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Memory for action events in the bottlenosed dolphin

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Abstract We investigated whether a bottlenosed dolphin's ability to recall and repeat actions on command would immediately generalize to actions performed with specified objects. The dolphin was tested on her ability to repeat 18 novel behaviors performed with potentially interchangeable objects specified using an artificial gestural language. Such "action events" were correctly repeated at above chance levels, indicating that the dolphin had access to memories of those events. Performance levels were, however, lower than in previous tests. The dolphin appeared to have difficulty recalling which object an action was performed with. Previous research has demonstrated that animals can recall features of their environment and features of their actions independently of one another. The results of this study demonstrate (1) that the dolphin's concept of repeating extends beyond simply accessing memories of movement patterns, and (2) that dolphins' memories of past events incorporate representations of both self-performed acts and objects, locations, or gestural instructions.

Key words Memory · Dolphin · Action Events · Motor

Introduction

Internal representations of movements have been investigated from various perspectives. Studies of invertebrates have focused on the neural circuitry underlying motor programs/action patterns (Kien et al. 1992), while studies of vertebrates have concentrated on processes involved in the acquisition and adaptation of motor patterns (Bloedel et al. 1996; Holding 1981). Motor learning is often viewed as an unconscious process that depends on implicit (or non-declarative) memory systems (Engelkamp and Wippich 1995; Squire and Zola 1996). In contrast, the ability to recall past actions has been described as a conscious process that relies on explicit (or declarative) memory systems. Movement recall (or motor memory) studies have explored how well humans remember past actions by having subjects attempt to reproduce movements in standardized tasks (Goodman et al. 1985; Magill 1983; Pepper and Herman 1970). Researchers have also examined how actions performed in response to symbolic cues in the form of verbal instructions (called action events) can affect a subject's ability to recall the instructions (Cohen 1989; Engelkamp and Zimmer 1989). Past approaches to investigating motor representations have generally reflected the perceived complexity and flexibility of motor representations in different species as well as the constraints of available methodologies. For example, tests of movement recall have been largely restricted to humans. The few tests of motor recall that have been conducted in other animals (Beninger et al. 1974; Kramer 1982; Morgan and Nicholas 1979; Shimp 1982, 1984), have not addressed questions concerning how flexibly different species can access memories of past actions. The methods used in these tests often involve training a subject to discriminate a small number of events, and to report these discriminations through arbitrary responses (e.g., pressing different levers). Although such methods can provide evidence that subjects differentiate certain events, they do not clearly reveal what features of these events the subjects recall.

Recently, a technique was developed to test whether bottlenosed dolphins (*Tursiops truncatus*) could recall actions that they had recently performed (Mercado et al. 1998). Dolphins were taught to respond to a gestural instruction by repeating the last sequence of actions performed. The dolphins proved to be able to recall and repeat a wide variety of actions involving multiple coordinated movements, including combinations of movements that the dolphins were not specifically trained to perform. Furthermore, the dolphins were able to generalize the re-

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peating rule to novel behaviors and novel experimental contexts. The methods developed by Mercado et al. (1998) provide a new way to investigate motor representations in dolphins and potentially other species as well. Unlike previous methods used to test motor recall in other species, the repeating task provides a flexible way to test the dolphin's ability to recall numerous actions in a wide variety of situations. Additionally, the dolphins' responses when requested to repeat an action provide clear evidence of whether the dolphin has recalled specific components of past actions.

Dolphins have also been taught to respond to an artificial gestural language by performing specified actions to specified objects (Herman et al. 1984). Using this gestural language, dolphins can be instructed to perform novel action sequences. Dolphins have demonstrated the ability to (1) respond appropriately to such novel instructions, (2) modulate the form of responses to action gestures to accommodate contextual constraints, and (3) follow an instruction correctly even when objects were not introduced until 30 s after the instruction was given. Additionally, dolphins have been taught to report on actions performed by other dolphins (Bauer and Johnson 1994; Xitco 1988) and to report on the presence or absence of objects (Herman and Forestell 1985). Collectively, these experimental tasks provide powerful tools with which to investigate the cognitive abilities of dolphins.

