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The object behind the echo: dolphins (*Tursiops truncatus*) perceive object shape globally through echolocation

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Abstract

Two experiments tested a bottlenosed dolphin's ability to match objects across echolocation and vision. Matching was tested from echolocation sample to visual alternatives (E–V) and from visual sample to echolocation alternatives (V–E). In Experiment 1, the dolphin chose a match from among three-alternative objects that differed in overall (global) shape, but shared several 'local' features with the sample. The dolphin conducted a right-to-left serial nonexhaustive search among the alternatives, stopping when a match was encountered. It matched correctly on 93% of V–E trials and on 99% of E–V trials with completely novel combinations of objects despite the presence of many overlapping features. In Experiment 2, a fourth alternative was added in the form of a paddle that the dolphin could press if it decided that none of the three-alternatives matched the sample. When a match was present, the dolphin selected it on 94% of V–E trials and 95% of E–V trials. When a match was absent, the dolphin pressed the paddle on 74% and 76%, respectively, of V–E and E–V trials. The approximate 25% error rate, which consisted of a choice of one of the three non-matching alternatives in lieu of the paddle press, increased from right to center to left alternative object, reflecting successively later times in the dolphin's search path. A weakening in memory for the sample seemed the most likely cause of this error pattern. Overall, the results gave strong support to the hypothesis that the echolocating dolphin represents an object by its global appearance rather than by local features. © 2002 Elsevier Science B.V. All rights reserved.

1. Introduction

What does a dolphin perceive when it inspects an object through echolocation? Does it perceive only the raw acoustic characteristics of the echoes (e.g. amplitude, frequency spectra), and subse-

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quently relate those through associative learning to some visually perceived object? Alternatively, does it perhaps perceive only some particular local feature, such as the presence of an open area or of a protruding arm? Or, does it directly perceive the object globally, as an integrated whole? This is the problem of object recognition, how objects are perceived and how they are represented in memory. This problem has been studied extensively within the field of visual perception (e.g. Tarr and Bulthoff, 1998). Humans, and likely many other animals, have the remarkable ability to recognize objects visually after a single glance, based on their shape (Biederman, 1995). Some examples from research on animal visual perception include findings that pigeons are sensitive to the spatial configuration of a picture's features (Wasserman et al., 1993; Kirkpatrick-Steger et al., 1998; cf. Cerella, 1980), and that chimpanzees (as well as humans) discriminate visually between complex figures by attending to their outer contours (i.e. their overall shape) (Tomonaga and Matsuzawa, 1992; see also Fagot and Tomonaga, 1999 for global precedence effects in these species). Clearly, direct shape perception characterizes much of visual perception.

Of course, the question of the basis of object perception is germane to any sensory system capable of shape perception. Recent cross-modal matching-to-sample studies at our laboratory have suggested that dolphins can directly perceive object shape through echolocation. These studies (Pack and Herman, 1995; Herman et al., 1998) demonstrated that a bottlenosed dolphin (*Tursiops truncatus*) could spontaneously (i.e. on the first trial, without reliance on associative learning) recognize an object through echolocation alone that it had inspected previously through vision alone. The reverse was also true. Performance was at or near ceiling levels in both directions, indicating a high degree of integration of the percepts arising from these two senses. Popper et al. (1997) argued that 'raw' acoustic cues present in the echoes returning from targets inspected by dolphins through echolocation (such as, highlight structure, echo spectrum, and target strength) were insufficient to explain the cross-

modal matching results reported by Pack and Herman (1995). However, raw acoustic cues, in conjunction with the learning of associations between these cues and reward contingencies, have often been invoked to explain dolphin capabilities for object discrimination through echolocation (e.g., see summaries in Au, 1993). In contrast, the data from our cross-modal matching studies support the hypothesis that the dolphin is capable of directly forming 'object-based' representations through echolocation (i.e. representations having characteristics of objects) without the necessity for associative learning (Pack and Herman, 1995; Herman et al., 1998; Pack et al., in press).

In these prior cross-modal studies, the dolphin chose between two-alternative objects, one of which matched the 'sample' object inspected previously. Theoretically, the dolphin could have perceived the sample at different levels of complexity, ranging from attention to a single local feature to apprehending the object's overall (global) shape. In the present studies, to determine whether the dolphin represents an object by its global shape, or attends primarily to local features, we examine its matching accuracy and its search behavior among objects that differ in shape but share particular local features. Suppose that following sample exposure the dolphin focuses on a local feature. If so, either of the two search behaviors might result. One would be characterized by considerable vacillation before choosing, as the dolphin goes back and forth between the two-alternatives, each of which contains the key local feature. Alternatively, the dolphin might simply choose the first object it encountered in its search path that contained the key feature. In either case, over a large number of trials, matching accuracy would be at chance levels, assuming that the location of the correct alternative along the dolphin's search path is a random variable. However, if the dolphin represented the sample by its global shape, and assuming the objects are clearly perceptually different, there should be little vacillation, and performance should be at levels well above chance.

In the new cross-modal matching studies presented here, we contrasted objects sharing 'local

class features' to determine whether the dolphin searched among the alternative objects for a local feature, or features, present in the sample, or searched for a global match. A class feature was defined as a general characteristic common to at least two different objects. For example, an 'L' and a 'l' share the same class feature 'vertical linear orientation'. A circle and a square share two class features, 'symmetry' and 'closure.' Several previous studies have demonstrated that dolphins can be taught to attend to specific class features such as symmetry (von Fersen et al., 1992) linear orientation (Hoffmann-Kuhnt, 1994) and closure (Herman et al., 1984). Depending on the degree to which the dolphin's representation of the sample in the cross-modal task preserves information about its global spatial structure, the dolphin may or may not confuse objects of different shape but with overlapping class features.

In our previous cross-modal studies, matching performance was well above chance levels on initial trials with novel objects, and vacillation was extremely rare. However, the use of only two-alternatives limited any detailed investigation of the dolphin's search strategy, and its use of local features versus global shape. Theoretically, the dolphin could make an *A/not A* type of judgment (i.e. if the first alternative does not match the sample, the second one must). Examination of the second alternative was not necessary. In the current cross-modal study, we instead used *three-alternative* objects taken from a set with overlapping class features (Experiment 1), or three-alternative objects plus a fourth possibility that we called, 'none of the above' (Experiment 2). With three-alternative objects present, if the first alternative is rejected, the dolphin must examine at least one more alternative. It cannot simply assume the next object to be correct. This procedure can help reveal the dolphin's search strategy (for example, random versus systematic, partial vs. exhaustive). Inasmuch as the local features of the non-matching alternatives overlap with those of the sample, the three-alternative procedure can also help to determine the dolphin's reliance on local features versus global shape. The latter should re-

sult in high matching accuracy, while the former, in a substantial number of errors by selection of non-matching objects when they are encountered prior to the match. The logic of adding the fourth 'null' possibility rests on the assumption that if the dolphin were searching for a local feature or features, it should find it or them, in one or more of the offered alternatives and select that alternative even though neither it nor the other alternatives are an exact match for the sample. On the other hand, if the dolphin were searching for a particular global shape, the mere presence of particular local features should not be sufficient for response. The dolphin should, therefore, reject all alternatives when no match is present, choosing instead 'none of the above'. In effect then, when no alternative matches the sample object, the dolphin must examine all three to conclude reliably that no match is present. Its search strategy can then be delineated in detail, and conclusions about reliance on local features versus global shape can be made more definitively.

In Experiment 1, we developed the three-alternative cross-modal procedures and, after training, tested the dolphin with objects that differed in global shape but had overlapping class features. In Experiment 2, we extended the cross-modal matching task to the fourth possibility, allowing the dolphin to press a paddle if it decided that a match was not present among *any* of the three-alternatives. For these tests, we used eight objects of abstract shape, all constructed of the same polyvinyl chloride (PVC) materials. The eight had been experienced previously by the dolphin (Herman et al., 1998), but only as four fixed pairs (i.e. only four pairings were tested out of the possible 28 that can be constructed among eight objects). The dolphin had demonstrated that it could match these shapes, as well as others (Pack and Herman, 1995), significantly above chance on the first trial that it encountered new objects, and hence without reliance on associative learning. For the current tests, all three-way combinations of objects were novel to the dolphin, having never been encountered previously.
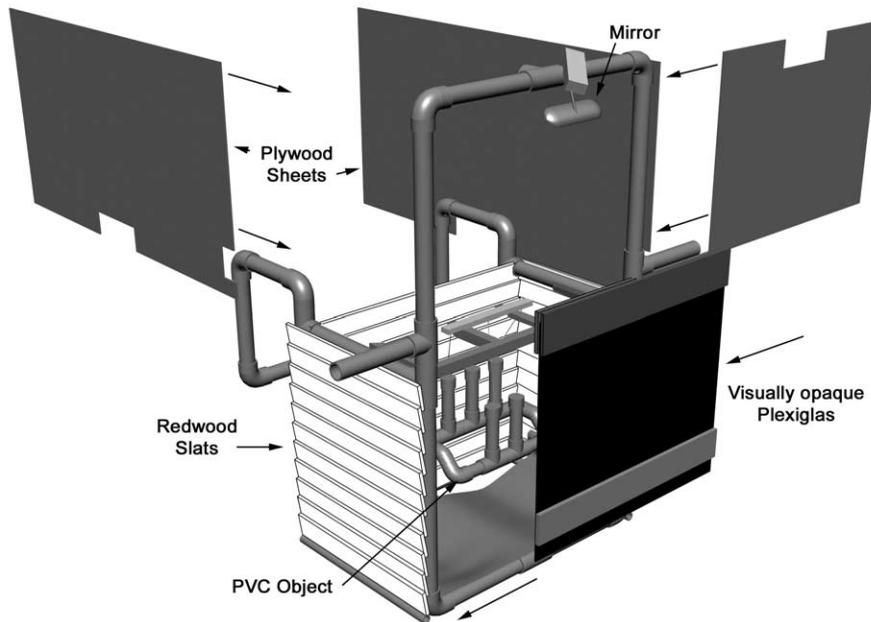
Fig. 1. Computer schematic (not to scale) of an exploded view of the anechoic box used for presenting sample objects to the dolphin's echolocation sense in echoic–visual (E–V) matching. The box measures 1.1 m wide × 0.6 m deep × 1.0 m high, and is composed of a PVC frame with angled redwood slats attached to each side and the back. The front Plexiglas panel is partially open to reveal an object suspended inside from monofilament line. The bottom of the box is covered by a thin sheet of PVC with a small opening at the back to allow seawater to fill the box when suspended from the tank wall. Two of the three opaque screens that are normally attached to the sides and front of the top half of the box have been retracted to reveal the interior. The mirror used to view the dolphin touching the Plexiglas panel is attached to the top of the box. Anechoic boxes used in visual–echoic (V–E) matching are similar in construction to the box used in E–V, except that no mirror is present, and a response paddle is attached to the side of the box.

