SHORT TERM MEMORY FOR BEHAVIOR IN THE BOTTLENOSE DOLPHIN (TURSIOPS TRUNCATUS)

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Abstract

We tested an adult female bottlenose dolphin's ability to repeat self-performed behaviors after a delay interval. Her memory fidelity was tested using four sets of increasingly long delay intervals. Repeat performance decreased as length of delay increased. However, the dolphin's repeat performance was significantly greater than would be expected by chance at all delay intervals tested (up to 120 seconds). Another study tested the dolphin's ability to transfer her delayed repeat ability to five behaviors not previously tested after incrementally increasing delay intervals. The dolphin was able to repeat three behaviors without error. A post-test analysis characterized the dolphin's posture and any behaviors occurring during delay intervals, in an attempt to identify memory strategies utilized by the dolphin. A final experiment introduced a distracter task, paddle pressing, during the delay interval, to study interference effects. Paddle pressing disrupted the dolphin's memory, but not so much that she remembered nothing.

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Chapter 1
Introduction

General Animal Memory. An animal's short-term, or working, memory, contains newly received information (Herman, 1980). Researchers have long been interested in how and how well this information is represented, what factors affect short-term memory, and how animals can demonstrate what they have remembered. Memory in animals has been studied for decades (see Roitblat, 1987; Kendrick, et.al., 1986). A variety of different types of memory have been examined, including: visual short-term memory in monkeys (D'Amato & Worsham, 1974), spatial short-term memory in rats (Beatty & Shavalia, 1980a,b), and long-term visual memory in pigeons (Vaughan & Greene, 1984). However, less attention has been given to animal memory for behavior or actions. The focus of this thesis is to test the duration of, and processes involved with, memory for self-performed motor behaviors by the dolphin.

Dolphin Memory. Dolphin short-term memory for sounds (Herman & Gordon, 1974; Herman & Thompson, 1982), visual materials (Forestell & Herman, 1988; Herman, Hovancik, Gory, & Bradshaw, 1989), spatial location (Thompson, 1976), and motor behaviors performed by other dolphins (Xitco, 1988) has been examined.

Herman and Gordon (1974) tested a dolphin's auditory short-term memory using a delayed matching to sample (DMTS) task. The DMTS test required the dolphin to listen to a brief auditory "sample" sound, and then find the matching sound again from among two alternative sounds presented after a delay. The dolphin was exposed to more than 300 unique sample tones and tested with delays ranging from 1 to 120 seconds. Performance across trials and blocks ranged from 79% correct to 100% correct. From the method used, the authors determined the dolphin's lower performance levels were related to task acquisition, and not to auditory memory abilities. Overall, the dolphin showed a fairly rapid acquisition of the general matching task, and was able to match sounds with more than 80% accuracy at even the longest delay interval tested (120 seconds). Within the delay limits tested, the dolphin's performance was similar to that reported for primates in a visual short-term memory test (D'Amato & Worsham, 1972).

Herman (1975) tested the effect of interference in the dolphin's auditory short-term memory, again using the DMTS test. Of interest were both proactive and retroactive interference effects. In proactive interference, information from a previous trial interferes with memory for a future trial. In retroactive interference, a stimulus presented after the information to be remembered, but before the memory test, interferes with the information to be remembered (Roitblat, 1987). In one experiment, the inter-trial interval (ITI) and the delay interval were manipulated, and a small set of auditory stimuli (two sounds) were utilized, in order to study the effects of proactive interference. Delays ranged from 1 to 30 seconds; ITIs ranged from 7.5 seconds (the shortest practical time possible between trials) to 60 seconds. An ITI of 15 seconds or less resulted in significantly poorer performance across delay intervals than an interval of 30 seconds or more. Also, more errors occurred in trials where the S+ changed from the previous trial. A change in sample from trial to trial combined with less time between trials made it more difficult for the dolphin to remember which was the most recently heard sample sound.

In a second experiment, auditory stimuli were interposed during the delay interval to assess the effects of retroactive interference. The location of the sound occurrence within the delay interval, and the duration of the sound, was varied independently. In the first part of this experiment, a 4 second tone was played either early (3 seconds into) or late (8 seconds into) a 15 second delay interval. Due to the dolphin's rapid habituation to the interference sound regardless of location in the interval (5 total errors in 48 trials, 4 of which occurred in the first block of trials), this part of the experiment was discontinued. There was no effect of short duration interference either early or late in the delay interval. In the second part of this experiment, a 13 second sound was played in the middle of the same 15 second delay interval. The dolphin performed significantly less accurately during trials with near continuous interference than in control (no interference) trials, and the degree of interference did not lessen over time. From these experiments it is clear that the amount of interference (long duration vs. short duration sounds) has a greater memory effect than the location of interference (early or late) in the delay interval. And, this interference effect may indicate that the dolphin must actively rehearse information in working memory; if not, information is lost.

