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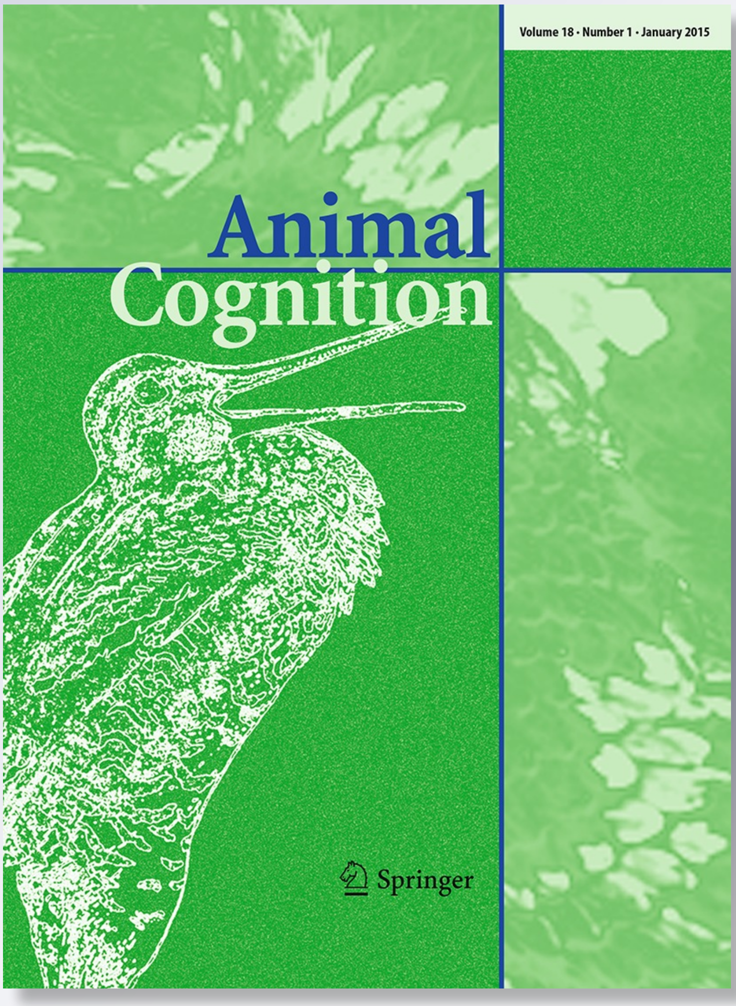

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ORIGINAL PAPER

Visible and invisible displacement with dynamic visual occlusion in bottlenose dolphins (*Tursiops* spp)

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Abstract Anticipating the location of a temporarily obscured target—what Piaget (the construction of reality in the child. Basic Books, New York, 1954) called "object permanence"—is a critical skill, especially in hunters of mobile prey. Previous research with bottlenose dolphins found they could predict the location of a target that had been visibly displaced into an opaque container, but not one that was first placed in an opaque container and then invisibly displaced to another container. We tested whether, by altering the task to involve occlusion rather than containment, these animals could show more advanced object permanence skills. We projected dynamic visual displays at an underwater-viewing window and videotaped the animals' head moves while observing these displays. In Experiment 1, the animals observed a small black disk moving behind occluders that shifted in size, ultimately forming one large occluder. Nine out of ten subjects "tracked" the presumed movement of the disk behind this occluder on their first trial—and in a statistically significant number of subsequent trials—confirming their visible displacement abilities. In Experiment 2, we tested their invisible displacement abilities. The disk first disappeared behind a pair of moving occluders, which then moved behind a stationary occluder. The moving occluders then reappeared and separated, revealing that the disk was no longer behind them. The subjects subsequently looked to the correct stationary occluder on eight of their ten first trials, and in a statistically significant number of subsequent trials. Thus, by altering the stimuli to be more ecologically valid, we were able to show that the dolphins could indeed succeed at an invisible displacement task.

Keywords Object permanence · Invisible displacement · Bottlenose dolphins · Occlusion · Secondary representations

Introduction

The natural world is a cluttered, dynamic place. When a moving object of consequence—predator, prey, or conspecific—is obscured by an occluder, any animal that cannot act prepared for its reappearance would be at a disadvantage. One cognitive adaptation to this problem is maintaining perceptual coherence. This can involve, for example, forming sustained representations of objects and their movements, despite fluctuations in the availability of environmental information about them. In this study, we tested bottlenose dolphins' (*Tursiops* spp) ability to anticipate the paths of occluded objects and consider the role of mental representations in this process.

Developmental psychologist Piaget (1954, 1974) recognized the importance of organisms' ability to track occluded objects and described the cognitive ontogeny, in humans, of what he calls "object permanence." According to Piaget, early in the development, if an infant watches while an object is moved behind an opaque occluder, it acts as if the object no longer exists. For example, the infant

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loses interest and acts surprised when the object reappears. But, after repeated experience with handling and observing moving objects, Piaget claims that the infant will begin to represent, and draw inferences about, objects' unseen movements and locations.

According to Piaget, this development proceeds through six stages, within what he calls the "Sensorimotor Period" (Piaget 1954). Of special interest to us here will be the distinction between Stage 5 and Stage 6 of Piaget's ontogeny. By Stage 5, the infant will act to retrieve a hidden object, suggesting that the infant has somehow represented or remembered the existence and location of that object. For example, if a ball is placed in an opaque cup, an infant at Stage 5 will reach into the cup to retrieve the ball. At the final Stage 6, the infant will successfully seek the object even when it was first placed inside one occluder (the "displacement device") and then "invisibly displaced" to one of multiple other occluders. For example, consider a case where (1) a ball is placed within an opaque cup; (2) the cup is placed in an opaque box; and then (3) the cup emerges empty. An infant who successfully tracks the ball during this invisible displacement event will infer that the ball is in the box, even though she never saw the ball actually move from the cup to the box, that is, when the displacement device is revealed as empty, the infant recognizes that the object had been carried by, and left behind in, the container visited by the displacement device. Such performance on "invisible displacement" tasks require, according to Piaget, not only representing the invisible object, but also using that representation, in what he calls "symbolic" ways, to make inferences about the object's likely location.

Contemporary interpretations recast this "symbolic" activity as involving "secondary representations" (Leslie 1987; Perner 1991; Suddendorf and Whiten 2001). These models suggest that success on an invisible displacement task requires that the infant can maintain multiple simultaneous models of the world (one that directly represents its recent sensory experience and one that does not). In the above example, this might include representing the ball disappearing into the cup, as well as imagining the unseen transfer of the ball from cup to box. Working within this paradigm, researchers interested in animal cognition have aimed to use advanced object permanence tasks as a way to investigate mental representation in non-humans (see Chevalier-Skolnikoff and Poirier 1977; Doré and Dumas 1987; Pepperberg 2002).