2. General method

2.1. Subject

The subject throughout was an 11-year-old female bottlenosed dolphin (*T. truncatus*) named Elele. She was housed with three other dolphins in two interconnected seawater pools (each 15.2 m in diameter and 1.8 m in depth) at the Kewalo Basin Marine Mammal Laboratory (KBMML) in Honolulu, HI, USA. All matching tests were conducted in one of these pools. Elele was fed approximately 9.1 kg of a combination of smelt, herring, sardines and capelin daily, a normal dietary intake. A portion of her feed was available during test sessions. Elele was the subject in the prior referenced cross-modal studies (Herman and Pack, 1992; Pack and Herman, 1995; Herman et

al., 1998). She was, therefore, highly experienced in two-alternative echolocation-to-vision (E–V) matching-to-sample (MTS) and in vision-to-echolocation (V–E) MTS, as well as in within-modal visual (V-V) MTS and echoic (E-E) MTS.

2.2. Apparatus

2.2.1. Exposing objects for echolocation inspection alone

As in our previous studies (e.g. Pack and Herman, 1995), we exposed objects to the dolphin's echolocation sense alone by presenting them within customized sound attenuation (anechoic) boxes. Fig. 1 shows a schematic of an 'exploded' view of an anechoic box. The sides and back of the box consist of a series of angled redwood slats that when soaked in water disperse and attenuate

echoes. The critical feature of the box is its front panel, a visually opaque but acoustically transparent 0.32 cm-thick black Plexiglas sheet (shown partially open in Fig. 1). In water, the thin Plexiglas sheet transmits sound well and consequently, allows objects suspended within the box to be inspected through echolocation. The dolphin's echolocation signals reflect off the object suspended in the water column inside the box and return as echoes.

Depending on the particular matching task in effect (e.g. E–V or V–E), one or more anechoic boxes were suspended inside the dolphin's pool from the wall and filled with seawater through an opening at the bottom. Objects were suspended underwater within the box from thin monofilament lines. Black plywood blinders attached to the front and sides of the box (two are shown retracted in Fig. 1) prevented the dolphin from seeing objects as they were placed in the box. The box used to expose a sample object (Fig. 1) was fitted with a mirror at its top to allow an assistant located behind the box to see the dolphin's rostrum (beak) when it was directly in front of the Plexiglas sheet. Each box that was used to expose an alternative object was fitted with an underwater response paddle that when pressed deflected an attached arm. The arm extended in air and ended in a red buoy, making deflections highly visible from the surface.

2.2.2. Exposing objects for visual inspection alone

Objects (either the sample or the alternatives) to be presented strictly to the dolphin's visual sense were held in air, a medium in which dolphin echolocation is ineffective (Pack and Herman, 1995). Objects were held approximately 30 cm above the water surface by assistants donned in white shirts (to present a uniform background) and wearing opaque goggles (to prevent any view of the dolphin). The assistant displaying the sample object had no knowledge of the location at which the matching alternative would appear, and the assistants displaying the alternatives had no knowledge of whether the object they held was a match or not for the sample object.

2.3. Objects

2.3.1. Baseline objects

There were six 'baseline' objects that were highly familiar to Elele, a terra-cotta flower pot, a green fiberglass grating, a sand-filled PVC cross, a letter 'I' constructed from aluminum I-beams, a stainless-steel bowl, and a black hard rubber roller. They differed from each other in size, material composition, and shape, and had been experienced previously by the dolphin in within-modal and cross-modal matching tests (e.g. Herman and Pack, 1992). The baseline objects were used in part to train the three- and four-alternative cross-modal tasks, and were also interleaved during transfer tests among trials using the less familiar PVC transfer objects. Baseline objects were easy discriminations for Elele, and were employed throughout to help insure a reasonably high level of performance when she experienced new contexts or new procedures, thus guarding against negative emotional behavior that might obscure her potential.

2.3.2. PVC training objects.

A set of six pairs of 12 objects constructed exclusively of PVC pipes and fittings were used together with the baseline objects to teach the three-alternative task. Computer-scanned images of the PVC objects and pairings appear in Fig. 2. Elele had previously experienced these PVC objects (Pack and Herman, 1995; Herman et al., 1998). Each object within a pair was constructed from schedule 40 and/or 80 PVC pipe and fittings, ranging in diameter from 0.5 to 1.5 in (1.27–3.81 cm). Within pairs, the same diameters of PVC pipe were used, and the surface areas of the two objects were equated to within 4%. Objects were filled with dry sand to achieve negative buoyancy for immersion in water and to reduce internal reflections, to emphasize surface features.

2.3.3. PVC transfer objects

The transfer objects were eight PVC objects used in Herman et al. (1998), Experiment 2 (see Fig. 3). Each object had been experienced previously by Elele exclusively as a member of a par-
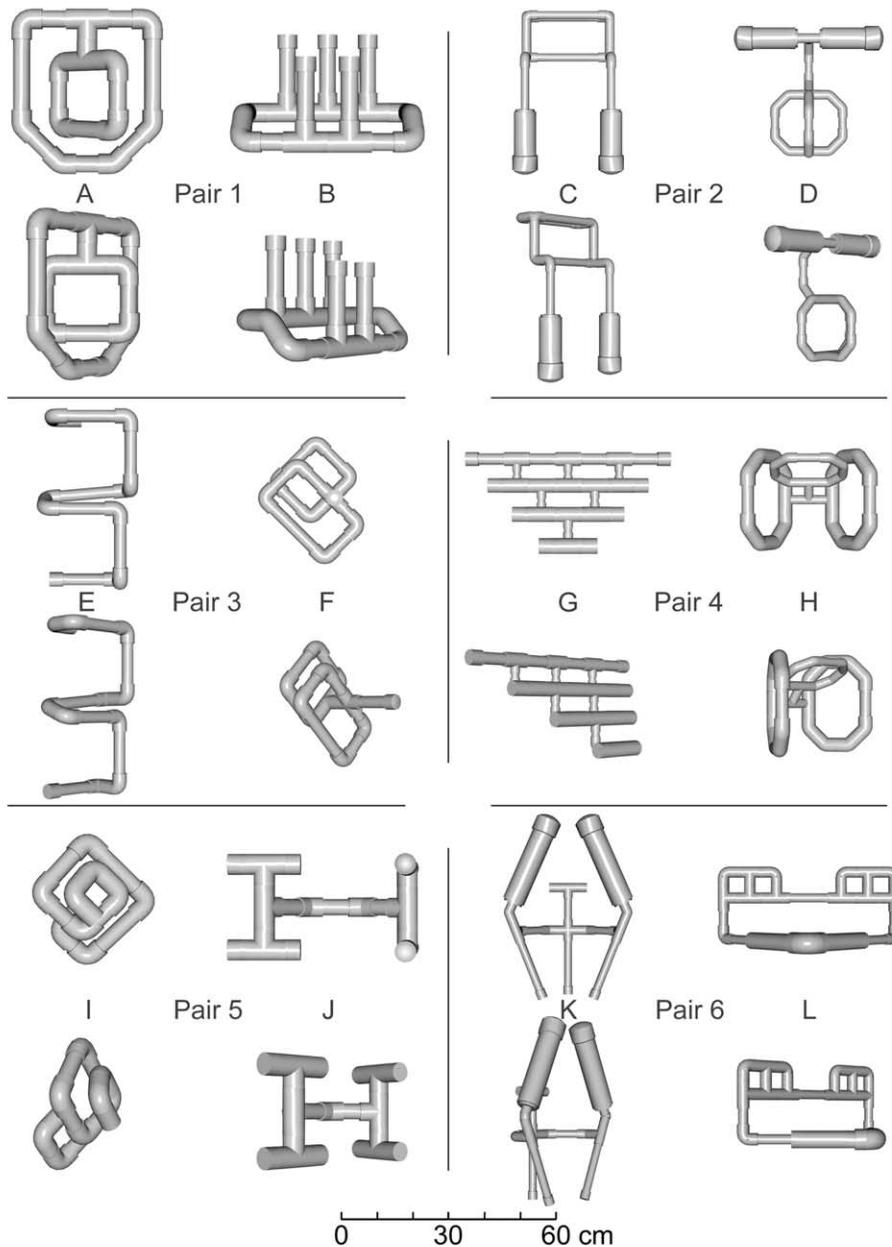
Fig. 2. Computer-scanned images of pairs of the PVC training objects numbered 1 through 6. Both a frontal view (shown to the dolphin) and a 45° view of the objects are displayed to reveal their three-dimensionality.

ticular test pair for 48 trials each in E–V and V–E MTS and for 24 trials each in V–V and E–E MTS. These previous pairings were: object 1 versus 2, 3 versus 4, 5 versus 6, and 7 versus 8. No other pairings of these objects had been used before the current study, and Elele's previous experience with these objects was limited to the number of trials noted. Further, there was a hia-
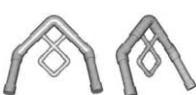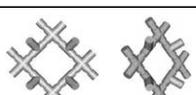
Test Objects Front View / 45° View	Vertical Piping	Horizontal Piping	Diagonal Piping	Closure	Symmetry	Protrusions
1	+	+	0	0	+	+
2	+	+	0	+	0	+
3	0	0	+	+	+	+
4	+	+	0	+	+	+
5	0	0	+	+	+	+
6	+	+	+	0	+	+
7	+	+	+	+	0	0
8	0	0	+	0	0	+

Fig. 3. Computer-scanned images of the PVC transfer objects numbered 1 through 8. Both the frontal view (shown to the dolphin) and the 45° view of the objects are displayed to reveal their three-dimensionality. The row adjacent to each object's image indicates the presence (by a ' + ') or absence (by a '0') of six class features: vertical piping, horizontal piping, diagonal piping, enclosed space, symmetry, and protrusions.

tus of 20 weeks since the last use of these eight objects by Herman et al. (1998) and their use in the current study.

