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What do dolphins (*Tursiops truncatus*) understand about hidden objects?

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Abstract Object permanence, the ability to mentally represent and reason about objects that have disappeared from view, is a fundamental cognitive skill that has been extensively studied in human infants and terrestrial animals, but not in marine animals. A series of four experiments examined this ability in bottlenose dolphins (*Tursiops truncatus*). After being trained on a "find the object" game, dolphins were tested on visible and invisible displacement tasks, and transpositions. In Experiments 1 and 2, dolphins succeeded at visible displacements, but not at invisible displacements or transpositions. Experiment 3 showed that they were able to pass an invisible displacement task in which a person's hand rather than a container was used as the displacement device. However, follow-up controls suggested they did so by learning local rules rather than via a true representation of the movement of hidden objects. Experiment 4 demonstrated that the dolphins did not rely on such local rules to pass visible displacement tasks. Thus, like many terrestrial animals, dolphins are able to succeed on visible displacement tasks, but seem unable to succeed on tasks requiring the tracking of hidden objects.

Keywords Dolphins · Object permanence · Visible displacement · Invisible displacement · Secondary representation

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Introduction

A basic element of spatial cognition is the ability to reason about the location and movements of objects that are not directly visible. In non-human animals, this ability has adaptive significance for tracking predators, prey, and social partners. In humans, research on this ability has played a prominent role in studies of cognitive development.

According to Piaget (1954), the development of this ability—which he termed "object permanence"—proceeds through six stages. In the earliest stage, infants simply do not search for objects that go out of sight. With development, they begin to search for partially hidden objects (Stage 3), then fully hidden objects (Stages 4 and 5), and eventually progress to the point that they can track or reconstruct the possible movements of hidden objects (Stage 6).

This transition between Stage 5 and Stage 6 object permanence is of particular importance due to the claim that attainment of Stage 6 marks the emergence of a new representational capacity (Piaget 1954). To understand why, consider the problems presented to the child. In traditional Stage 5 visible displacement tasks, an experimenter places an object directly into one of several opaque containers, then allows the child to search for it. Solving this task requires the child to remember the location at which he/she saw the object disappear. In traditional Stage 6 invisible displacement tasks, the experimenter hides a target object inside a displacement device (such as a small box), places the displacement device inside one of the opaque containers, and surreptitiously transfers the object to that container. Then the experimenter removes the displacement device from the container, shows the child that the device is empty, and allows the child to search. Because the movements of the object in this task are hidden, solving it requires the child to mentally reconstruct the object's possible paths. Thus, according to Piaget, it is at Stage 6 where the child acquires the ability to use and manipulate mental representations.

Perner's (1991) theory of representational development provides a similar analysis, in which he argues that passing the invisible displacement task is one of several related abilities, such as mirror self-recognition, imitation, and understanding external representations, that mark the emergence of the capacity for secondary representation. With this new type of representation the child gains the ability to consider multiple models of a situation—including past, future, or hypothetical models—rather than simply relying on what is immediately perceivable. So when solving an invisible displacement task, for example, the child is no longer bound by his present model of the situation (e.g., "The object is not in the displacement device."), but can also use his past models of the situation (e.g., "The object was in the displacement device. The displacement device was in that container.") to reconstruct where the object must have gone.

Although the bulk of theoretical work and empirical research on object permanence has been conducted within the field of human cognitive development, over the past few decades this topic has gained considerable attention in studies of cognition in other animals as well (for reviews, see Doré and Goulet 1998; Tomasello and Call 1997). Results to date seem to support this idea of a conceptual watershed between organisms that can solve invisible displacement tasks (Stage 6) and organisms that can solve only visible displacement tasks (Stage 5) (Doré and Goulet 1998).

Among primates, the general consensus in the field is that apes—including chimpanzees (Barth and Call 2006; Beran and Minahan 2000; Call 2001, 2003; Collier-Baker et al. 2006; Mathieu et al. 1976; Wood et al. 1980), bonobos (Barth and Call 2006; Beran and Minahan 2000), orangutans (Barth and Call 2006; Call 2001, 2003; de Blois et al. 1998), and gorillas (Barth and Call 2006; Natale and Antinucci 1989; Natale et al. 1986)—are capable of passing invisible displacement tasks. The results for monkeys are more controversial. Although a number of studies have claimed that monkeys of various species are capable of invisible displacement—e.g., squirrel monkeys (Vaughter et al. 1972), rhesus macaques (Wise et al. 1974), capuchin monkeys (Mathieu et al. 1976; Schino et al. 1990), cotton-top tamarins (Neiworth et al. 2003), and marmosets (Mendes and Huber 2004)—the results of many of these studies are circumspect due to methodological shortcomings, most notably their failure to control for the use of simple associational rules such as "pick the last location touched" (Doré and Dumas 1987; Natale et al. 1986). A similar number of studies have failed to find invisible displacement capabilities in the same or similar species—e.g., rhesus macaques (de Blois and Novak 1994), squirrel monkeys (de Blois et al. 1998), Japanese macaques (Natale and Antinucci 1989; Natale et al. 1986), crab-eating macaques (Natale and Antinucci 1989; Schino et al. 1990), and capuchin monkeys (Natale and Antinucci 1989). Lemurs, the only prosimians tested on object permanence to date, also fail invisible displacement tasks (Deppe et al. 2009).

Among non-primate mammals, early studies suggested that both dogs and cats can succeed at invisible displacement tasks (e.g., Gagnon and Doré 1992, 1993; Triana and Pasnak 1981; Pasnak et al. 1988; Dumas 1992). However, these studies have also been criticized on methodological grounds (e.g., Collier-Baker et al. 2004; Doré and Dumas 1987). The vast majority of more recent studies have found either that these animals cannot pass the task, or that they solve it with low-level associative rules rather than via a true conceptual understanding of invisible displacement (e.g., Collier-Baker et al. 2004; Doré 1986, 1990; Doré et al. 1996; Fiset and LeBlanc 2007; Goulet et al. 1994).

Finally, it has also been claimed that psittacine birds (Funk 1996; Pepperberg and Funk 1990; Pepperberg and Kozak 1986; Pepperberg et al. 1997) and corvids (Pollok et al. 2000; Zucca et al. 2007) pass Stage 6 tests of object permanence. Unfortunately, all of these studies have used Uzgiris and Hunt's (1975) testing procedure, which has been criticized on the grounds that it systematically tests easier, visible displacement problems before gradually working its way up through the more difficult invisible displacement problems (e.g., Gagnon and Doré 1992). This procedure thus gives the birds the opportunity to learn low-level local rules such as "pick the last cover that was lifted" during the visible displacement tasks, which could then theoretically be used to pass the invisible displacement tasks without a conceptual understanding of the movement of hidden objects. Of course, given the results of other cognitive studies with psittacines and corvids that seem to suggest a capacity for symbolic and/or secondary representation—e.g., means-ends reasoning (Heinrich and Bugnyar 2005; Weir et al. 2002) and the ability to utilize symbols (Pepperberg 1999)—it does not seem unreasonable to suggest that these animals might understand invisible displacement. However, additional controlled studies are required to solidify this claim.

In summary, studies to date have shown unequivocal understanding of invisible displacement only for great apes. This is consistent with Suddendorf and Whiten's (2001) analysis of the evidence for secondary representation in non-human animals, in which they concluded that apes show a cluster of abilities indicative of secondary representation, but that the evidence for monkeys and other animals is scant.