Herman, et. al. (1989) examined a dolphin's memory for visual stimuli. Their study was divided into four experiments, one of which tested the dolphin's ability to sustain a visual representation in memory over time. The dolphin studied, Phoenix, was familiar with a symbolic language-like system in which object classes, such as balls or Frisbees, were referred to by a specific acoustic symbol. The authors conducted a visual DMTS task using language objects, non-language familiar objects, and novel objects. The dolphin was asked to match these objects cross three different delay sets of increasing maximum delay intervals. During delay set 1, intervals ranged from 1 to 20 seconds. During delay set 2, intervals ranged from 1 to 40 seconds; and during set 3, intervals ranged from 1 to 80 seconds. ITIs averaged 30 seconds for each trial. In past studies (Herman, 1975), this ITI value was sufficient to avoid proactive interference.

The dolphin's performance remained above 90% correct for delays less than 40 seconds, and declined to a low of 73% at the longest delay interval (Herman, et. al., 1989). Also, performance with language objects was significantly worse across delay intervals than performance with non-language or novel objects. One possible interpretation of this result was that the dolphin was using categorization (i.e., "language object" or "not language object") as a strategy to facilitate remembering. In trials of delays longer than 40 seconds, where the matching alternative was in the same category as the non-matching alternative, more confusion occurred. In general, the dolphin's overall performance was comparable to results obtained in an auditory delayed matching to sample task with a dolphin subject (Herman, 1975; Herman and Gordon, 1974).

Thompson (1976) studied dolphin spatial memory. In one experiment, two pairs of paddles were spatially separated, one to either side of the dolphin. One of each pair of speakers was closer to the dolphin, and one each far from the dolphin. The duration of an initial tone heard from a central speaker indicated to the dolphin whether press of a close or far paddle would be rewarded with food. After a delay interval, a second tone from either a left or ride side speaker indicated which close or far paddle to press. This procedure restricted the dolphin from orienting her body towards the paddle she should press after the delay interval, a strategy utilized by other animals in spatial memory tasks (Miles, 1971). Delays of up to 70 seconds were used, and the dolphin's spatial memory was above chance levels for delays as long as 30 seconds.

In a second experiment, only the left hand or right hand pair of speakers was present in the water for a given trial. Again, a sound from a central speaker indicated directly that either a press of the near or far paddle would be rewarded with food. However, the dolphin was not allowed to press the correct paddle until a second tone from a speaker "released" her to do so, after the required delay interval. The dolphin quickly developed a postural strategy during the delay interval, such that her location (forward or not) in the listening area was predictive of which paddle she would press. This posturing was a form of spatial coding, and resulted in the dolphin successfully remembering the correct paddle significantly more often that would be expected by chance at delays as long as 50 seconds. Thus, the dolphin was able to remember spatial information without the use of posture or location cues, although such cues did prove helpful when they could be utilized.

Xitco (1988) studied delayed imitation in dolphins. In one study, Xitco taught each of two dolphins to copy a variety of motor behaviors performed by the other. The dolphins each had a trainer and worked at the same training station, but were separated by a partition. This partition fit over the tank wall, and extended out from the wall and above the water. A dolphin on one side of the partition could see her trainer and the other dolphin, but not the other dolphin's trainer (and vice versa). For some trials, one dolphin was the demonstrator of a behavior, and the other dolphin was given a non-specific gestural instruction, "mimic," which directed her to copy the behavior of the first dolphin. For other trials, the roles of demonstrator and imitator were reversed. Each dolphin was able to imitate a variety of behaviors, both familiar and novel. One dolphin successfully imitated seven of 12 familiar, and two of three novel behaviors. The other dolphin successfully imitated six of 12 familiar, and one of three novel behaviors.

In a second study, Xitco introduced a delay interval between the demonstrator's performance of a behavior, and the mimic instruction given to the imitator dolphin. The testing procedures varied slightly for each dolphin, although each was tested on delays ranging up to 80 seconds. For each dolphin, imitation performance declined as delay intervals increased (from 95% correct to 59% correct for one dolphin, and from 88% correct to 57% correct for the other dolphin). Both dolphins correctly imitated behaviors at levels significantly greater than would be expected by chance at all delay intervals. The dolphins' performance in this experiment implied they were relying on mental representations of each other's behavior.

Animal Memory for Motor Behaviors. The study of action memory in animals is a more recent endeavor (see Herman, 2002 for a review). Cutting (1997) examined the dolphin's ability to repeat, or avoid repeating, a previously performed behavior which was self-selected. A dolphin was previously taught a gesture, called "any," which allowed her to self-select one of five behaviors in a set (Taylor, 1995; Taylor-Gaines & Herman, 1993). The behaviors in the set were "over" (jump over an object), "under" (swim ventral up under an object), "tail touch" (touch an object with your tail), "pec touch" (touch an object with your pectoral fin), and "mouth" (open your mouth about an object). Correct responses to the "any" behavior required that, when asked for the first time, the dolphin select and perform any one of the five behaviors listed; when asked again after performing a selected behavior, the dolphin was required to pick and perform any of the four remaining behaviors (i.e., avoid performing the one last performed).

