Sensory integration in the bottlenosed dolphin: Immediate recognition of complex shapes across the senses of echolocation and vision

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In matching-to-sample tests, a bottlenosed dolphin (*Tursiops truncatus*) was found capable of immediately recognizing a variety of complexly shaped objects both within the senses of vision or echolocation and, also, across these two senses. The immediacy of recognition indicated that shape information registers directly in the dolphin's perception of objects through either vision or echolocation, and that these percepts are readily shared or integrated across the senses. Accuracy of intersensory recognition was nearly errorless regardless of whether the sample objects were presented to the echolocation sense and the alternatives to the visual sense (E–V matching) or the reverse, with samples presented to the visual sense and alternatives to the echolocation sense (V–E matching). Furthermore, during V–E matching, the dolphin was equally facile at recognition whether the sample objects exposed to vision were "live," presented in air in the real world, or were images displayed on a television screen placed behind an underwater window. Overall, the results suggested that what a dolphin "sees" through echolocation is functionally similar to what it sees through vision. © *1995 Acoustical Society of America.*

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INTRODUCTION

Studies of shape discrimination by bottlenosed dolphins (*Tursiops truncatus*) through echolocation have been restricted principally to a few simple geometric forms: cylinders versus cubes (Nachtigall *et al.*, 1980), cylinders versus spheres (Au *et al.*, 1980), and flat circles versus either flat triangles or squares (Barta, 1969, cited in Nachtigall, 1980). In each case, the objects were constructed of the same materials, and size differences were controlled. The dolphin subjects successfully discriminated between these shapes. Among other things, the investigators examined how different echo characteristics such as amplitude, waveform, or frequency spectra may have contributed to the discriminations. Au (1993, p. 259) pointed to the likely cues for shape discrimination by dolphins (and bats) as "variation in echo intensity as the animal scans across a target, and fluctuations in echo intensity as a target is ensonified from different aspects." However, that only a few shapes were used in the cited studies limited any generalizations about the extent of echoic shape discrimination attainable by dolphins. Also, the procedures of these studies did not allow for a determination of whether shape was a feature directly perceived by the echolocating dolphin, or whether the discriminations were based primarily on the noted acoustic differences, which then served as cues for learning a differential response to the different sounds received. To understand capabilities for shape recognition better, it is necessary, at least, to (1) test many different shapes, while insuring that shape is the only feature on which discrimination can be based, and (2) examine the immediacy with which discriminations are attained. The immediate correct discrimination or classification of shape supports the view that shape is a feature apprehended directly through the echoic perceptual system. Nonetheless, even should discrimination be immediate, an element of uncertainty remains in that two different shapes may be discriminated, once again, not because echolocation directly yields a shape percept but because the echoes returned from the differently shaped objects sound different to the dolphin. These heard differences, and not a sense of the shape of the object, may then reliably guide the dolphin's discrimination responses.

Compelling evidence for the formation of shape percepts through echolocation would come, however, from a demonstration of immediate *cross-modal* recognition, specifically the immediate recognition through vision of an object initially inspected through echolocation, as well as the reverse, the immediate recognition through echolocation of an object initially inspected through vision. In these instances, immediate recognition must be based on the construction of shape percepts common to or coordinated between the senses of echolocation and vision because there is no opportunity for associative learning. Anything less than immediacy is subject to interpretations based on associative learning, in which coordination between the senses develops as the dolphin is exposed over time or training trials to the spatial and temporal contiguities between echoes received and things seen.

A procedure which lends itself well to the exploration of capabilities for intramodal or cross-modal shape perception is the matching-to-sample (MTS) task, or a variant, the "same/different" task. In the MTS task, the subject is shown a "sample" figure or object, and is then required to select an identical figure or object from among two or more subsequently presented alternatives. In the same/different task the dolphin must classify a single test figure or object (usually

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termed the "probe") as the same as or different from a previously presented sample figure or object. Both tasks allow for a meaningful examination of performance on the very first trials on which the dolphin is exposed to new stimuli. In the cross-modal test, if the dolphin's performance on the initial unique trials of new discrimination problems is significantly above chance, for a variety of new problems, then an interpretation of direct shape perception is strongly supported.

A few echoic MTS or same/different studies have been reported with dolphins (Nachtigall and Patterson, 1981; Roitblat *et al.*, 1990). However, these studies used objects which differed in multiple dimensions (e.g., material, size, shape), and thus could not meaningfully address questions of shape recognition. Furthermore, immediacy of echoic recognition in these studies was either not reported in sufficient detail for any evaluation (Nachtigall and Patterson, 1981) or not reported at all (Roitblat *et al.*, 1990).

Bottlenosed dolphins have good visual resolution acuities in air or underwater (Dral, 1972; Herman *et al.*, 1975), and MTS and same–different procedures have been used successfully in the study of visual recognition of shapes by dolphins (Herman, 1990; Herman *et al.*, 1989, 1994; Hunter, 1988; Reeve *et al.*, 1991; Shaw, 1990). These studies have found that dolphins are capable of visually recognizing a wide variety of arbitrarily shaped two-dimensional figures and three-dimensional objects. Many of the figures and objects used in these various visual studies were new to the dolphin's experience, yet were immediately matched or correctly classified on the first unique test trials. Although in some of these studies (e.g., Herman *et al.*, 1989) objects differed in several dimensions in addition to shape (e.g., size and/or brightness), in other studies (Hunter, 1988; Shaw, 1990), shape was the only controlling variable. The immediacy with which recognition occurred in these latter studies (discriminations occurred on the first unique trials of many new pairings of shapes) suggested that shape or form is a fundamental stimulus feature preserved by the visual perceptual system of the dolphin.

If it can be shown that the construction of detailed shape percepts does characterize the dolphin echolocation perceptual system, it would provide a close link with the demonstrated capabilities of dolphins for visual recognition. It would also provide a link with capabilities for echoic shape recognition found for various species of bats (Simmons, 1989; Simmons and Grinnell, 1988).

In theory, the correspondence between the percepts developed across the senses can range from functional integration to virtual independence. Studies of human recognition of objects across the senses of vision and active touch (the haptic sense) have revealed immediate recognition, supporting an integration view (Bryant *et al.*, 1972; Bushnell and Weinberger, 1987; Gibson and Walker, 1984; Jones, 1981; Meltzoff and Borton, 1979; Rose and Ruff, 1987; Ruff and Kohler, 1978). These results suggest that certain fundamental features of objects, like size or form, "may register directly in perception regardless of the modality of presentation" (Marks, 1978). In humans, the existence of multisensory neurons and multisensory convergence areas may provide mechanisms for sensory integration (Stein and Meredith, 1993).

Immediate cross-modal recognition of objects through vision and active touch has also been found in several species of great apes and monkeys (Davenport and Rogers, 1970; Davenport *et al.*, 1975; Savage-Rumbaugh *et al.*, 1988; Tolan *et al.*, 1981), providing unequivocal support for sensory integration as a fundamental characteristic of the visual and haptic perceptual systems of these species, and encouraging the study of sensory integration in other species.

