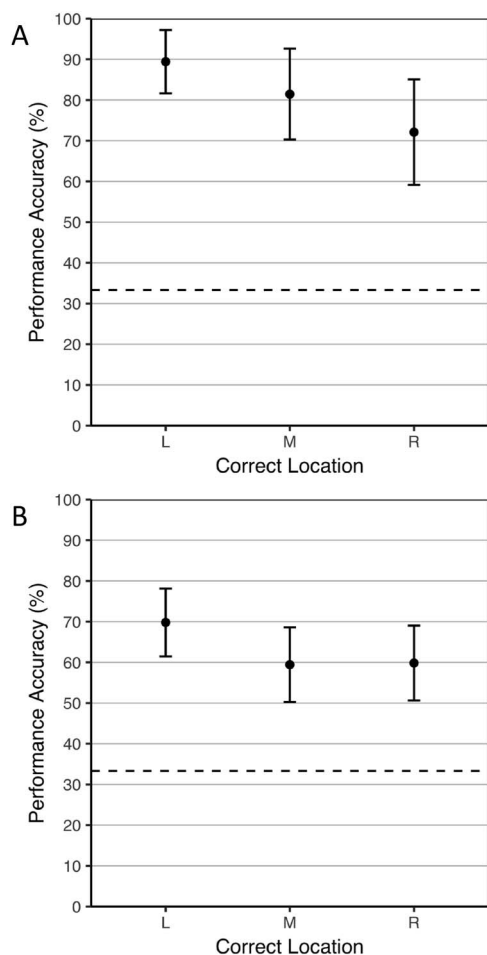
Figure 10. The performance accuracy of the dolphin when the correct choice was in the left, middle, and right positions shown for the picture plane rotation test (A) and the depth plane rotation test (B). Accuracies are shown along with 95% simultaneous Tukey-adjusted confidence intervals. Chance performance of 33.3% is shown as a dashed line.

Discussion

The purpose of the current study was to investigate a bottlenose dolphin's ability to recognize visually objects presented at six different orientations in two rotation planes. The dolphin's performance accuracy was significantly better than chance across all aspect angles in both rotation planes. When viewing objects rotated in the picture plane, the dolphin displayed a significant linear decline in accuracy as the sample was rotated from 0° toward 180°. In contrast, when viewing objects rotated in the depth plane, there was a significant quadratic trend in accuracy with the lowest performance at ±90°. As predicted, the dolphin's overall performance was better during the picture plane rotation test versus the depth plane rotation test, and performance with familiar object sets exceeded performance with novel object sets. Finally, in the picture plane rotation test, the dolphin consistently approached the sample and alternative objects in a stereotypical fashion instead of aligning his head and body to match the aspect angle of the object when it was not upright.

The dolphin's performance in this study is best described as showing evidence of both viewpoint-independent and viewpoint-dependent processes. The dolphin matched objects at all aspect angles in both rotation planes, suggesting he achieved object constancy. These results would be consistent with the view that a single underlying 3-D representation is constructed of the object specifying structural relations between geons, consistent with viewpoint-independence (Biederman & Gerhardstein, 1993; Marr, 1982). However, the dolphin's recognition accuracy was a function of viewing angle in both rotation planes. These results are consistent with the theory that the visual system stores a number of 2-D object representations, and recognition occurs if the stored view is close to the presented view, consistent with viewpoint-dependence (Tarr & Pinker, 1989). These two possibilities are not mutually exclusive in that an organism may rely on a viewpoint-dependent 2-D representation for some purposes and a viewpoint-independent 3-D representation for others. The dolphin's pattern of results in the current study (success at all aspect angles, but aspect-dependent performance) has been found in studies with other animals, like pigeons (for a review see Peissig & Goode, 2012).