Tests of object permanence have been conducted with a variety of non-humans subjects. A review of this literature suggests that, while many can operate at Stage 5, relatively few species appear capable of Stage 6 performance. For example, among the primates, the great apes are the most successful at Stage 6 tasks (e.g., Collier-Baker et al. 2006; Bräuer et al. 2006; De Blois et al. 1998). While some monkeys may also be capable of Stage 6 performance (e.g., cotton-top tamarins: Neiworth et al. 2003), most tested, with careful controls for practice effects and the use of local cues, seem to only perform at Stage 5 (e.g., De Blois and Novack 1994; De Blois et al. 1998). Similarly, both dogs and cats only achieve Stage 5 performance (Goulet et al. 1994; Doré et al. 1996; Collier-Baker et al. 2004; Bräuer et al. 2006; Fiset and Le Blanc 2007; Rooijakkers et al. 2009). Among the birds, Stage 6 performance has been observed in some parrots (Pepperberg and Funk 1990; Funk 1996) as well as various members of the corvid family (such as Eurasian jays, Zucca et al. 2006 or ravens, Bugnyar et al. 2007), while others (such as magpies, Pollock et al. 2000) have produced more ambiguous results, or failed even at Stage 5 (such as ring doves; Dumas and Wilke 1995). Thus, it would seem that these tasks, involving visible (Stage 5) versus invisible (Stage 6) displacement, discriminate a level of sophistication in subjects' object permanence abilities.

Bottlenose dolphins (*Tursiops* spp) have also been tested on object permanence tasks (Doré et al. 1991, cited in Doré and Goulet 1998; Jaakkola et al. 2010). Both of these studies report that their dolphins succeeded at Stage 5 visible displacement, using a standard "containment" (ball-in-cup) procedure. This converges with earlier evidence from Herman and Forestell (1985), done with "language-trained" dolphins. In that study, the animals were trained to touch a "No" paddle when an object referenced by a symbolic command sequence (such as "Frisbee Fetch") was absent from their tank. With further study, they found that the dolphins could also respond to an "interrogative" signal paired with an object name (such as "? Frisbee") and, after visually scanning their environment, touch either a "Yes" (object present) or "No" (object absent) paddle appropriately. Indicating when an expected object is not visible and looking for an object hidden in an opaque container are both consistent with the dolphins being able to form representations of these unseen objects.

However, in both the Jaakkola et al. (2010) and the Doré et al. (1996) studies, the dolphins failed at Stage 6 invisible displacement. As Jaakkola et al. suggest, this is a particularly "puzzling" result because, in other research, bottlenose dolphins have been found to perform well on the sorts of tasks that tend to cluster with Stage 6 success. For example, bottlenose dolphins have demonstrated a capacity for the comprehension of symbolic combinations (Herman et al. 1993; Herman 2006), for performing means-end analyses (Kuczaj and Walker 2006), and perhaps for mirror self-recognition (Reiss and Marino 2001, although see Harley 2013). In fact, in general, they tend to perform at a level similar to that of the great apes on many cognitive tasks (see Marino et al. 2007; Johnson 2010). Dolphins are renowned for their inventive playfulness (e.g., Tavolga 1966; Kuczaj and Trone 2001) and can be trained to produce novel behaviors on command (Herman 2002, 2006; see also Pryor et al. 1969). They are also proficient imitators, doing both behavioral and vocal mimicry (e.g., Taylor and Saayman 1973; Herman 2002; Kuczaj and Yeater 2006; see also Rendell and Whitehead 2001). This includes imitating non-delphinid models, including the behaviors of humans or pinnipeds, which requires the dolphin to map a human's hand to its own pectoral fin, or a seal's rear flippers to its own tail flukes.

All the above behaviors seem to demand forming links between perception, memory, and imagination. These seem to be just the sort of "secondary representations" that Suddendorf and Whiten (2001) argue are required in tasks of invisible displacement. Thus, Jaakkola et al. (2010) conclude that it "seems unlikely that the dolphins' failure to pass invisible displacement in the current study should be explained by a general incapacity for secondary representation."

Instead, they argue that this apparent failure "might have more to do with a lack of understanding of containment than a lack of understanding of hidden movements." Containment involves a complex set of relationships between containers and their contents. Regularities in how contents are supported, transported, and emptied from containers arise and may be learned, at least in part, through repeated experience (e.g., Hespos and Baillargeon 2001; Aguiar and Baillargeon 2002). In their natural habitat, dolphins have little opportunity to concern themselves with containment; all the objects of interest to them—predators, prey, and conspecifics—are seldom contained. Even the fish hiding in the sand that dolphins seek with echolocation are not subject to key containment features, like the transportation of content. Plus, certain assumptions that tend to hold for objects in air—such as the effects of gravity—may not hold as often in an aquatic environment where many objects float, get caught up in currents, etc. It is interesting, then, that the Jaakkola et al. (2010) dolphins showed their best performance on invisible displacement tasks in which the trainer's hand was used as the displacement device. This may reflect the dolphins' enculturation by humans (see Pepperberg 2002) and their consequent frequent exposure to objects being handled by their trainers.

An alternative perspective is that dolphins have failed at previous tasks testing their understanding of object permanence because they may, in fact, not *need* to understand such relationships. For example, in reviewing the bottlenose dolphin's failure on invisible displacement to date, Mitchell and Hoban (2010) suggested that echolocation may make understanding object permanence "unnecessary" for dolphins. However, this view sounds unlikely to us. Echolocation does penetrate the flesh of an ensonified target, and even fish buried shallowly in the sand can be located with it (Roitblat et al. 1995; Rossbach and Herzing 1997). Nonetheless, just because echolocation enables a dolphin to "see past" the visual surface of an object (sending back echoes, for example, from the bones and air sacs within an ensonified animal), it does not follow that nothing is hidden from it. An echolocated object both reflects and absorbs the incoming sound energy, allowing that object to both visually and acoustically occlude another object behind it (Au 1993).

It is certainly the case that the dolphins' primary sensory modality is audition, but vision also plays a critical role in their sensory lives, and these two systems are intimately connected. For example, bottlenose dolphins can visually recognize objects to which they had had only echolocative access and vice versa (Pack and Herman 1995; Harley et al. 1996; Herman et al. 1998). This cross-modal facility also extends to higher-level cognitive tasks, at which the dolphins do quite as well with vision as they do with echolocation, as long as the stimuli are suited to the constraints of their visual system (Herman et al. 1989). As a result, faced with designing a visual task to test for object permanence, we aimed to adapt our stimuli to those sensory constraints.

The dolphin's visual system differs from that of other animals tested for object permanence (Dawson 1980; Madsen and Herman 1980; Ridgway 1990; see Thomas and Kastelein 1990). Their laterally placed eyes give them panoramic visual access to their surroundings, as well as small, binocular fields directly ahead and behind the animal. With no fovea, and only one cone type, they do not discriminate the color and details that primate and avian eyes tend to do. Rod-dominant, the dolphin eye is, instead, particularly sensitive to motion. Resolution is good enough to enable a dolphin to recognize human faces, but their performance at visual tasks is best when moving stimuli are used (see Herman 1991). Trainer hand signals, for instance, can be degraded to point-light displays without significant detriment to animal performance (Herman et al. 1990). In the dolphin's brainstem, in addition to the expansion of the auditory areas expected in an echolocator, one also sees a hypertrophy of the superior colliculus (Ridgway 1990). This midbrain structure is responsible, across mammals, for processing visual motion and plays a central role in orienting behavior.

The above visual system is well suited to a dolphin's natural habitat, where most of the elements are in continual motion. Whether it is the swaying of kelp or sea grass, the morph and veer of a cluster of fish, or the maneuvering of their own schoolmates, objects in the dolphin's environment continually move and occlude one another. Objects of particular importance to a dolphin—such as prey and conspecifics—both live in schools, so there are often multiple layers of occlusion occurring at once. These important objects are also animate and so start, stop, and change direction on their own initiative.