In the current exploratory study, we investigated whether a dolphin's ability to recall and repeat actions would immediately generalize to actions performed to symbolically specified objects. To perform this task, the dolphin must recall not only movement patterns, but also specific environmental cues in relation to which the movements were performed. Performance at above chance levels would thus suggest that the dolphin was encoding and recalling both self-performed acts and environmental cues. Given that the dolphin was never explicitly reinforced for attending to any cues other than actions in past experiences with the repeating task, successful performance would also suggest (1) that bottlenosed dolphins naturally attend to and encode environmental cues as part of their memories for past events involving self-performed acts, and (2) that the subject's repeating rule is more abstract than was shown in previous tests.

Methods

Subjects

The subject in this study was a 12-year-old, female, Atlantic bottlenosed dolphin, named Elele. Elele was housed in a seawater tank 15.2 m in diameter and 2 m deep, with three other dolphins. She was fed approximately one-quarter of her daily ration of 9.1 kg of smelt during each experimental session. Elele has received extensive training, and served as one of the subjects in the study of Mercado et al. (1998). She is proficient at matching-to-sample tasks (Pack and Herman 1995; Shaw 1990), has experience in reporting on the presence or absence of objects (L. Herman, unpublished work), and in performing specified actions to specified objects in response to gestural commands (L. Herman, unpublished work).

Table 1 Gestural instructions used in the tests. Body parts and actions were combined to form six action instructions (used with each object for a total of 18 instructions):

Over	Jump over one of the three objects
Under	Swim under one of the objects with belly facing up
Mouth	Open mouth near an object
Pectoral touch	Place either pectoral fin over an object
Rostrum toss	Use rostrum to toss an object out of the water
Fluke toss	Use fluke to toss an object out of the water

Objects	Body parts	Actions
Ball	Pectoral fin	Over
Basket	Fluke	Under
Frizbee	Rostrum	Mouth
		Touch
		Toss

Gestures and their referents

The gestures used to instruct Elele consisted of movements of the arms and hands of a trainer standing beside the tank wall (described in detail by Herman et al. 1984). Such gestures have been shown to be highly discriminable by dolphins (Herman et al. 1990). Elele has been taught that specific gestures made by a trainer refer to specific objects (e.g., a ball, basket, frizbee, cone, or surfboard), specific body parts (e.g., the fluke, belly, rostrum, dorsal fin, or either pectoral fin), and specific actions (e.g., jump over, swim under, touch, or toss an object). A subset of the gestures understood by Elele was used in the current experiment (see Table 1); these gestures were combined to form a set of 18 instructions according to a set of combinatorial rules. When instructions were given to Elele, gestures were presented in rapid succession. Object signs always preceded body part signs, which always preceded action signs. For example, the gestural sequence "Frizbee Rostrum Toss" instructed her to toss a frizbee out of the water using her rostrum. Elele has also been previously taught a gesture that instructs her to repeat the action just performed (see Mercado et al. 1998). It is important to note that Elele had never been instructed to repeat actions performed with specified (and functionally interchangeable) objects prior to these tests.

Procedure

Before formal tests using the "Repeat" instruction were conducted, Elele was tested on her ability to follow each of the 18 instructions. These tests established baseline performance levels on the behavior set.

The general experimental procedure for the repeating task has been described in detail by Mercado et al. (1998). Elele was tested in eight sessions, consisting of 20 trials each. Each trial began with a gestural instruction indicating an action to be performed to a specified object. Elele's response was then evaluated by the experimenter as being either correct or incorrect. If the response was correct, either a second instruction was given (15 of 20 trials) or reinforcement (vocal praise and a fish) was given and the trial ended (5 of 20 trials). The second instruction either required the dolphin to repeat the previous action or to perform another specified action. Elele's response to a second instruction was described by a *blind* observer (i.e., with no knowledge of which instructions were given), using prescribed labels. If the observer's description indicated that the correct action had been performed with the correct object, Elele was given reinforcement. A response was considered to be incorrect if either the action or the object the action was performed with was incorrect. Whenever a response was incorrect, Elele was simply instructed to return to station and await the next trial. Controls against inadvertent cueing included: (1) the trainer wore opaque goggles to prevent eye-gaze cues, (2) the trainer was only informed of instructions one at a time (by a tankside assistant) im-