Notably missing from the literature on object permanence, however, are any published studies of marine mammals. In particular, data on bottlenose dolphins may be particularly relevant. Evolutionarily, the ancestors of dolphins and apes split approximately 90–95 million years ago, and adapted to radically different physical and ecological niches, yet cetaceans and primates show a striking convergence in higher cognitive abilities (Marino 2002). Most relevant for current purposes, dolphins have been shown to possess a variety of cognitive characteristics relevant to symbolic and/or secondary representation, such as imitation (Bauer and Johnson 1994; Herman 2002; Richards et al. 1984), mirror self-recognition (Reiss and Marino 2001), means-ends reasoning (Kuczaj and Walker 2006), and the ability to understand symbols and other external representations (Herman and Forestell 1985; Herman et al. 1984, 2001).

The goal of the current study was to examine whether dolphins can reason about the movements of hidden objects. Dolphins were first trained on a "find the object" game, and then, over several studies, were tested on traditional visible and invisible displacement tasks, as well as on a conceptually related "transposition task" which has begun to gain attention in studies of hidden objects (e.g., Barth and Call 2006; Beran and Minahan 2000; Call 2003; Doré et al. 1996; Pepperberg et al. 1997; Sophian 1984, 1985; Sophian and Sage 1983). In this task, the target object is hidden in one of several containers, and then the container itself is moved or switched with another container. As with standard invisible displacement tasks, the subject must infer the location of the target object without having seen its movements directly. There is debate, however, as to which task is more difficult. Whereas great apes seem to perform better on transposition tasks (Barth and Call 2006), human children seem to find standard invisible displacement tasks the easier of the two (Barth and Call 2006; Sophian and Sage 1983).

Following previous research (e.g., Collier-Baker et al. 2004, 2006; de Blois and Novak 1994; de Blois et al. 1998), we also included control tasks to ensure that any successes could not be explained by the learning of local strategies.

Experiment 1

Method

Subjects

Four male and two female Atlantic bottlenose dolphins (*Tursiops truncatus*) housed at Dolphin Research Center in Grassy Key, Florida participated in this study. The dolphins ranged in age from 3 to 27 years ($M = 17.3$; SD = 13.2), and lived in social groups in natural seawater lagoons (ranging in size from 22.9 × 13.7 × 3.7 m deep to

Fig. 1 Photograph depicting the experimental apparatus and testing set-up. (The displacement cylinder was not present for the single and double visible displacement conditions.)

70.1 × 29.0 × 9.1 m deep) situated on the Gulf of Mexico. One adult male dolphin (Rainbow) had previously participated in a test of relative numerosity (Jaakkola et al. 2005). The dolphins were fed according to their normal daily routine, which typically included capelin, herring, and either smelt or sardines, three times per day, approximately 33% of which they received during experimental sessions. During non-experimental sessions, they continued to participate in other training sessions, including public programs and in-water interactions with trainers and guests. The dolphins were never deprived of food in any way, regardless of performance. Any remaining fish allocation was given to the dolphins at the end of each experimental session, either coupled with other training behaviors or in a free-feed format.

Apparatus and stimuli

Figure 1 shows the basic apparatus and testing set-up. Three black, rectangular polyethylene office waste paper baskets (37 × 27 × 38 cm) were used as hiding buckets. The bottom of each bucket was filled with approximately 2.5 cm of concrete for weighting purposes. During trials, the buckets were positioned 30.5 cm apart in a straight line at the front edge of the dock, and were covered by three dark blue Rubbermaid lids (41 cm × 27 cm), connected by a PVC bar (2 cm in diameter). The PVC bar allowed the lids to be lifted simultaneously from their starting position on the dock behind the buckets to their final position on top of the buckets.

The target object was a green plush stuffed alligator (55 × 19 × 8 cm).[1] The displacement device for the invisible

[1] For one dolphin, the target object initially consisted of three interlocking rings (each 16 cm in diameter), made from flexible plastic tubing (1 cm in diameter) and covered with colored electrical tape. When these rings seemed to be contributing to problematic behavior, the object was switched to the plush alligator.

displacement condition was an opaque PVC cylinder (20 cm × 16.5 cm diameter) with a small metal handle for gripping. The cylinder was covered on one side with an opaque, detachable PVC cap attached to a short length of nylon rope that was used to pull the cap off.

All sessions were videotaped using a camera located across the lagoon from the testing dock.

Procedure

For blinding purposes, all test trials were conducted by two experimenters—the hider, who knew where the object was hidden, and the asker, who did not. In addition, a note-taker sat on the steps or boardwalk behind the testing dock, positioning a clipboard in front of her face during trials to avoid any possibility of cueing. At the start of each trial, the hider stood centrally positioned behind the buckets, facing the front of the dock. The asker stood at the back of the dock with his/her back turned, so as to remain unaware of which bucket the object would be hidden in. To begin the trial, the hider called the dolphin to the front of the dock, then hid the object using one of three displacement procedures described below. The hider then placed the lids on the array of buckets, turned and walked to the rear of the dock, tapped the asker on the shoulder, and remained facing to the rear. Upon being tapped, the asker turned and walked to the front of the dock, to a position centered behind the buckets, made eye contact with the dolphin and gave the hand signal while saying “Where is it?”

The dolphin made its choice by touching a bucket with its rostrum (i.e., “snout”). Once the dolphin had chosen, the asker removed the lids to see where the object was hidden. If the dolphin was correct, the asker removed the object from the chosen bucket and blew a whistle, then provided the dolphin positive reinforcements of fish and social interaction. If the dolphin was incorrect, the asker tilted the incorrect bucket forward to show the dolphin it was empty, removed the object from the correct bucket and showed it to the dolphin, but otherwise remained neutral in response.

If, during a trial, the dolphin performed another behavior or did not respond when the signal to choose was given, the signal was repeated. If the dolphin swam away from the dock, touched a bucket before the signal was given, or touched something other than one of the buckets (e.g., the lid handle between two buckets), the trial was aborted, set up again, and repeated.[2] If the dolphin performed any of these behaviors three times for the same trial, that trial was skipped and coded as incorrect.

During sessions, any other dolphins present in the lagoon were kept busy at a separate dock by another trainer. On those rare occasions when one of those other dolphins swam away from its trainer and approached the testing dock, the session was immediately discontinued until the non-subject dolphin had returned to its own dock and trainer.

Displacement conditions

Across sessions, there were three types of displacement tested.

1. In single visible displacements, the object was placed in a single bucket before the lids were placed on the array.
2. In double visible displacements, the object was placed in one bucket, then taken out and placed in a second bucket before the lids were placed on the array.
3. In invisible displacements, the object was placed in a cylinder held in an upright position (see Fig. 1). The cylinder was then placed in a bucket, emptied, and removed from the bucket. Next, the cylinder was tipped forward to show the dolphin that it was now empty, and the cylinder cap was removed so the dolphin could see entirely through the cylinder. The cylinder and cap were then placed on the dock to the far right or left of the buckets, before the lids were placed on the array.

Training

Because dolphins do not naturally forage on land or reach into containers, we trained the dolphins how to play the “find the object” game before the testing conditions just described, using two types of training trials. In choice trials, the object was placed onto or partially into one of several buckets, in such a way that the object remained visible, and the dolphin was rewarded for selecting the associated bucket. In errorless trials, only one bucket was present, and the object was placed entirely within it. The purpose of these errorless trials was to familiarize the dolphin with the idea that the object might disappear entirely into a bucket, in a situation where no tracking was necessary. Training consisted of several intermediate steps or components, including:

1. Introducing the object and signal—the trainer placed the object on the dock, showed the dolphin the “where is it” signal, and pointed to the object. The dolphin was rewarded for touching the object. Eventually, the point cue was faded out, and the dolphin was expected to

[2] For the first dolphin tested, the protocol differed slightly. Any test trial in which she touched early was aborted, and then repeated at the end of the session. If the aborted trial was the last trial of the session, a training trial (i.e., with a partially hidden object) was added before the repeated test trial. However, because the first dolphin continually touched early, this protocol led to an unfortunate cycle of repeatedly adding trials. Therefore, after her first condition, we switched to the current protocol.

touch the object no matter where it was placed. If necessary, the dolphin was explicitly trained to wait for the signal before responding.