In our tests of object permanence in dolphins, we aimed to design visual stimuli that would share these regularities. As a result, we investigated visible and invisible displacements with high-contrast, animated shapes that dynamically occluded—and were occluded by—one another. These stimuli also moved in "animate" ways, starting and stopping unpredictably, including briefly "hiding" behind an occluder. By keeping ecological validity in mind (see Dumas 1992; Shettleworth 1998), we hoped that we would maximize our chances of obtaining an accurate read of the dolphins' object permanence abilities.

Experiment 1: Visible displacement

Methods

Subjects and setting

During the course of these studies, 9–16 bottlenose dolphins (*Tursiops* spp.) were present in the pool at Rocky Point Preserve at Sea World San Diego. The animals ranged from 2 to approximately 37 years of age and included four males and 12 females. During the day, this habitat was the "petting pool" at which the public could feed and interact with these animals, including during trainer-mediated sessions. Our experiments were all run in the evening, when the public was not present in the park, and all feeding sessions were finished for the day. Participation in these studies was voluntary; no training or reinforcement was involved. Only animals who came to a full stop at the presentation window (see below), and remained observing for the full duration of a given stimulus, were included in our analyses. Presentations continued for as long as any dolphin showed an interest in the stimuli. As can be seen in Table 1, 10 animals participated in Study 1.

Table 1 Subject participation and first-trial results

Subject	Age	Gender	Study 1 Track hidden disk on first trial?	Study 2 Orient to displaced disk on first trial?
A	Juvenile	Male	–	Yes (1/1)
N	Juvenile	Female	–	Yes (2/2)
Y	Juvenile	Female	Yes (2/2)	No (4/6)
H	Juvenile	Female	Yes (1/1)	–
Z	Juvenile	Female	Yes (5/5)	Yes (1/1)
D	Subadult	Male	Yes (1/1)	Yes (2/3)
B	Subadult	Female	Yes (3/3)	Yes (4/7)
P	Subadult	Female	Yes (7/7)	Yes (3/4)
C	Adult	Male	Yes (1/1)	–
G	Adult	Female	Yes (4/4)	–
K	Adult	Female	–	No (0/1)
O	Adult	Female	No (2/4)	Yes (3/3)
R	Adult	Female	Yes (3/4)	Yes (3/3)

Juvenile = 2 to 5 year olds, Subadult = 6 to 10 year olds, Adult >20 years old. Fraction in parentheses indicates the number of correct trials over total number of trials completed by that subject. A field with a "–" indicates subject did not participate in that study

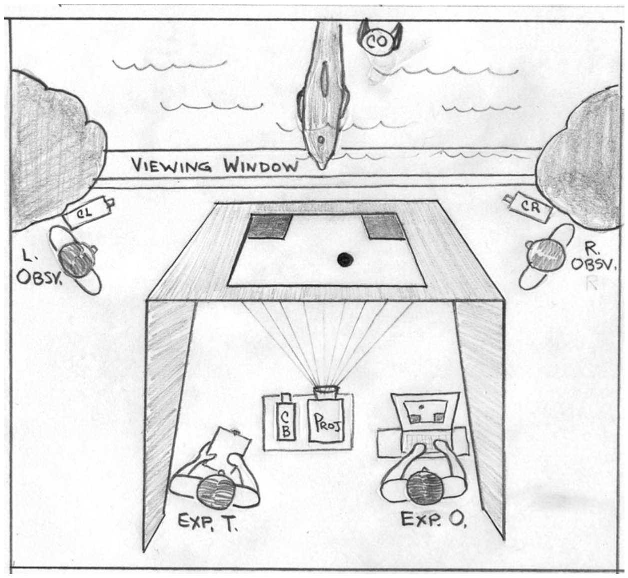

Fig. 1 Projection setup used in this study. Four cameras include "CB" (in Booth, recording what stimulus is being projected), and "CO" (*Overhead*), "CL" (*Left*), and "CR" (*Right*) for recording the dolphin's response. "OBSV" on *left* and *right* are observers who identified the subjects. In the booth are experimenters: "EXP. T." who tracked which animals saw, and needed to see, which stimuli, and "EXP. O" who operated the projection system

Stimuli and protocol

For this project, a projection booth was set up at each session that allowed us to back-project our stimuli, via a 2004 MacBook laptop and video projector, onto a 1.5 × 1.2 M white screen (see Fig. 1). The screen was centered in front of a 5-m-wide, 1.4-m-tall viewing window, such that the projected video was visible to the animals below the water line. Four Canon Powershot 960 video cameras, each with an 8-GB card that enabled about 45 min of continuous filming, recorded all sessions. One camera was trained on the projection screen from within the projection booth, capturing footage of the video being presented. One was suspended above the water at the window, providing an overhead view of the dolphins' activity at the screen. Two additional cameras were located to the right and left of the window, and captured the dolphins' motions from the sides. All cameras were synchronized and then positioned, before each projection session began. Synchronization was achieved by directing all four cameras at a clapperboard and, in postproduction, zeroing all videos to that same frame.

Dynamic images—such as videos of other dolphins or of a single, erratically moving disk—were first displayed to attract the subjects' attention. Once one or more animals were stably positioned in front of the screen, presentation of the actual stimuli would begin. The stimuli used in these studies were animated using *Keynote* software and are described in the procedures below.

During all sessions, two observers were located at the sides of the viewing window to identify each dolphin as it approached the projection area, and to indicate whether it stayed or passed by the window (see Fig. 1). These experimenters did not observe what was being projected on the screen. Two other experimenters were located inside the projection booth. One operated the projection apparatus, while the other, by incorporating information provided by the observers, kept track of which animals had been exposed to which stimuli and recommended which stimuli be projected next (to help keep the presentations as counterbalanced as possible and ensure that animals only saw test trials after having seen familiarization trials). The experimenters in the projection booth could not see, or be seen by, the animals, so no inadvertent cuing was possible.

Procedure

There were two phases to our design. During Phase I, the animals were familiarized with the stimulus format. During Phase II, testing began. After three sessions of exposure to the Phase I stimuli, the dolphins were presented with mixed trials of Phase I and Phase II stimuli in six additional sessions, all during March 2010.

Phase I: Exposure to samples

During Phase I, the animals were exposed to sample stimuli in which a small black disk (~12 cm in diameter) moved, at a fixed velocity, along a soft-cornered rectangular path (~1.25 × 0.75 M) near the perimeter of the projection screen (see Fig. 2a). At the bottom of the screen were three gray rectangular occluders. On the disk's traverse along the top and sides of its path, the disk was unobscured. On its traverse along the bottom of its path, it would vanish temporarily as if passing behind and reappearing between the occluders. Each full circuit by the disk took 4 s, and the disk did four continuous circuits in each 16-s stimulus. In each stimulus, in both Phase I and Phase II, the disk moved in either all clockwise, or all counterclockwise circuits.