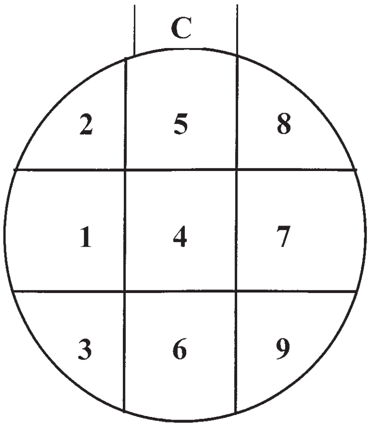

Fig. 1 Diagram showing how object positions in the tank were recorded in terms of regions. At the beginning of a test session, objects were placed in *regions 1, 2, and 3* (which object was placed in each region was arbitrary). Elele was stationed and given instructions in *region 1*. A second dolphin was stationed in *region 7* during trials. The channel *(C)* leads to a second tank where two more dolphins were present. This channel was closed during test sessions. If objects floated into the channel, or region 7, they were moved to some other region (chosen arbitrarily) during the next inter-trial interval

mediately before they were given, and (3) observers judging the dolphin's behaviors were located on a raised platform, out of the dolphin's sight.

Each session began with two "warm-up" trials requiring Elele to repeat familiar actions from previous tests (squirting water out of the mouth, and swimming at the surface with head hunched over). A test session was continued only if she was successful on these initial trials. The remaining 18 trials consisted of 9 trials requiring Elele to repeat actions to objects, 4 trials requiring her to perform two explicitly instructed actions to objects (i.e., upon returning from the first behavior, she was immediately instructed to perform a second behavior from the test set), and 5 trials requiring her to perform a single action to an object. Trial types were randomly ordered within sessions, and instructions were randomly ordered within trials. A session was divided into two blocks (11 trials followed by 9 trials) separated by a minimum of 2 min; trials were separated by at least 30 s. The interval between instructions was timed with a stopwatch.

Objects were placed in the tank at the beginning of each session. They were allowed to drift freely around the tank with only minor repositioning if they drifted together, or into areas near other dolphins. Object locations were recorded during each trial (Fig. 1). The movement of objects within and between trials was primarily a function of wind conditions and small waves generated by the actions of dolphins in the tanks.

Data analysis

Elele had four opportunities to repeat each of 18 actions to specific objects across the eight sessions. Performance levels were evaluated for significance using the summed binomial test. Probability of a correct response was considered to be 1 correct response in 18 trials based on an "independent elements" model (Herman et al. 1984). The probability of guessing the correct object was 0.33, and the probability of guessing the correct action can be taken to be 0.17 (note that this is a conservative estimate because Elele could respond to the repeat gesture with actions other than those she was being tested on). Assuming independence of trials, Elele had to perform correctly in two out of four trials for her performance to be statistically significant ($P < 0.05$) for a particular instruction.

Results

Elele correctly performed 62 of 66 (94%) trials correctly in initial pre-tests requiring her to perform actions to specified objects. This performance level is comparable to those reported for another dolphin in a previous study of comprehension of similar gestural sequences (Herman et al. 1984). Most errors (3 of 4) involved choosing the wrong object in response to the Ball gesture.

Table 2 summarizes Elele's performance on tests of repetition. Overall, she correctly repeated her previous actions (to the same object) in 30 of 72 trials (42%, $P < 0.05$), and performed at above-chance levels on 10 of the 18 object-action sequences tested. Performance levels remained stable across the testing period; her responses were correct in 7 of 18 (39%, $P < 0.05$) first exposure trials, and in 8 of 18 (44%, $P < 0.05$) fourth exposure trials. Trials involving Ball, Fluke toss, and Mouth accounted for a majority of the errors (31 of 42, 74%). Errors consisted of either (1) a correct action performed to an incorrect object (29/42, 69%), (2) an incorrect action performed to the correct object (5/42, 12%), or (3) an incorrect action performed to an incorrect object (8/42, 19%; 4 of these errors involved actions not in the test set). Table 3 provides a detailed description of incorrect responses to the repeat instruction. Considering objects and actions independently

Table 2 Performance levels for each instruction. Data are given as number correct divided by number of trials. Values in parentheses reflect performance levels if objects and actions are assessed independently of one another (e.g., although the action Mouth was repeated perfectly, it was seldom performed to the correct object)

	Frizbee	Ball	Basket	Totals
Over	2/4*	1/4	3/4*	6/12 (9/12)
Under	3/4*	1/4	3/4*	7/12 (10/12)
Mouth	2/4*	1/4	0/4	3/12 (12/12)
Pectoral touch	3/4*	0/4	2/4*	5/12 (10/12)
Rostrum toss	3/4*	3/4*	2/4*	8/12 (11/12)
Fluke toss	0/4	0/4	1/4	1/12 (6/12)
Totals	13/24 (16/24)	6/24 (9/24)	11/24 (11/24)	30/72*