In the current studies, we examined the ability of a dolphin to recognize a wide variety of arbitrarily shaped objects through echolocation alone, through vision alone and, importantly, *across* these two senses, using MTS tests and objects in which shape was the only controlling variable. Questions addressed in these studies included: (i) To what extent does dolphin echolocation preserve the multidimensional spatial features of objects, i.e., their unique shapes; (ii) how does shape recognition through echolocation compare with shape recognition through vision, for the same objects; (iii) is shape recognition through echolocation immediate, indicating that perception of shape is a basic property of this system as well as the visual system; (iv) can a dolphin recognize objects "cross-modally," across the senses of echolocation and vision and, if so, can cross-modal recognition be immediate; and (v) are the spatial percepts developed through echolocation functionally similar to those obtained through vision?

I. GENERAL METHOD

We first examined the ability of a dolphin to recognize objects separately *within* the senses of echolocation and vision, before testing for cross-modal recognition. It is apparent that if a particular object is not easily recognized within each of these senses, then cross-modal recognition cannot be effective either (Bryant, 1968; Rose and Orlian, 1991; Pack, 1994). Therefore, only those objects shown to be easily recognized within vision alone and within echolocation alone were further tested for cross-modal recognition.

A. Subject

The subject was an 8-yr-old subadult female bottlenosed dolphin named Elele. Elele was also the subject in an earlier, preliminary study of cross-modal recognition through echolocation and vision in which some of the procedures used in the current studies were first developed (Herman and Pack, 1992; Pack, 1994). For the current studies, Elele was tested once daily over a 5-day work week in her circular, concrete seawater tank (diameter 15.2 m and depth 1.8 m) at the Kewalo Basin Marine Mammal Laboratory in Honolulu, Hawaii. The walls of the tank rose 1.22 m above the surrounding deck. Elele was fed 9.1 kg of smelt and herring daily. She received a portion of this ration during test sessions.

B. General procedure

Both within- and cross-modal recognition were tested using an MTS task. Objects were organized into pairs and at each MTS trial one of the two pair members was used as the "sample" object and exposed to either the dolphin's visual or echolocation sense alone. After the dolphin had inspected the sample object, both pair members were presented, one to each side of the sample object (duplicates of every object were available). For within-modal matching, the alternatives were presented to the same sense as was the sample, and for cross-modal matching they were presented to the other sense. In either case, the dolphin was rewarded for choosing the alternative which physically matched the sample object. The pair member serving as sample varied randomly across trials with the constraint that over the total number of trials given within a testing session, each pair member serve as sample equally often.

C. Limiting exposure of objects to one sense only

Objects to be exposed only to the dolphin's echolocation sense were presented inside of customized "anechoic" boxes suspended from the wall of the tank and allowed to fill with seawater through the partially open bottom. Figure 1 (top) shows the configuration of the box in which the sample was displayed, and Fig. 1 (bottom) shows the configuration of one of the two boxes used to display the two alternative objects. Each of the latter boxes was fitted with an underwater response paddle and a visual shield around the upper portions of the box. The shield prevented the dolphin from viewing activities occurring behind the box. The response paddle was attached to a length of PVC pipe extending vertically approximately 82 cm into the air and terminating in a bright red oval foam float. When the response paddle was deflected by the dolphin, an easily observable large movement of the red float occurred. The black Plexiglas panel at the front of all boxes was visually opaque but transmitted waterborne sound well.[1] In a preliminary test, we confirmed that a dolphin could use echolocation alone to choose an air-filled container over an identical water-filled container, with both containers presented underwater behind a sheet of opaque Plexiglas identical to the one used in the current study. The redwood slats on the sides and back of all boxes tended to absorb sound (see Johnson, 1967), and were arranged at an angle approximately 30° from the vertical plane to disperse any echoes from sounds not absorbed. An object suspended inside of the box thus became salient echoically, but was not available to the visual sense.

Each member of a tested pair of objects appearing inside a box was always suspended from the same number of strands of monofilament 60-lb (27.3-kg) plastic test line attached to a wooden bar. The bar was placed across two horizontal PVC tubes fixed inside the box above the water surface and above the Plexiglas shield. The orientation of the object suspended inside the box always remained the same across trials.

Objects to be presented only to the visual sense were exposed in air. When viewing these objects the dolphin typically assumed a near-vertical posture, positioning its eyes above water such that it regarded an object from the rostral/ventral plane, possibly binocularly. This position is favorable for in-air viewing (Dral, 1972; Herman *et al.*, 1975), but unfavorable for echolocation, since the transmitting beam of the echolocation signal of *T. truncatus* emanates from the region of the melon and is directed forward and slightly upwards by 5° with respect to the tip of the rostrum (Au *et al.*, 1986). Hence the direction of the beam is away from the object being inspected visually when the dolphin is in the indicated viewing position. The physics of sound transmission also argues against the usefulness of dolphin echolocation in air. The large density differences of the air medium and the lipid substances of the melon[2] yield a gross imped-