Phase II: Visible displacement tests

During Phase II, each stimulus would, during Circuit 1, look exactly like the Phase I stimuli described above. However, at the onset of each subsequent circuit, the occluders would suddenly shift to being slightly wider, incrementally decreasing the gaps between them, while maintaining the same outer edges on the far left and right of the display (see Online Resource 1). As a result, on Circuit 2 (Fig. 2b), the gap between the occluders reduced to only slightly wider than the diameter of the disk and on Circuit 3 (Fig. 2c), the gap was reduced to slightly less than the diameter of the disk. Therefore, on Circuits 1, 2, and 3, the disk was partially occluded. On Circuit 4 (Fig. 2d), the occluders became one solid block without any gaps, causing the disk to be entirely occluded. See Online Resource 1 for an example of one version of this stimulus.

Scoring

For Phase I, we tallied the numbers of times each animal was exposed to clockwise or counterclockwise stimuli. For the Phase II tests, we cropped five segments from each video for blind coding. The first segment cropped was the initial, unoccluded traverse by the disk across the top of the screen. Since the disk began this leg from a standstill (unlike on its later circuits, which were part of a continuous trajectory), this initial leg was presumed to be the most salient incident of the disk's unoccluded motion. The remaining segments were cropped starting from the frame

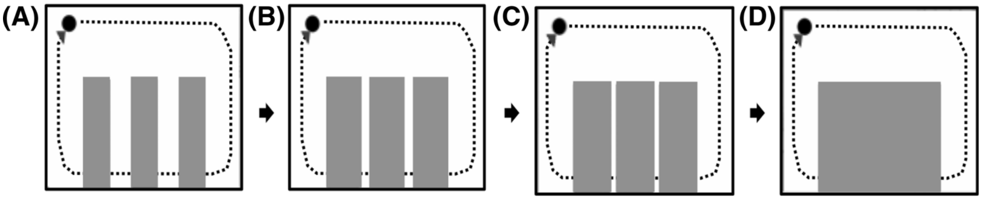

Fig. 2 Phase II stimuli for Experiment 1. *Dotted line* (not seen by subjects) indicates the trajectory of the moving disk. **a**–**d** Phases of a continuous display, with the occluders changing suddenly when the disk reached its starting point in each circuit. In figure, **a** was also presented in the Phase I exposure period. See also Online Resource 1

in which the disk first disappeared behind the first occluder, until the frame just before it reappeared from behind the last occluder, that is, for the partially occluded segments, Segment 1 captured the disk moving from one end to the other of the standard, unchanged occluders. Segment 2 captured that same traverse behind the slightly gap-closed occluders and Segment 3 behind the more gap-closed occluders. In Segment 4, during which the occluder was a single, solid block, the disk was not visible at all during the scored segment. Each of these segments was approximately 700 ms long.

During scoring of these video segments, the part of the image showing the projection screen was masked, so only the dolphin was visible. Most trials were scored from the overhead view; a few trials, in which one animal obscured the other from the overhead view, were scored from the less-optimal side view. The three scorers were familiar with the animals but blind to which stimuli they were scoring. They scored each segment, in random order, as to whether and how many times the animal shifted its head to the left or right. Our dependent measure of interest was the direction of the animal's first head turn, which is the measure that we used for all analyses. Coders could also indicate that the dolphin had made no movement, or that they could not tell the direction of motion. After these data were collected, the responses were recoded as to whether they constituted a "track" of the object (i.e., head moving the same direction as the object) or not.

Agreement

Two coders scored every segment. Out of 160 segments, the two coders agreed on the dolphin's head motion 140 times, resulting in an agreement rate of 87.5 % (Cohen's Kappa = .812). When there was disagreement, the third coder, blind to both the experimental condition and the coding choices of the other two coders, coded the segment. Out of the 20 segments requiring the third coder's input, 14 trials were resolved, resulting in a data loss of only 6 trials due to coder disagreement.

Results: Experiment 1

Exposure

Dolphins who remained at the screen tended to orient perpendicularly to the window, facing the screen directly. From their first exposure to a moving disk, attentive animals often tracked the disk. Occasional acoustic tests, involving placing a hydrophone in the water adjacent to the screen, indicated that no echolocation by the animals was involved. Similarly, while on rare other occasions, echolocation directed at the windows could be heard by the researchers, none reported hearing any echolocation during any presentation.

The dolphins were exposed to clockwise versus counterclockwise stimuli approximately the same number of times. For Phase I stimuli, participants saw the disk move clockwise 47 % of the time and counterclockwise 53 % of the time; for Phase II stimuli, the disk move clockwise 53 % of the time and counterclockwise 47 % of the time. Chi-squared tests revealed that none of these differed from a 50–50 distribution (all $P > .25$). We also tested whether dolphins displayed a side bias (e.g., preferring to turn to the left vs. the right). Across all stimuli, dolphins looked left (clockwise) 41 % of the time, right (counterclockwise) 46 % of the time, and in no direction 12 % of the time, suggesting no side bias. We describe the looking behavior for each occlusion condition separately below, but in no cases did the dolphins show evidence of a side bias.

Main analyses

If the animals were able to represent the disk, even when it was occluded, we hypothesized that they should "track" the disk's movement even when it was not directly visible, that is, the critical test here occurred on Segment 4, where the "closed" occluders completely hid the (presumably moving) disk. Because the animals varied in their participation, viewing from one to seven test trials, we analyzed these data in two ways. First, we assessed whether the animals tracked the disk the first time they participated in the test. Next, we averaged each dolphin's performance (so that each dolphin was represented by a proportion of trials tracked).

Nine out of ten animals "tracked" the fully occluded disk on their first test exposure to Segment 4; the other animal moved its head in the opposite direction, toward where the disk had disappeared (see Online Resource 2 for a sample response). This rate is much higher than we would expect by chance alone, which we would expect to be 50 %, because all ten responses were coded as either a turn to the left, or a turn to the right. By this measure, we find a binomial $P < .025$, indicating that the dolphins "tracked" the disk more often than would be expected by chance. Considering all coded Segment 4 tests ($N = 32$), the dolphins tracked the disk 29 times. This results in an overall success rate of 91 %. We can compare this to a chance value of 50 % by constructing a generalized linear mixed effect model using *glmer* in R, predicting binomial accuracy from participant (as a random factor). We found that dolphins responded correctly more often than would be expected by chance alone ($B = 3.24$, $SE = 1.03$, $P = .00157$). In fact, eight of the ten animals tracked the occluded disk on 100 % of their Segment 4 tests.

Finally, we computed an average rate of tracking for each dolphin and used these values to ask whether, as a group, the dolphins tracked the disk more often than would be expected by chance. Two-tailed t tests were comparing performance to 50 % chance performance ($t(9) = 7.96$, $P < .0001$), and this was confirmed by Wilcoxon signed-rank tests, which allow us to compare performance to chance even if our data fail to meet some of the assumptions required by t tests ($W = 22.5$, $P < .01$).