The eight PVC transfer objects were constructed in the same way and of the same materials as the PVC training objects. Additionally, each object subtended a 43 cm² area. We classified each transfer object in terms of the presence or absence of six local class features: vertical piping, horizontal piping, diagonal piping, enclosed space (closure), horizontal symmetry, and protrusions (Fig. 3).

3. Experiment 1

Experiment 1 was conducted in three parts. In part A, we tested Elele in the three-alternative E−V MTS procedure. We used the baseline and PVC training objects to teach her the new procedure, by extending several of the already familiar two-alternative E−V MTS procedures. We then proceeded to formal tests of three-alternative E−V MTS using the PVC transfer objects. In part B, we tested Elele on three-alternative V−E MTS. Again, we used the

baseline and PVC training objects to teach the three-alternative V–E procedure, and then conducted tests with the PVC transfer objects. Finally, in part C, we evaluated Elele's search strategies among the three-alternatives in each MTS paradigm to examine whether her behavior was consistent with a search for local class features or global shape.

3.1. Part A: three-alternative E–V MTS

3.1.1. Method

A single anechoic box was placed at the east end of the dolphin's pool. Three-alternative objects were presented in air by assistants located at the west-end of the pool (ca. 15.2-m diameter distance from the east end). Objects were separated from each other by 2.5 m, with the central alternative located directly opposite the position of the sample box. At the beginning of each trial the dolphin remained with her trainer at a remote station 14-m circumferential distance from the anechoic box. While the dolphin's head was held out of water, to prevent any use of echolocation, an assistant immersed the sample object in the anechoic box. A second assistant simultaneously immersed and then immediately withdrew two 'masking' objects. The masking objects were always identical to the two non-matching objects presented as alternatives, and served to preclude any potentially useful sound cues made by the sample object as it was immersed in the water. When the sample object was in place, the trainer signaled the dolphin to approach the anechoic box. The dolphin approached and inspected the object inside through echolocation. When the first assistant, looking through the mirror, viewed the dolphin's rostrum in front of the box for approximately 2 s, he/she verbally signaled the assistants on the opposite side of the pool to display their alternative objects. The assistant's loud vocalization also signaled the dolphin to swim across the pool and choose among the alternatives by stationing in front of one of them for 3 s. An observer having no knowledge of the correct choice timed the dolphin's stationing response and verbally indicated which alternative was chosen (by calling out 'right', 'center', or 'left'). A

correct choice was followed by a whistle sound, fish reward, and social praise from the trainer. These were omitted following an incorrect choice.

3.1.1.1. Training. Elele was first familiarized over two sessions (39 trials) with the new location of the alternative objects at the west end of the pool (with the sample at the east end) using the baseline objects and two-alternative E–V MTS. These locations differed from those used in Elele's previous experience with two-alternative E–V MTS (e.g. Herman et al., 1998). Elele remained errorless throughout the two sessions. In each of the following two sessions, Elele was exposed to 12 trials of three-alternative E–V MTS using the baseline objects interleaved among 12 trials of two-alternative E–V MTS using the PVC training objects. She was again errorless. Thus, she transferred her matching concept spontaneously from two to three-alternatives in the E–V MTS task.

3.1.1.2. Testing. Elele was next tested on three-alternative E–V MTS with the eight PVC transfer objects (Fig. 3). There are 336 unique permutations of three-alternative objects taken from the pool of eight PVC transfer objects. The permutations represent the six possible arrangements of each set of three as right, center, and left alternative object. Further, any of the three could be the matching alternative, so that altogether there were 1008 (336×3) unique trial types that could be tested. From these, we chose a one-third sample (336 trials), such that all 56 combinations of three-alternative objects were tested, with each object serving as sample in two of the six possible trial configurations. Over all transfer trials, objects sharing local class features were, therefore, contrasted as sample and non-match on numerous occasions (see Fig. 3).

Each of the 28 three-alternative E–V MTS test sessions consisted of 12 transfer trials using the PVC transfer objects interleaved among 12 trials using the baseline objects. Trials were pseudorandomly ordered with the restriction that no more than three successive identical locations for the matching alternative could occur. Over two consecutive sessions, each of the eight PVC trans-

Table 1
Experiment 1: the number of correct first matches per sample object for each unique combination of sample object and two non-matching alternative objects ($n = 168$) in E–V and V–E MTS using the PVC transfer objects for partial and full transfer tests (see text)

Task	Sample object	1	2	3	4	5	6	7	8	Total
E–V	Partial transfer tests ($n = 9$)	9	8	9	8	8	9	9	9	69 (95.8%)
	Full transfer tests ($n = 12$)	12	12	12	11	12	12	12	12	95 (99.0%)
V–E	Partial transfer tests ($n = 9$)	9	5 ns	9	9	9	8	9	8	66 (91.7%)
	Full transfer tests ($n = 12$)	11	10	12	9	12	12	11	12	89 (92.7%)

ns, not significant; all other cell values significant at $P < 0.005$ (cumulative binomial test, chance = 0.33).

fer objects appeared three times as sample, and each of the six baseline objects appeared four times as sample (twice per session). Within-trial procedures remained as described earlier.

3.1.2. Results and discussion

Elele matched the echoic sample correctly on 331 (98.5%) of the 336 test trials using the PVC transfer objects, and was errorless on the 336 baseline trials. Table 1 shows the number of correct *first-trial* matches with each object acting as sample (i.e. the first occurrence of each unique combination of sample and alternative objects). The results are shown separately for 'partial' transfer tests and 'full' transfer tests. Partial transfer tests were those trials in which two of the three-alternative objects had been tested together previously in two-alternative E–V, and the third object had been tested for an equal number of trials as a member of a different pairing (Herman et al., 1998). There were nine partial transfer test trials per sample object. Elele was correct on eight or nine of these tests ($P < 0.001$, cumulative binomial test, chance = 0.33) for all eight PVC transfer objects acting as sample.

Full transfer tests were those trials involving *completely* novel combinations of objects (i.e. combinations whose members had never been tested together pair-wise previously). There were 12 full transfer test trials per sample object. Elele was errorless on full transfer test trials for seven of the eight sample objects, and made only a single error on the eighth ($P < 0.001$, cumulative binomial test). Thus, she demonstrated spontaneous transfer of her cross-modal matching concept to completely novel three-way combinations of familiar objects in the three-alternative E–V task.

3.2. Part B: three-alternative V–E MTS

3.2.1. Method

To present the echoic alternatives in V–E MTS, three anechoic boxes fitted with response paddles were suspended from the pool wall at the east end and separated from each other by 2.5 m. An assistant wearing opaque goggles presented the visual sample at the west end of the pool. On each trial, the assistant stood in view of the dolphin with the object hidden behind the wall. The dolphin stationed in front of the assistant in response to a signal from the trainer. Upon hearing a verbal signal from a coordinator located on an elevated observation platform, the assistant showed the sample object to the dolphin, by bringing it forward over the pool wall and holding it stationary about 30 cm above the water surface. After approximately 5 s, the coordinator verbally signaled the assistants behind the anechoic boxes to suspend their objects inside the boxes. As in E–V MTS, each alternative object was plunged into a box simultaneously with two masks that were then immediately withdrawn. The same three objects were plunged into each box. The dolphin swam to the boxes, inspected the alternatives echoically, and pressed the paddle on the selected box. Reinforcement contingencies were identical to those used in E–V MTS.

3.2.1.1. Training. Using the V–E MTS procedure, Elele was first familiarized over seven sessions (139 trials) with the new location of the sample

object (previously, in Herman et al., 1998, Experiment 2, it had been shown at the remote station). She was also made aware that there were now three-alternative boxes rather than two. These familiarization trials used baseline objects only. However, the alternative objects were placed in only two of the three boxes (randomly chosen). The third remained empty. Initially, some cueing was used to teach Elele how to use the response paddle on the central anechoic box. Overall, Elele was correct on 128 (92.0%) of the uncued trials, including 45 (93.8%) of the 48 uncued trials occurring in the final two sessions.

In the subsequent two sessions we presented mixed trials of three-alternative V–E MTS using the baseline objects and all three anechoic boxes, and two-alternative V–E MTS using the PVC training objects placed in two of the three boxes (randomly chosen), with the third remaining empty. Elele was correct on 23 (95.8%) of 24 trials in each condition.

3.2.1.2. Testing. Elele was next tested on three-alternative V–E MTS with the eight PVC transfer objects (Fig. 3). The same experimental design used for testing three-alternative E–V MTS was used again, but with a different ordering of the 336 test trials and the 336 baseline trials.

3.2.2. Results and discussion

Elele chose the matching echoic alternative on 316 (94.0%) of 336 transfer trials in V–E MTS and made but a single error on the baseline objects. Table 1 shows the number of correct *first-trial* matches with each object acting as sample for both partial transfer tests ($N = 9$ trials per sample) and full transfer tests ($N = 12$ trials per sample). For partial transfer tests, Elele was correct on eight or nine trials ($P < 0.001$, cumulative binomial test, chance $= 0.33$) for seven of eight samples. She was correct on only five of nine partial transfer trials with Object 2 as sample. For full transfer tests, Elele was correct on nine or more trials ($P < 0.005$, cumulative binomial test, chance $= 0.33$) for all eight sample objects. Clearly then, Elele performed at near ceiling levels in both the three-alternative E–V and V–E MTS tasks using novel three-way combinations of familiar objects having overlapping local class features. Her performance accuracy on the first trials of completely novel combinations of objects (i.e. full transfer tests) did not differ significantly across E–V and V–E MTS (χ^2 [1,192] $= 3.26$, $P > 0.05$).