Cutting also taught the dolphin to repeat a just previously performed behavior, in response to a "repeat" instruction. Cutting then created trials which varied combinations of the "any" and "repeat" instructions, in order to test the dolphin's memory for a previously performed, and self-selected, behavior. Trials were four instructions long, beginning with the specific instruction for one of the five behaviors in the "any" set. The specific instruction was then followed by some combination of "any" and "repeat" instructions. The dolphin had to correctly respond to each instruction of the sequence, by repeating (in response to a "repeat" instruction) or NOT repeating (in response to an "any" instruction) the most recent behavior of the sequence. For example, one trial sequence was "behavior-repeat-any-any," and would have begun with the gestural instruction for tail touch. Once the dolphin touched the object with her tail, she would be signaled "correct" and return to her trainer for the next instruction. On seeing the "repeat" gesture, she should then touch the object again with her tail and return to the trainer. The "any" gesture should then elicit a behavior other than tail touch (e.g. "over"), and the final "any" gesture should elicit a behavior different from over. The dolphin received a fish reward only if she correctly performed each behavior in the sequence. If she was in error at any point in the sequence, the sequence was terminated and no reward was given. Sequences were constructed using each of the specific behaviors as the first instruction, and any combination of subsequent "any" and "repeat" instructions to make up a four-item sequence.

For each of the eight possible different sequence types, the dolphin's performance ranged from 76-99% correct. The sequence type that best demonstrates the dolphin's ability to repeat a self-selected behavior is the following: behavior-any-any-repeat.

Because it contains two "any" instructions in a row prior to the "repeat," it is the sequence which most stringently requires the dolphin to self-select the behavior to be repeated. Likewise, this type of sequence forces the dolphin to represent (in some form) the most recently performed behavior, and not the gesture, which elicited the behavior. To encode the gesture would provide no advantage, since the "any" instruction is only a general one (i.e., does not elicit any single specific response), and is contingent upon a behavior having been performed prior to it. The dolphin was 97.5% correct on this sequence type, indicating that the dolphin was quite proficient at repeating a self-selected behavior.

Mercado, Murray, Uyeyama, Pack, and Herman (1998) examined dolphin memory for a wide variety of different behaviors by asking for a specific behavior through a gestural instruction, and then asking for that behavior again through the "repeat" instruction. Initially, each of two dolphins was asked to repeat 32 behaviors, including simple motor actions and actions towards objects. From the initial training and calibrating of the repeat instruction, four baseline behaviors were identified. The dolphins became highly proficient at repeating these behaviors, and they were incorporated into test sessions along with behaviors not previously formally tested with the repeat instruction (test behaviors). One dolphin was correct on 90% of test behaviors and 94% of baseline behaviors; the other on 57% of test trials and 88% of baseline trials. In many cases, errors consisted of a partial replication of the initial behavior.

The dolphins were also asked to repeat behaviors that they innovated, in order to determine whether they were recalling the previous gesture or the previous behavior. Previously (Braslau-Schneck, 1994), the dolphins had been taught to innovate a behavior in response to a non-specific gestural instruction, "creative." In response to a creative prompt, the dolphin could perform any behavior or its creation. In response to a second creative, the dolphin could again perform any behavior, as long as it was not the just previously performed behavior. The creative instruction required the dolphin to perform a behavior not previously performed in response to that instruction. Both dolphins were able to repeat at least one innovated behavior. Since the instruction to select (create) a behavior was non-specific (i.e., doesn't elicit only one behavioral response), the dolphins' ability to repeat an innovated behavior implied they were recalling the previously performed behavior, not the instruction. Also, inherent in the creative instruction is a non-repeat rule; the dolphin has to perform a "new" behavior in response to each subsequent creative sign. In a repeat trial, if the dolphin were recalling the previous gesture ("creative") instead of the previously performed behavior, she should avoid repeating herself and offer a different behavior.

Next, the dolphins were tested on their ability to repeat newly trained, and thus never previously repeated, behaviors. Each dolphin was trained to perform four novel behaviors that had never been tested with the repeat instruction, to examine whether the dolphins had learned a generalized repeat rule. Again, there were differences in performance: one dolphin repeated novel behaviors correctly on 79% of the trials; the other dolphin repeated 50% of novel behavior trials correctly. These levels translated to above chance performance on two of four novel behaviors for the first dolphin and on one of four behaviors for the second dolphin. These results demonstrated the dolphins had indeed learned a generalized rule of repeat.

Lastly, one dolphin was tested on her ability to perform multiple, sequential recalls of a previously performed behavior. This test was done to provide further confirmation that the dolphins were indeed recalling the previously performed behavior, and not the gestural instruction which prompted performance of the behavior. During this test, only baseline behaviors from the initial experiment were probed. They were done so in a double repeat fashion, where the dolphin was given two repeat instructions following the initial behavior-specific gestural instruction. The dolphin performed all of these trials correctly.