One concern might be that, because the test trials showed the disk moving through a successively more occluded space (Segments 1–3), the animals may have gotten into a rhythm of moving their heads that carried through to the fully occluded Segment 4. By this view, the animals were not tracking the occluded object, but merely continued making a repetitive motion that they had made earlier when tracking the visible or semi-visible disk. This did not appear to be the case. If the animals tracked the disk on the initial segments and simply carried this motion forward to Segment 4, we would expect similar rates of tracking across all the segments. However, this is not what we found. The animals tracked the disk 33 % of the time on the segment involving no occlusion, and 74, 67, and 63 % (on average, 68 %) of the time during the partially occluded Segments 1, 2, and 3, respectively. Thus, the animals were *more* likely to "track" the disk on the fully occluded Segment 4 segments (91 %) than they were on any of the earlier segments. To statistically test this occlusion-based difference in performance, we constructed a model that predicted binomial accuracy from occlusion (full, partial, and no occlusion), with participant as a random variable. We found a significant effect of occlusion such that both the partial and no occlusion segments showed significantly different rates of accuracy relative to the full occlusion segments (no occlusion: $B = -3.51$, $SE = .77$, $P < .0001$; partial occlusion: $B = -1.89$, $SE = .69$, $P = .0059$). This finding was independently confirmed by two-tailed matched samples t test (full vs. no occlusion: $t(9) = 5.54$, $P = .0003$); full vs. partial occlusion: $t(9) = 4.03$, $P = .003$). Furthermore, in 12 of these 29 successful Segment 4 responses, coders noted that the animals quickly moved their heads to the far side of the occluder, outstripping the pace of the invisible moving disk, as if in anticipation of its eventual reappearance (Fig. 3).

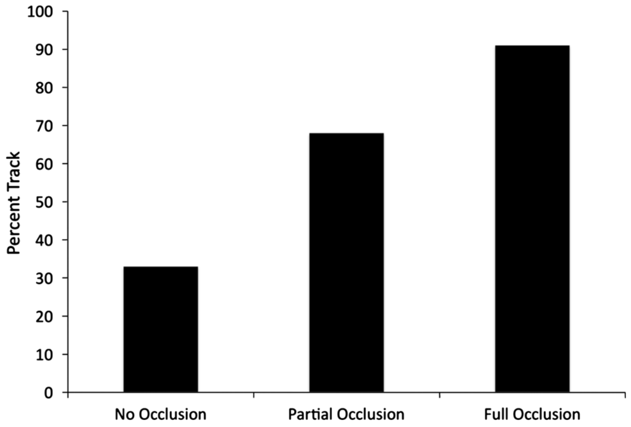

Fig. 3 Percent tracking of stimulus, by the amount of occlusion. All differences significant at $P < .05$ or better

Discussion: Experiment 1

In this study of visible displacement, we shifted from the typical paradigm of containment to one of visual occlusion, that is, instead of testing our subjects with the placement of a target object into an opaque container, we presented a moving target that temporarily disappeared behind shifting occluders. The animals' success on this task is essentially a replication of the previous work on visual displacement in bottlenose dolphins, in which the containment paradigm was used (e.g., Doré and Goulet 1998; Jaakkola et al. 2010). Apparently, in both types of task, the relative movements of the stimulus elements—i.e., a smaller stimulus disappearing inside/behind a larger one—are similar enough that either task can lead to Stage 5 performance. In our study, the dolphins' voluntary interest in the task, and high level of first-trial success, suggests that this occlusion task did indeed "come naturally" to them. Tracking a target as it moves behind various occluders is exactly the sort of capacity that we would expect to have evolved in a hunter of clustered, dynamic prey like the bottlenose dolphin.

In addition, the findings that the dolphins were most likely to "track" the object while it was fully occluded, and more when it was partially occluded than when non-occluded, support a claim that occlusion affects attentional behavior. Inasmuch as such changes in head orientation are effortful, we can say that our subjects invested more effort in orienting to a target, the less visually accessible that target became.

Given their nearly hemispheric, lateral visual fields, a dolphin positioned at our screen could easily see the entire display without moving its head. It may be that the kinesthetic, as well as visual, feedback from tracking behavior could have helped the dolphins to maintain an accompanying mental simulation. In addition, abrupt head turns, such as those often observed in the "full occlusion" condition, may be a particularly useful measure for studying a dolphin's expectations about the activity of objects around occluders. This orienting response will be exploited in investigating invisible displacement in Experiment 2.

Experiment 2: Invisible displacement

Methods

Subjects

Subjects were exposed to the stimuli in this study using the same projection system described in Study 1. Up to sixteen bottlenose dolphins were available in the pool to observe these stimuli, and overhead videos of the 10 animals that stopped long enough to observe the full sequences described below were analyzed. As in Study 1, participation in this study was entirely voluntary and included seven of the same animals who participated in that study, plus three additional animals (see Table 1).

Phase I: Exposure to samples and controls

For all the stimuli used in this study, the backdrop was the same—a white background with stationary, one-foot square, solid gray occluders at the lower right-hand and left-hand corners of the screen (see Figs. 4, 5). Two types of moving images were used in this setting: a small (~12 cm) black disk of the sort used in Study 1 that served as the target and one or two moving occluders. The moving occluders were ~25-cm-long, bar-shaped (flat-sided) ovals, each dark gray, outlined in black. Each oval was half as wide as the disk, so the disk could be partially occluded by one oval and fully occluded by two ovals side by side.

The disk moved quickly, in erratic (unpredictable) ways, sometimes disappearing briefly and variably (1–4 s) behind one of the stationary occluders or behind a pair of the moving oval occluders. The ovals moved more slowly, along a steady trajectory that led (predictably) on a vertical path through the center of the display and then curving off to make a circuit around the left and/or right halves of the screen. Often, these ovals would come together, their long edges touching, and move side by side along the same trajectory, sometimes for multiple circuits, before separating and moving along different trajectories. Whether moving alone or together, the ovals would pass, on every circuit, completely behind one or both stationary occluders at the bottom corners of the screen. No moving object ever passed in front of these stationary occluders in any stimuli. Ovals would typically take 3 s to do one full circuit of half the screen. Overall, the presented stimuli lasted from 8 to 14 s each.

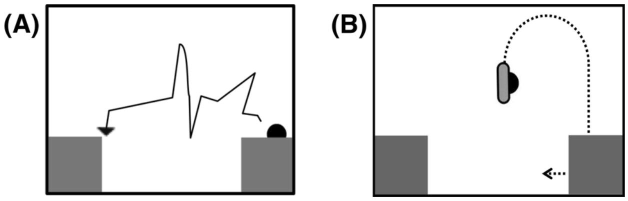

Fig. 4 Sample stimuli shown during exposure phase. *Solid line* (unseen by subjects) indicates rapid irregular path of disk, while *dotted line* (also unseen by subjects) is slower, regular path of oval. In **a**, the disk is the only moving object. In **b**, the disk is partially occluded by the moving oval for part of the stimulus. See Online Resources 3 and 4 for examples of videos

To attract the dolphins' interest, assess their responsiveness to such stimuli, and acclimate them to the dynamic relationships between the moving elements, we first presented the animals with a set of sample stimuli involving different combinations of the disk and ovals (see Fig. 4). There were two versions of each of these stimuli, which involved slightly different paths and passing behind different (right vs. left) stationary occluders.

One pair of sample stimuli involved a single disk, moving erratically, occasionally occluded by one or the other stationary occluders (Fig. 4a and Online Resource 3). The animals that stopped and watched this display typically tracked this lively disk, as they had the disk in the previous study. Another pair of sample stimuli involved one moving occluder (oval) and one target (disk; Fig. 4b and Online Resource 4). The oval moved on its customary smooth path, while the disk moved independently and erratically until it joined the oval. From that point, half of the disk was obscured behind the oval, and they moved together along the same trajectory, including behind a stationary occluder. After some time, the disk suddenly separated from the oval and, appearing fully round again, moved off independently. This stimulus was designed to illustrate that the disk could be partially, but not fully, occluded by a single oval.