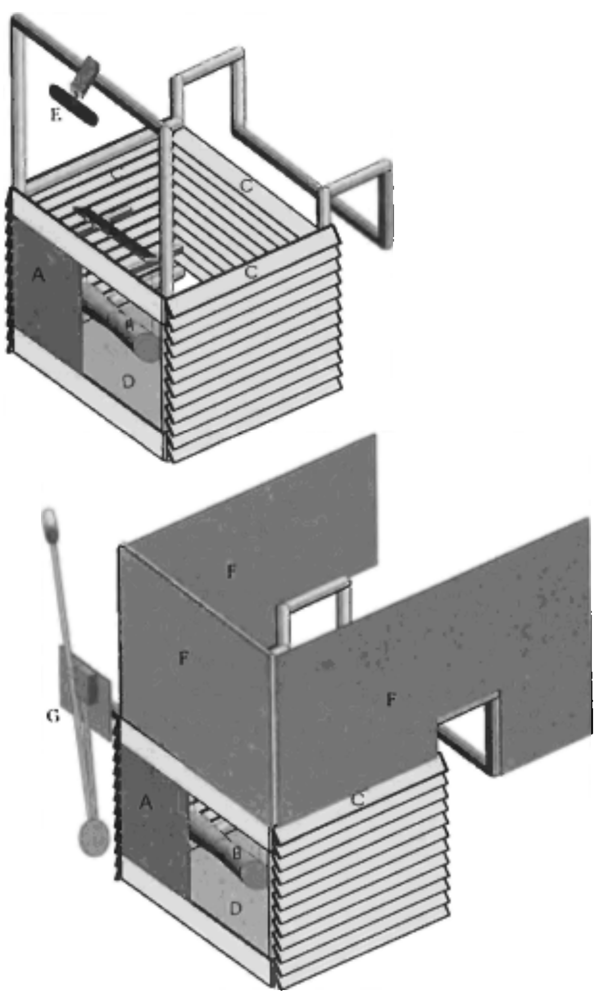

FIG. 1. Schematic representation (not to scale) of the anechoic box used for displaying sample objects (top), and one of two anechoic boxes used for displaying an alternative object (bottom). Each box was 1.1 m wide by 0.6 m deep by 1.0 m high and was suspended into the dolphin's tank from the tank wall. The bottom of the box extended approximately 0.8 m below the water surface. Each box was framed with 6.4-cm-diameter PVC tubing which extended above the front of the box 0.8 m on each side and was joined at the top. An object to be inspected through echolocation (B) was immersed underwater inside the box, which was open at the top. The sides and rear of the box were constructed of lengths of 11.4-cm-wide redwood slats (C), and the bottom was covered by an opaque polyvinyl chloride (PVC) sheet (D), except for a small opening through which seawater could enter. The front of the box was covered by a sheet of black Plexiglas (acrylic polymer resin), 1 m wide by 0.6 m high by 0.32 cm thick (A). Additionally, a mirror (E) is attached to the sample-object box, and wooden blinders (F) and a response paddle (G) are attached to the alternative-object box. The two alternative-object boxes differed only in the location of the response paddle, to the left side of the box (for the alternative-object box positioned to the left of the sample box, from the dolphin's perspective), or to the right side of the sample box (for the alternative-object box positioned to the right of the sample box). See text for additional details.

ance mismatch and suggest that any emitted signals would be highly attenuated (Au, 1993; Norris and Harvey, 1974).

As a further definitive control against any imputation that echolocation in air might be providing useful information to the dolphin, an additional test is reported using television as the medium for displaying sample objects to the visual sense.

D. Construction and selection of objects

Cross-modal recognition through vision and through echolocation was tested for the 16 pairs of objects shown in Fig. 2. All pairs were constructed from schedule 40 and/or schedule 80 0.5- (1.27 cm), 0.75- (1.91 cm), 1.0- (2.54 cm), or 1.5-in. (3.81 cm), gray PVC pipe and fittings. The pipes and fittings were filled with dry sand to displace the air and to weight the objects so that they were negatively buoyant. The sand also may have reduced any idiosyncratic resonating characteristics of the pipes during echolocation, and thereby may have promoted an emphasis on surface features. Within each of the first 15 pairs, the combination of PVC sizes used was the same across the two objects. Also, the two objects of a pair were equated to within 4% for their three-dimensional frontal surface area (i.e., the hemispheric surfaces of the pipes and fittings comprising an object that were potentially exposed to echolocation signals arriving through the Plexiglas panel, taking account of the standard positioning of the object inside an anechoic box). The only exceptions were pair 1 (20%) and pair 4 (9%). The use of identical materials and the equating of surface areas within pairs were intended to encourage the dolphin's attention to differences in shape alone.

II. EXPERIMENTS

A. Experiment 1: Testing for within-modal object recognition

In tests for echoic matching-to-sample (E–E MTS), both the sample object and the two alternative objects were presented strictly to the echoic sense; for visual matching (V–V MTS) all objects were presented strictly to the visual sense.

Each of the 16 pairs of objects of Fig. 2 was tested in both E–E MTS and V–V MTS. For 8 of the 16 pairs, V–V MTS was tested first and for the remaining 8 pairs, E–E MTS was tested first. Each MTS test consisted of two daily sessions of 24 trials each. Twelve of the trials within a session presented the particular PVC "test" pair, and the remaining 12 presented mixed pairings of six other "baseline" objects of various composition and shape which were found to be highly discriminable in the earlier, preliminary study of Herman and Pack (1992).[3] Trials using a PVC test pair were embedded in random locations among trials using the baseline objects. Constraints on pure randomization included the following: no more than two test trials were given consecutively; no more than three matches occurred successively on the same side; the first two trials were always baseline trials; each half-session was composed of six baseline trials and six test trials; for each test pair, the initial four test trials given were the four unique combinations of the two samples and the two possibilities for placement of the matching alternative—either left or right of the sample object.

1. E–E recognition

To test abilities for E–E MTS, three anechoic boxes were used, arranged in a series along the tank wall at intervals of 3.1 m. The central box (Fig. 1, top) was used to display the sample object, and the two boxes to each side (Fig. 1, bottom) were used to display the alternative objects.

Between trials, the dolphin remained with a trainer at a remote station along the tank wall located approximately 12-m circumferential distance from the central box. While the trainer placed his or her hands over Elele's eyes, occluding the dolphin's view of the apparatus,[4] a sample object was suspended inside the central anechoic box and remained there throughout the trial. The sample object was placed either to the left or to the right of center of the box, approximately 5 cm in back of the Plexiglas panel. Placement to the left or right followed a preplanned, pseudorandom balanced schedule. To guard against the dolphin detecting any passive acoustic cues associated with a given object entering the water, the sample object was immersed in the box simultaneously with two other masking objects which were then removed promptly from the box. One masking object was always identical to the nonmatching object for that particular trial and the second mask was any one of the six baseline objects. Over the course of a 24-trial session each of the six baseline objects served as a second mask four times. When the sample object was in place and the masks removed, Elele's eyes were uncovered and she was signaled gesturally by her trainer to approach the central box. Once there, she was required to touch the front panel with her rostrum in a position corresponding to the left or right location of the sample, to indicate that she had located the sample object echoically. The trainer observed Elele's touch of the front panel through a rear-view mirror (Fig. 1, top, E) attached to the PVC frame above the front of the box and called for a continuation of the trial only if Elele correctly identified the left–right location of the sample. The angle of the mirror did not allow the dolphin to view any activities within or behind the box. The location response was normally rapid and over the course of the experiment Elele never failed to identify the location of the sample object correctly. When the location response was confirmed by a vocal response by the trainer, the two alternative objects were immediately immersed in the side boxes by assistants positioned at each side box. The side box within which each member of a pair was suspended on any particular trial was randomized across trials with the constraint that each side box contain the matching alternative 12 times during a 24-trial session and that a particular alternative not appear in the same side box for more than three successive trials. On each trial all assistants were "blind" to the side box containing the matching object. Likewise, the trainer had no knowledge of the side on which the correct match would appear. Neither the assistants nor the objects they were handling could be seen by Elele. As with the central box, two masking objects were immersed simultaneously with each alternative and then immediately withdrawn. Also, immersion in the left and right side boxes was simultaneous.