3.3. Part C: analysis of search strategies

The dolphin's search behavior, together with its performance accuracy, can provide information about its representation of the sample. To investigate whether Elele was searching among alternatives for a local class feature or features in parts A and B, we analyzed the experimenter's hand-written records of each transfer trial for the order in which Elele searched among the alternative objects before finally selecting 1. During trials, the experimenter had recorded the order in which Elele viewed each visual alternative object in E–V MTS (e.g. right, then center, then left, etc), and the order in which she pointed her rostrum at the different alternative anechoic boxes in V–E MTS. This latter measure reflects findings that echolocation signals of *Tursiops* are directed forward of the head in a narrow beam (e.g. see Au, 1993). We analyzed search path for each first trial in which Elele experienced each unique combination of sample and two non-matching alternative PVC transfer objects in E–V and V–E MTS. The search path was available for 286 PVC transfer trials, 150 in E–V MTS and 136 in V–E MTS. Fig. 4 represents Elele's search path when choosing objects at the right, center, and left positions. For example, within a bar, 'RCL' means that Elele first searched the right position, then the center, and finally chose left. It is evident that on the majority of trials Elele performed a right-to-left serial non-exhaustive search among the alternatives. This strategy, summarized as 'search only R, if R is a match, if R is not a match, search C, and if C is not a match, choose L,' accounted for 90.0% of the trials in E–V MTS and 76.5% of the trials in V–E MTS. These percentages are well above what might be expected from a random search strategy, which should yield an approximately equal number of first approaches to each box, and no systematic path thereafter. The low
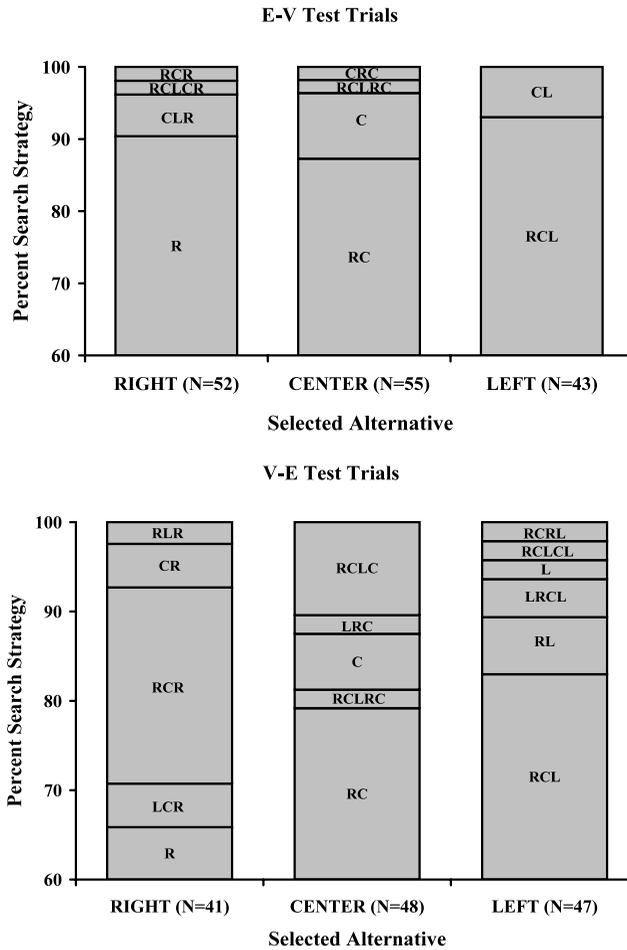
Fig. 4. The percentage of times the dolphin used particular search paths among the alternatives in three-alternative E–V and V–E MTS tasks with baseline objects when it selected the right, center, or left object. Search path is read from left to right where R, inspection of right object; C, inspection of center object; and L, inspection of left object.

incidence of vacilation in Elele's search among the alternatives combined with her high performance accuracy does not support a search for local features. The sequential search path typically followed, R, then C, then L, if necessary, clearly shows that Elele rejected non-matching alternatives, even though they shared local class features with the sample. Indeed, of the 48 permutations of sample and non-matching alternative that Elele had never experienced previously, she correctly rejected the non-match on its first encounter dur-

ing her search on 47 occasions in E–V MTS and on 46 occasions in V–E MTS.

4. Experiment 2

The serial non-exhaustive search strategy used by Elele in Experiment 1, and the high level of performance she achieved in the presence of many overlapping local features between sample and alternative PVC objects, together suggested that

Elele operated on the basis of a global 'search image' (Tinbergen, 1960; Vreven and Blough, 1998) that corresponded representationally to the structure of the sample object. It appeared that she searched serially among the three PVC alternatives until an exact match was found, and then stopped. Of course, a matching object was always present and Elele may well have developed that expectation. But what if none of the alternatives was an exact match for the sample? Would Elele be able to indicate the absence of a match? If she could, this would provide compelling evidence that her search was not for a specific local feature or features, inasmuch as a correct rejection of all PVC alternatives would mean that: (a) all alternatives had been inspected (which was not necessary in Experiment 1 given her serial, non-exhaustive search strategy) and (b) that despite many overlapping local features among the three-alternatives, and between the alternatives and the sample, she recognized that no object wholly matched the sample (i.e. she was not simply generalizing to the 'best-fit' match from among the available alternatives).

To examine this issue, in Experiment 2 we added a fourth alternative, in the form of a paddle that Elele could press if none of the three-alternative objects matched the sample. We termed this paddle the 'none of the above' or NA paddle. If Elele were searching for the global shape of a specific object, and it was not present among the three-alternative objects, she should reject all three and press the NA paddle. Alternatively, if she were searching for a local class feature or features, she should select one of the objects that contained that local feature(s), even if no object was identical to the sample.

Experiment 2 was carried out in three parts. The baseline objects and the PVC transfer objects from Experiment 1 were again used. The PVC training objects from Experiment 1 were no longer used. In part A, we familiarized Elele with the use of the NA paddle in E–V and V–E MTS. In Part B, we tested whether Elele would demonstrate spontaneous and appropriate use of the NA paddle in E–V and V–E MTS with the PVC transfer objects. Inasmuch as the PVC transfer objects had many overlapping local features, if

Elele could correctly select a matching alternative object, or correctly reject all objects if none matched the sample, it would provide compelling evidence that she was not representing the sample as a local class feature or features, but as a global shape. Finally, in part C, we examined Elele's search strategies among the four alternatives in each matching task of part B.

4.1. Part A: using the NA paddle with baseline objects

In this Part, Elele was introduced to the NA paddle and attendant procedures using the E–V paradigm. After training and testing within E–V MTS was complete, we introduced the NA paddle in the V–E paradigm and again tested her performance.

4.1.1. E–V matching with the NA paddle present

4.1.1.1. Method. The same anechoic sample box from Experiment 1 was used here. The NA paddle consisted of a black oval float attached to a 22-cm PVC arm and frame. The frame was suspended from the side of the pool, allowing the float to rest just above the water surface.

Only the six baseline objects from Experiment 1 were used when the NA paddle was present. When it was absent, either baseline objects or the PVC transfer objects from Experiment 1 were used. This latter condition thus partially replicated that of Experiment 1, part B.

The NA paddle was introduced using the two-alternative E–V MTS paradigm with the sample object at the east end of the pool and the alternative objects located at the west end and separated by 2.5 m. When present, the NA paddle was located 7.0 m to the left of the left alternative object (from the dolphin's perspective). After familiarizing Elele to the two-alternative E–V condition, plus the NA paddle, we gradually transitioned to the use of the NA paddle in three-alternative E–V MTS. The NA paddle continued to be located to the left of the alternative objects. Elele indicated her choice of an alternative object, as she had in Experiment 1, by stationing in front of it for a 3 s hold. Alternatively, to indicate her

Table 2
Experiment 2: results of E–V matching tests for using the 'None-of-the-Above' (NA) paddle to report on the absence of a match among the alternatives for a baseline object appearing as sample

Number of alternatives	Match present		Match absent	
	Number of trials	Number correct	Number of trials	Number correct
(a) Two objects + NA	8	8	8	8
(b) Three objects + NA	9	8	9	9
(c) Three objects only	40	39	–	–

choice of the NA paddle, Elele pressed it. The matching alternative object, if present, appeared equally often, or nearly so, in each available position. An observer having no knowledge of the correct solution judged all of Elele's responses.

Three sessions were run, the first of 26 trials, and the remaining two of 24 trials each. Each session consisted of mixed trials of three types, representing three different arrangements of alternatives. These were: (a) two-alternative objects plus the NA paddle, (b) three-alternative objects only, and (c) three-alternative objects plus the NA paddle. Over the three sessions, there were 16 trials of Type a, half containing a matching alternative object, and half not, all using the baseline objects only. There were 40 trials of Type b, 3 using the baseline objects and 37 using the PVC transfer objects. Finally, there were 18 trials of Type c, using the baseline objects only, given as 'probes' in increasing density over sessions. There were two 'probe' trials during Session 1, four during Session 2, and 12 during Session 3. For half the probes, one of the alternative objects matched the sample and for the remaining half, none did.

To acquaint Elele with the use of the NA paddle, it was suspended from the pool wall. The trainer, using gestures familiar to Elele, signaled her to touch the paddle with her rostrum. Elele did so, for which she received social praise and a fish reward. This was the full extent of her training to use the NA paddle. The remaining trials of the session, using mixed trial types, began immediately thereafter.

4.1.1.2. Results and discussion. Elele successfully pressed the NA paddle on the first NA trial of Session 1 in which there was no match for the sample among the two-alternative objects. Table 2 summarizes the results over all three sessions. It can be seen that Elele made no errors on Type a trials, a single error on Type b, and a single error on Type c (in all cases, $P < 0.001$, cumulative binomial test). Thus, Elele spontaneously used the NA paddle to report correctly the absence of a match for the sample from among either two or three-alternative baseline objects.

4.1.2. V–E matching with the NA paddle present

Immediately after completing E–V testing, we examined whether Elele could transfer her facility with the use of the NA paddle to the V–E paradigm.

4.1.2.1. Method. For the initial transfer test we used two anechoic boxes, located at the pool's east end and separated by 2.5 m. The visual sample was located at the west end. The NA paddle, when used, was located 7.0 m to the left of the left box (from the dolphin's perspective). As in the earlier E–V test, only the six baseline objects from Experiment 1 were used on V–E trials in which the NA paddle was present. After the assistant exposed the sample object in air to Elele, the alternatives were presented in the anechoic boxes (along with their masks, which were removed promptly). If one of the alternatives matched the sample, Elele was required to press the response paddle on the box containing the match. If neither matched the sample, she was required to press the NA paddle. Both the baseline objects and the PVC transfer objects from Experiment 1 were used on trials in which the NA paddle was absent. On these trials, a match for

Table 3

Experiment 2: results of V–E matching tests for using the 'None-of-the-Above' (NA) paddle to report on the absence of a match among the alternatives for a baseline object appearing as sample

Number of alternatives	Match present		Match absent	
	Number of trials	Number correct	Number of trials	Number correct
A				
Two objects + NA	4	4	4	1
B				
One object + NA	30	30	30	29
Two objects + NA	18	18	18	18
Three objects + NA	18	17	18	18

A, initial V–E test results; B, V–E tests with 1, 2, and 3 objects following brief training.

the sample was always present in one of the two boxes.