* $P < 0.05$, summed binomial test

Table 3 Responses to Repeat instruction (✓ behavior was correctly repeated, *FZ* Frizbee, *BL* Ball, *BK* Basket). Actions without objects reflect ambiguous responses (e.g., performing an action near, but not to an object). *Subscript numbers* indicate the order of test trials/responses (e.g., the very first object-action sequence tested was BK Mouth). Patterns of successive error responses suggest strategies Elele may have used to determine response requirements. For example, she initially responded by performing actions to no objects, then began performing actions to objects (typically defaulting to the FZ), then began performing actions to specific objects (note the increased number of errors on FZ trials)

Correct response	1st Attempt	2nd Attempt	3rd Attempt	4th Attempt
FZ Over	✓$_{8}$	Leap, belly-up$_{21}$[a]	✓$_{37}$	Leap, belly-up under FZ$_{69}$[a]
FZ Under	✓$_{16}$	Under$_{19}$	✓$_{48}$	✓$_{64}$
FZ Mouth	✓$_{12}$	✓$_{28}$	BL Mouth$_{54}$	BK Mouth$_{71}$
FZ Pectoral touch	✓$_{14}$	✓$_{25}$	✓$_{46}$	BK Pectoral touch$_{72}$
FZ Rostrum toss	✓$_{4}$	✓$_{23}$	BK Rostrum toss$_{45}$	✓$_{65}$
FZ Fluke toss	Fluke above water, near BK$_{17}$[a]	FZ Fluke touch$_{34}$[a]	FZ Fluke touch$_{43}$[a]	BK Fluke toss$_{62}$
BL Over	Over$_{18}$	FZ Over$_{29}$	BL Fluke toss$_{52}$	✓$_{57}$
BL Under	BL Mouth$_{5}$	FZ Under$_{26}$	✓$_{51}$	BK Under$_{70}$
BL Mouth	FZ Mouth$_{3}$	Mouth$_{20}$	✓$_{44}$	BK Mouth$_{68}$
BL Pectoral touch	Mouth$_{2}$	FZ Pectoral touch$_{24}$	FZ Pectoral touch$_{47}$	BK Pectoral touch$_{61}$
BL Rostrum toss	✓$_{7}$	✓$_{35}$	FZ Rostrum toss$_{38}$	✓$_{55}$
BL Fluke toss	FZ Over$_{15}$	FZ Fluke touch$_{33}$[a]	FZ Fluke toss$_{49}$	BK Fluke toss$_{59}$
BK Over	FZ Over$_{10}$	✓$_{32}$	✓$_{53}$	✓$_{66}$
BK Under	✓$_{9}$	BL Rostrum toss$_{31}$	✓$_{41}$	✓$_{58}$
BK Mouth	Mouth$_{1}$	FZ Mouth$_{30}$	FZ Mouth$_{39}$	FZ Mouth$_{60}$
BK Pectoral touch	BL Mouth$_{6}$	✓$_{36}$	FZ Pectoral touch$_{40}$	✓$_{63}$
BK Rostrum toss	FZ Rostrum toss$_{11}$	✓$_{27}$	FZ Rostrum toss$_{50}$	✓$_{67}$
BK Fluke toss	FZ Fluke toss$_{13}$	FZ Fluke touch$_{22}$[a]	✓$_{42}$	FZ Fluke toss$_{56}$

[a] Behavior was not part of the test set

of one another, Elele successfully recalled 59 of 72 (82%, $P < 0.05$) actions and 35 of 72 objects (49%, $P < 0.05$). When she made errors repeating object-action sequences involving specified body parts, she usually recalled the correct body part (19 of 22 trials, 86%), but not the correct generic action. For example, when incorrectly repeating Fluke toss, Elele typically (4 of 6 errors) performed a Fluke touch (see Table 3). Elele performed very well (170 of 176 correct, 97%) when explicitly instructed to perform actions with objects during test trials.