Through this experiment, the dolphins demonstrated that they had developed a generalized rule of repeating, one of the first demonstrations of such ability in a non-human animal. It is unclear, however, what strategies the dolphins used to remember the previously performed behavior. The dolphins may have adopted or retained postures associated with or required by the initial behavior performed, and accessed these associations when required to repeat the behavior. Another explanation for the dolphins' repeat ability is that they simply continued, completely or in part, the first behavior until given the gestural instruction for the second (either repeat or not). This is within the realm of possibility, given that there was no standardized delay between the gestural instruction for the first behavior to be performed and the request for the second behavior. Or, the dolphins may have performed some type of mental rehearsal of the behavior to be repeated, in the event they were instructed to do so. Lastly, there may also be kinesthetic cues, which are specific to specific behaviors, which linger and/or are remembered.

An additional test of the dolphin's memory for past actions was conducted by Mercado, Uyeyama, Pack, and Herman (1999). In this study, one of the dolphins previously tested on her ability to remember previously performed motor behaviors was tested on her ability to remember a variety of different actions performed towards objects.

Such behaviors were called "action events," because they required the subject to encode representations not only of motor actions but also of environmental features corresponding to those motor actions. The dolphin had previously been trained in a gestural language, which allowed her to respond to novel action sequences or combinations of actions and objects upon which to be acted (Herman, et al., 2001). She had also demonstrated proficiency with body part/action combinations. She was now being required to repeat an action to a specified object.

The method for this study was similar to the previous one. In this case, however, the first behavior requested in a given trial consisted of three parts: a specific object gesture, a specific body part, and a specific action (in that order). Although the dolphin had demonstrated proficiency with language instructions previously, she had no experience with such instructions in the repeat experiment context. In the repeat context, a trial was considered correct only if the dolphin responded again to the same object with the same action.

The dolphin was not as accurate at repeating action events as she was at repeating simple motor behaviors. Overall, she was correct on 42% of action event repeat trials. However, she appeared to be more accurate at remembering the action previously performed than the object to which the action was performed. Specifically, she remembered the action correctly in 82% of repeat trials, and the object correctly in 49% of trials. These results (that it seems easier to recall a previously performed action than the action's corresponding object) parallel results of human action event memory studies (Engelkamp and Zimmer, 1997). This study demonstrated the extreme flexibility of the dolphin's repeat concept.

However, this study does not successfully illuminate the dolphin's strategy used for remembering previously performed behaviors. It is possible that the dolphin relied, at least in part, on some recollection of the initial gestural instruction, to carry out the task. It is also possible that, during some trials, she monitored the object toward which to direct a repeated action from the time she performed the initial action event until the time she was asked to repeat it.

The focus of this thesis was to test the duration and processes involved with memory for motor behaviors by a dolphin. Three experiments were conducted. In the first experiment, we assessed the dolphin's performance with a variety of behaviors in the repeat task. This allowed us to select a set of behaviors to be used in the subsequent two experiments. In Experiment 2, the dolphin's ability to remember a previously performed behavior after a delay interval was tested. During this experiment, we introduced the delayed repeat procedure and tested the dolphin's repeat ability using gradually increasing lengths of delays and one set of behaviors; we then tested her conceptual ability further by probing another set of behaviors never previously tested in delayed repeat, and without the gradual increase of delay length. This experiment explored several alternate explanations to the dolphins' repeat ability by imposing a delay interval between the dolphin's performance of the first behavior and the subsequent gestural instruction for a second behavior (either repeat or not). Through this method we could better ascertain the strategies utilized by the dolphin to remember a previously performed behavior. This methodology illuminated (in some trials) whether the dolphin was relying on postural codes or behavioral continuation to carry out the repeat task. With such lengthy delays (up to 120 seconds), this study tested the dolphin much more stringently than the initial repeat work. This study also further explored the breadth, in general, of the dolphin's short term memory ability in relation to previously performed behaviors. In Experiment 3, we introduced a simple motor task (paddle pressing) as an interference variable during the delay interval. We manipulated the location of the interference during the delay interval (occurring either early or late). We expected interference to degrade the dolphin's performance in the delayed repeat task, especially if it were evident the dolphin was relying on postural codes or behavioral continuation as a delayed repeat strategy.

Chapter 2
General Method

Subject. The subject of this study was a 24-year old Atlantic bottlenose dolphin (*Tursiops truncatus*) named Akeakamai (Ake). Ake was housed together with other dolphins in two 15.2 m diameter circular seawater tanks connected by a channel at the Kewalo Basin Marine Mammal Laboratory in Honolulu. Prior to this study, Ake had demonstrated proficiency with numerous cognitive tasks, including: sentence comprehension (Herman, Richards, & Wolz, 1984), vocal and behavioral mimicry (Herman, 2002), video comprehension (Herman, Morrel-Samuels, & Pack, 1990), understanding of indicative gestures (Herman, Abichandani, Elhajj, Herman, Sanchez, & Pack, 1999), judgment of similarity and difference (Mercado, Killebrew, Pack, Macha, & Herman, 2000) and reporting on the presence or absence of objects in her environment (Herman & Forestell, 1985). During test sessions for this study, Ake received a portion (approximately 2.7 kg) of her daily ration of silver smelt, capelin, herring, sardines, and squid.