Prior to any trials, the NA paddle was suspended from the pool wall and Elele's trainer signaled her to press it. She pressed the paddle without hesitation and a single session of 24 trials then followed immediately. On eight trials the NA paddle was present. On four of these trials a match was present in one of the two boxes (equally distributed between both boxes), and on four trials a match was absent. These eight trials were interleaved among 16 trials in which the NA paddle was absent. These latter trials used either the baseline objects ($N = 3$ trials) or the eight PVC transfer objects ($N = 13$ trials).

Due to this initial transfer test showing only marginal success, we instituted brief NA paddle training during the following V–E session of 18 trials, using only a single anechoic box and with the NA paddle present on all trials. Only baseline objects were used. On four trials, a match for the sample was present in the box, and on 14 trials it was not. To assist Elele in correctly choosing the NA paddle when a match was absent, the anechoic box was empty on some trials. Elele then spontaneously pressed the NA paddle. If the box contained an object, an assistant cued Elele to press the paddle by 'jiggling' it. This type of assistance or cueing occurred on five of the first 12 trials. In the final six trials of the session, no further assistance or cue was given.

Three 20-trial V–E MTS sessions using a single anechoic box with the NA paddle present were then conducted. Across these sessions, using the six baseline objects only, each of the 30 permutations of sample and non-matching alternative was tested once, and each of the six combinations of sample and matching alternative was tested five times for a total of 60 test trials. Each session consisted of 10 match trials and 10 non-match trials. These three sessions were then followed by an additional four 24-trial sessions using the baseline objects only, during which the number of anechoic boxes was increased to two, and then to three. Within each of these sessions, half the trials contained a match and half did not.

4.1.2.2. Results and discussion. Table 3A shows the results of Elele's initial V–E MTS test using the NA paddle with the baseline objects. Elele selected the box containing the matching object on all four trials in which a match was present, but pressed the NA paddle on only one of the four trials when a match was absent. Her correct response occurred on the first 'match-absent' trial. On the remaining trials she inspected and rejected the right box and then selected the left box, which was closest to the NA paddle.

During the subsequent 18-trial training session instituted with baseline objects to improve her V–E performance with the NA paddle present, Elele was cued on only five trials in which a match was absent. She responded correctly on a total of 11 of 13 uncued trials ($P = 0.011$, cumulative binomial test), including correct responses on seven of nine trials in which a match was absent and all

four trials in which a match was present. Elele thus demonstrated the appropriate use of the NA paddle with the baseline objects after only brief training with minimal cueing.

Table 3B summarizes Elele's subsequent performance with one, two, or three anechoic boxes. She made only two errors throughout, one on a match-present condition and one on a match-absent condition ($P < 0.0001$, cumulative binomial test).

4.2. Part B: testing use of the NA paddle with PVC transfer objects

In this part, we tested Elele's ability to use the NA paddle appropriately when making discriminations among the PVC transfer objects. These tests again contrasted objects with overlapping local class features to determine more conclusively whether Elele was searching among alternative objects for particular local features or for global shape. Trials specifically germane to this goal were those in which none of the alternatives matched the sample, but nevertheless shared one or more local features with the sample.

4.2.1. Method

4.2.1.1. Objects. Six of the eight PVC transfer objects from Experiment 1 (Objects 3–8, see Fig. 3) were tested in four-alternative E–V and V–E MTS. The transfer set was limited to six objects to keep the overall number of trials manageable. Although the transfer objects were familiar to Elele, they had not been used previously in trials in which the NA paddle was available.

4.2.1.2. Procedure. The apparatus and procedures were the same as in the final E–V and V–E MTS configurations of Part A. We tested 30 of the 120 possible permutations of the six transfer objects taken three at a time. Each permutation of three-alternative objects was tested on four trials. For three of these trials one of the alternative objects matched the sample (i.e. each alternative object was the correct match once). For the fourth trial, none of the alternatives matched the sample, requiring therefore a press of the NA paddle. Thus, a total of 120 trials were run (30 permutations × four trials

per permutation) in E–V MTS and 120 in V–E MTS. Sessions of E–V and V–E MTS were counterbalanced to control for order effects. The location of particular alternatives at the right, center, and left positions was balanced across trials.

At each of 20 sessions, there were 12 transfer trials using the PVC transfer objects interleaved among 12 trials using the 6 baseline objects. The baseline trials were organized under the same rules and constraints described above for the transfer trials (i.e. 30 permutations × four trials per permutation per matching task). Within each session, for both transfer trials and baseline trials, each of the four alternative choices (right, center, left and NA paddle) was correct 25% of the time. Over the course of two consecutive sessions, each matching object appeared once in each alternative position and also once as sample in trials in which there was no matching alternative. The same control procedures described in Experiment 1 were used here. Research sessions were videotaped for subsequent determination of the dolphin's search behaviour among alternatives.

4.2.2. Results and discussion

4.2.2.1. Accuracy. Fig. 5 summarizes Elele's performance when the matching alternative was at the right, center, or left position, and when it was absent. For both E–V and V–E, Elele reported the presence of a match with high accuracy, 97% or better with baseline objects and 93% or better with PVC transfer objects. Elele made no errors in reporting that a baseline object was absent. However, for PVC transfer objects, she reported absence correctly for 77% of E–V trials and 73% of V–E trials. Inasmuch as chance accuracy is 25% (assuming a random choice among the four alternatives), her performance in reporting absence of PVC matches was nonetheless highly significant ($P < 0.0001$, cumulative binomial test).

An analysis of variance compared conditions (E–V vs. V–E), object type (baseline vs. PVC) and alternative position (R, C, L or NA). There was no significant difference between conditions. Overall performance with baseline objects signifi-cantly exceeded that with PVC objects ($F(1,464) = 16.38$, $P = 0.0001$), and the effect of alternative position
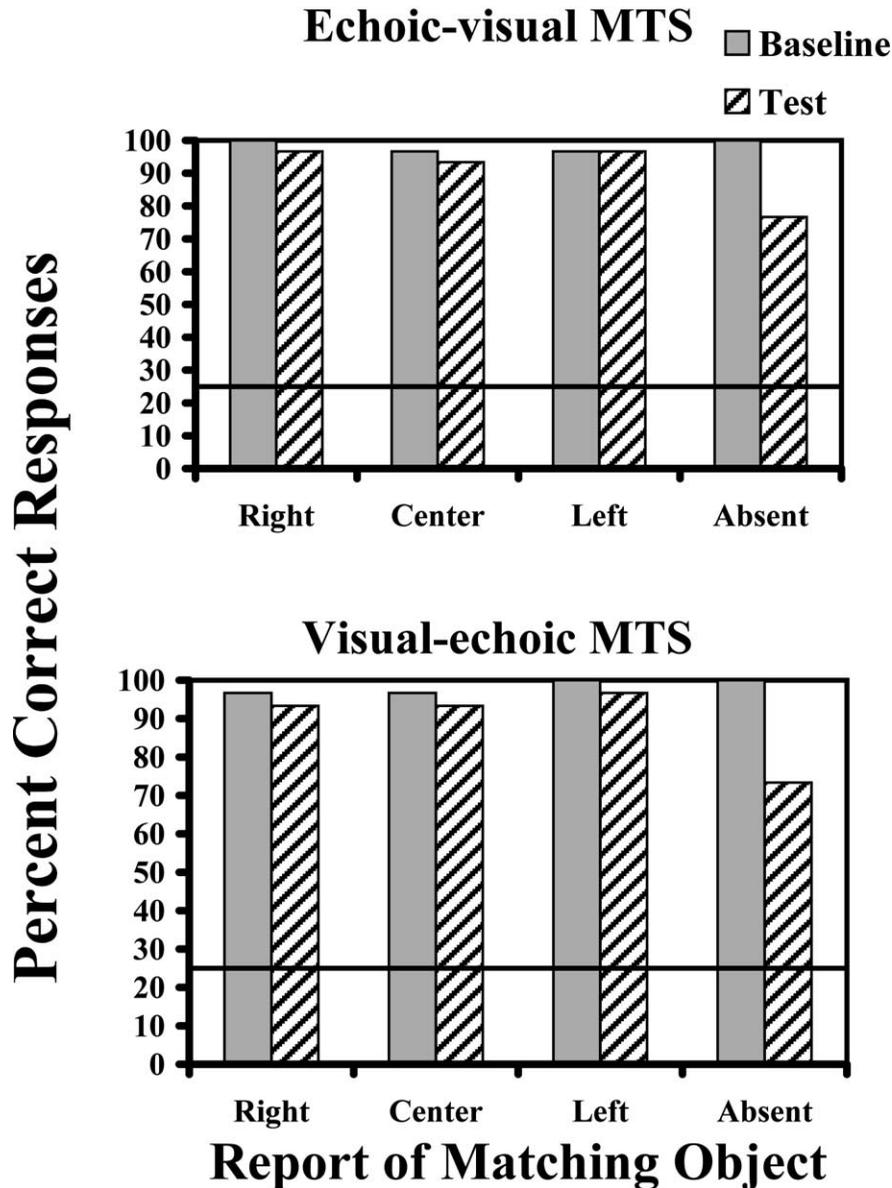
Fig. 5. Percent correct responses in four-alternative echoic-visual and visual-echoic matching with baseline objects (gray bars) and test objects (striped bars) for trials in which either a match was located in the right, center, or left position, or no match was present (absent). Each bar represents 30 trials. A chance performance line is shown at 25%.

was significant ($F(3,464) = 4.92$, $P = 0.0023$). Although Elele performed equivalently reporting that a match was present in each of the alternative positions (i.e. right, center, or left), she was less accurate reporting a match's absence on the NA paddle trials (Duncan's Multiple Range, $\alpha = 0.05$; df $= 464$; MSE $= 0.051$; critical range $= 0.057$ for two means, 0.060 for three means, and 0.062 for four means). In addition, the interaction of object type and position was significant ($F(3,464) = 7.32$, $P = 0.0001$), and as can be seen in Fig. 5, was driven by the lowered performance with the NA paddle with the PVC objects.

Table 4
Experiment 2: performance accuracy on the first trial in which a particular sample was displayed and none of the alternatives was identical to the sample (chance = 25%) in E–V and V–E four-alternative MTS

Object	3	4	5	6	7	8	Number correct
E–V	+	0	+	0	+	0	3
V–E	+	+	+	0	+	+	5
Total							8[a]

Objects are as shown in Fig. 3. Note: '+' indicates correct NA response, '0' indicates false alarm (i.e. choice of an object when no match was present).