The recognition of objects that are presented at novel viewpoints in relation to a comparator is a complex process. Attempts to infer an organism's ability to reconcile differences between the encoded representation and the new exemplar to be recognized have focused not only on the nature of the underlying representation in memory but also on the process of mental transformation. In the process of transformation, an image can be transformed to reduce differences between the image and a view-specific stored representation. Mental rotation has been invoked as a process allowing the recognition of rotated stimuli in many species (Köhler et al., 2005; Mauck & Dehnhardt, 1997; Shepard & Metzler, 1971) and can be detected by observing increased reaction time (RT) as well as more errors with increasing angular disparity from the stored view. The results of the picture plane rotation tests in the current study reveal a linear relationship between the dolphin's accuracy and absolute distance from 0° of rotation, which might be suggestive of the process of mental rotation. Our results agree with studies with planar-rotated 2-D stimuli showing systematic decrements in performance as a function of object rotation (Hamm et al., 1997; Mauck & Dehnhardt, 1997; Peissig et al., 2005). However, our dolphin showed the lowest performance at 180°, which contrasts with the sea lion in Mauck and Dehnhardt's (1997) study showing lowest performance at 90° (but highest RTs at 180°). Our results contrast with studies that have not shown systematic decrements in performance with planar-rotated 2-D stimuli as a function of aspect angle (fish: DeLong et al., 2018; lion-tailed macaques: Burmann et al., 2005). Our results showing that performance with planar-rotated objects was significantly better at 0° than 180° agree with other studies. For example, rhesus monkeys and chimpanzees showed significant linear impairment as rotation angle increased, but stimulus type mattered (faces vs. nonfaces; Parr, 2011; Parr & Heintz, 2008). RT is a key dependent variable in studies that invoke the process of mental rotation, but we did not measure that variable in the current study. Therefore, we cannot assert that the dolphin was mentally rotating the stimuli. Future research in this area could incorporate RT to further explore this possibility.
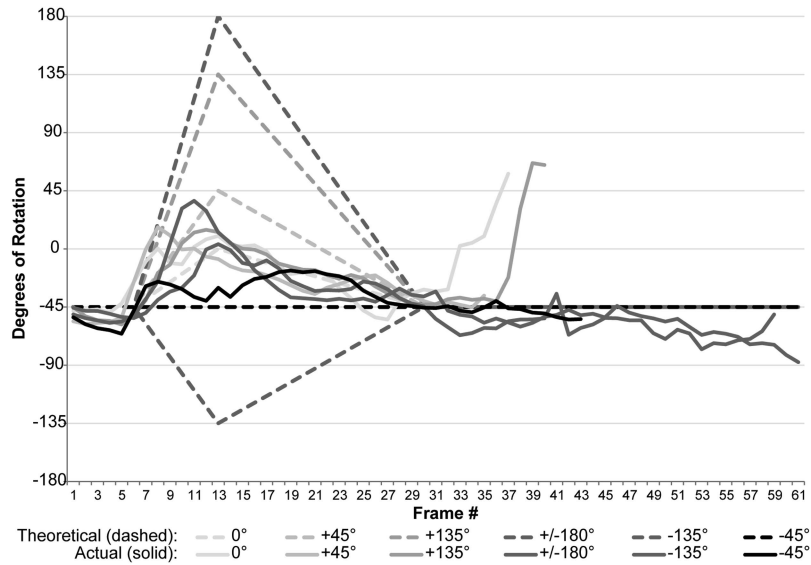
Figure 11. A comparison of how the dolphin could have rotated his body to match the sample ("theoretical" = dashed lines) versus his actual body rotation ("actual" = solid lines) as measured in sequential frames of video. If he had rotated his body to align with the rotation of the object, the solid and dashed lines would overlap. However, the dolphin performed similar movements during each trial, irrespective of the sample object's orientation.

In addition to examining the nature of the underlying representation in memory or the process of mental transformation, another way to explain an organism's ability to recognize rotated objects is to explore the presence of distinctive, rotation-invariant features. This account may explain some results in this study. First, the dolphin's performance accuracy was higher when viewing objects rotated in the picture plane than when viewing objects rotated in the depth plane. This is likely because when rotating objects in the picture plane, all object features remain in view at all aspect angles, whereas when rotating objects in the depth plane, a diagnostic feature can disappear and another can reappear at different aspect angles. The dolphin's superior performance with picture-plane rotation could mean that he used diagnostic features. Second, when viewing objects rotated in the depth plane, there was a significant quadratic trend in accuracy with the lowest performance at ±90°. For many of the object sets, object features that were present at 0° are no longer present at ±90° (Figure 4, Appendixes A and B). For example, in Set D1, the two vertical bars in the dumbbell and the two ears on the elephant are not present at ±90°. In addition, many of the objects when viewed at ±90° strongly resemble one another. For example, within Set D4, the penguin and the purse when viewed at ±90° both look like vertical bars and share almost no features with their 0° aspects. In most object sets, many if not all object features present at 0° are also present to some degree at all aspects except the ±90° aspect.