There was only a weak relationship between performance levels and either the interval between gestures or the positions of objects (Fig. 2); Elele was, however, most accurate when the correct object was closest to her starting position. The relative movements of objects during trials were generally not predictive of whether she would perform a correct response. The correct object remained within the same region in 62 of 72 (86%) trials; Elele chose the correct object in 26 of these 62 trials (42%). Of the ten trials in which the correct object was not in the same region it was during performance of the first behavior (i.e., the object had moved by the time the repeat instruction was given), Elele chose four correct objects (40%). These performance levels are not significantly different based on the chi-square test of independence: $\chi^2(1, n = 72) = 0.01$, $P > 0.1$. When the correct object was the only object in a specific region (31 of 72 trials), Elele correctly chose that object in 14 trials (45%). In the remaining 41 trials, in which one or two incorrect objects were in the same region as the correct object, she chose the correct object 16 times (39%). Again, these performance levels are not significantly different: $\chi^2(1, n = 72) = 0.27$, $P > 0.1$.

Discussion

This exploratory study was conducted to investigate whether a bottlenosed dolphin could generalize a previously learned repeating rule to a novel situation, and if so, what information the dolphin would use to solve this new problem. Elele demonstrated the ability to generalize the repeating task to actions performed with specified objects. In previous work, it was shown that dolphins learned an abstract concept of repetition that could be applied to novel actions (Mercado et al. 1998). The results of the current study demonstrate an untrained flexibility of this concept that suggests Elele's performance in the repeating task involves more than just the recollection of movement patterns.

Generalization of the repeating rule

Dolphins have shown an exceptional ability to conceptualize experimental tasks (Herman et al. 1993, 1994). The generalization shown in the current study is particularly notable, however, because Elele had never been explicitly reinforced for attending to the identity or location of objects in her previous training with the repeat instruction.

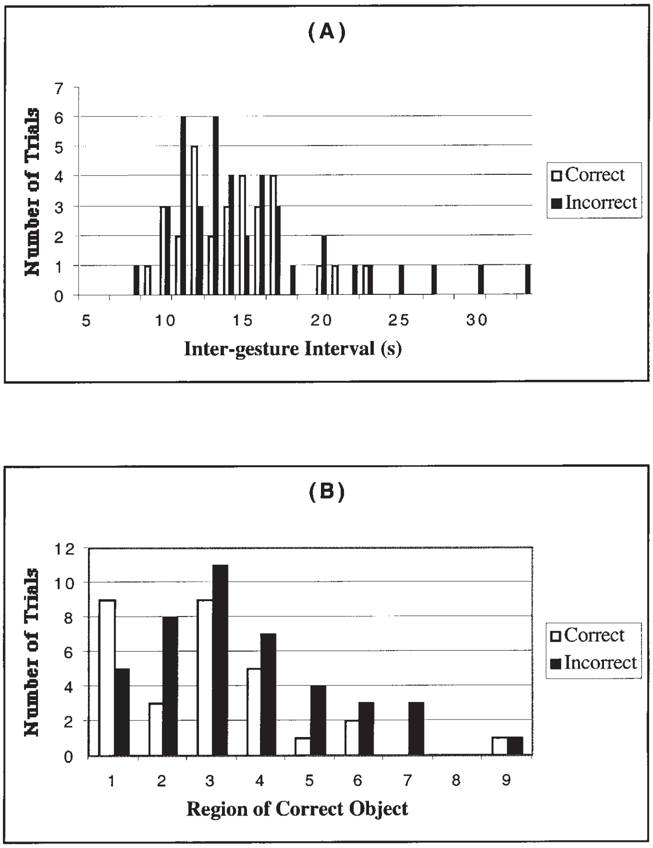

Fig. 2 **A** Frequency distributions of correct and incorrect responses to the Repeat instruction as a function of the duration between the first gestural sequence and the repeat gesture. When data are pooled into trials with inter-gesture intervals (IGIs) either above or below the mean (15 s), there is no significant difference between performance levels on trials having shorter or longer duration IGIs; χ^2 (1, $n = 71$) = 1.2, $P > 0.1$. Note that one IGI was inadvertently not measured. **B** Frequency distributions of correct and incorrect responses to the repeat instruction as a function of the position of the correct object. When data are pooled into trials in which the correct object was either near the training station (regions 1, 2, and 3) or farther away from the station (all other regions), there is again no significant difference between performance levels; χ^2 (1, $n = 72$) = 0.24, P > 0.1

When the task was initially trained, no objects were used. Additionally, when objects were first introduced in test trials, there was no requirement that actions be repeated to the same object and objects floated freely about the tank. Pretests suggested that the presence of multiple objects in the tank degraded performance levels even on trials that did not involve objects (Mercado et al. 1998, Part A). In later tests, Elele performed well (87% correct) on trials requiring her to repeat actions to unspecified objects when only one object was available (Mercado et al. 1998, Parts B and C). Because the location and identity of objects were not predictive of the correct response in her past experiences with the repeating task, it was not clear in past tests whether Elele attended to either of these cues. The results of animal learning studies suggest that representations of such extraneous cues would likely degrade as training progressed (cf. Bonardi and Hall 1996; Cole et al. 1995; Miller and Matute 1996; Miller et al. 1992).