During this phase, we also presented two pairs of control stimuli. One of these was the "No Disk" control (Fig. 5.1a–c and Online Resource 5). In these stimuli, two ovals moved along smooth paths, at first separately. They then came together, side by side, for two or three circuits, and then once again separated, at center screen, to go off in opposite directions. The ovals disappeared behind a stationary occluder once per circuit. No disk was present in these sequences. Critically, this stimulus was nearly identical to the test stimulus (described below), except that there was no disk to be occluded.

The other control stimulus—"Occluded Disk, Revealed"—involved one target disk and two ovals (Figs. 5.2a–c and Online Resource 6). As above, the erratic disk intersected with the ovals' smooth paths. However, in this case, when the disk joined two side-by-side ovals, it was completely occluded behind them. After completing most of a circuit in this way, including passing behind one of the stationary occluders, the pair of ovals would separate, again at center screen, revealing the disk behind them. From that point, the ovals would continue on independent

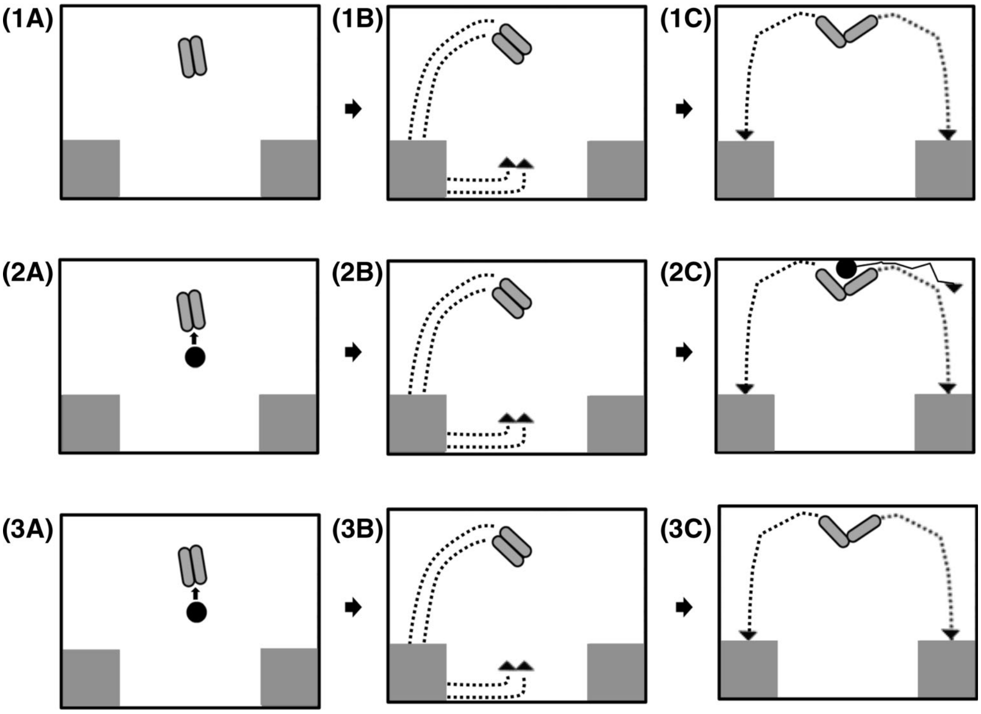

Fig. 5 Control and test stimuli. Each panel (**a–c**) is a phase of a continuous stimulus. The *dotted lines*, indicating paths, were not visible to subjects. **5.1** "No Disk" control. **5.2** "Occluded Disk, Revealed" control. **5.3** is "Occluded Disk, Displaced" test. See also Online Resources 5, 6 and 7, respectively, for examples of these videos

circuits to the right and left, and the disk would move off on a rapid, erratic path. This stimulus showed that the disk could be fully occluded by the paired ovals and would serve as a control for the "Occluded Disk, Displaced" tests, described below.

The animals observed all of the above stimuli, ad libitum, in random order. Once an animal had observed at least one full set of these stimuli, designed, in part, to illustrate the "rules" governing the behavior of the ovals and disk, that animal could then be shown the test stimuli.

Phase II: Invisible displacement tests

In the test phase, animals were presented with the test stimuli "Occluded Disk, Displaced" (see Fig. 5.3a–c and Online Resource 7). These stimuli were nearly identical to the "Occluded Disk, Revealed" controls described above, in that the disk would join the paired ovals, disappearing behind them, and the pair would then pass behind the right or left stationary occluder. As in the controls, the oval pair would then reemerge and, once reaching center screen, would split apart, and circle off in opposite directions. However, unlike in the "Occluded Disk, Revealed" controls, when the ovals separated, no disk was visible behind them. The absence of the disk, in these "Occluded Disk, Displaced" tests, implied that it had been "invisibly displaced" behind the stationary occluder the ovals had just visited.

If the dolphins recognized, by the revealed absence of the disk, that it had been invisibly displaced, we postulated that they would look toward the stationary occluder behind which the ovals had passed. After a 2-s delay, during which the ovals continued to circle around, the disk suddenly reappeared from behind its stationary occluder and moved off on an independent path. Thus, the critical measure here was whether the dolphin turned its head to look toward the appropriate occluder, in the brief (2 s) interval between when the ovals separated, revealing the disk's absence, and the time the disk reappeared from behind its stationary occluder.

Scoring

The animals' responses to the test trials and the two control trials were scored. In all three cases, 2-s segments were cropped from the overhead videos of the dolphins, beginning at the moment, in the stimulus, when the side-by-side pair of ovals splits apart at center screen. As described above, in the "Occluded Disk, Revealed" condition, the disk, which had been seen earlier moving behind the pair of ovals, was revealed, in the 2-s segment, when the ovals separated. In the "No Disk" condition, no disk had been present at any time during the sequence, and none was seen when the ovals separated. In the "Occluded Disk, Displaced" condition, the scored 2-s clip was identical to the "No Disk" clip, in that no disk was seen when the ovals separated. However, in the “Occluded Disk, Displaced” sequence, the disk had been present earlier, before disappearing behind the ovals. We hypothesized that the animals would tend to track equally often to the right and left in the “No Disk” condition, would tend to track the lively, suddenly revealed disk in the “Occluded Disk, Revealed” condition, and if capable of understanding invisible displacement, would tend to turn toward the appropriate stationary occluder in the “Occluded Disk, Displaced” condition.

For blind scoring, the image of the presentation screen was masked on all the cropped segments, so the scorers could not determine which condition was being presented to the animals. The same scorers used in Study 1 again indicated whether the dolphins shifted their heads to the Left, Right, None, or Can’t Tell, during these 2-s segments. They scored each head movement within the 2-s window. Our dependent measure of interest was the direction of the animal’s first head turn.

Agreement

Out of 82 segments, the two coders agreed on the dolphin’s head motion 67 times, resulting in an agreement rate of 81.7 % (Cohen’s Kappa = .745). When there was disagreement, the third coder, blind to both the experimental condition and the coding choices of the other two coders, coded the segment. All 15 segments requiring the third coder’s input were resolved.