In the picture plane rotation tests, the dolphin had greater success recognizing rotated stimuli with familiar object sets than with novel object sets. This result is in agreement with studies finding that repeated exposure to a stimulus set during training sessions increases accuracy and allows viewpoint-independent strategies to develop (by increasing awareness of rotation-invariant features; Jolicoeur, 1985; Jolicoeur & Milliken, 1989). The dol-

phin had only 24 to 36 training trials with the familiar sets in the upright (0°) position before the start of the test sessions, yet this seemed to be enough exposure to lead to an advantage over the novel sets. The dolphin in the current study had relatively few training trials compared to the thousands of trials it took for monkeys to generalize to rotated stimuli more than 30° away from upright (Nielsen et al., 2008). During the test sessions with the novel sets, after the first five sessions with rotated samples, the dolphin was given five sessions of "practice" with upright samples, then a final five sessions with rotated samples. Interestingly, these five practice sessions (90 trials) did not improve the dolphin's performance on the novel sets, whereas 24 to 36 trials of exposure helped the dolphin with the familiar sets. The training trials for the familiar sets took place in the context of a two-alternative matching task, so perhaps that increased the dolphin's awareness of the differences between the objects better than the three-alternative matching task done during the five practice sessions for the novel objects.

Alternately, we may have inadvertently placed more similarly shaped objects within the novel object sets as compared with the familiar object sets, making the task more difficult for the dolphin when viewing the novel object sets (Figures 2 and 3). Objects within a set with different shapes are easier to recognize when rotated then objects within a set with more similar shapes (Logothetis et al., 1994). It should also be acknowledged that the dolphin showed ceiling-level performance in familiar Sets F1 and F2, which could account for the difference in performance between the familiar and novel sets. The familiarity, or amount of exposure, to the familiar sets may have been less of a factor in the dolphin's performance than the high discriminability of the objects within Sets F1 and F2. Familiar Set F3 appears to have been challenging for the dolphin despite its familiarity. Overall performance when

two of the objects within Set F3 were presented as sample objects was high (battleship = 73.3%, binoculars = 83.3%), whereas the dolphin's choices when presented with the clown as the sample object were distributed across all three alternatives (accuracy = 46.7%). The reason for the dolphin's confusion with this object is not known. Given that we only had three familiar and three novel object sets, it is difficult to conclude what accounted for the dolphin's performance advantage on the familiar objects. Future studies could use a larger number of both familiar and novel object sets and could also control the setting in which the objects are exposed to the dolphin (e.g., use the same number of alternatives for training and testing).

Despite being free to adopt any posture while inspecting the sample during the picture-plane rotation test, the dolphin did not align his head and body to the aspect angle of the sample object (e.g., he did not turn his head or body 90° when the sample was positioned at 90°). He swam toward the sample then turned left and inspected the alternatives with his right eye (the windows were on his right side). When making a choice, he did a headstand in front of his chosen object. He may have made his selection while using his right eye only. The dolphin's stereotypical movement pattern and use of his right eye could be attributed to the side-by-side layout of the two viewing windows, but it was possible for him to stop in front of each object and view each one with both eyes. He may have preferred using his right eye. There was no evidence to suggest that the dolphin's vision varied between eyes, and because dolphins' eyes are on the sides of their heads, they likely do not rely on binocular vision in most circumstances. Several other studies have shown that dolphins show superior performance during visual tasks when using their right eye as opposed to their left eye. This is the case for a 2-D shape discrimination task (von Fersen et al., 2000), a spatial working memory task (Kilian, von Fersen, & Güntürkün, 2000), and a numerosity task (Kilian et al., 2005). These studies suggest that dolphins show visual lateralization and have left hemispheric dominance for visual processing. However, our experiment was not set up in a way that would allow us to detect which eye was preferred.

There is a strong possibility that the dolphin's swimming pattern was a function of the design of the facility as shown in Figure 1. This factor may also explain the side bias throughout the study, showing the dolphin's performance was highest when the correct alternative was on the left (although it was above chance in all three choice positions). The dolphin viewed the sample in one window then swam toward his left, encountering the alternatives at an adjacent window where he first saw the left alternative, then the middle alternative, and finally the right alternative. Because the window was slightly curved and he swam close to it, he may not have immediately seen the right alternative as early in his approach as the left and middle alternatives. His occasional tendency to forget to check the right alternative may have impacted his performance. Therefore, the results may actually be a conservative estimate of the dolphin's ability to recognize rotated objects. Overall performance may have been higher with a different experimental setup in which all three alternatives are equidistant from the sample object.