Prior relevant training. In an earlier study, Ake was trained to repeat a previously performed behavior in response to a gestural instruction from a trainer (Herman, 2002). This training was well documented, and included the following steps: the dolphin was given a specific gestural instruction for a motor behavior (one of four used in training). If correct, the dolphin received a whistle reward and returned to station. The dolphin was then given the repeat instruction followed by the specific gestural instruction previously given (cueing). The dolphin executed the same motor behavior and received a whistle/fish reward. On some subsequent trials, the second specific gestural instruction (cue) was omitted. Trials which required the dolphin specifically not to repeat the initial behavior were interwoven between repeat trials, to be sure the dolphin was processing each instruction conceptually and not relying on some other strategy. This procedure was implemented until the dolphin reached an 80% performance criterion over two sessions on probe (uncued) repeat trials. It took five sessions to reach this criterion.

Ake was then tested on her repeat ability over 24 sessions, using 15 behaviors not previously exposed to the repeat instruction. On each trial, a trainer gestured to Ake to perform a first behavior (B1). After completing B1, Ake was given another gestural instruction for a second behavior (B2). This second instruction either signaled Ake to perform B1 again (a repeat trial) or to perform one of several specific behaviors different from B1 (a non-repeat trial). The repeat gesture was the same for all B1 behaviors regardless of the specific behavior to be repeated; a correct response to the repeat instruction was contingent upon the dolphin's recollection of its last performed behavior. The repeat gesture was given using the trainer's right arm and hand. Holding the elbow to the hip, and the forearm pointed to the right side at a 90 degree angle from the torso, the trainer swung the forearm (hand in a fist) directly across the torso and back to the original position. For a non-repeat trial, B2 was directed by any one of many different specific gestures, each controlling a particular behavior (e.g., back dive, pirouette, twisting jump, butterfly swim, etc.).

Repeat trials included actions towards objects and non-object actions. Overall Ake was 76% correct on repeat trials. There was a significant difference in performance on repeat trials with actions towards objects (84.5% correct) versus non-object actions

(69% correct) (p<.01). In sum, these results are consistent with those demonstrated by two other dolphins in the Mercado et al (1998) repeat study.

General procedure. The repeat gesture and trial sequence described above was employed in the current study. All sessions were organized and run by a supervisor using a pre-planned schedule of trials. Each trial was of the same format, and consisted of two behaviors (B1 and B2) controlled by unique gestures. The supervisor was located on an elevated deck overlooking the tank in which the dolphin was tested. The dolphin's testing station was located at one side of the tank. A trainer, standing on a platform adjacent to the tank wall, interacted with the dolphin socially between trials and provided all gestures to the dolphin during trials. An assistant, with a copy of the pre-planned trials, stood behind the platform (out of the dolphin's view), and verbally directed the trainer as to which gesture to give for each part of the trial.

In response to the supervisor's verbal instruction to begin a trial, the trainer donned opaque goggles and then gave a "pay attention" gesture (consisting of an extended arm and an extended index finger) that required the dolphin to position vertically on her tail flukes facing the trainer. The goggles prevented the trainer from seeing the dolphin's behaviors, and therefore guarded against inadvertent social cueing. As the trainer gave the pay attention instruction, the assistant told the trainer the gesture to be signed for B1. When the supervisor called "ready," the trainer gave the gesture for B1. The supervisor vocally judged the dolphin's response to B1 as correct or incorrect; if correct, the trainer blew a whistle and the dolphin returned to station. The supervisor then instructed the trainer to again give the "pay attention" gesture. The delay interval (if any) then began, and at its completion the trainer was instructed to give the B2 gesture. During the delay interval, the assistant told the trainer the gesture to be signed for B2.

A "blind" observer located on the elevated deck judged the dolphin's performance of B2. This observer stood with his back to the training station, and could not see either the gestural instruction for, or the dolphin's response to, B1. The observer also wore headphones attached to a radio, and listened to music during each trial. This was to prevent him from hearing any sounds coincident with the performance of a particular behavior. Thus, the observer had no knowledge of the first behavior given. Likewise, the observer could not see the instruction given for B2. After the instruction for B2 was given, the supervisor prompted (by tapping on the shoulder) the observer to watch the dolphin's B2 response and label it out loud. If the observer's label of the behavior matched the B2 instruction, then the trial was called correct; a whistle blast was given, and the dolphin received a fish reward and social praise from the trainer. If the blind observer's label did not match the instruction, these reward contingencies were omitted and the dolphin was called back to station by the trainer splashing the tank water with his/her hand. Each trial was video taped for subsequent independent analysis of results. For example, in the event that the "blind" observer was unable to readily label the dolphin's response, the session supervisor labeled the behavior and that judgment was later verified by review of the videotape. This review was done by experienced observers having no knowledge of the required behavior or the supervisor's label.

If Ake's performance of B1 was incorrect or inadequate, she was called back to station by the trainer and the trial ended. Ake was given two additional opportunities at the end of scheduled trials to re-run those in which she missed B1.