Results: Experiment 2

Exposure

Presentation of these stimuli occurred in seven sessions, between April 13 and May 24, 2010. The dolphins often tracked the disk when it was the only moving stimulus and preferred to track the erratic disk over the more slowly moving and predictable ovals. As in Study 1, participation varied (see Table 1), with some animals remaining for multiple trials in a row, while others stayed for only a single trial, possibly returning for one or more additional trials later in the 45-min session. As above, presentation sessions were continued for as long as any dolphin showed a sustained interest in the stimuli.

We also analyzed for a side bias in these compiled data and found none. While we could not control when an animal might come up to view a stimulus, and thus which version it would see, we monitored who was present and worked to keep the left and right presentations balanced. As a result, in the “Occluded Disk, Displaced” tests, the dolphins saw the ovals pass behind the right occluder on 16 trials and behind the left in 14 trials, in the “Occluded Disk, Revealed” condition, they saw 14 right and 10 left, and in the “No Disk” condition, they saw 13 right and 14 left. Across all trials, there was no difference in the likelihood of the dolphins turning right versus left (chi-squared = .49, $P > .25$) in response to these stimuli, and this was true for each condition considered separately (all chi-squared <.4, all $P > .25$).

In the “No Disk” controls, there was no disk to track, only the two ovals moving in opposite directions. The direction of the dolphins’ orienting behavior was at chance on these trials. Of the dolphins who did head turns, 56 % of their first turns were to the right and 44 % were to the left; on four trials, they showed no head turns. Interestingly, dolphins watching these “No Disk” stimuli also tended to vacillate in their response, making multiple head turns (e.g., first looking left, then right, and sometimes left again) on many trials, that is, on 12/27 trials with the “No Disk” stimulus, the animals made more than one head movement, compared to only 2/24 trials in the “Occluded Disk, Revealed”, and 1/31 in the “Occluded Disk, Displaced” conditions. To test this observation empirically, we constructed a model predicting whether or not a dolphin vacillated on a given trial from stimulus type (“No Disk;” “Occluded Disk, Revealed;” and “Occluded Disk, Displaced”), with subject as a random variable. This allowed us to compare rates of vacillation to the baseline rate found in “Occluded Disk, Displaced.” While the rate of vacillation did not differ between “Occluded Disk, Displaced” and “Occluded Disk, Revealed” ($B = 1.00$, SE = 1.23, $P = .42$), it did differ between “No Disk” and “Occluded Disk, Displaced” ($B = 3.18$, SE = 1.09, $P = .003$). This suggests that dolphins vacillated significantly more often in the “No Disk” case than in the “Occluded Disk, Displaced” case.

Main analyses

If the dolphins recognized that the disk had been invisibly displaced behind the last occluder that the side-by-side ovals had passed, we hypothesized that they would look toward that occluder. To explore this, we first examined the subjects’ first-trial performance. First-trial success is particularly pertinent here, since on these trials the dolphins had not yet seen an invisibly displaced disk reemerge from behind the stationary occluder.

Overall, eight out of ten dolphins oriented in the correct direction (i.e., toward the occluder where the disk had been invisibly displaced) on their first trial with the “Occluded Disk, Displaced” stimuli (see Online Resource 8 for a sample response). If we consider only trials in which a dolphin actually turns its head during the critical 2 s, the likelihood of turning in the correct direction is 50 % (left or right). Of the nine dolphins that made head turns on the first test trial they observed, eight of them turned the correct direction. Again, this indicated a rate of success well above what would be expected by chance (binomial $P < .025$).

Next, we computed an average rate of tracking for each dolphin, for each test stimulus. As above, we did this in two ways. We computed the average accuracy after excluding trials where there was no movement. We then constructed a model predicting binomial outcome (looking to the correct vs. incorrect side) from stimulus, with subject as a random variable—this model compared the binomial outcomes to chance rates of 50 %. Orientation was significantly predicted by the location of the correct stationary occluder for the "Occluded Disk, Displaced" stimulus (Accuracy = 79.3 %, $B = 1.06$, SE = .41, $P = .01$). A second model that compared binary accuracy in each stimulus to that observed for "Occluded Disk, Displaced" revealed that there was no significant difference between "Occluded Disk, Displaced" and "Occluded Disk, Revealed" on this score ($B = .45$, SE = .69, $P = .52$). This suggests that, as a group, the dolphins were as likely to anticipate the location of the invisibly displaced disk as they were to track the revealed one.

One possible explanation of these data is that dolphins did not represent the occluded disk and instead used the low-level strategy of looking to the occluder behind which the ovals last passed. We tested for this possibility by analyzing the rate of "correct" responding to the "No Disk" stimulus (here, "correct" responding is—as in our other stimuli—looking first to the occluder behind which the oval just passed). Critically, this stimulus does not include a disk that the dolphins could have represented. Dolphins responded correctly on 43 % of trials, a success rate that did not differ from chance in our model ($B = -.26$, SE = .42, $P = .53$), but that did differ from the "Occluded Disk, Displaced" stimulus ($B = -1.32$, SE = .59, $P = .025$).

Discussion: Experiment 2

In the critical test in this study, a smaller, moving disk disappears behind a pair of larger, moving ovals, and those ovals then pass behind one of two stationary occluders. After reappearing, the ovals separated, revealing no disk behind them. Eight out of ten of our subjects looked toward the correct occluder on their first exposure to these stimuli, and overall, the dolphins maintained this performance in three quarters of their subsequent trials. These data support the claim that bottlenose dolphins can solve an invisible displacement task, based on the dynamic occlusion of visual stimuli.

Traditionally, the invisible displacement task is divided into two phases—the discovery (implication) phase and the search (information-seeking) phase (Piaget 1954; see discussion Dumas 1992; Doré and Goulet 1998). In our scenario, the first phase occurred when the two ovals that had formerly hidden the disk separated. The dolphins had seen earlier displays illustrating that the disk could not be fully occluded behind a single moving oval, so it was not plausible that the absent disk was hiding behind one of the ovals. Furthermore, in the critical 2 s during which we scored their head movements, the dolphins viewed identical displays in the "Occluded Disk, Displaced" trials and in the "No Disk" controls, that is, in both displays, the ovals moved apart and no disk was seen. Nevertheless, the dolphins responded to these two perceptually identical events in different ways. In the "No Disk" trials, they looked equally often to right and left, but in the "Occluded Disk, Displaced" trials, they oriented significantly more often toward the pertinent stationary occluder. Thus, it seems reasonable to conclude that something earlier in that segment that differed between these two conditions—i.e., the disk disappearing behind the moving pair of ovals—impacted the way the dolphins responded to the ovals' separation. Such a response might be interpreted as the subjects having expected the disk to be visible when the ovals separated, and being surprised at its absence, were thus motivated to seek it elsewhere.

In the search phase of an invisible displacement task, the subject indicates the occluder behind or in which it predicts the target object is hidden. In our study, this requires remembering which stationary occluder the paired ovals passed behind on the current trial, and, farther back in the sequence, that the disk had disappeared behind them. It further requires an assumption that, as the ovals moved, the unseen disk moved with them. This assumption apparently held until the ovals were observed to separate, revealing that the disk was "no longer" behind them, since that was the point at which the subjects reoriented their heads. The dolphins showed high confidence in this move, maintaining their new orientation until the disk reappeared, and showing none of the vacillation that characterized their response to the "No Disk" controls. And, as noted above, they displayed this performance from their very first exposure to the test stimuli.