[a] $P < 0.005$ by the cumulative binomial test.

4.2.2.2. Spontaneous reports of absence. As noted earlier, the PVC transfer objects had never been used previously in the four-alternative cross-modal task. In Table 4, we examined the details of Elele's use of the NA paddle on the first trial given with each PVC sample in which a match was absent. Elele was correct on eight of 12 first trials in E–V and V–E MTS combined ($P = 0.0028$, cumulative binomial test, chance = 0.25). Elele's spontaneous and appropriate use of the NA paddle in these cases indicates that the presence of shared local features (Fig. 3) between alternatives and the sample generally was not sufficient to induce the selection of an alternative not wholly matching the sample. That is, when confronted with a situation in which none of the alternatives matched the sample, Elele did not simply respond to the 'best fit' match. Rather, her overall high levels of rejection of non-matches in favor of the NA paddle indicate that her representation of the sample was highly faithful to the overall spatial structure of that object.

4.2.2.3. False alarms and missed detections. Table 4 showed four false alarms among the 12 initial match-absent trials with each PVC sample object. A false alarm occurred on a match-absent trial when Elele incorrectly selected a non-matching alternative object instead of pressing the NA paddle. Overall, false alarms occurred on 15 of 60 NA trials. These 60 trials actually represented 180 individual comparisons of the dolphin's representation of the sample and a non-matching alternative object, inasmuch as there were three objects available for comparison at each trial. False alarms did not appear to be random selections among the alternative objects. Table 5 shows the identities of

the sample object and selected non-matching alternative on false alarms. Although there were 15 false alarms, they occurred with only six of 15 possible combinations of sample object and non-matching alternative. Six of the false alarms (40%) occurred between Objects 3 and 6. Fig. 3 shows that these objects shared three of the six local class features (diagonal piping, symmetry, and protrusions). However, Objects 3 and 5 shared these same features but were never confused. Thus, the basis for these few false alarms remains in question. It is interesting that in 11 of 15 false alarms the same confusions occurred in both E–V and V–E (Objects 3 vs. 6, 4 vs. 7, and 6 vs. 5). This symmetry provides additional evidence for the functional equivalence of the representations of objects derived through echolocation and vision, as first proposed by Pack and Herman (1995).

A missed detection occurred on a match-present trial in which Elele incorrectly pressed the NA paddle when a match was actually present among the alternatives. Only four missed detections occurred in 180 match-present trials (combining E–V and V–E), significantly fewer than the number of false alarms (Fishers exact test, $N = 240$, $P < 0.0001$). The PVC samples associated with the four missed detections were Objects 4 (three missed detections) and 6 (one missed detection).

4.3. Part C: analysis of search strategies with NA paddle present

We analyzed the archival videotape records of each available trial in Experiment 2, Part B, to determine Elele's search behavior among the four alternatives after her inspection of the sample

Table 5
Experiment 2: the number of times a particular non-matching alternative was selected in error for a particular sample object (i.e. a false alarm) when none of the alternatives matched the sample in the four-alternative E–V and V–E MTS

Task	Sample	Selected alternative	Number times selected ($N = 3$)	Positions of false alarm object
E–V	3	6	1	C
V–E	3	6	2	L, C
E–V	6	3	1	L
V–E	6	3	2	L, R
E–V	4	7	1	L
V–E	4	7	2	L, C
E–V	6	5	1	C
V–E	6	5	1	L
E–V	4	3	1	C
V–E	8	3	1	L
E–V	8	6	2	L, C

Objects are designated as in Fig. 3. Note, R, right; C, center; and L, left.

object. In Experiment 1, Elele most often conducted a right-to-left serial non-exhaustive search of the alternative objects, both in E–V and V–E MTS. However, dfletailed inspection of the left object was not in theory necessary inasmuch as a match for the sample always appeared among the alternatives. Consequently, when the match was positioned left, the dolphin could have adopted a strategy of 'If not right, and not center, then choose left.' This strategy would not have been effective in Experiment 2 in the presence of the NA paddle.

4.3.1. Method

Two raters independently viewed taped E–V and V–E MTS trials to determine Elele's search path, and to measure her response time after presentation of alternative objects. For E–V MTS, without knowledge of the sample object, the raters recorded the order in which Elele viewed each alternative object. For V–E MTS, without knowledge of the identity of alternatives, they noted the order in which Elele pointed her rostrum at each anechoic box (as a measure of echoic inspection strategy, see Experiment 1).

The raters used the digital tape's chronometer record to determine response time. For E–V MTS, they measured the time from the box assistant's verbal command 'In' (signaling the assistants on the opposite side of the pool to present the alternative objects in air) to the moment when the dolphin either stationed in front of the object

of its choice or touched the NA paddle. For V–E MTS, they measured the time from the experimenter's verbal command 'In' (signaling the assistants to suspend the alternative objects in the anechoic boxes) until the dolphin began its press of a response paddle (either one of the paddles on the anechoic boxes or the NA paddle).

4.3.2. Results and discussion

Each rater independently examined 427 videotaped trials to determine the dolphin's search pattern. Overall, the raters were in exact agreement on 377 trials (88.3%). This included 98.2% agreement on 109 of 111 E–V PVC test trials, 96.3% agreement on 103 of 107 E–V baseline trials, 84.0% agreement on 89 of 106 V–E PVC test trials, and 73.8% agreement on 76 of 103 V–E baseline trials. Each of the 50 trials in which there was disagreement was then viewed independently by a third rater who had no knowledge of the previous judgements. If two of the three judges were in agreement, this was selected as the final description of search behavior. There was agreement between the third rater and one of the two original raters on 36 trials, leaving 14 trials on which none of the raters agreed. The total of 413 final descriptions ($377 + 36$) are summarized in Fig. 6, which shows the percentages of different search strategies used by Elele when responding to each position (i.e. right, center, left, or NA paddle). Results are shown for both PVC transfer
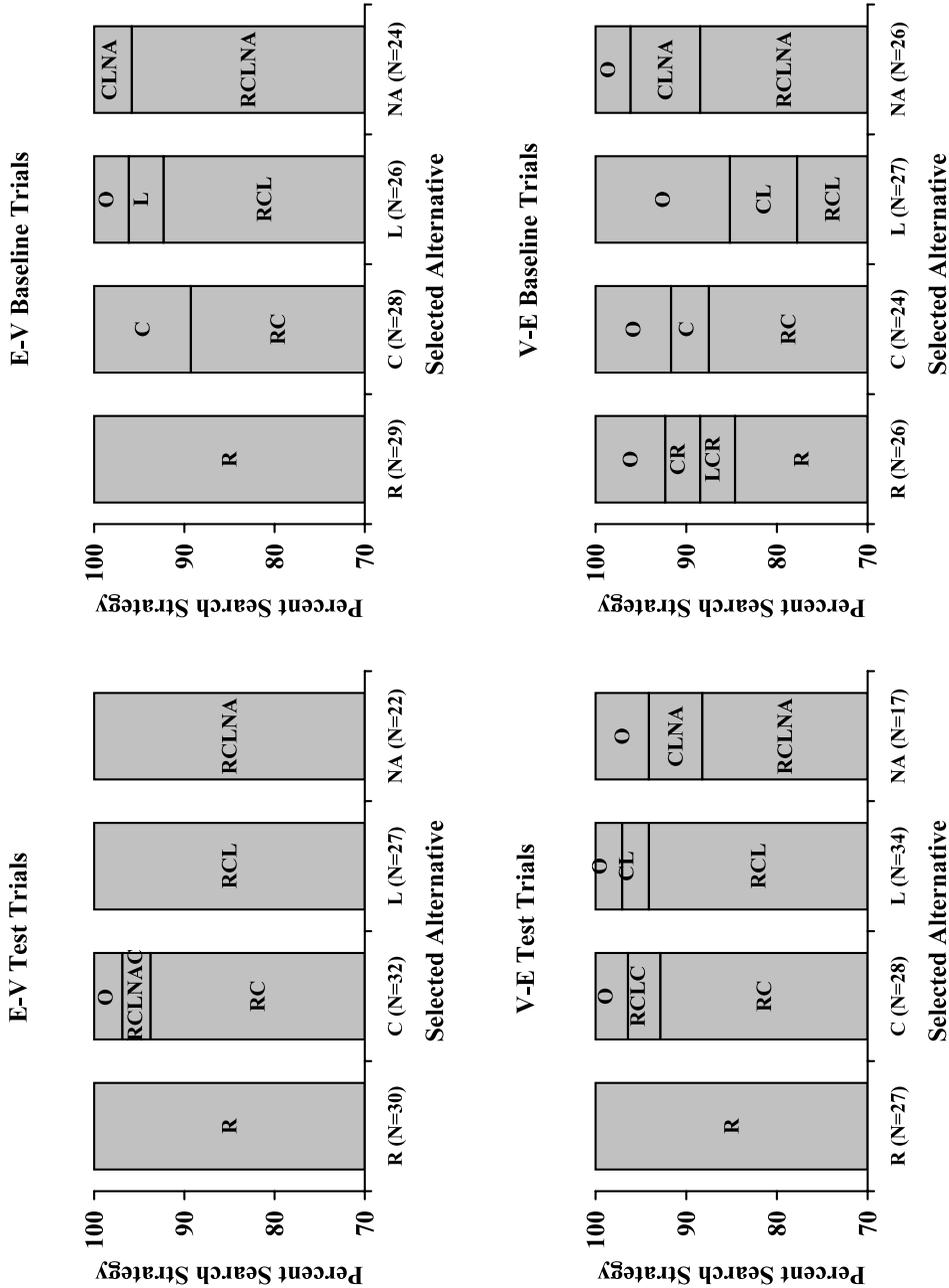
Fig. 6. The percentage of times the dolphin used particular search strategies (as determined by independent raters viewing video records) in echoic-visual and visual-echoic matching tasks with baseline and test trials when it responded to either the right, center, or left object or the NA paddle. Search strategy is read from left to right where R, inspection of right object; C, inspection of center object; L, inspection of left object; and NA, press of NA paddle. 'O' signifies a trial for which there was no agreement among raters of dolphin's search pattern.
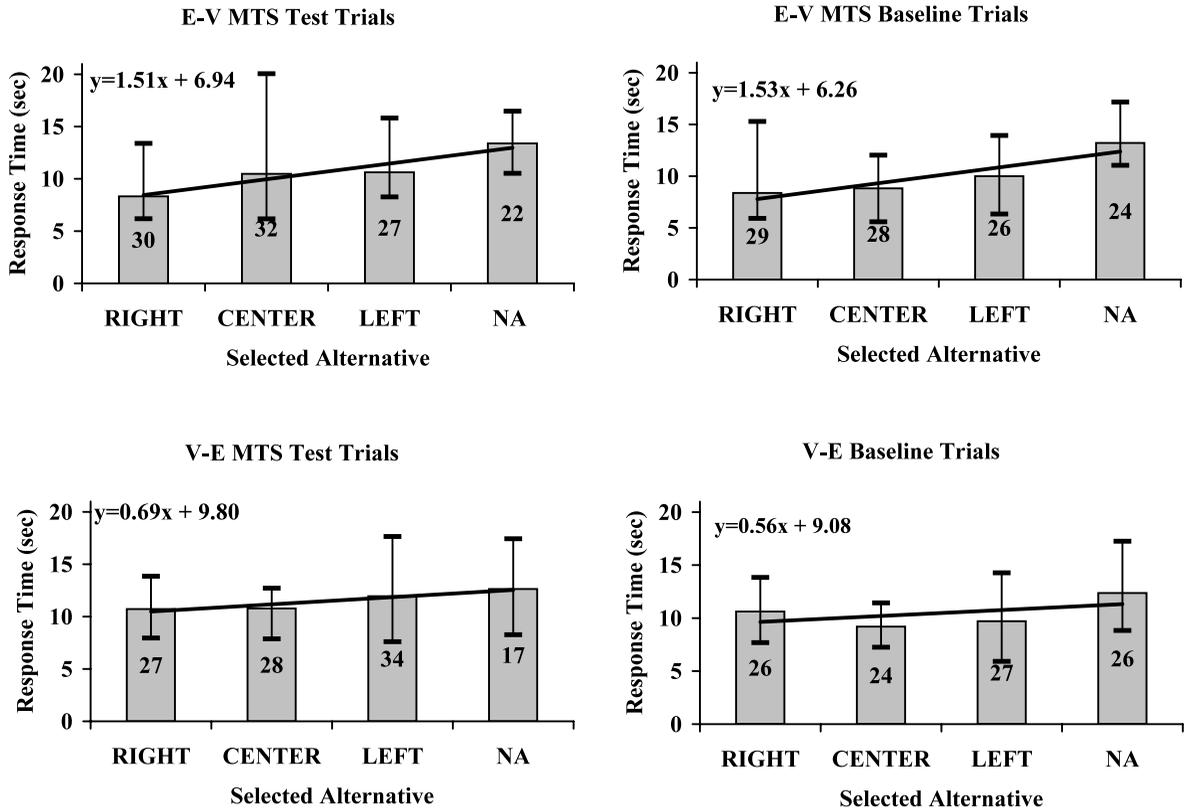
E-V MTS Test Trials