Methodological differences between the current test and past tests made it even less likely that Elele would be able to successfully generalize the repeating rule. For example, the delay between performance of an action and reproduction of the action was increased relative to past tests because objects were allowed to float freely throughout the tank. There was also increased potential for interference effects because three objects were present in the tank during all trials, and every trial involved an action performed with an object. Furthermore, each trial required Elele to search the tank for a specific object before repeating her previous action; previous tests did not require such searching. Combining the artificial language task with the repeating task could also have led to some confusion concerning what stimuli were to be encoded (e.g., in artificial language tests, the emphasis is on correctly interpreting gestures, whereas in the repeating task the emphasis is on remembering a previous action).

Given these numerous obstacles, it would not have been surprising if Elele had failed to correctly repeat any object-action sequence. Her immediate generalization (7 of 18 responses correct in first trial exposures) of the repeating rule in this novel context thus provides an impressive demonstration of conceptual and behavioral flexibility. Elele's modest overall performance level (42% correct) in comparison to previous levels (familiar actions, 90%; novel actions, 79%, Mercado et al. 1998) suggests that the current task was more difficult than previous ones. This increased difficulty can be attributed, at least in part, to the requirement that actions be performed with a specific object. Most errors involved a correct action performed to an incorrect object, and accuracy at repeating actions (81%) was comparable to previous levels. If Elele had simply repeated each action to a randomly selected object, she would have chosen the correct object in one out of three trials simply by chance. The fact that she chose the correct object in 35 of 72 (49%) trials suggests that she was not randomly choosing objects. When Elele chose an incorrect object, she could have (1) forgotten or failed to encode the identity or location of the object, (2) forgotten or failed to encode the gestural instruction used to specify the object, and/or (3) been confused regarding the requirements of the task. Unfortunately, the methods used in the current study do not provide any way to differentiate these possible sources of error.

What do dolphins remember?

The results of this study demonstrate that Elele had access to representations of past events that enabled her to correctly repeat actions to specified objects. Mercado et al. (1998) provided strong evidence that when dolphins perform the repeating task, they do so by accessing representations of past actions stored in working memory. This is not an intrinsic requirement of the task. Subjects could have learned to perform correctly by recalling the gestural sequences used to instruct initial behaviors. Several pieces of evidence indicate that this is not what the dolphins learned to do. First, previous data show no relationship between the complexity of gestural sequences and the difficulty of repeating actions associated with these sequences (Mercado et al. 1998). Second, dolphins immediately generalized the repeating rule in trials containing sequences of multiple repeat gestures; i.e., having repeated an action once, dolphins could readily repeat the same action a second or third time, in response to additional repeat gestures (Cutting 1997; Mercado et al. 1998). Finally, dolphins also immediately generalized the repeating rule to self-selected actions (i.e., actions not explicitly instructed by a trainer), including actions that had never been trained and thus were not associated with gestures (Cutting 1997; Mercado et al. 1998). Such generalization capabilities strongly suggest that the dolphins recollect actions rather than (or in addition to) instructions. One limitation of the current study is that the results do not show conclusively whether Elele was recalling past actions and objects or recalling past instructions, or both. Studies of action event memory in humans have led to similar ambiguities, with some researchers suggesting that motor representations are involved (Engelkamp 1991), and others suggesting that they are not (Kormi-Nouri et al. 1994). Although Elele could potentially have based her responses on recollections of gestural sequences in these novel tests, it is more parsimonious to assume that she used the same strategy as in previous tests than it is to claim that she adopted an entirely new strategy exclusively for this experiment.

The results of the current study also do not clearly reveal whether Elele was encoding the identity of objects, their location, or both. Because the positions of objects did not vary much between Elele’s initial response and her repetition of that response, she could often perform correctly by simply recalling her action and the location where it occurred, rather than recalling which object was the focus of the action. Two findings that suggest Elele was not relying only on spatial memory are (1) her performance level did not drop on the occasions when the correct object moved into a different region before she repeated the action, and (2) her performance level did not drop when incorrect objects were in the same region as the correct object. Anecdotally, Elele performed actions during trials that seemed inconsistent with sole reliance on spatial cues. For example, when instructed to repeat an object-action sequence, Elele would sometimes approach each of the three objects before performing an action to any of the objects. Additional tests are clearly needed, however, to clarify the role spatial cues play in dolphins’ memories of the past.