Chapter 3
Experiment 1

This first study was used to select a set of behaviors that were typically performed reliably by Ake, and that could be used therefore for B1 behaviors. In the study described in Herman (2002), Ake had been required to perform any of 19 different behaviors as B1 (Table 1, middle column), and then to either repeat or do a different specific behavior as directed by the gestures already described. The 19 behaviors used in that study were: toss, under, mouth, pec touch, pec carry, over, tail touch, head shake, flyback, pirouette, hunchback swim, blow bubbles, snob swim, tail wave, back dive, mermaid, spiral swim, somersault, and butterfly swim. Each of these behaviors is described in the first column of Table 1. Ake was able to repeat all but two behaviors multiple times (two were never repeated), and was able to successfully apply the repeat rule to a variety of behaviors not used in training. The two behaviors never repeated were snob swim and flyback.

Method. For the current study, we reevaluated Ake's performance on twelve of the same behaviors used previously: head shake, flyback, pirouette, hunchback swim, blow bubbles, snob swim, tail wave, back dive, mermaid, spiral swim, somersault, and butterfly swim. The seven behaviors not re-tested for the current study were actions towards objects or tank locations: toss, under, mouth, pec touch, pec carry, over, and tail touch. We opted not to include actions towards objects or specific locations in the current study, in order to minimize the availability of environmental cues for repeating. Past literature has suggested that other non-imitative phenomena (stimulus enhancement, local enhancement, etc.), resulting from environmental cues, could explain some proposed cases of imitation in animals (Howard & Keenan, 1993; Whiten & Ham, 1992). Given that the current task can be considered self-imitation, we wanted to exclude these phenomena as possible explanations for the dolphin's repeat ability. We also probed her repeat ability with five additional behaviors: body wiggle, spit, roll over, tail slap, and twisting jump (see Table 1, last column).

This reevaluation took place over the course of seven sessions. Each session was conducted using the general procedure previously described. The first session consisted of 34 trials. There were 17 repeat trials (one trial each per behavior) and 17 non-repeat trials (where each behavior was used one time each as B1 and B2). After the first session we deleted two behaviors, snob swim and flyback, from the experiment. Ake never repeated these behaviors in the initial repeat study, and she did not repeat them during the first session of Experiment one. Each of the remaining sessions consisted of 30 trials, 15 repeat and 15 non-repeat. All sessions were divided into blocks of trials (approximately 8 trials per block); there was a 30 second ITI between trials, and a two-minute break between blocks. A 0 second delay interval was used; this meant that the dolphin received her instruction for B2 immediately upon adopting the pay attention posture after performance of B1.

Results and Discussion. Aside from the two behaviors deleted after the first session (snob swim and flyback, which Ake never repeated) her repeat performance on individual behaviors ranged from 28.6% to 100% correct (see Table 1, last column). She was 100% correct on nine of the behaviors: head shake, pirouette, blow bubbles, back dive, mermaid, somersault, spit, roll over, and twisting jump.

Table 1. The behaviors tested in the prior study (Herman, 2002) and those selected for current studies (starred items).

Behavior Description (Label)	Prior Study	Retest
	Repeat *N (% correct)*	Repeat *N (% correct)*
Object-oriented behaviors		
Toss an object (Toss)	35/45 (77.8)	
Swim under an object (Under)	35/37 (94.6)	
Place mouth about object (Mouth)	27/28 (96.4)	
Touch object with pectoral fin ["pec"] (Pec Touch)	19/20 (95)	
Inverted swim, object held between pecs (Pec Carry)	4/12 (33.3)	
Jump over an object (Over)	#	
Touch object with tail (Tail Touch)	#	
Behaviors not involving object		
Shake head left and right (Head Shake)*	40/41 (97.6)	7/7 (100)
Lean over backwards (Flyback)	0/10 (0)	0/1 (0)
Pirouette, head and torso out of water (Pirouette)*	6/12 (50)	7/7 (100)
Swim with head hunched over (Hunchback Swim)	4/12 (33.3)	2/7 (28.6)
Blow bubbles underwater (Blow Bubbles)*	28/28 (100)	7/7 (100)
Swim with head held high (Snob Swim)	0/12 (0)	0/1 (0)
Wave tail in air (Tail Wave)	20/20 (100)	3/7 (42.9)
Leap out of water, belly up (Back Dive)*	7/12 (58.3)	7/7 (100)
Arch body on top of tank scupper (Mermaid)@	3/12 (25)	7/7 (100)
Swim underwater while spiraling (Spiral Swim)	10/12 (83.3)	3/7 (42.9)
Somersault vertically (Somersault)*	#	7/7 (100)
Swim inverted while slapping pecs on water (Butterfly Swim)*	#	6/7 (85.7)
Behaviors not used in Herman (2002) but tested for use in the current study		
Wave pecs (Body Wiggle)*		6/7 (85.7)
Spit water from mouth (Spit)*		7/7 (100)
Turn around (Roll Over)*		7/7 (100)
Slap tail on surface of water (Tail Slap)*		6/7 (85.7)
Jump out of water and slap tail stock on surface at re-entry (Twisting Jump)*		7/7 (100)

#: These behaviors were used for initial training of the repeat concept, and thus, their data are excluded from this table

@: This behavior is performed to a specific location in the tank, and was therefore omitted from the current study.