$y=1.51x + 6.94$

RIGHT 30 CENTER 32 LEFT 27 NA 22

Response Time (sec) — Selected Alternative

E-V MTS Baseline Trials

$y=1.53x + 6.26$

RIGHT 29 CENTER 28 LEFT 26 NA 24

Response Time (sec) — Selected Alternative

V-E MTS Test Trials

$y=0.69x + 9.80$

RIGHT 27 CENTER 28 LEFT 34 NA 17

Response Time (sec) — Selected Alternative

V-E Baseline Trials

$y=0.56x + 9.08$

RIGHT 26 CENTER 24 LEFT 27 NA 26

Response Time (sec) — Selected Alternative

Fig. 7. The dolphin's response times in E–V and V–E MTS for baseline and test trials as measured from the time of the presentation of the alternative objects until the dolphin's response to a particular position (R, C, L, or NA). Each bar represents mean response times for a particular alternative selected by the dolphin. Range data is shown within each bar, as is the number of trials that a particular alternative was selected. The linear regression line and the regression equation based on all the response data are shown for each set (test and baseline trials) and each task (E–V and V–E MTS). All regression lines showed a positive gradient ($P \leq 0.0014$).

objects and baseline objects, in both E–V and V–E MTS. As in Fig. 4, the nomenclature used to describe the particular search strategy is shown within each bar and reads from left to right. The letter 'O' indicates that there was no agreement between the three raters and therefore the search behavior was deemed ambiguous. As in Experiment 1, Elele most often performed a serial non-exhaustive search among the alternatives, starting from the right-positioned object and working her way left until either a match was found, in which case she ceased searching, or no-match was found, resulting in a press of the NA paddle. There were some exceptions, most notably in V–E MTS with the baseline objects. Here, she sometimes appeared able to make her echolocation decisions from

slightly less than the midway point in the pool, making it difficult for the rater to judge the dolphin's rostrum orientation. Additionally, with the baseline objects she sometimes appeared either to examine the contents of the center box before the contents of the right box, or on her way to the right box, cocked her head toward the center box and then back to the right box. Nevertheless, on majority of V–E trials with the baseline objects (84.5%), she appeared to follow the serial non-exhaustive search strategy. Furthermore over all tasks vacillation between alternatives was relatively rare.

An analysis of Elele's response times largely confirmed her serial search strategy. A total of 427 trials were used to measure response times. A comparison of the raters response time measure-

ments for each trial revealed significant inter-rater reliability ($r = 0.973$, $P < 0.0001$). We therefore used the mean of the rater's response time measurements for each trial. If Elele performed a right-to-left serial non-exhaustive search (as indicated by the qualitative judgements, Fig. 6), we would expect her response time to be shortest when responding to the right-positioned object and longest to the NA paddle. Fig. 7 shows Elele's response times as a function of the alternative selected (R, C, L, and NA) for both PVC test and baseline trials in E–V and V–E MTS. There was a significant positive slope for each plot ($P \leq 0.0014$) from R to NA, providing support for the serial non-exhaustive search strategy commencing with the alternative at the right.

Elele's search strategy on NA paddle trials helped to clarify the nature of her representation of the sample. Recall that Elele committed 15 false alarms on NA paddle trials. These errors were not evenly distributed between the three-alternative positions containing a non-match. Elele committed eight false alarms to the non-match positioned left, six false alarms to the non-match positioned center, but only one false alarm to the non-match positioned right. Indeed a greater number of false alarms occurred to the non-match in the left position ($n = 8$) than to the non-match in the right position ($n = 1$), the first alternative object examined during the Elele's search ($N = 120$, $P = 0.032$, Fishers' exact test). Given that every sample/non-match permutation of the six PVC transfer objects was represented in each position, Elele's correct rejection of right-positioned non-matches on 59 of 60 trials (29 in V–E and 30 in E–V) provides substantial evidence that her representation was not of a local feature or features, but rather of the overall global shape of the sample. That is, she did not simply select the non-match at the right even though it contained overlapping local features with the sample and no exact match was present among the alternatives.

5. General discussion

The findings from the current studies support our earlier contentions (Pack and Herman, 1995;

Herman et al., 1998) that dolphins can form a percept or internal representation of the spatial structure of an ensonified object. The major distinguishing features of our current approach were: (a) the use of a cross-modal matching-to-sample procedure that required the matching of objects across the senses of echolocation and vision in both directions, echolocation to vision (E–V) and vision to echolocation (V–E); (b) the use, in transfer tests, of multiple objects of complex, abstract shapes, all constructed of the same PVC materials and all having almost the same degree of reflective surface and the same peripheral extents; (c) the requirement (in Experiment 1) that the dolphin select a match for the sample object from among three-alternative objects with overlapping features with the sample; and (d) the use (in Experiment 2) of a unique fourth alternative that allowed the dolphin to indicate that none of the three offered alternative objects matched the sample object. Items *a* and *b* also characterized portions of our earlier studies, which had used a two-alternative matching-to-sample procedure (Pack and Herman, 1995; Herman et al., 1998). Items *c* and *d* were unique to the current studies. Item *a* insured that raw acoustic cues could not be invoked as an explanation of object matching performance (Popper et al., 1997; cf. Au, 1993), as there are no inherent physical correlates between acoustic and visual cues. Further, inasmuch as objects were never exposed to the dolphin's echolocation and visual senses contemporaneously, and if successful matching occurred significantly often on the first trial with new objects (as occurred in the studies reported by Herman et al., 1998), associative learning could be ruled out as an explanation for the dolphin's performance. Item *b* helped to insure that the only reliable difference among objects was shape. Further, the abstract and complex shapes of the objects used meant that generalization from previously encountered familiar shapes was quite unlikely. Items *c* and *d* allowed us to examine the dolphin's search strategy among alternatives and to determine whether that search was for some local feature or features or for the overall (global) shape of the object. A search with little vacillation among alternatives having many overlapping fea-

tures, coupled with a high level of matching accuracy and correct rejection of all alternatives if no match were present, would argue strongly against a feature-based interpretation of the dolphin's search strategy and for an interpretation based on representing the sample object by its global shape.

The results of Experiments 1 and 2, including search strategy and matching accuracy, clearly supported the latter hypothesis. In the three-alternative condition, the dolphin's search strategy was best characterized as serial and non-exhaustive. For both E–V and V–E MTS, the dolphin typically began its search with the right-most alternative, then the center, and finally the left, stopping immediately when a match was found. Exceptions to this pattern were relatively rare, as was retracing of the search path in reverse order, or traveling back and forth between alternatives (vacillation), as might be expected in a search for local features that were present in more than one alternative. The right-to-left search strategy was most clearly seen during Elele's inspection of the visual alternatives (E–V matching), because she approached the alternatives closely, sometimes looking at them through the water–air interface as she swam by, and sometimes raising her head above the surface (bottlenosed dolphins have good visual resolution acuity both underwater and in air—Herman et al., 1975). The right to left search strategy was still apparent during Elele's search among echolocation alternatives (V–E matching), though more difficult to classify on some trials because objects were sometimes inspected from 1 to 3 m distance.

Clearly, in the three-alternative condition, and given the dolphin's search strategy, not all alternatives need be inspected for the dolphin to make a decision. This was not the case in the four-alternative condition when no matching object was present. In that instance, the dolphin most often continued its search path, right, center, left, NA paddle, in that order, despite the presence of many local features among the alternatives that overlapped those of the sample object. When false alarms occurred (on 15 of 60 match-absent trials) they most often were in choosing a non-match in either the center ($n = 6$) or left position ($n = 8$). A false alarm occurred to the non-match at the right position only once. What factors might explain this

pattern of false alarms? Consider the dolphin's task when a match is absent, in light of her typical search strategy: examine the right-hand alternative first, then the center, and finally the left. During that process, two conditions affecting memory for the sample can occur. The first is, hypothetically, a time-dependent weakening of the integrity of the representation of the sample object as the dolphin proceeds along her search path. The second is retroactive interference, arising from the successive inspection of each alternative. Theoretically, then, we would expect false alarms to be rare to the right-hand alternative, and to increase for the center and left-hand alternatives, which is precisely what occurred. It is significant that missed detections, pressing the NA paddle when a match was in fact present, were extremely rare, occurring on only four of 180 trials, suggesting that the dolphin's decision criterion was set low to favor detections.