2. Introducing the buckets—the trainer placed one bucket on the dock, then placed the object on the dock, away from the bucket, and asked the dolphin to touch the object on signal. With repetition, the trainer moved the object closer to the bucket, until it was eventually on top of the bucket in a highly visible position. Once the dolphin was comfortable touching the object on the bucket, the other two buckets were incorporated, one at a time.
3. Introducing the lids—first, the trainer placed the lids behind the buckets during trials. Next, the trainer bent to touch the lids between object placement and the signal. Over many repetitions, the trainer began to lift the lids, gradually higher, until the lids were placed on the buckets during trials (with the object still visible beneath the lids).
4. Introducing errorless trials—for these trials, the trainer positioned a single bucket at the front of the dock, placed the object entirely into the bucket, and gave the signal. The dolphin was rewarded for touching the bucket. If a dolphin was reluctant to touch the bucket, the trainer utilized a point cue, which was then gradually faded out.
5. Introducing the second trainer—in this step, trainer 2 (the asker) initially stood directly behind trainer 1 (the hider), facing forward. The hider hid the object, then quickly stepped to the side, so that the asker could give the signal quickly. Over many repetitions, the asker moved farther back on the dock, necessitating a longer delay, and eventually turned his or her back.
6. Making the object less visible during choice trials–over the course of training, the object was hidden in ways that gradually decreased its visibility. For example, the alligator was first placed apart from the bucket, then on top of the bucket, then eventually was placed in the bucket with only the end of its tail visible. Once a dolphin evidenced success with a partially hidden object, the position of the object during choice trials was allowed to vary, as long as part of the object remained visible.
7. Randomizing trials—during early training, the order and composition of trials was left to the discretion of the trainers. By the end of training, trial composition was standardized, with six choice trials and three errorless trials, and randomized as in testing (see below).

Although each dolphin's training included each of these steps, there was flexibility between dolphins with respect to the order, duration, and rigidity with which the steps were incorporated. For example, a dolphin may have been introduced to errorless trials before or after the lids were introduced. Or, when the second trainer was introduced, we may have temporarily stopped using the lids. The goal was that by the end of training, each dolphin would be successful with trials utilizing all of the components (i.e., both errorless and choice trials, using lids and two trainers, with a partially hidden object).

Our criteria for moving from training to testing were: with all components in place, the dolphin was correct on at least five out of six choice trials on two consecutive days, during which time it never attempted to make its selection before the signal was given. (Training durations for individual dolphins in all experiments are presented in the "Appendix".)

Testing design

Each of the three conditions was tested during a separate week, with order of conditions counterbalanced across dolphins. Testing for each condition was divided into two sessions that took place over two consecutive days in the week. Each session consisted of six choice trials (two per location) and three errorless trials (one per location).[3] For the double visible displacement condition, the object's initial location was counterbalanced across trials. For the invisible displacement condition, the final location of the displacement cylinder (i.e., at the far left or far right of the buckets) was counterbalanced across trials. Order of trials was randomized, with the constraints that there were never more than three choice trials in a row, and the object was never hidden more than two consecutive trials in any particular location.

On the day preceding the first testing session each week, a refresher training session (i.e., consisting of errorless and partially hidden choice trials) was conducted. If the dolphin missed more than one of the six choice trials, testing for the condition scheduled for that week was postponed. Instead, additional training sessions were conducted until the dolphin once again reached criteria, at which point testing was resumed.

Coding

A dolphin was coded as making a choice when its rostrum contacted a bucket, the lid, or the displacement cylinder. Accuracy of the choices was coded live during the sessions and double checked against the video immediately thereafter.

[3] For the first dolphin tested, the design also included three training (i.e., partially hidden) trials in addition to the errorless and testing trials in each session. However, when this dolphin encountered difficulties during her first two testing sessions (see footnote 2), these training trials were dropped for all remaining test sessions.

A second experimenter later independently coded two-thirds of the testing sessions from the videotapes. Reliability between the two coders was 100%.

Results

The dolphins' motivation to attend to the manipulations was high across all conditions. None of the trials in the single visible and double visible conditions, and only 5.0% of the trials in the invisible displacement condition, had to be repeated due to inattention or off-task responses. In the invisible displacement condition, however, one of the dolphins (Rainbow) repeatedly chose a bucket before the object was hidden, and we were forced to terminate his testing without generating useable data. This occurred during both of the testing sessions for this condition, but not during any other testing sessions, and seemed to be the result of the dolphin's extreme confusion with this condition. For purposes of analysis, we therefore scored his performance in this condition at chance. Alternately coding his responses as missing data did not change any of the statistical outcomes.

Overall accuracy

Table 1 presents the proportion of correct responses for each dolphin for each type of displacement tested. Overall, the dolphins performed above chance for single visible displacements, $t_5 = 4.67$, $P = 0.005$, but not for double visible, $t_5 = 1.55$, $P = 0.158$, or invisible displacements, $t_5 = 1.53$, $P = 0.187$. Individual performance above chance levels (binomial test, $P < 0.05$) was reached by three dolphins for single visible displacement, one for double visible displacement, and none for invisible displacement.

A repeated-measures one-way ANOVA on these data found a significant difference between conditions, $F_{2,10} = 18.59$, $P < 0.001$. Specifically, performance on single visible displacement was better than performance on both double visible displacement, paired $t_5 = 5.49$, $P = 0.003$, and invisible displacement, paired $t_5 = 5.85$, $P = 0.002$. There was no significant difference between performance on double visible and invisible displacements, paired $t_5 = 1.00$, $P = 0.362$.

Table 1 Proportion of correct responses per displacement type for each dolphin in Experiment 1

Dolphin	Type of displacement		
	Single visible	Double visible	Invisible
Aleta	0.67*	0.50	0.33
Delphi	0.83*	0.75*	0.58
Pandora	0.67*	0.42	0.50
Pax	0.42	0.33	0.33
Rainbow	0.58	0.33	0.33
Tanner	0.50	0.33	0.33
Mean	0.61*	0.44	0.40

*$P < 0.05$. See details for statistics in main text

Order effects

Because the data from individual dolphins suggested a possible boost in performance for those dolphins who experienced the single visible displacement condition first, we next divided the dolphins into two groups—those who received the single visible displacement condition first (Aleta and Delphi), and those who received that condition later in testing (Pandora, Pax, Tanner, and Rainbow). Because of the small number of dolphins in each group, this analysis was undertaken for exploratory purposes only, and should be viewed only as preliminary and suggestive.

Figure 2 shows the mean proportion of correct trials in each condition for dolphins in each group. A 2 (order) × 3 (condition) mixed ANOVA was performed on these data. In addition to the earlier main effect of condition, found again here, $F_{2,8} = 39.15$, $P < 0.001$, this analysis revealed a significant interaction between order and condition, $F_{2,8} = 6.50$, $P = 0.021$. Dolphins who received the single visible displacement condition first performed better than dolphins who received the single visible displacement condition later on both single visible displacements, one-tailed $t_4 = 2.18$, $P = 0.047$, and double visible displacements, one-tailed $t_4 = 3.27$, $P = 0.016$. There was no significant difference between groups in the invisible displacement condition, one-tailed $t_4 = 0.84$, $P = 0.224$.