Error responses to the other eight behaviors included many that could be categorized as similar to the behavior that should have been repeated, in one of two ways. One of Ake's eighteen error responses was a hunchback swim (swim with head hunched over) offered as the response to a snob swim repeat trial. In this case, the error fell into the same behavioral category (swims) as the behavior that should have been repeated. Twelve additional error responses preserved behavioral components of the behaviors that should have been repeated. For example, four of the errors offered for hunchback swim repeat trials were blow bubbles (submerge blowhole underwater and expel air, creating bubbles). Typically, the dolphin's head is hunched when blowing bubbles; this hunching during the blow bubbles errors does preserve a key component of the hunchback swim behavior that should have been repeated. This type of response could be considered a partial replication of the behavior to be repeated, which is an important detail in the discussion of imitation. Since the repeat task can be considered self-imitation, it is noteworthy that behavioral replications may not exactly represent all elements of the initial behavior (Whiten & Custance, 1996; Whiten & Ham, 1992). Ake repeated an additional three of the behaviors (hunchback swim, tail wave, and spiral swim) correctly less than half the time, and we opted to exclude those from future experiments.

We excluded one additional behavior, mermaid, from use in further experiments. This behavior, during which the dolphin curls its head and tail into the air while on its side, is done to one of two scuppers (top drains) on the tank wall. In spite of Ake's perfect performance on this behavior, we excluded it since it was done to a particular tank location. Thus, based on this retesting, and on our exclusion of behaviors towards objects/locations, the resulting set included 11 behaviors: head shake, pirouette, blow bubbles, back dive, vertical somersault, spit, roll over, twisting jump, tail slap, butterfly swim, and body wiggle. Ake repeated these behaviors correctly on six or seven attempts of seven total opportunities, $p<.01$ (summed binomial test; see Table 1, last column).

Chapter 4
Experiment 2

During this experiment, Ake's ability to recall a previously performed behavior after a delay interval was tested for the first time. The experiment was run in three parts. In Part A delays were tested incrementally, which consisted of exposing the dolphin to sets of delays that increased in length of time both within and across sets.

Part A – Incremental Delay Testing

Method. There were four delay sets, consisting of six delay intervals each. Within a given test session, consisting of approximately 16 trials, repeat trial density was approximately 75%. Density varied only if the dolphin was unable to successfully perform B1 for one or more repeat trials during a given session. Trials were run in blocks of four with a two-minute break between blocks, and an equal number of repeat and non-repeat trials per block. Trials were balanced within delay sets such that each behavior appeared an equal number of times both as B1 and B2 with a given delay interval. We selected 6 of the 11 behaviors to be used as test behaviors during incremental delay testing with each of the four delay sets: butterfly swim, vertical somersault, roll over, tail slap, head shake, and twisting jump. We reserved the other five behaviors for Part B.

The delay interval and the inter-trial interval were prompted, timed, and standardized using a computer program. This program was generated with Max 3.5 custom software, and was keyboard controlled by a research assistant in a remote room observing trials on a video screen. The delay interval for each trial was predetermined by a balanced schedule of trials and entered into the computer program. For the balanced schedule, no specific delay interval appeared twice in a row, each block of trials contained four different delay intervals, and each delay interval was represented an equal number of times within a given session. The delay interval was started by the press of a computer key as soon as Ake returned to the training station and went into the "pay attention" posture after performing B1. The computer projected the verbal cue "ready" through an outdoor speaker to the trainer when the specified delay interval was complete. The trainer gave the instruction for B2 on hearing the "ready" cue. A standardized ITI of at least 30 seconds was maintained after each trial.

Four delay sets were used, consisting of the following intervals: Set 1 (0, 5, 10, 15, 30, 45 sec), Set 2 (5, 10, 15, 30, 45, 65 sec), Set 3 (5, 15, 30, 45, 65, 90 sec), and Set 4(10, 30, 45, 65, 90, 120 sec). Delay intervals and sets were designed based on previous short-term memory studies with dolphins (Herman, 1975; Herman, et al. 1989) and took into account logistical and dolphin mood considerations. Typical research designs consist of sessions containing, on average, anywhere from 12-30 trials, which can be conducted during the course of a 30- to 45-minute long research session. Deviations from these guidelines can result in a drop in the dolphin's mood and/or performance. We deliberately increased not only the total range of delay intervals within a set, but also the increase between delay intervals within a set, from the first to last delay set. For example, the range of Delay Set 1 was 45 seconds, and the biggest increase from one delay to the next in that set was 15 seconds. In Delay Set 4, the range was 110 seconds, and the biggest increase between intervals was 30 seconds.

In order to familiarize Ake with the delay procedure, we began Delay Set 1 using only the first three shortest delay intervals for two sessions. During sessions 3 and 4, we added the fourth, next longest, delay interval. During sessions 5 and 6, we added the fifth delay interval. The remaining three sessions of Delay Set 1 utilized all 6 delay intervals.

Table 2. Number of trials per delay interval per delay set.