Elele's matching performance also gave strong support to the hypothesis that the sample object was represented in memory by its global shape. The three-alternative procedure of Experiment 1 demonstrated that the dolphin was able to select the matching alternative with high reliability even though there were many overlapping features among alternatives and between the alternative objects and the sample object. During the PVC transfer tests, Elele chose the matching alternative on 94% of V–E trials and on 98% of E–V trials. Elele had never experienced many of the combinations of alternatives previously, yet her performance remained at a high level and included numerous successes on the first occasion that a particular combination appeared.

These results were strongly reinforced by findings from the four-alternative procedure. Here, for the first time, the dolphin was able to reject all alternatives (by pressing the NA paddle) despite the presence of local features among the alternatives that were also present in the sample object. When Elele was presented with a trial in which no alternative exactly matched the sample, she did not simply choose the 'best fit' match. Nor did she vacillate between alternatives. Instead, she most often examined each non-matching alternative once and then pressed the NA paddle. When a match was present among the alternatives during

the PVC transfer tests, Elele chose it on 94% of V–E trials and on 95% of E–V trials, results very similar to those of Experiment 1. When a match was absent, and a press of the NA paddle was therefore required, performance declined to 74% and 76%, respectively, in V–E and E–V. We noted earlier that the decline was possibly associ-ated with uncertainty of the memory for the sample.

There are several possibilities for how an echoically inspected object may be represented by the dolphin. At a complex level, the representation may contain information about the spatial arrange-ment of object features relative to each other, which in essence preserves the shape of the object (see Biederman, 1987 for a model of visual object recognition that contains similar properties). How-ever, simpler levels are possible theoretically, one of the most elementary being the representation of one or more perceived features (we have focused on 'class features' here). The findings of the present study indicate that echoically inspected objects are not represented simply as one or more features. Elele's lack of vacillation among alternatives sharing class features with the sample, combined with her high levels of accuracy in reporting the presence or absence of a match from among three-alternatives, provide substantial inferential evidence that her representation of the sample object was of its global shape. A theory of feature representation would predict that the dolphin se-lects the first alternative object along its search path that contains the key feature or features. This would be the right-most object, given the dolphin's typical search path, and the abundance of overlapping features among the alternatives and the sample object. However, when a match was present, errors were rare overall, and were no more frequent to the right-most object than to the objects in the remain-ing positions. When a match was absent, errors were least frequent to the right-most object.

Another possibility is that the dolphin represents a sample object as an unorganized list of features that it matches against the features of an alternative. When a discrepancy is found, the alternative is rejected. If all features in the list match the sample, the alternative is selected. We have limited evidence arguing against this theory from pairings of Objects 3 and 5 (Fig. 3). Each of these objects contained the same four class features. Nevertheless, the objects were never confused. This suggests that the location of features and their spatial relationship relative to each other may be preserved in the dolphin's representation of echoically perceived objects.

Further evidence supporting this theory comes from our earlier findings of spontaneous cross-modal recognition between televised miniaturized images of PVC objects presented as samples to the dolphin's visual sense and 'live' alternatives unal-tered in size presented to the echolocation sense (Pack and Herman, 1995). Four pairs of PVC objects had overlapping features and had never been exposed previously in the television condition. The televised images of the samples were 40–49% smaller than the live objects making the actual lengths and widths of PVC components different between sample image and matching alternative object, although the relationship between the struc-tural features of the objects remained unaltered. Nevertheless, Elele spontaneously matched the tele-vised sample to the correct echoically perceived alternative on first trials without error across four PVC pairs, including one with which she had no previous cross-modal experience.

If, as suggested, the dolphin represents the struc-tural relationship between features in an echoically inspected object, an obvious question is what mechanisms might allow for this representation. The question is similar in some respects to the dilemma of how in vision a three-dimensional object is recognized from a two-dimensional retinal array of photon activated cells that varies over differences in viewpoint, object size, and illumination (Marr and Nishihara, 1978). In the case of the echolocating dolphin, a shape percept must be constructed from returning echoes that may vary significantly with angle of ensonification and changes in object size, orientation, and material composition. Herman et al. (1998) hypothesized that echoic shape perception is a result of specialized peripheral and central processing, arranged hierarchically and resulting ultimately in a representation of the contours of an object. Theoretically, the dolphin can take advan-tage of both spatial and temporal information in the echoes returning from an ensonified object to create a spatial-temporal representation that is then inter-

preted by central auditory mechanisms as a three-dimensional shape.

Pack and Herman (1995) and Herman et al. (1998) suggested that fine range-difference resolution and cross-range (angular) resolution capabilities might be important auditory processes contributing to shape perception. Range-difference resolution is a function of the ability to perceive temporal differences in echo arrivals. Echoes reflecting from different points along an object will arrive at slightly different times resulting in a temporal array that represents the array of different range values along that object (cf. Simmons, 1989). Range-difference resolution capabilities as small as 0.9 cm at a range of 1 m were reported in a dolphin subject by Murchison (1980) who trained the dolphin to respond to the closer of two identical foam spheres separated in azimuth by 40°[1]. To achieve this level of resolution, it is theoretically necessary for the dolphin to detect echo-delay differences of approximately 12 μs, applying the same model as Simmons (1989). This value is in close agreement with the time resolution constants of 12 to 15 μs for *Tursiops* reported by Au (1993) (Table 10.1), which translate to resolvable ranges of 1.0 to 1.1 cm between point targets. Murchison's results are also consistent with those of Au (1993) who showed that a dolphin could perceive time differences between echo highlights as small as 500 ns, a value that translates to a resolvable distance of 0.76 cm.

Cross-range (angular) resolution has recently been obtained for the bottlenosed dolphin. Branstetter (2001) reported a horizontal angular difference threshold of 1.6° by an echolocating dolphin. The echolocating dolphin was required to discriminate horizontal angular differences between two arrays of vertically oriented PVC pipes, in a procedure similar to that used with echolocating bats (Simmons et al., 1983). Branstetter's results agree well with those from passive sound localization experiments conducted by Renaud and Popper (1975) who found a minimum audible angle threshold of approximately 0.9° for clicks sounds

and 2.1° for pure tones. Clearly, the dolphin's range-difference resolution and cross-range resolution capabilities are fine enough to provide significant temporal and spatial information for the direct perception of the types of relatively large complex shapes used in our cross-modal studies.

Movement by the dolphin during object ensonification may also enhance shape perception (Azzali et al., 1995; Pack and Herman, 1995; Herman et al., 1998). During our cross-modal tasks, the dolphin is free to echolocate at any time as it approaches the anechoic box containing an object. Echolocation from different aspects relative to the front panel of the box provides some degree of different viewpoints of the object suspended within the box.

The central neuronal processes involved in cross-modal recognition by the dolphin remain speculative. However, there are several intriguing possibilities. Herman et al. (1998) referred to multisensory neurons (see Stein and Meredith, 1990, 1993) that respond to both visual and auditory stimuli as a possible mechanism for integrating visual and auditory input. For example, Maunsell et al. (1989) found that neurons at level V4 of the visual cortex of the monkey that are tuned to a particular line orientation respond regardless of whether the line orientation is examined visually or haptically. Although some evoked potential studies have reported on the principal sensory projection zones in the dolphin's cerebral cortex (e.g. see Ridgway, 1986), none of these studies have searched for the presence of multisensory neurons that respond to both visual and acoustic input. Supin et al. (1978) noted, however, an unusual organization of the dolphin brain in that auditory and visual cortex lie immediately adjacent to each other. This proximity may promote auditory-visual integration.

Knudsen and Konishi (1978) demonstrated that nerve cells in the midbrain auditory nucleus of the barn owl (*Tyto alba*) had spatial receptive fields that were topographically organized. Adjacent sound sources in auditory space trigger corresponding adjacent areas in the midbrain, thus creating a physiological map of auditory space. In addition, Knudsen (1982) discovered spatiotopic neurons in the tectum of the owl that responded to both visual and auditory stimuli. The spa-

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[1] Au (1993) (p. 206) considered the study by Murchison (1980) to be better characterized as a range difference discrimination experiment rather than a range resolution experiment, because 'true' range resolution involves resolving targets at different distances along the same line of acoustic propagation.

tiotopic map responded to either light or sound in specific locations in space and had the same receptive fields, thus suggesting that areas of the tectum may provide an amodal representation of space. There appear to be no studies that have examined comparable spatial mapping in the dolphin brain, but it is clear that such amodal mapping could benefit cross-modal matching.

In summary, our studies have revealed that the dolphin is a sophisticated perceiver of object shape. Our previous work (e.g. Pack and Herman, 1995; Herman et al., 1998) provided compelling evidence for direct perception of shape through vision, through echolocation, and across these senses. The findings of the current study extend our understanding of *what* aspects of object shape are perceived, represented, and transferred across the senses of echolocation and vision. These findings indicated that the dolphin's representation of the sample object was highly faithful to the overall spatial structure of the object inspected, and not easily confused with alternative objects sharing features with the sample. Consequently, it appears that objects were represented globally (holistically) by the dolphin whether perceived through vision or through echolocation. Similarly, visual object perception research with humans, chimpanzees, and pigeons has in many cases also found reliance on global appearance rather than on local features (e.g. Navon, 1977; Tomonaga and Matsuzawa, 1992; Wasserman et al., 1993; Kirkpatrick-Steger et al., 1998; Fagot and Tomonaga, 1999; cf. Cavoto and Cook, 2001). The current finding that E–V and V–E performances closely mirrored each other is consistent with our earlier results (Pack and Herman, 1995; Herman et al., 1998) and supports the theory that echolocation and vision are functionally equivalent in their representation of object shape. Finally, perceptual mechanisms, in particular temporal acuity and azimuthal acuity, are available to the dolphin that appear to have sufficient resolution for representing faithfully the spatial/temporal array of returning echoes, which in turn preserves the global shape of the ensonified object.

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