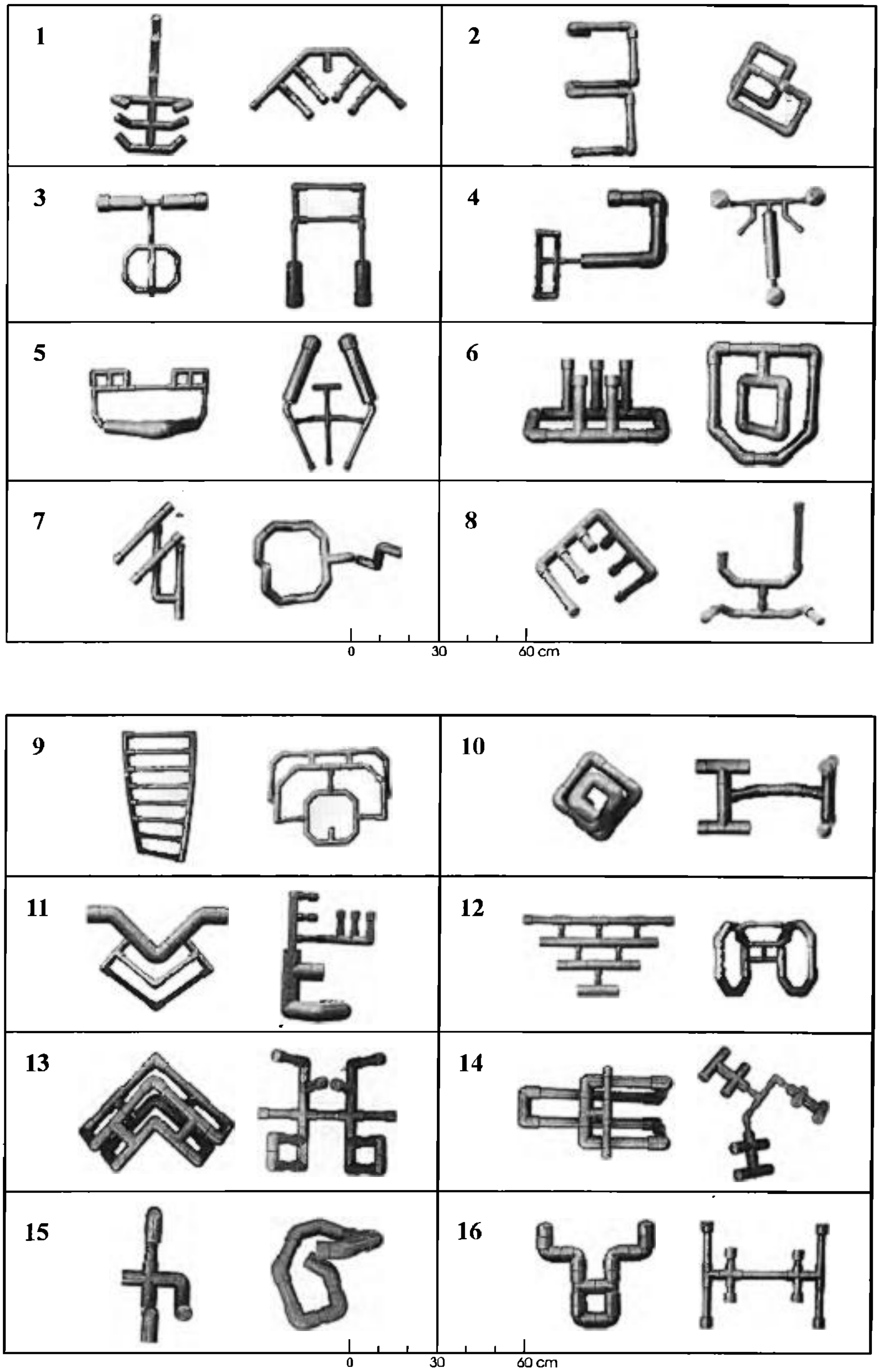

FIG. 2. Computer scans of photographs of the 16 pairs of PVC objects used in within-modal and cross-modal matching tests. All pairs are shown to the same scale.

For the side box containing the matching object, one of the masks was identical to the nonmatching object and the other mask was identical to the baseline object used as the second mask in the central box. For the side box containing the nonmatching object, one of the masks was identical to the matching object and the other mask was again identical to the baseline object used as the second mask in the central box. Thus the same three objects were submerged together initially in each of the alternative boxes. On hearing the splashing sound of the objects being immersed, Elele turned toward or approached the side boxes, inspected their contents echoically, and then pressed one or the other response paddle to indicate her choice. She was rewarded for pressing the response paddle on the anechoic box containing the matching alternative. A correct response was followed by a blast from the trainer's whistle, and then by fish reward and social interaction with the trainer. These were omitted after an incorrect response, in which case Elele simply returned to her station to await the next trial. A blind observer unaware of the identity of the sample object judged the dolphin's response by observing the movement of the red float and announcing which paddle (right or left) had been pressed by Elele.

2. *V–V recognition*

The sample object and the two alternative objects were all presented in air, strictly to the visual sense. No anechoic boxes were used. To begin a V–V trial, Elele was signaled to leave the remote station and position herself in front of an assistant standing on a 0.7-m-high platform just outside the tank wall. Only the approximate upper half of the assistant's body was visible above the tank wall. The location of the remote station was the same as in E–E matching, and the assistant was in the same location as was the central anechoic box during E–E matching. The assistant wore a white T-shirt. Also, opaque goggles were worn to guard against any knowledge by the assistant of the location of the matching object. The goggles also guarded against any eye gaze cues that might possibly direct the dolphin's responses. The white T-shirt provided a uniform, homogeneous background for objects held by the assistant.

When Elele was properly positioned, the assistant was directed by a supervisor located on an observation tower to present the sample object. The object was presented in a standard manner by the assistant, by bringing it forward from behind the tank wall where it could not be seen by the dolphin and then holding it with two hands with arms fully extended in front of his/her chest. The object thus extended over the tank wall with the bottom of the object approximately 30 cm above the water surface. The object remained exposed in that position throughout the trial.

Prior to Elele's approach to the sample object, the assistant was directed to extend his/her left hand out over the water surface and to raise the left index finger. In response, Elele was trained to position her body vertically with her ventral side toward the assistant, head out of the water with rostrum raised approximately 75°–90° above the horizontal plane and eyes facing forward. This is a common viewing position for dolphins inspecting objects elevated in air and is consistent with findings of an in-air emmetropic field of view in the nasal–ventral plane (Dral, 1972; Herman *et al.*. 1975). Once Elele assumed this position, the supervisor directed the assistant to present the sample object. After a 5-s exposure interval for the sample, the two alternative objects were presented in the same manner as was the sample by two assistants positioned on platforms 3.1 m to the right and left of the central assistant. These assistants also wore opaque goggles over their eyes, to guard against any knowledge of the sample object, and were dressed in white T-shirts identical to that of the assistant displaying the sample object. Elele selected one of the alternatives by leaving the central station and stationing herself for 3 s in front of one or the other alternative. She was rewarded for selecting the alternative object that matched the sample. An assistant located in a remote tower overlooking the dolphin tank judged Elele's response. The assistant held an opaque card in front of his/her gaze to block any view of the sample object, while allowing a view of the alternative objects. The assistant therefore was blind to the identity of the matching object. Reward was as described for E–E MTS.