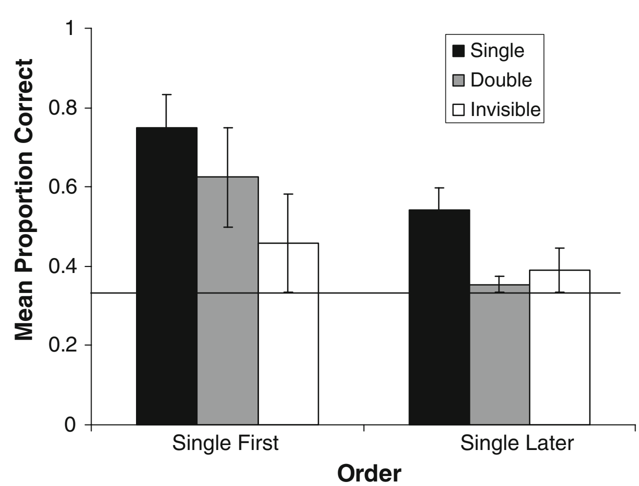

Fig. 2 Mean (±SE) proportion of correct trials for each condition of Experiment 1, as a function of whether dolphins received the single visible displacement condition first

Individual strategies

Next we examined the dolphins' individual strategies for responding. We identified four possible strategies: (1) correct responding; (2) selecting the first bucket in which the object was placed (in the double visible displacement condition); (3) selecting the cylinder or the bucket closest to the cylinder (in the invisible displacement condition); and (4) choosing a particular favored bucket (left, middle, or right). For each of the first three strategies, we counted a dolphin as following it if 8 or more of its 12 choices fit the pattern (binomial test, $P < 0.05$). However, for the fourth (favored bucket) strategy, because any of three different response patterns (i.e., predominantly left, predominantly middle, or predominantly right) could satisfy the criteria, 9 rather than 8 out of 12 choices at any particular location (left, middle, or right) were required to reach significance (binomial test, $P < 0.05$).

Table 2 shows the response strategies identified for each dolphin. When dolphins did not follow a correct bucket strategy (primarily in the single visible displacement condition), they tended to default to a favored bucket, or showed no identifiable strategy. No dolphin followed the alternative strategies of selecting the first bucket in the double visible displacement condition, or selecting the bucket adjacent to the cylinder in the invisible displacement condition.

Discussion

Overall, the dolphins succeeded on single visible displacement, but not on double visible or invisible displacement tasks. Also, unlike the case with dogs and some monkeys (e.g., Collier-Baker et al. 2004; Fiset and LeBlanc 2007; Natale et al. 1986; Schino et al. 1990), dolphins' choices in the invisible displacement condition did not seem to depend on the location of the displacement device (i.e., the cylinder). Rather, when unsure of the correct response, they tended to default to a favored bucket.

Table 2 Response strategies for each dolphin in Experiment 1

Dolphin	Type of displacement		
	Single visible	Double visible	Invisible
Aleta	*	Fav	Fav
Delphi	*	*	–
Pandora	*	Fav	–
Pax	–	Fav	–
Rainbow	–	Fav	–
Tanner	Fav	–	Fav

* Correct responding, *Fav* selecting a favored bucket (left, middle, or right); – no identifiable response strategy

It may be important to note, however, that dolphins who received the single visible displacement condition first performed significantly better than the other dolphins on both single and double visible displacements. This difference suggests that one problem may have been too great a leap between the training situation and the more complicated testing conditions. Unlike other animals tested in these kinds of studies, dolphins do not forage on land. They do not naturally reach for things. We tried to teach them the "find the object" game using an object that remained visible, but perhaps the jump between that training situation and the more complicated disappearances was just too large for them to handle all at once.

Because Experiment 1 demonstrated that dolphins can succeed on single visible displacement tasks, we next decided to train this task directly, to determine whether that would enable the dolphins to succeed on the more difficult displacements as well. To streamline the testing procedure, we also eliminated errorless trials. These trials had been included in Experiment 1 to mitigate the dolphins' frustration levels if they had been unable to solve a given condition. However, after testing, it seemed that this concern was unwarranted and that, if anything, switching between errorless and choice trials may have been distracting.

Experiment 2

Method

Subjects

One female and three male Atlantic bottlenose dolphins (*Tursiops truncatus*), ranging in age from 4 to 18 years, and housed at the same facility as in Experiment 1, participated in this study. Two of the dolphins (Tanner and Pax) had previously participated in Experiment 1. We chose the two dolphins who had performed the most poorly in Experiment 1 under the assumption that their performance might benefit the most from further training. The other two dolphins (AJ and Calusa) were experimentally naïve.

Apparatus and stimuli

The same buckets, hiding object, and displacement cylinder were used as in Experiment 1. However, instead of three dark blue Rubbermaid lids connected by a PVC bar, the lid for Experiment 2 consisted of a solid rectangular PVC frame (198 cm × 46 cm) with blue canvas stretched over it, and a PVC handle spanning the top. This alteration was made to accommodate the changing bucket configuration for the transposition condition.

Procedure

The basic procedure for trials was the same as in Experiment 1, with the following three differences: (1) instead of positioning a clipboard in front of her face, the note-taker simply sat with her back turned during trials. (2) When a dolphin chose an incorrect bucket, the asker removed the object from the correct bucket and showed it to the dolphin, but did not tip the incorrect bucket forward to show the dolphin the empty bucket, as in Experiment 1. This action had not seemed to help them in Experiment 1, and we felt that such extraneous movement after the choice may have been confusing. (3) If, during a trial, the dolphin performed another behavior, swam away from the dock, touched a bucket before the signal was given, or touched something other than one of the buckets (e.g., the lid between two buckets), the trial was aborted, and the experimenters stepped back from the testing platform to take a "timeout". When they returned, they proceeded with the following trial, and the skipped trial was placed at the end of the session. If the dolphin performed any of these alternative behaviors three times in a row, the session was discontinued.

Displacement conditions

Across sessions, there were three primary types of displacement tested.

1. In double visible displacements, the object was placed in one bucket, then taken out and placed in a second bucket before the lid was placed on the array, just as in Experiment 1.
2. In invisible displacements, the object was placed in a cylinder. The cylinder was then placed in a bucket, emptied, and removed from the bucket. However, instead of pulling the object from the open top of the cylinder to empty it, as in Experiment 1, the object was instead pushed through the removable cap on the bottom of the cylinder. The cylinder cap remained in the bucket, so when the dolphin was shown that the cylinder was now empty, there was no added step of removing the cap so the dolphin could see entirely through the cylinder. The cylinder was then placed on the dock to the far right or left of the buckets, before the lid was placed on the array.
3. The transposition condition was new to Experiment 2. In this condition, the object was placed in a bucket. One of the three buckets was then moved to a new location before the dolphin was asked to choose. The moved bucket was always lifted over at least one other bucket to an outside position. So either the far left bucket was moved to the far right position, the far right bucket was moved to the far left position, or the middle bucket was moved to either the far left or far right position.