This study utilized a single subject design, so care should be taken in interpreting the results. This match-to-sample task required an extensive training period as well as a lengthy time commitment to complete the experiment. At the present time, few dolphins are available to undertake behavioral research and they are expensive to care for. Thus, it is common to use very few subjects in marine mammal cognition and perception studies (Harley et al., 1996; Herman et al., 1984; Jaakkola et al., 2005; Kilian et al., 2000). However, it would be beneficial to replicate these results with other dolphin subjects using different experimental setups and different stimuli.

The dolphin represents a special case in the analysis of visual object recognition because vision is not the only sense it brings to bear on the task of recognizing objects at a distance. Vision and echolocation are complementary senses that work together to form an integrated representation of the world (Harley & DeLong, 2008; Harley et al., 1996) and, because dolphins often navigate visually opaque environments, vision is likely to be secondary to echolocation. Interestingly, some of the same aspects of object recognition that present challenges in the visual domain are similar in the echoic domain, in that when objects are rotated in space, they result in strikingly different proximal sensory inputs. Echolocation and vision often are used simultaneously and can provide complementary information. When encountering a small, aquatic animal, the dolphin's echolocation system may detect the presence of cartilaginous material while the visual system recognizes a cigarlike shape, bright underbelly bioluminescent photophores, and dark collar marking, which is then integrated into the recognition of a cookiecutter shark (*I. brasiliensis*), even when viewed from a novel perspective.

Although dolphins have remarkable acoustic abilities and are capable of recognizing objects using echolocation (Au, 1993; Harley & DeLong, 2008), they are also capable of visual object identification. Not only is their visual acuity good both in air and underwater (Herman et al., 1975), they are also capable of recognizing objects across orientation shifts in the picture and depth planes. Their performance is similar to some mammals and birds that do not echolocate (Peissig & Goode, 2012). Dolphins likely use both viewpoint-dependent and viewpoint-independent representations to accomplish this complex but ecologically valuable feat.

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(*Appendices follow*)