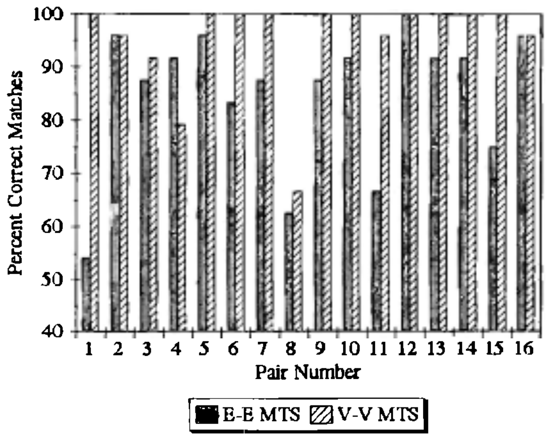

FIG. 3. Dolphin's performance accuracy in E–E and V–V MTS with the 16 pairs of novel objects of Fig. 2. Each bar represents 24 trials.

3. *Controls: Separating vision and echolocation information*

During the within-modal tests, no object was ever exposed to vision and echolocation simultaneously. Also, for each of the 16 pairs, tests of discriminability in one sensory modality were separated from tests in the other modality by a minimum of 5 days (range=5–18 days; mean=median =11 days). During the intervening days between testing of a given pair in one modality and subsequent testing of that same pair in the second modality, tests were conducted with two other pairs of objects. Hence the suite of controls used make it implausible to suppose that there was somehow an opportunity for the dolphin to develop learned associations between visual and echoic representations of specific pairs. These controls may be summarized as follows: no object or pair of objects was ever exposed simultaneously to the echoic and visual senses; the dolphin never viewed an object being placed inside of or taken out of an anechoic box; for given pairs, the tests of E–E and V–V matching were widely separated temporally; several intervening pairs were tested before a given pair tested with one sense was exposed to the second sense.

4. *Results and discussion*

Figure 3 shows the percentage of correct responses during E–E and V–V MTS for each of the initial 16 pairs of objects of Fig. 2. Elele scored 92% correct matches or better (at least 22 correct matches during the 24 trials, $p<0.0001$ by the cumulative binomial test) under both conditions for

TABLE I. Immediacy of within-modal object recognition. For each of the 16 pairs of objects, the results are shown for the first matching trial with object A of the pair as sample and for the first matching trial with object B of the pair as sample. A plus sign indicates a correct response (a choice of the matching alternative) and a zero an incorrect response. Results are shown for pure echoic matching (E–E) and for pure visual matching (V–V).

		Pair number																
Test	Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	No. correct
E–E	A	+	+	+	+	+	+	+	+	+	0	0	+	0	+	+	+	13
	B	0	+	0	+	+	+	+	+	+	+	0	+	+	0	+	+	12
																total:		25[a]
V–V	A	+	+	+	0	+	+	+	+	+	+	0	+	+	+	+	+	14
	B	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	0	14
																total:		28[a]

[a] $p \leq 0.001$.

seven pairs and was 75.0% correct or better (at least 18 correct matches in 24 trials, $p<0.02$) under both conditions for 13 of the 16 pairs. Over all 16 pairs she performed significantly more accurately during V–V MTS, matching correctly on 366 (95.3%) of 384 V–V trials, compared with 326 (84.9%) of 384 E–E trials (x^2 [1,N=768]=22.21, $p<0.001$). Performance on the 384 baseline trials remained errorless throughout all within-modal tests. The exceptional level of performance with these baseline pairs likely reflects Elele's long experience with these objects during the preliminary study of Herman and Pack (1992).

Table I summarizes the immediacy with which objects were recognized during E–E and during V–V MTS. The two members of a pair are symbolized as "A" and "B" and performance is shown for the first trial of the test with A as the sample, and for the first trial with B as the sample. A plus (+) sign indicates a correct response, and a zero an incorrect response. During E–E MTS Elele was correct on 25 of 32 first trials, and during V–V MTS she was correct on 28 of 32 first trials (for both cases, $p<0.002$ by the cumulative binomial test). Immediacy of recognition during E–E and V–V MTS did not differ significantly (x^2 [1, N=64]=0.44, $p>0.05$).

Clearly, Elele was capable of immediately recognizing most of the novel objects through echolocation alone and through vision alone. Her performance accuracy in E–E recognition suggests that shape recognition may be a fundamental property of the dolphin's echolocation perceptual system. Earlier studies showing echoic discrimination of shape by dolphins (Au *et al.*, 1980; Nachtigall *et al.*, 1980; Barta, 1969 cited in Nachtigall, 1980) were limited to discriminations of a few basic shapes or forms and did not report on the immediacy of echoic discriminations. The current results reveal immediate echoic recognition of many different complex shapes.

Elele's high level of V–V recognition extends earlier findings of immediate visual recognition of objects in V–V MTS (Herman, 1990; Herman *et al.*, 1989, 1994), to include complexly shaped objects made of the same materials and largely equated for surface area within pairs (see Hunter, 1988 for similar findings with two-dimensional figures).

B. Experiment 2: Testing for cross-modal object recognition

Cross-modal testing began after completion of all within-modal tests. From the 16 pairs of objects in Fig. 2, 9 were selected for cross-modal tests (pairs 2, 3, 6, 9, 10, 12, 14, 15, and 16). All nine pairs had yielded performance levels during each within-modal test of at least 75% correct matches over 24 trials (Fig. 3) (13 of 16 pairs actually met this criterion, but the four remaining pairs meeting criterion were used in other types of tests not reported here). Within each of the first eight of these nine pairs, the pair members were constructed from the same combinations of diameters of PVC pipe and fittings. Pair 16, whose members were constructed from PVC pipe of different diameters, was used only for the tests of cross-modal matching through television. The number of days intervening between the final day of within-modal testing and the first day of cross-modal testing for the nine pairs was, respectively, 113, 166, 179, 84, 104, 79, 153, 98, and 394 days.

For each of the first eight pairs, each cross-modal test consisted of 96 MTS trials given over four consecutive sessions of 24 trials each. At each session, 12 trials were cross-modal tests of a particular PVC pair (for a total of 48 trials over the four sessions with that pair), and 12 were cross-modal tests of the same baseline objects used during the within-modal tests and presented in all possible two-way combinations. Tests of the particular PVC pair were embedded among tests of baseline pairs using the same rules employed during the within-modal tests.

1. E–V recognition

For echoic–visual (E–V MTS), the sample object was presented to the echolocation sense and the alternatives to the visual sense. A single anechoic box was used (Fig. 1, top), in which the echoic sample was presented using the same procedures as described for E–E MTS. When Elele touched the front panel of the central anechoic box in the correct location corresponding to the position of the sample object, the alternatives were presented in air, under procedures identical to those described for V–V MTS.