Because the first dolphin tested in the invisible displacement condition repeatedly selected the displacement cylinder when asked to choose, we also ran an additional variation of this condition after the primary tests were completed:

4. The vanishing cylinder condition was identical to the invisible displacement condition, except that after the object was emptied from the cylinder into a bucket, the hider removed the cylinder from the testing area rather than placing it to the left or right of the buckets. Call (2001) suggested that apes and human toddlers have difficulty inhibiting a tendency to search adjacent hiding places on standard double invisible displacement tasks. Similarly, we wondered if dolphins might have difficulty inhibiting search in the immediate vicinity of the cylinder into which they had initially seen the object disappear (cf. Collier-Baker et al. 2004). Thus, the purpose of this manipulation was to examine whether the dolphins might show evidence of better object tracking when the distraction of that cylinder was removed.

Training

For the two dolphins who had participated in Experiment 1, training consisted of refresher sessions using a visible object, and then gradually hiding more of the object during trials until the object was completely hidden in a bucket. The new rectangular lid was also introduced, gradually incorporating earlier training steps as necessary until the dolphin was comfortable with the new lid. For the two dolphins who had not participated in Experiment 1, training consisted of all of the training steps in Experiment 1 with the exception of errorless trials, and with the object eventually being completely hidden in the buckets. As in Experiment 1, the order and composition of training trials was initially left to the discretion of the trainers. By the end of training, sessions were standardized to consist of 12 single visible displacement trials, randomized as in testing.

Our criteria for moving from training to testing were: with all components in place, the dolphin was correct on at least 22 out of the 24 single visible displacement trials over two consecutive sessions. In addition, because testing for each condition was to occur over two sessions in a day, we also required that the dolphin had performed two training sessions in a single day prior to testing.

Testing design

Each of the conditions was tested in 24 trials, divided into two equal sessions on the same day. Testing of the three primary conditions took place over three consecutive days. Each of the dolphins received the double visible displacement condition first, followed by the invisible displacement and transposition conditions, counterbalanced across dolphins at each experience level. That is, one of the experimentally naïve dolphins saw invisible displacement before transposition, as did one of the dolphins who had previously participated in Experiment 1. For each dolphin, the vanishing cylinder condition was run within 5 days after the primary tests were completed.

Each test session consisted of four trials with the object hidden in each location. For the double visible displacement condition, the object's initial location was counterbalanced across trials. For the invisible displacement condition, the final location of the displacement cylinder (i.e., at the far left or far right of the buckets) was counterbalanced, with the order randomized across trials. For the transposition condition, the correct bucket was moved in half of the trials, the incorrect bucket was moved in half of the trials, and each bucket (Left, Middle, Right) was moved an equal number of times. In each session for all conditions, order of trials was randomized, with the constraints that there were never more than two consecutive correct answers in any particular location.

Coding

Coding was identical to that of Experiment 1. A second experimenter later independently coded half of the testing sessions from the videotapes. Reliability between the two coders was 99%.

Results

The dolphins' motivation to attend and search was again high. Very few trials had to be repeated due to inattention or off-task responses—only 0.7% in the double visible condition, 3.1% in the invisible displacement condition, none in the transposition condition, and 2.8% in the vanishing cylinder condition.

Overall accuracy

Table 3 presents the proportion of correct responses for each dolphin for each type of displacement tested.[4] Overall, the dolphins performed above chance for double visible displacements, $t_3 = 7.78$, $P = 0.004$, but not for either invisible displacements, $t_3 = -0.84$, $P = 0.464$, or transpositions, $t_3 = 0.33$, $P = 0.760$. Individual performance above chance levels (binomial test, $P < 0.05$) was reached by all of the dolphins for double visible displacement, and by none for either invisible displacement or transposition.

Table 3 Proportion of correct responses per displacement type for each dolphin in Experiment 2

Dolphin	Type of displacement			
	Double visible	Invisible	Transposition	Vanish cylinder
AJ	0.64*	0.33	0.38	0.38
Calusa	0.83*	0.38	0.38	0.38
Pax	0.88*	0.33	0.38	0.63*
Tanner	0.71*	0.00	0.25	0.42
Mean	0.76*	0.26	0.34	0.45

* $P < 0.05$. See details for statistics in main text

We next compared performance across conditions for new subjects versus subjects who had participated in Study 1. A 3 (condition) × 2 (experience) mixed ANOVA on these data found a significant effect of condition, $F_{2,4} = 50.79$, $P = 0.001$. Specifically, performance on double visible displacement was better than performance on both invisible displacement, paired $t_3 = 5.95$, $P = 0.009$, and transposition, paired $t_3 = 7.81$, $P = 0.004$, but there was no significant difference between performance on invisible displacement and transposition, paired $t_3 = 1.48$, $P = 0.235$. There was no significant main effect of experience, $F_{1,2} = 0.33$, $P = 0.622$, nor a significant interaction between condition and experience, $F_{2,4} = 2.62$, $P = 0.188$.

Effect of cylinder presence

We next compared the dolphins' performance on the invisible displacement and vanishing cylinder conditions. Recall that these conditions were identical except for the final placement of the displacement cylinder (i.e., it either remained on the dock or was removed from the testing platform).

A 2 (cylinder presence) × 2 (experience) mixed ANOVA on these data found a significant effect of cylinder presence, $F_{1,2} = 32.43$, $P = 0.029$, and a significant interaction between cylinder presence and experience, $F_{1,2} = 25.59$, $P = 0.037$. Both of the dolphins who were new to this study (AJ and Calusa) showed virtually identical chance performance regardless of whether the cylinder was present or absent at the time of selection (with performance between 0.33 and 0.38 correct). In contrast, removing the cylinder from the testing platform seemed to have a dramatic effect on the performance of both dolphins who had

[4] Note that during the invisible displacement condition, one of the dolphins (Tanner) repeatedly chose the displacement cylinder itself, except for two trials in which he touched the bucket closest to the displacement cylinder. For purposes of analysis, we scored his performance in this condition at zero. Alternately coding his responses as chance did not change any of the statistical outcomes.

previously participated in Experiment 1. Tanner switched from fixating almost exclusively on the cylinder when it was present (and thus scoring zero) to selecting the buckets at chance levels, while Pax moved from chance to above chance performance (0.63 correct, binomial test, $P = 0.003$).

Individual strategies

Finally, we examined the dolphins' individual strategies for responding, using the same strategies identified in Study 1, as well as an additional possible strategy of selecting the moving bucket (in the transposition condition). For ease of comparison with Study 1, we calculated the strategies for each of the two testing sessions for each condition separately, again using the criterion of 8 choices out of 12 for each strategy (or 9 out of 12 in the case of favored bucket strategy).

Table 4 shows the response strategies identified for each dolphin. As in Study 1, when dolphins did not choose the correct bucket, their primary strategy was to default to a favored bucket. However, unlike in Study 1, we now also see a strategy of choosing based on the location of the cylinder in the invisible displacement condition, but only among the two dolphins who had also participated in Study 1. No dolphin followed the alternative strategy of selecting the first bucket in the double visible displacement condition, and only one dolphin (for one session) followed a moving bucket strategy in the transposition condition.

Discussion

When trained explicitly on single visible displacement, dolphins were also able to succeed on double visible displacement. However, like in Experiment 1, they were still unable to succeed on invisible displacement tasks. Interestingly, unlike in Experiment 1, the dolphins with the most experience with the task followed a strategy of selecting a bucket on the basis of the final location of the displacement cylinder. Subsequently removing the distraction of this cylinder from the testing platform during the dolphins' choices affected their performance, but even so, only one of the dolphins scored above chance. So while it could be that removing the distraction unmasked this dolphin's underlying understanding of invisible displacement, his success could also be explained by a learned response strategy of selecting the only bucket that the trainer had paid attention to. The dolphins also failed an alternative invisible displacement task using a transposition procedure, in which there were no potentially distracting extraneous containers involved.