Finally, it could be argued that Elele performed trials correctly without storing either the identity or the location of objects in memory. Because the objects remained in the tank as Elele returned to her station to receive the second instruction, it is conceivable that she could have visually monitored the position of the correct object until (and while) the second instruction was given. This possibility seems unlikely because she would have had to simultaneously attend to both the trainer in front of her and an object located behind her. It is doubtful whether dolphins even have such capabilities. Additionally, this explanation does not account for why Elele performed best when the specified object was Frisbee (see Table 2), an object smaller and less visible than either Ball or Basket.

Despite these ambiguities, the results strongly suggest that Elele did more than just recall and repeat past action patterns when instructed to repeat object-action sequences. If she was not attending to either the identity or positions of objects (or recalling gestures), then she should not have been able to perform correctly when an object moved into a different region before the repeat instruction was given. Her performance levels on such trials, however, did not differ significantly from trials in which the correct object was stationary. Given that the correct object remained within the same region in 86% of trials, Elele could have done quite well simply by precisely replicating the previous action pattern. All of the available evidence suggests that she did not adopt this strategy. Rather, it appears that Elele attempted (with moderate success) to choose an object based on her memories of the past, and then performed a remembered action to that object. Further experiments are needed to determine whether object choice was based on memories of gestures, locations, object identity, or some combination of these cues.

Comparative perspectives

It is not yet clear how the dolphin’s ability to remember past events compares with other species’ (especially humans’) abilities. The learned skills (or motor programs) that dolphins must acquire to perform various actions likely involve long-term, procedural memory systems. The ability to recall that a specific action has been performed in the recent past, however, likely depends on short-term, working memory systems. The repeating task is similar to human motor memory tasks in that movements must be reproduced to match some standard. This task differs from human motor memory tasks in that human subjects are typically required to exactly replicate their movements, whereas the dolphins are only required to repeat an action such that it is recognizable by a blind observer as being of a particular type (e.g., a dolphin can Fluke toss an object in various ways). The task is also similar to action event tasks in that movements are directed using symbolic instructions (e.g., whereas humans might be instructed to “snap your fingers” or “open a book,” dolphins are instructed to “slap your fluke” or “toss a basket”). In human action event tasks, however, subjects are given long lists of actions and then tested on their ability to recall items from the list. It seems appropriate to describe the ability of a dolphin to repeat actions performed to specified objects as requiring memory of action events, given that actions are instructed using sequences of symbols and that both actions and environmental cues must be recalled. Further research is needed to determine whether or not this ability involves processes similar to those involved in human motor memory and/or memory for action events, processes that in the past have often been classified as part of declarative rather than procedural or working memory systems.

An interesting similarity between the findings on memory for action events in humans and the abilities seen in dolphins is that humans also have more difficulty recalling actions performed with specified objects than actions performed without objects. Engelkamp and Zimmer (1997) distinguished "body-related" actions from "object-related" actions and suggested that body-related actions are easier to encode because the number of actions that can be performed with body-parts is more constrained. Several studies have found consistently better memory for body-related actions than for actions performed with external objects (Cohen et al. 1987; Engelkamp and Zimmer 1994; Norris and West 1991; Nyberg et al. 1991). The reasons for these differences are still under investigation. Although findings of similar limitations in the memory abilities of dolphins are suggestive of similar constraints in event memory processing, more data are needed to assess whether such parallels are robust or superficial.

A large number of memory systems have been described in the human literature (for review, see Schacter 1995; Squire and Knowlton 1995; Tulving 1995), including verbal and visual short-term stores (Baddeley 1998 a, b), as well as long-term semantic, episodic, and procedural systems (Neiworth 1995; Squire and Zola 1998). Of these systems, only episodic memory has yet to be shown in non-humans (Tulving and Markowitsch 1998). Episodic memory has been described as the ability to mentally travel back in time to consciously re-experience past events (Levine et al. 1998; Wheeler et al. 1997). Event memory, in contrast, does not necessarily involve either conscious introspection or mental time travel. In Mercado et al. (1998) and the current study, dolphins demonstrated the ability to represent self-performed acts in working memory. It is tempting to infer from these performances that (1) dolphins are aware that they are performing specific actions (i.e., that they are self-aware), and (2) that the dolphins remember that they were just performing a specific act (i.e., that they have episodic memories). Although the ability to represent and report on ones own past actions is clearly consistent with (and likely necessary for) states of self-awareness and episodic recollection, evidence of this ability can only compel the inference that mental representations of events from the recent past exist and can be flexibly accessed.