2. V–E recognition

For visual–echoic (V–E MTS), the sample object was presented to the visual sense and the alternatives to the echolocation sense. Two anechoic boxes (Fig. 1, bottom) separated by 6.20 m were used. The sample object was presented in air by an assistant positioned centrally between the two anechoic boxes, using procedures identical to those described for V–V MTS. After a 5-s exposure period, the alternative objects (along with the two masking objects) were

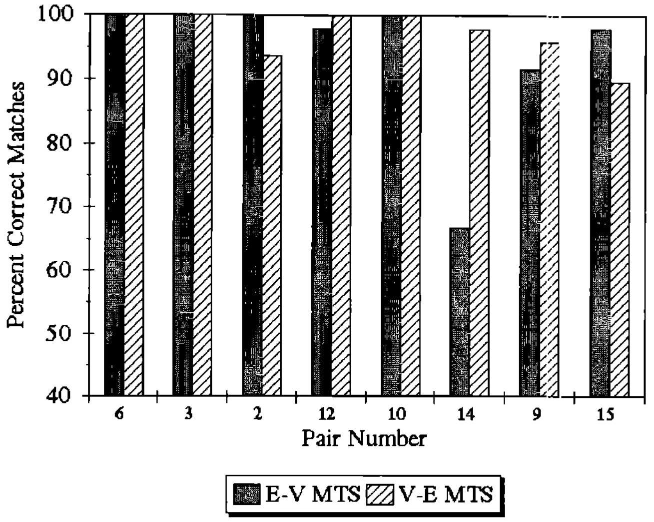

FIG. 4. Dolphin's performance accuracy in E–V and V–E MTS with eight pairs of objects which had yielded performance levels of 75% correct matches or better during E–E and V–V tests (Fig. 3). Each bar represents 48 trials. Pair numbers refer to numbers in Figs. 2 and 3 and are shown, left to right, in the order in which they were tested.

immersed in the anechoic boxes, using the same procedures for the presentation of alternatives described during E–E MTS. During these tests, as well as during the E–V tests, the occurrence of dolphin vocalizations was monitored and recorded using a Labcore customized hydrophone, a customized Archer miniamplifier, and a Marantz professional cassette deck model PMD430. The system was sensitive to frequencies between 50 Hz and approximately 11 kHz, well below the upper limit of dolphin echolocation signals (see Au, 1993), but sufficient to confirm the occurrence of these broadband signals.

3. Order of cross-modal tests

E–V MTS was tested first for four of the eight pairs (pairs 6, 12, 14, and 9, in that order) and V–E MTS was tested first for the remaining four pairs (pairs 3, 2, 10, and 15, in that order). Testing of a pair was completed in both cross-modal conditions before testing with the next pair was begun. The sequence in which the eight pairs were tested was: pair No. 6, 3, 2, 12, 10, 14, 9, and 15. This was a counterbalanced sequence to control for any effects of testing E–V or V–E first.

4. Results and discussion

Figure 4 shows the percentage of correct cross-modal matches for each pair, arranged according to the order in which pairs were tested. Elele produced 89.6% correct responses (43 matches in 48 trials), or better, during both V–E and E–V MTS for seven of the eight pairs, including errorless performance on three pairs ($p<0.001$, cumulative binomial test). The only pair giving some difficulty was pair 14, but the difficulty was limited to E–V MTS. Nonetheless, Elele's E–V performance with this pair was still significantly above chance (32 correct matches out of 48 trials, $p=0.01$).

TABLE II. Immediacy of cross-modal object recognition. For each of the nine pairs of objects, the results are shown for the first matching trial with object A of the pair as sample and for the first matching trial with object B of the pair as sample. A plus sign indicates a correct response (a choice of the matching alternative) and a zero an incorrect response. Results are shown for E–V matching in which the sample is presented echoically and the alternatives visually, and for V–E matching in which the sample is presented visually and the alternatives echoically. The pair numbers correspond to the same pair numbers in Table I.

		Pair number								
Test	Sample	6	3	2	12	10	14	9	15	No. correct
E–V	A	+	+	+	0	+	0	+	0	5
	B	+	+	+	+	+	+	+	+	8
									total:	13[a]
V–E	A	+	+	+	+	+	+	+	+	8
	B	+	+	0	+	+	+	0	+	6
									total:	14[a]

[a] $p\leq0.01$.

Altogether, Elele matched correctly on 94.3% of 384 E–V trials and on 97.1% of 384 V–E trials, a nonsignificant difference (x^2 [1, $N=768$]=3.17, $p>0.05$). In all tests, echolocation signals were confirmed through acoustic recordings.

There was a significant effect of order of testing only for E–V matching, favoring those pairs for which E–V was tested after V–E (95.8% correct matches versus 89.1%, X^2 [1, $N=384$]=5.4, $p<0.05$), but this effect was entirely accounted for by the relatively low performance on pair 14. Without pair 14, performance with E–V tested first yielded 96.5% correct matches, and when tested second yielded, as before, 95.8% correct matches, differences that are not significant (X^2 [1, $N=336$]=0.002, $p>0.05$).

To test for immediacy of recognition, we examined the dolphin's performance on the very first cross-modal trial with one member of a pair as the sample, and the very first trial with the other member as the sample, as was done for within-modal matching (Table I). This measure allows virtually no opportunity for associative learning as it is restricted to the first trial on which the dolphin experiences each object as sample in the cross-modal task. If cross-modal matching is primarily the result of learned associations between echoic and visual experiences, chance performance on these trials would be expected. Table II gives the first-trial results for the eight pairs, for E–V MTS and for V–E MTS, and is interpreted in the same way as was Table I for within-modal tests. Elele was correct on 13 of 16 (81.3%) first trials in E–V tests and on 14 of 16 (87.5%) first trials in V–E tests ($p=0.011$ and $p=0.002$, respectively, by the cumulative binomial test). These data provide strong evidence that the dolphin *immediately* recognized complexly shaped objects across the senses of echolocation and vision, under conditions in which there was no prior opportunity to inspect these objects through both senses simultaneously or in close temporal contiguity. Recognition proceeded approximately equally well in either direction, from echolocation to vision or from vision to echolocation.