Given dolphins' aforementioned proficiency on other tasks requiring secondary representation, this apparent inability to understand invisible displacement was surprising. It occurred to us, however, that their difficulty might have more to do with a lack of understanding of moving containers than with a lack of understanding hidden movement, per se. After all, dolphins have nothing like moving containers in their natural environment, nor much experience with them in their current living situation. Therefore, in Experiment 3 we decided to use a displacement device that these dolphins have had ample experience with—human hands. Specifically, we examined whether dolphins can track the movements of an object hidden in a person's hand rather than in a moving bucket or cylinder, and if successful, whether this is due to a learned response strategy or a conceptual understanding of hidden movement.

Table 4 Response strategies for each dolphin in Experiments 2–4

Dolphin	Sess	Type of displacement							
		Experiment 2				Experiment 3			Experiment 4
		Double vis	Trans	Invis	Vanish cyl	Hand	Drop first	Drop last	Vis drop first
AJ	1	*	Fav	Fav	Fav	*	Fav	Fav	*
	2	–	–	Fav	Fav				–
Calusa	1	*	Fav	Fav	Fav	*	–	–	*
	2	*	Fav	Fav	Fav				*
Pax	1	*	–	Fav	–	*	Fav	Fav	*
	2	*	Mov	Cyl	*				*
Tanner	1	*	–	Cyl	–	*	Fav	–	*
	2	*	–	Cyl	Fav				*

* Correct responding, *Fav* selecting a favored bucket (left, middle, or right), *Mov* selecting the bucket that moved, *Cyl* selecting the cylinder or bucket closest to the cylinder; – no identifiable response strategy

Experiment 3

Method

Subjects

The same four dolphins in Experiment 2 also participated in this study.

Apparatus and stimuli

The same buckets and lids were used as in Experiment 1. However, because the hiding object needed to be small enough to fit completely into an experimenter's hand, we used a small toy mouse ($6 \times 4 \times 3$ cm, with a 7 cm tail) instead of the plush alligator used in Experiments 1 and 2.

Procedure

The basic procedure for trials was identical to that of Experiment 2.

Displacement conditions

Across sessions, there were three types of displacement tested.

1. In hand displacement, the hider first dangled the object from one hand, then closed his hand around the object, hiding it completely. He next placed his hand in a bucket, dropped the object, removed his hand from the bucket, and showed the dolphin that his hand was empty before placing the lids on the buckets.
2. In the drop-first condition, the hider dangled the object, then closed his hand around it. He then placed his hand in a bucket, dropped the object, took his hand out and showed the dolphin his empty hand, using the same hand motions as if he were dangling the object. Then he put his hand into a second bucket, took it out, and showed the dolphins his empty hand again.
3. In the drop-last condition, the hider dangled the object, then closed his hand around it. He placed his hand in a bucket, took his hand out and showed the dolphin that he was still holding the object, dangling it a second time. Then he closed his hand around the object again, put his hand into the second bucket, dropped the object, and took his hand out and showed the dolphin his empty hand.

Training

Training consisted of continued single visible displacement sessions, first using the stuffed alligator, and then slowly introducing a variety of new objects such as shoes, sunglasses, and mangrove pods. When new objects were introduced, earlier training steps were incorporated as necessary, until the dolphin was comfortable with the objects. In addition, the segmented lids from Experiment 1 were either re-incorporated, or introduced for the first time to the two dolphins who had not participated in Experiment 1. As a final step, the toy mouse was introduced.

Our criteria for moving from training to testing were: with the toy mouse as the hiding object and all components in place, the dolphin was correct on at least 22 out of the 24 single visible displacement trials over two consecutive sessions.

Testing design

Each of the three conditions was tested in single 12-trial sessions. Testing of all three conditions took place over three consecutive days.

Each test session consisted of four trials with the object hidden in each location. For the drop-first condition, the final bucket that the experimenter placed his hand in was counterbalanced across trials. For the drop-last condition, the initial bucket that the experimenter placed his hand in was counterbalanced across trials. In each session for all conditions, order of trials was randomized, with the constraints that there were never more than two consecutive correct answers in any particular location.

Coding

Coding was identical to that of the previous experiments. A second experimenter later independently coded half of the testing sessions from the videotapes. Reliability between the two coders was 100%.

Results

The dolphins' motivation to attend was again very high. None of the trials in the hand or drop-first conditions, and only 4.2% in the drop-last condition, had to be repeated due to inattention or off-task responses.

Overall accuracy

Table 5 presents the proportion of correct responses for each dolphin for each type of displacement tested. Overall, the dolphins performed significantly above chance for hand displacement, $t_3 = 19.12$, $P < 0.001$, but not for the drop-first condition, $t_3 = 1.56$, $P = 0.216$, or the drop-last condition, $t_3 = 3.00$, $P = 0.058$. Individual performance above chance levels (binomial test, $P < 0.05$) was reached by all of the dolphins for hand displacement, and none for either the drop-first or drop-last conditions.

Table 5 Proportion of correct responses per displacement type for each dolphin in Experiment 3

Dolphin	Type of displacement		
	Hand	Drop first	Drop last
AJ	0.75*	0.33	0.58
Calusa	0.83*	0.50	0.58
Pax	0.83*	0.33	0.33
Tanner	0.75*	0.42	0.58
Mean	0.79*	0.40	0.52

*$P < 0.05$. See details for statistics in main text

A repeated-measures one-way ANOVA on these data found a significant difference between displacement conditions, $F_{2,6} = 22.96$, $P = 0.002$. Specifically, performance on hand displacement was significantly better than performance in both the drop-first condition, paired $t_3 = 9.90$, $P = 0.002$, and the drop-last condition, paired $t_3 = 3.44$, $P = 0.041$, but there was no significant difference between performance in the drop-first and drop-last conditions, paired $t_3 = -2.32$, $P = 0.103$.

Individual strategies

We next examined the dolphins' individual strategies for responding. In addition to the relevant strategies from Experiments 1 and 2 (i.e., correct responding, first bucket, and favored bucket), we also included a possible strategy of selecting the last bucket in the drop-first condition, using our standard criterion of 8 choices out of 12 (binomial test, $P < 0.05$).

Table 4 shows the response strategies identified for each dolphin. Uniformly, the dolphins followed the correct responding strategy in the hand condition, and either the favored bucket or no identifiable strategy in the other conditions. No dolphin followed the alternative strategies of consistently picking the first or last buckets.

Discussion

When tested in a more naturalistic invisible displacement condition in which the object was displaced using the experimenter's hand rather than an additional displacement device, all four dolphins appeared to succeed at the task. However, follow-up controls suggested that they likely succeeded by using a response strategy of selecting the bucket the experimenter had paid attention to. When presented with a situation in which the experimenter paid attention to more than one bucket, they were unable to determine which of the buckets contained the hidden object, and often defaulted to a favored bucket.

Due to this result, it seemed prudent to ensure that the dolphins' earlier success on visible displacement could not similarly be explained by a simple response strategy. In Experiment 2, the dolphins had shown success on double visible displacement, which is the visible analog to the drop-last condition of Experiment 3. To complete the control set, Experiment 4 tested the visible analog to the drop-first condition as well.

Experiment 4

Method

Subjects

The same four dolphins that participated in Experiments 2 and 3 also participated in this study.

Apparatus and stimuli

The same apparatus and hiding object (i.e., stuffed alligator) were used as in Experiment 2.

Procedure

The basic procedure for trials was identical to Experiment 2.