The ability to recall and reproduce self-performed actions may be related to the ability to recall and reproduce the actions of others. Imitation has often been viewed as a cognitively advanced form of social learning, limited to a few select species (for review, see Byrne and Russon 1998; Galef 1988; Heyes 1994; Whiten 1998; Whiten and Ham 1992). Recent findings suggest, however, that imitation may be an ability possessed by many species (Bugnyar and Huber 1997; Zentall et al. 1996). In humans, deferred imitation tasks have been used to show that infants have memories of action events (Cohen 1989). Studies of amnesic patients suggest that performance levels in such tasks can be used as a nonverbal measure of declarative memory systems (McDonough et al. 1995). Collectively, these results suggest that the ability to recall and reproduce perceived actions is a basic skill.

Some human memory researchers suggest that the processes underlying this ability are somewhat independent of how actions are perceived (Cohen et al. 1987; Jeannerod 1994), whereas others claim that the processes involved in recalling perceived acts are radically different from those involved in recalling performed acts (Engelkamp and Zimmer 1997). The latter interpretation has been weakened by recent cognitive neuroscience studies that indicate that an action observation/execution matching system is present in the motor cortex of primates (Hari et al. 1998; Rizzolati et al. 1996).

Dolphins have shown an impressive ability to imitate actions involving objects (Kuczaj et al. 1998; Tayler and Saayman 1973; Xitco 1988). It is possible that the flexibility with which dolphins recall and repeat self-performed object-action sequences parallels the flexibility with which they can imitate similar observed events because both abilities involve comparable or shared mechanisms for encoding and accessing representations of events. Interestingly, the only other species that appears to have learned an abstract repeating rule is, like the dolphin, an accomplished mimic. Pepperberg (1994) reported that after a parrot (Alex) had learned to mimic certain vocal sequences, he could be instructed to reproduce a recently produced sequence using the vocal command "Say better." Comparative studies investigating which species are able to imitate and repeat actions may clarify how these two abilities are related.

Conclusions

Past studies of working memory in animals have emphasized visual and spatial recognition abilities (Olton et al. 1992). For example, matching-to-sample (MTS) tasks are commonly used to test delayed conditional discriminations of visual stimuli. Researchers have discovered that subjects in such tasks often base their responses on multi-component representations of past events rather than visual cues alone (Lionello and Urcuioli 1998; Urcuioli and DeMarse 1994). The repeating task learned by the dolphins could be viewed as a MTS task in which the dolphins "choose" features from a sequence of samples (e.g., gestures, actions, objects, and locations) such that they can later identify the correct response among a large number of alternatives. Mercado et al. (1998) showed that dolphins based their responses on representations of actions in the repeating task, and the results of the current study show that at least one dolphin also bases her responses on environmental cues. Thus, dolphins choose a sample that incorporates both internal events, such as the production of actions, and external events, such as the observation of a particular object or location. Such proclivities provide important clues towards understanding how dolphins naturally represent past events.

The repeating task provides a useful way of investigating event representations in the bottlenosed dolphin, and potentially other species as well. The constraints of past methods used to study event representations in nonhumans have made comparisons with performance in humans difficult. The flexibility of the dolphins' concept of repeating is exemplified by the fact that the specificity of event encoding is neither inherent nor fixed within the concept. Because of this flexibility, the repeating task provides a unique and powerful tool for assessing how different species represent the past. Many questions remain concerning dolphins' memories of events, including:

1. How are action events represented in a dolphin's memory?
2. Would a dolphin's ability to recall such events improve if she were specifically taught to attend to the identity of objects?
3. How long can a dolphin retain memories of action events?
4. Would performing an action in synchrony with another dolphin affect each dolphin's ability to remember the action?

It would be surprising to discover that dolphins cognitively process events in ways comparable to humans, given the vast differences in evolutionary history, social structure, linguistic proficiency, and ecology between these two species. Such parallels between the cognitive abilities of humans and non-humans (or the lack thereof) can provide important clues about the basic representational mechanisms involved in event processing.

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