Appendix A

Additional Object Sets Used in the Depth Plane Rotation Test

This appendix shows three of the nine object sets used for the depth plane rotation test (D2, D3, D5). The line in the bottom left corner of each object set is a 5-cm scale bar (near the 0° view of the snail, scallop, and gopher tortoise). Other object sets used for the depth plane rotation test can be found in Figure 4 and Appendix B.
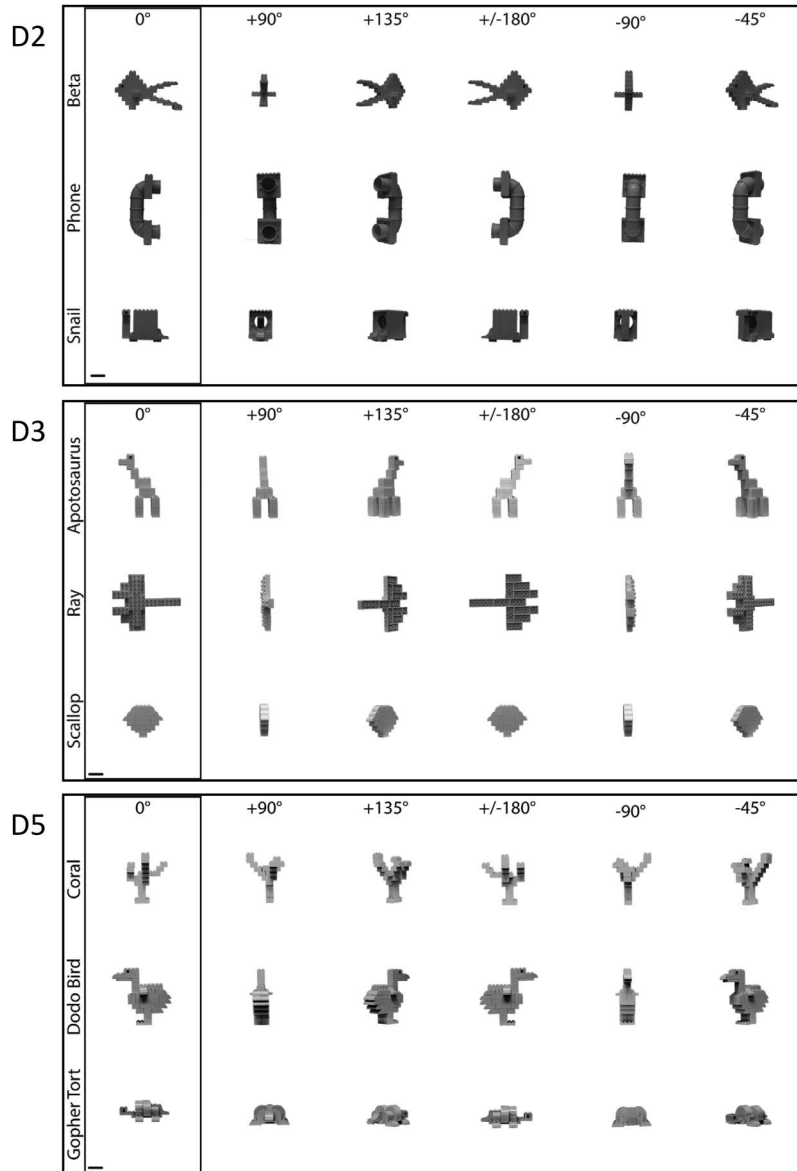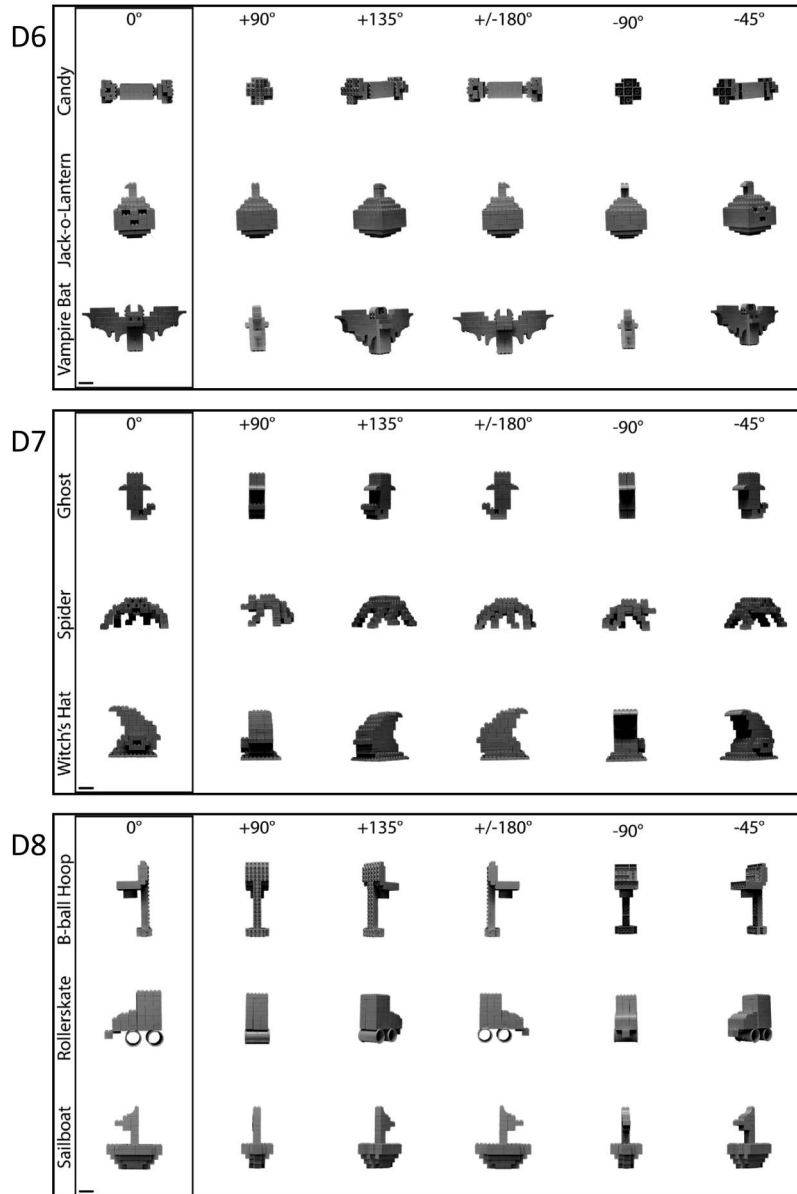
Appendix B

Additional Object Sets Used in the Depth Plane Rotation Test

This appendix shows three of the nine object sets used for the depth plane rotation test (D6, D7, D8). The line in the bottom left corner of each object set is a 5-cm scale bar (near the 0° view of the vampire bat, witch's hat, and sailboat). Other object sets used for the depth plane rotation test can be found in Figure 4 and Appendix A. A sentence similar to this should appear at the end of Appendix A.