Thus, while the method we used to assess the subjects' object permanence abilities differed from those traditionally used in "containment" paradigms, the critical aspects of the task were present, and the animals were able to respond appropriately.

General discussion

While, in the past, the use of a containment protocol did not prevent correct dolphin performance on visible displacement tasks (Herman and Forestell 1985; Doré et al. 1996; Jaakkola et al. 2010), it may have been an issue in their poor performance (Doré et al. 1996; Jaakkola et al. 2010) on invisible displacement. The choice, in those studies, to deploy such a protocol, similar to that used with other animals, was no doubt made to facilitate cross-species comparisons. However, in prioritizing ecological validity—by shifting from containment to occlusion—the current study was apparently able to more easily tap into the dolphins' natural capacities for solving object permanence tasks.

While success at Stage 5 visible displacement requires that a subject maintain a memory for a no-longer visible target, some additional representational abilities would seem to be required for Stage 6 invisible displacement. In our study, for example, the disk disappeared behind the moving ovals while they were still in the center of the display. Thus, the head turns most typically produced by our dolphins would constitute their shifting *away* from where the disk had last been seen. This suggests that the dolphins may have been operating not with a memory of the target's last known position, but instead with an updated expectation about its new location. Thus, it seems reasonable to suggest that these dolphins are capable of coordinating their representations of both seen and imagined events, the hallmark of "secondary representations" (Perner 1991; Suddendorf and Whiten 2001).

However, we would caution that, for most studies of invisible displacement in non-humans, including this one, the data do not really discriminate between alternative possible mental representations involved. This is not to say that considerable research has not been devoted to assessing the cognition involved in these tasks (see Bräuer et al. 2006). Many studies institute controls to examine, for example, limitations from memory demands (e.g., De Blois et al. 1999), the primacy of spatial representations over sequential ones (e.g., Rooijakkers et al. 2009), and the role of inhibition in making a correct response (Call 2001). Still, these leave several issues concerning the nature of the representations themselves unaddressed. In most cases, several different types of mental processes are consistent with a successful subject's response.

For example, in our study, while tracking the moving ovals after the disk had disappeared behind them, a subject might have maintained a mental image of the disk itself, moving along that same trajectory. In this case, the disk's already-modeled motion behind the stationary occluder would cue the animal to search for it there. Alternatively, the dolphin might form some kind of more generalized association between the disk and the ovals, and use their recollection of the ovals' path to infer the disk's likely position. For instance, a subject could first solve the visible displacement problem presented by the ovals' movement behind the stationary occluder and then substitute the disk into that solution.

Other questions regarding the mental representations that may have guided our dolphins' responses also remain. Do they have an abstract representation of "occlusion," based on previous experience with obscured objects, that drives their search? Might this include feasibility constraints, such as that an occluder must be larger than the target? Or, alternatively, do the dolphins simply default to a heuristic of tracking backward in time along the observed trajectory, attending any familiar object along the way?

Many of the above are empirical questions which presumably could be tested under the appropriate conditions. But, to date, most studies of invisible displacement in animals have not directly tested for alternative forms of mental representation. If such studies, including this one, do not discriminate between specific mental processes, just what cognitive claims do they enable us to make? We would argue that two such claims are justified.

First, both Stage 5 and Stage 6 object permanence tasks require a response in the absence of direct sensory access to a target, that is, at the time of choice, the target is invisible in both cases. At Stage 5, subjects respond as though the target had continued along its same trajectory, either stopping behind the occluder, or reemerging on its far side. In contrast, in Stage 6 tasks, the subject's representation of the target must also have undergone some kind of *invisible transformation*. Whether this transformation involves—as discussed above—the simulation of a modified path, an associative substitution, a propositional inference, or some other kind of mental process, some change in the representation of the unseen target was required.

Furthermore, any transformations of a mental representation must be linked—or "anchored"—to concurrent input from the world. As discussed in Study 1, even representing the continuation of a target's perceived motion may involve such a link between the representation of an object and the object's actual motion in the world, such as in the animal's own tracking motion supporting its Stage 5 performance. In Stage 6, however, the invisible transformation of the dolphin's representation of the disk must somehow be provided through a link with the perceived transposition and reconfiguration of the visible moving occluders. It is this link between the recollection of a perceived event, and the consequent transformation of the representation of an invisible event, that enabled the animals to orient to the appropriate occluder. It is in this sense, then, that these data support the claim that bottlenose dolphins are capable of integrating memory and imagination.

Further research in this area could benefit from a closer examination of how objects move in the dolphin's world. Such constraints can lead, through evolution or learning, to species-specific biases concerning which models of the world are entertained (see Shepard 1994). Hauser (2001), for example, working with Rhesus monkeys, argues that those arboreal animals show a "gravity bias" in dynamic object permanence tests, that is, after seeing an object dropped behind a tall occluder, the monkeys tended to search for the object, after the occluder was removed, in a lower box aligned with the drop, rather than in the higher-positioned box into which the object actually fell. Dolphins, too, may be biased to presume which things will sink or float. For example, Mitchell and Hoban (2010) report that their captive dolphins tended to first search under surface containers into which a fish had been thrown. Plus, captive dolphins' well-documented facility at maneuvering and playing with buoyant toys (e.g., Kuczaj and Trone 2001; Greene et al. 2011) or bubbles (e.g., McCowan et al. 2000; Pace 2000) suggests they would also be adept at predicting the motion of these stimuli.

Finally, a note on the manner of stimulus presentation was used in this work. There were both advantages and disadvantages to the use of "volunteer" subjects in these studies. One obvious disadvantage is that we had little control over the number of trials that were run. For example, the 82 trials seen by ten animals over three conditions, in Experiment 2, apparently exhausted the animals' interest in our stimuli. If offering food reinforcement for the subjects' continued attention had been an option for us, it would most likely have enabled us to collect more data, making more robust and subtle analyses available. Similarly, exposure to the type and order of stimuli was difficult to control under these conditions, since animals could approach an already-in-progress video. Keeping non-participating animals preoccupied, and regulating access to the presentation screen, could also have helped limited distractions and reduce other social factors.

However, the "volunteer" approach also worked, to some degree, in our favor. With no extrinsic reinforcement involved, we can be more confident that the dolphins are bringing preexisting skills to bear on these tasks. Plus, given that first-trial success is the gold standard on perceptual tasks like these, perhaps a better goal than accumulating more trials might be to accumulate more subjects. Showing such stimuli to other captive dolphins, using a procedure like this with minimal impact on training and feeding regimes, could take advantage of the many oceanaria housing potential subjects, as well as enriching the environments of the dolphins involved.

Animating the stimuli also offers several advantages. It standardizes presentation and, since no knowledgeable trainer is visible to the subjects during the trials, eliminates the possibility of inadvertent cueing. Reducing the input to simple shapes, moving along designable trajectories, enables the researchers to manipulate essential features of the stimuli in systematic ways. As long as such stimuli are designed with ecological validity in mind (e.g., using high-contrast, dynamic stimuli suited to dolphin vision, and motions and interactions similar to those the animals might naturally encounter), they provide a useful way of addressing many fascinating questions on dolphin perception and cognition.

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