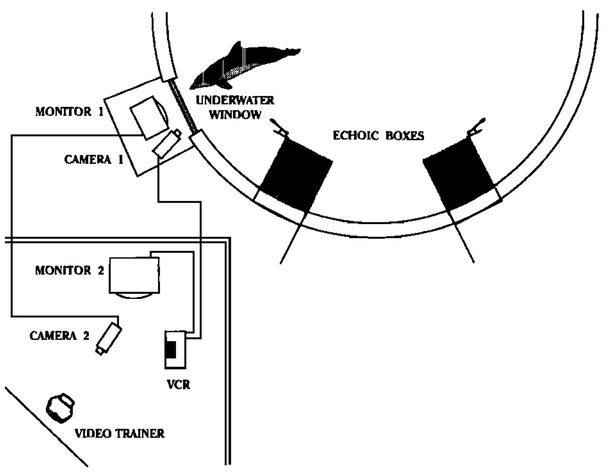

FIG. 5. Schematic representation of the apparatus and conditions for V–E MTS testing using a television monitor to expose sample objects to the dolphin. Monitor 1 and camera 1 are placed in a well (the "video studio") behind the underwater window. Monitor 2 and camera 2 are in a remote room located on an elevated deck beside the dolphin's tank. See text for details.

III. EXPERIMENT 3: CROSS-MODAL TESTS USING TELEVISION DISPLAYS

A. Rationale and method

To test whether Elele's success in cross-modal matching might be attributable to some latent ability to use echolocation in air, we exposed several pairs of objects as samples in V–E MTS on a 34.3-cm (diagonal measurement) Panasonic (model CT-1331Y) television monitor placed 16.5 cm behind an underwater window. If Elele were relying on echolocation to examine sample objects presented in air during V–E MTS, then chance performance levels would be expected when sample objects were presented on a television screen. That is, any echoes returned would be from the screen itself and, of course, not from the images on the screen. Elele's only previous experience with television had been a short but successful test of her ability to respond to gestural signals given by the image of a trainer on a television screen (cf. Herman *et al.*, 1990). Figure 5 is a schematic of the apparatus and conditions for the television tests. Images to be displayed on the television monitor located behind the underwater window (monitor 1) were filmed live in a remote enclosed room using camera 2. The images were either that of the "video trainer" alone, wearing a white T-shirt, and filmed only from the waist to the chin, or of the same trainer holding a sample object in front of his chest.

Camera 1, also located behind the underwater window, was positioned to provide a view of the dolphin looking at the television monitor. The output of camera 1 was presented on monitor 2 in the remote room, allowing the video trainer to observe the dolphin at the window. Note that, unlike the procedure for the earlier V–E tests, the location of the window required that the sample object be displayed to the side of the anechoic boxes (at 3.3 m circumferential distance from the closest anechoic box), rather than centrally between the two boxes.

B. Procedure

To begin a trial using the television display, a trainer located at the same remote station as in previous tests directed the dolphin to swim to the underwater window. On arriving there, Elele was shown a view of the video trainer with his left hand extended and index finger pointing up, the standard signal to "pay attention." In the current context, the proper response for the dolphin was to station herself in front of the window, with rostrum pointing toward the monitor or at a slight angle to it, both favorable underwater viewing positions (Dral, 1972; Herman *et al.*, 1975). The video trainer held the sample object to be displayed below his waist in his right hand and out of view of camera 2. When the dolphin was stationary in front of the window, watching the television monitor, the video trainer raised the sample object to his chest and held it stationary there, using both hands. After approximately 5 s of exposure, a supervisor vocally instructed assistants to immerse the alternative objects (and their masks) in the two anechoic boxes. On hearing the splashing sound of objects entering the water, Elele left the window to inspect the contents of the boxes and to make her choice, in the same manner as in the previous V–E study.

For this television experiment, we tested pairs 10, 3, and 6 (Fig. 2) from the previous experiment, in that order. Each of these pairs had yielded errorless performance during both E–V and V–E MTS (Fig. 4). Additionally, we used pair 16 (Fig. 2), which had been tested intramodally in E–E and V–V MTS more than a year earlier, under procedures described previously, but which had never been tested in either E–V or V–E MTS. Thus this final pair tested Elele's abilities to recognize a pair of objects novel to the cross-modal V–E condition with the visual component restricted to television viewing.

Pairs 10, 3, and 6 were each tested for 12 trials in a single session intermixed randomly with 12 trials using the standard baseline objects. Pair 16 was tested for a total of 24 trials over two successive sessions, using the same session procedures as for pairs 10, 3, and 6. Baseline objects as well as pairs 10, 3, 6, and 16 were all exposed visually only on television.

C. Results and discussion

Figure 6 shows that Elele responded correctly to all trials in each of the tests using pairs 10, 3, and 6, replicating the errorless performance level achieved when the sample objects were exposed "live" in air. With the new pair 16, she was correct on 23 of 24 trials. The single error occurred during the first session, but she responded correctly during the first trial on which each pair member served as sample. Finally, Elele responded correctly on all trials using baseline objects during all of these video tests.

These results show remarkable generalization of Elele's cross-modal matching ability to the novel television condition, and argue against any imputation that Elele was relying on echolocation in air in previous V–E tests (if indeed such were even practicable). The immediacy of recognition for pair 16 provides further evidence that shape recognition can be shared across the senses.

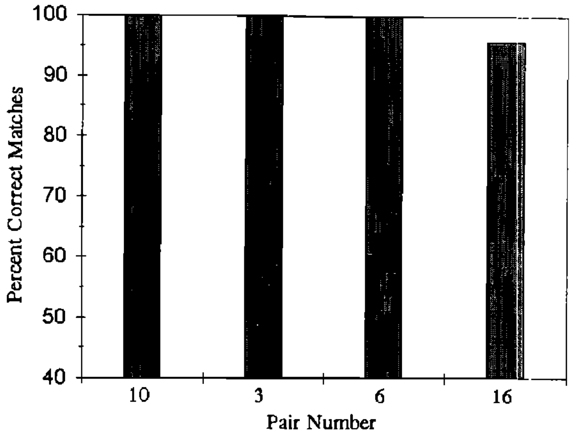

FIG. 6. Dolphin's performance accuracy in V–E MTS using television to expose sample objects, for three pairs of PVC objects previously tested in V–E and E–V MTS with samples shown in air at tankside (pairs 10, 3, 6), and for one pair of objects never before tested in V–E or E–V MTS (pair 16).

IV. GENERAL DISCUSSION

The immediacy of object recognition found within the visual sense, within the echolocation sense, and across these two senses, is evidence that (i) shape information "registers directly" in dolphin perception through vision or through echolocation and (ii) that functional integration of these two senses is a fundamental characteristic of dolphin perceptual processing of shape. The finding of immediacy of recognition, through echolocation, of a variety of complexly shaped objects greatly extends earlier findings on dolphin echoic shape recognition (e.g., Au *et al.*, 1980; Barta, 1969; Nachtigall, 1980; Roitblat *et al.*, 1990) and broadens concepts about the type and scope of mental representations that may be derived through the dolphin's echolocation sense. The immediacy with which objects were recognized across the senses (most objects were recognized on the very first trial in which they appeared as sample) makes explanations based on associative learning mechanisms between visual and echoic experiences untenable. Rather, it seems the dolphin apprehended certain features of the objects directly (in the least, features related to shape) through vision alone or through echolocation alone, and then shared these perceptions across the two senses. Thus, under the conditions of this study, echolocation and vision were found to be well integrated, suggesting that the mental representations constructed through the visual and echolocation systems are functionally similar and closely coordinated. Possibly, integration occurs within common multisensory convergence areas, as has been suggested for humans (Stein and Meredith, 1993).