Displacement condition

The visible drop-first condition was identical to the double visible displacement condition in Experiments 1 and 2, except that the object remained in the first bucket visited. That is, the trainer placed the object into a bucket, removed her hand from the bucket, then placed her empty hand into a second bucket before placing the lids on the array. The purpose was to control for the possibility that the dolphins were simply selecting the last bucket the trainer had touched or paid attention to.

Training

Training consisted of single visible displacement sessions using the stuffed alligator, and reintroducing the rectangular lid from Experiment 2. As always, this reintroduction was accomplished by slowly incorporating earlier training steps until the dolphin was comfortable with the change in apparatus.

Our criteria for moving from training to testing were: with all components in place, the dolphin was correct on at least 22 out of the 24 single visible displacement trials over two consecutive sessions.

Testing design

To parallel Experiment 2, the visible drop-first condition was tested in 24 trials, divided into two equal sessions on the same day. Each test session consisted of four trials with the object hidden in each location. The final bucket that the experimenter placed her hand in was counterbalanced across trials. Order of trials was randomized, with the constraints that there were never more than two consecutive correct answers in any particular location.

Coding

Coding was identical to that of Experiment 2. A second experimenter later independently coded half of the testing sessions from the videotapes. Reliability between the two coders was 100%.

Results

Motivation to attend was again very high. None of the trials had to be repeated due to inattention or off-task responses.

Overall, the dolphins performed significantly above chance levels, $t_3 = 5.68$, $P = 0.011$. Individual performance was also above chance levels (binomial test, $P < 0.01$) for all of the dolphins (with AJ, Calusa, Pax, and Tanner scoring at 0.67, 0.71, 1.00, and 0.71, respectively).

We next compared the dolphins' performance here with their performance in double visible displacement from Experiment 2. In essence, this provides a *visible* drop-first and drop-last comparison, analogous to the invisible drop-first and drop-last conditions in Experiment 3. There was no significant difference between these conditions, paired $t_3 = 0.15$, $P = 0.890$, with dolphins scoring a mean of 0.77 and 0.76 for the visible drop-first and drop-last conditions, respectively.

Individual strategies

Finally, we examined the dolphins' individual strategies for responding, using the relevant possible strategies identified in the previous experiments (i.e., correct responding, favored bucket, and last bucket). To parallel Experiment 2, we again calculated the strategies for each of the two testing sessions separately, using the criterion of 8 choices out of 12 for each strategy (or 9 out of 12 in the case of favored bucket strategy).

Table 4 shows the strategies identified for each dolphin. Almost uniformly, the dolphins followed the correct responding strategy in both sessions. No dolphin followed the alternative strategies of choosing the last bucket or a favored bucket.

Discussion

Unlike the difficulties they encountered with the invisible drop-first and drop-last conditions in Experiment 3, all of the dolphins succeeded on the visible drop-first condition. Combined with their earlier results on the visible drop-last condition (i.e., double visible displacement) from Experiment 2, this shows that the dolphins' success on visible displacement cannot be explained by a simple response strategy.

General discussion

The results of this study showed that, like many terrestrial animals, dolphins are able to succeed on visible displacement tasks. Surprisingly, however, they were unable to succeed on any task requiring the tracking of hidden objects—including both invisible displacements and transpositions. The one exception to this pattern seemed to be an invisible displacement task in which a person's hand was used as the displacement device. However, subsequent controls showed that the dolphins' apparent success there could be explained by their reliance on a local strategy of choosing the container the experimenter had paid attention to, and was therefore not indicative of understanding hidden movement.

As noted in the introduction, past research has demonstrated that dolphins are proficient in a number of tasks requiring symbolic and/or secondary representation. Therefore, given the generally accepted position that Stage 6 object permanence is an indicator of symbolic or secondary representation (Perner 1991; Piaget 1954; Suddendorf and Whiten 2001), the dolphins' pervasive failure at these tasks is puzzling. We can see three possible resolutions to this incongruity.

First, it could be that dolphins do in fact have the conceptual ability to pass Stage 6 object permanence tasks, but for whatever reason, the current study failed to uncover this ability. To that end, it should be acknowledged that our procedure differed from previous object permanence studies in that we used an explicitly trained response. One might argue that this training fundamentally changed the nature of the task, perhaps to the extent the dolphins did not understand what we were asking of them. We consider this explanation unlikely, however, based on the observed profile of successes and failures. That is, over the course of these experiments, the dolphins succeeded on multiple, novel versions of object displacement tasks, only running into difficulties in the presence of hidden movement. This suggests that the dolphins were in fact attempting to find the object, and were simply at a loss whenever hidden movement was involved.

One could also argue that testing the dolphins above water may have put them at a perceptual disadvantage. After all, dolphins spend the vast majority of their time underwater, and testing them in air prevented them from using echolocation to help them process the hiding situation. However, although it is possible that this made the testing situation more difficult for them overall, it again doesn't explain the specific pattern of results. The problem was not the dolphins' perception of the object, as shown by their success on visible problems. Rather, their difficulty was with inferences when the object was not perceivable at all.

A second possible resolution to the puzzle could be that dolphins do *not* have the conceptual resources to succeed on Stage 6 object permanence tasks because they do not in fact have symbolic or secondary representational abilities. We find this possibility unlikely as well. In Suddendorf and Whiten's (2001) review of the evidence for secondary representation in non-human animals across a variety of cognitive tasks, they concluded that the strongest case for secondary representation could be made for great apes. However, they also noted that dolphins showed evidence of secondary representation on some of the tasks they reviewed, and that further research was warranted to clarify the comparative picture. As detailed below, such further research, along with data not originally considered by Suddendorf and Whiten, has only strengthened the case for secondary representation in dolphins.

Imitation

Dolphins are highly proficient imitators, showing the ability to imitate both vocally and behaviorally, spontaneously or in response to an instruction to do so (e.g., Bauer and Johnson 1994; Herman 2002; Richards et al. 1984; Xitco 1988). They can also be trained to "self-imitate," which requires them to hold a representation of a previous action in mind, in order to repeat or not repeat that specific action, as instructed (Herman 2002; Mercado et al. 1998, 1999).

Mirror self-recognition

In the standard "mark test" for mirror self-recognition, a visible mark is surreptitiously placed on the subject's body in a location—such as the forehead—that cannot be seen without a mirror. To pass the test, the subject must, upon seeing the mark in the mirror, spontaneously touch the corresponding location on its own body (Gallup 1970). Clearly, this specific criterion is impossible to meet for animals without hands (or other relevant appendages such as the elephant's trunk, cf. Plotnik et al. 2006), and initial attempts to test behavioral analogs to this criterion with dolphins were unconvincing (see Marten and Psarakos 1995, and critical commentaries). However, a more recent study by Reiss and Marino (2001) examined dolphins' mirror-directed behavior when marked versus sham-marked. They found that the dolphins used the mirror to investigate the parts of their bodies that were marked, making a strong case for mirror self-recognition in an organism without hands.

Means-ends reasoning

In a study by Gory and Kuczaj (1998, described in Kuczaj and Walker 2006), dolphins were shown how to collect and drop four weights into a container—one at a time—in order to mechanically release a fish. Once the dolphins were proficient at this task, the experimenters moved the weights farther away from the device. Spontaneously, the dolphins began to carry multiple weights on each trip to the device, rather than carrying one weight at a time as they had been taught. This shows that the dolphins were not simply following the learned steps mechanically, but held the desired goal-state in mind and realized a more efficient way of achieving that state, demonstrating means-ends reasoning.

Recognizing mental states: attributing attention

Several studies suggest that dolphins understand something about the relation between head gaze and attention. Not only can they accurately select the object at which a person is gazing (Pack and Herman 2004; Tschudin et al. 2001), but they can also use the object of a person's gaze as a source of information for selecting a matching object in a distant location (Pack and Herman 2007)—demonstrating that they know the person is gazing at a particular object, rather than simply in a particular direction. Dolphins have also been shown to spontaneously monitor a human's gaze to determine whether the human is attending to them, and behave appropriately. In a study by Xitco et al. (2001), dolphins developed a spontaneous "pointing" gesture in which they would orient their bodies toward a jointly sought object and engage in gaze alternation with their human partner. When these same dolphins were later given an opportunity to use that gesture to indicate which of two containers had been baited (Xitco et al. 2004), the dolphins pointed significantly more often when their human partner was facing them than when he was facing away.

Understanding external representations

Two lines of evidence are relevant here. First, dolphins have repeatedly shown evidence of spontaneous understanding of televised images—correctly executing instructions from televised trainers (Herman et al. 1990), imitating televised dolphins (Herman et al. 1993), and performing match-to-sample tasks in which the sample was presented by a televised trainer (Pack and Herman 1995). Second, dolphins can answer yes–no questions. Although not addressed by Suddendorf and Whiten (2001), Perner (1991) describes this ability as requiring secondary representation. In order to answer the question, “Is there a ball in the room?”, for example, one must compare the described hypothetical proposition (e.g., A ball is in the room.) with the perceived situation in the real world, which clearly requires multiple models. Herman and Forestell (1985) demonstrated that a symbol-trained dolphin could accurately answer such questions about the presence of objects in her tank (e.g., “BALL QUESTION?”) by pressing one paddle for YES and another for NO.

In sum, the abilities evidenced by dolphins across a variety of tasks meet the criteria for secondary representation laid out by Perner (1991) and Suddendorf and Whiten (2001). It therefore seems unlikely that dolphins’ failure to pass invisible displacement tasks in the current study should be explained by a general incapacity for secondary representation.

Finally, it could be that dolphins do not have the conceptual resources to succeed on Stage 6 object permanence tasks, but possess symbolic and secondary representational abilities nevertheless. This of course begs the question “Why?” What is needed over and above secondary representation to succeed at these types of tasks?

Several researchers have noted that invisible displacement tasks place a higher load on memory than do visible displacement tasks (e.g., de Blois et al. 1999; Gagnon and Doré 1993). This same observation could be made for transposition tasks as well. That is, from the time the object disappears until the time the animal searches, more events occur and more time elapses in invisible displacement and transposition tasks than in visible displacement tasks. One possibility, therefore, is that these distracting movements and longer delays simply led the dolphins to forget which container held the object. If this were true, however, we would expect dolphins to have similar difficulties with the visible drop-first condition of Experiment 4, in which the experimenter performed additional actions after the object disappeared. This was not the case. On the contrary, all of the dolphins performed quite well in that condition (with one dolphin scoring 100%), suggesting that memory requirements are not to blame for their difficulties in the hidden movement tasks.

Another possible issue is the dolphins’ ability to inhibit preferred responses. Call (2001) and Barth and Call (2006), for example, found that all four species of great ape, as well as human toddlers, were biased to search adjacent boxes in double invisible displacement tasks. Similarly, Collier-Baker et al. (2004) suggested (and subsequently rejected) the possibility that dogs’ failure on invisible displacement tasks may have been due to problems inhibiting search in the vicinity of the displacement device. In the current study, this issue was tested in the vanishing cylinder condition of Experiment 2. We found that removing the cylinder from the testing platform affected performance for two of the dolphins, but only led to accurate performance for one of them. Subsequent experiments suggested that this dolphin had learned a local rule for solving the task. Thus, although the displacement device influenced these dolphins’ responses when it was available, releasing them from this influence did not allow them to succeed at the task. It therefore seems likely that something more fundamental underlies dolphins’ difficulties with invisible displacement tasks.

Finally, a lack of ecological validity has often been raised as a factor that may contribute to poor performance on invisible displacement and other cognitive tasks (e.g., Dumas 1992; Hare 2001; Tomasello et al. 2003). While this is certainly a valid concern in the present study, further specification is necessary. Simply noting that a given situation does not occur in an animal’s natural environment is not, by itself, a sufficient explanation. Like many animals, dolphins are capable of performing many tasks that are not within their natural repertoire. What is needed is an account of specifically which essential cognitive components are absent or divergent because of an animal’s ecological history. In dolphins’ natural environment, prey disappears behind occluders, but never into containers that subsequently change location. Furthermore, even when prey or other objects disappear behind visual barriers, dolphins may still be able to perceive these objects via echolocation (e.g., Pack and Herman 1995; Roitblat et al. 1995; Rossbach and Herzing 1997). This suggests two possibilities. First, as we proposed earlier, it may be that dolphins lack a fundamental understanding of moving containers. From studies of human infants, we know that the understanding of occlusion and containment follow different developmental time courses (Hespos and Baillargeon 2001, 2006), and that these are thus dissociable concepts. Because understanding containment is not required for the other tasks indicative of secondary representation, this missing concept could explain dolphins’ pattern of results observed to date. Second, it may be that, due to their echolocation abilities, dolphins are not often forced to confront the problem of tracking hidden objects, and therefore may not have gained the necessary empirical experience to develop this cognitive capacity.

In summary, the results of our experiments show that dolphins succeed on visible displacement tasks, but not on invisible displacement or transposition tasks. Given dolphins’ documented successes on a wide variety of other tasks requiring secondary representation, their failure on hidden movement tasks remains an open puzzle, but one that may be resolved if their difficulty lies in a lack of

Table 6 The total number of training/maintenance trials between experiments

Trial type	Dolphin							
	AJ	Aleta	Calusa	Delphi	Pandora	Pax	Rainbow	Tanner
Pre-Experiment 1								
Non-choice		49		30	40	31	74	95
Choice: object visible		444		276	53	99	149	144
Pre-Experiment 2								
Non-choice	10		14			0		3
Choice: object visible	363		348			98		137
Choice: object hidden	642		499			429		324
Pre-Experiment 3								
Non-choice	0		17			12		3
Choice: object visible	21		72			23		25
Choice: object hidden	272		376			141		250
Pre-Experiment 4								
Non-choice	0		0			0		0
Choice: object visible	1		1			0		1
Choice: object hidden	52		33			38		48

understanding of containment, or a lack of experience tracking objects that are hidden from both sight and echolocation. Further research could address these possibilities by examining other indicators of dolphins' understanding of containment, by devising invisible displacement tasks that rely on occluders rather than containers to accomplish the displacement, and by giving dolphins experience tracking objects behind visually and acoustically opaque barriers. In addition, we remain open to the possibility that a different invisible displacement task, perhaps one more closely tied to dolphins' natural foraging contexts, may yet reveal cognitive abilities not evidenced within the current procedure, just as previously undiscovered social cognitive abilities have been revealed when chimpanzees were tested in more natural competitive, rather than cooperative, social contexts (e.g., Hare 2001; Hare and Tomasello 2004). This possibility awaits further research as well.

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Appendix

Training trials before each experiment consisted of an incremental sequence of gradually introducing (or reintroducing) new components, along with any additional sessions between experiments for the purpose of maintaining the "find the object" game in the animals' repertoires. In no case did between-experiment sessions include the component which was to be tested in upcoming experimental sessions. The total number of training/maintenance trials between experiments is detailed for each animal in Table 6, divided into three trial types: non-choice trials, which were either errorless or no-container trials in which the object was placed directly on the dock; choice trials in which the object was visible; and (after Experiment 1) choice trials in which the object was hidden.

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