It seems appropriate to characterize the mental representations of objects perceived through echolocation by the dolphin as spatial "images," as has been proposed for the product of bat echolocation (Simmons, 1989; Simmons and Grinnell, 1988). Whether imaging by dolphins should be regarded as pictorial or propositional is arguable, although propositional theories that liken images to linguistic descriptions are clearly inappropriate for nonhuman animals (Kosslyn, 1980; Pylyshyn, 1981; Tye, 1991).

As postulated for some echolocating bats, the broadband echolocation signal of the dolphin may yield a total echo return composed of interfering partial echoes reflected from the irregularities and discontinuities of three-dimensional targets (Ostwald *et al.*, 1988; also see Altes, 1976). Simmons (1989) has proposed a model of acoustic imaging in bats based on the extremely fine sonar range resolution abilities of these animals. In behavioral tests of range resolution capability, the big brown bat (*Eptesicus fuscus*) was able to discriminate range differences on the order of 1–2 cm at distances from 30 to 240 cm (Simmons, 1973). Different reflecting points of a complex target will yield slightly different range values, creating a range profile, which in turn may be interpreted perceptually as shape. The bat thus creates "images having spatial dimensions from sounds having acoustic dimensions" (Simmons, 1989, p. 171).

The mechanisms for sonar imaging aided by fine range resolution capability also seem in place for dolphins. *T. truncatus* is capable of discriminating range differences as small as 0.9 cm, in two-choice discrimination experiments in which the targets were two static 7.62-cm foam spheres placed at an absolute distance of 1 m (Murchison, 1980).[5] To achieve this level of discrimination, echo-delay intervals as short as 12 μs are theoretically necessary, applying the same model used by Simmons (1989), but corrected for the water medium (also see Au, 1993, Table 10.1). Studies of discrimination by *T. truncatus* of rippled and unrippled noise stimuli indicate that echo-delay times as short as 13 μs can be resolved (Au and Pawloski, 1989). Also, studies of discrimination by the common dolphin, *Delphinus delphis*, of stepped pyramids indicated resolution of echo delay times as short as 4 μs (Bel'kovich *et al.*, 1969 cited in Au, 1993). The transformation of precise range data into detailed spatial data thus seems well within the capabilities of the dolphin's echolocation system.[6]

Good cross-range (azimuthal) resolution, in conjunction with fine range resolution, would further help to characterize the spatial features of an object. There seem to be no direct studies of azimuthal resolution by dolphins using active sonar. However, Renaud and Popper (1975), studying the passive sonar (passive listening) abilities of *T. truncatus*, reported discrimination of auditory angles (the angular separation of two sound projectors) as small as 0.7° for echolocation clicks having a center frequency of 64.4 kHz. In the studies reported in the present paper, the dolphin was able to swim freely about relative to the target as it carried out its echolocation task. Such movement while echolocating may yield detailed aspect information, enhancing azimuthal resolution, in analogy perhaps to the enhancement of spatial information that can be obtained from multiple, spatially separated sonar receivers. At our laboratory, a program of intensive study is planned to analyze the dolphin's echolocation behaviors and signal characteristics in the within-modal and cross-modal tasks, and to measure the acoustic properties of the objects used. This study will include the analysis of the role of relative movement in target recognition, as measured through the joint use of underwater video cameras and hydrophones. The results of such study should further the understanding of how the dolphin seeks and receives acoustic information in these object recognition tasks and may help in the understanding of how the spatial features of objects are represented by the dolphin.

Finally, several studies of cross-modal matching of objects through vision and touch by humans (Bushnell and Weinberger, 1987; Jones, 1981; Rose and Orlian, 1991) or by nonhuman primates (Dimattia *et al.*, 1990) have reported asymmetries in performance between visual–touch and touch–visual matching, generally favoring visual–touch over touch–visual matching. Under the conditions studied here, no significant functional asymmetry was observed: recognition proceeded approximately equally well in both directions, from echolocation to vision or from vision to echolocation.

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[1] Although Plexiglas (1.18 g/cm^3) and seawater (1.03 g/cm^3) have similar densities (Gross, 1977; Society for Automotive Engineering, 1969), because of different sound velocities, the acoustic impedance of Plexiglas (3.2×10^6) exceeds that of seawater (1.5×10^6). Transmissibility of the Plexiglas panel will therefore vary with sound frequency, being greater at lower frequencies than at higher frequencies. However, transmissibility is still high at 60 kHz (75%) and relatively high at 120 kHz (61%) (see, e.g., Kinsler *et al.*, 1982, p. 128). These transmission characteristics apparently provide sufficient echo information for the dolphin to complete its recognition task with high accuracy, as shown by results reported later.

[2] The density of air is 0.0013 g/cm^3 (Tipler, 1976); the density of the melon increases gradually from the core through the outer shell and eventually approximates the density of the surrounding water interface (1.03 g/cm^3).

[3] The six baseline objects were a stainless-steel bowl (33.0 cm diam. by 9.8 cm deep), an orange ceramic terra cotta flower pot (19.1 cm high by 21.6 cm wide), a green fiberglass grating (26.4 cm high by 35.6 cm wide), a black hard rubber roller (9.5 cm diam. by 30.5 cm wide), a sand-filled PVC cross (24.1 cm high by 24.1 cm wide), and a letter "I" constructed from aluminum I-beam (34.1 cm high by 22.9 cm wide). All 15 possible two-way combinations of these objects were used during the matching tests.

[4] Elele was trained to remain stationary while the trainer's hands were placed completely over her eyes. The occlusion of Elele's vision by this method was confirmed through tests of her ability to respond to familiar gestural signals signed both while Elele's eyes were covered and while the trainer's hands covered an area close to but not over Elele's eyes. In the former case Elele did not respond with any behaviors. In the latter case she responded with the behavior corresponding to the gestural signal.

[5] Range resolution decreased with greater target distances, unlike the case for bats for which it was constant over the absolute target distances studied. Au (1993) discusses this and other differences between bat and dolphin sonar capabilities that suggest different processing mechanisms may be involved in some cases.

[6] For a somewhat different view of acoustic imaging by dolphins see Altes (1992). Also, Au's (1993) discussion of shape discrimination by dolphins primarily focuses on the differences in echo intensity available to a dolphin as it scans across different targets, differences that may allow discrimination without the construction of a shape percept. In the present studies, however, the immediacy with which shape recognition occurred cross-modally argues that a shape percept must be obtained for each sense, and that these percepts are coordinated or shared across the senses.

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