Delay (sec)/ Set number	**0**	**5**	**10**	**15**	**30**	**45**	**65**	**90**	**120**
1	24	24	24	18	12	6			
2		12	12	12	13	12	12		
3		12		12	12	12	12	12	
4			12		12	12	11	12	12
Total	24	48	48	42	49	42	35	24	12

For all sessions, trials were balanced across behaviors and delay intervals. For the remaining three delay sets, all 6 delay intervals were incorporated and balanced from the very first session. Ake received a pro-rated number of fish for any correct trial based on the length of the delay interval. Correct trials with intervals of 30 sec or less were rewarded with one fish, correct 45-sec trials were rewarded with two fish, correct 65-sec trials were rewarded with three fish, correct 90-sec trials were rewarded with four fish, and correct 120-sec trials were rewarded with five fish. Table 2 shows the number of trials per delay interval per delay set.

Results and Discussion. We conservatively estimated chance performance at one correct repeat in six trials (p=.166), as there were six behaviors in the set used during Experiment 2, Part A. Specifically, there were six possible behaviors Ake could offer as correct responses to the repeat instruction. We erred on the side of a conservative estimate, although Ake could, and on occasion did, offer behavioral responses outside of the set tested.

Overall, Ake correctly repeated 282 (87%) of 324 of repeat trials. Her performance during this experiment exceeded her performance in the previous repeat study (Herman, 2002). Figure 1 shows the percentage of correct responses for each set of delays. In general, there was an inverse relationship between delay and performance level. However, her lowest level of performance was still a relatively high 66.7% (p<.01), occurring at 45 sec for both Sets 1 and 2 and at 120 sec for Set 4. Ake's performance at the longest delay interval in each of the four sets was statistically significantly above chance levels (p<.01), using the summed binomial test. While increasing the delay interval did make the repeat task more difficult, Ake still performed very well.

Figure 1. Repeat performance as a function of delay (seconds)

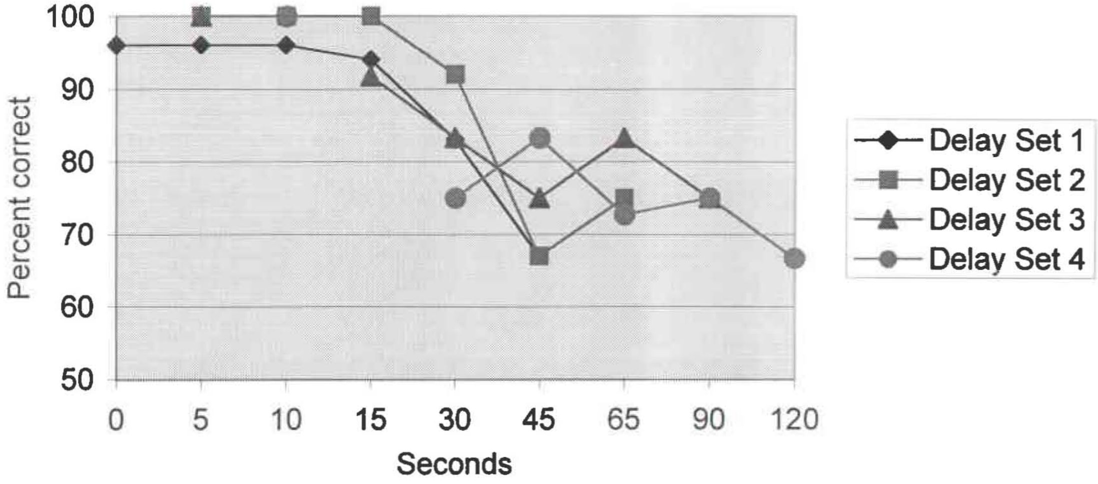


Figure 2. Repeat performance with and without the roll over behavior

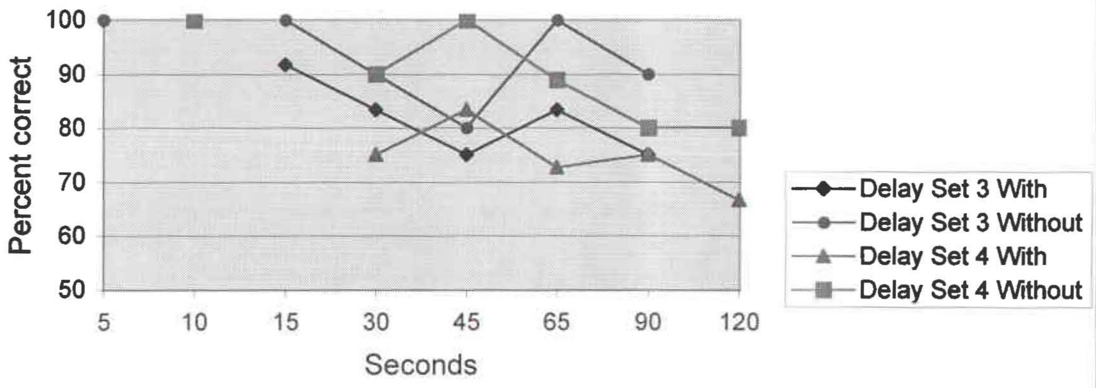
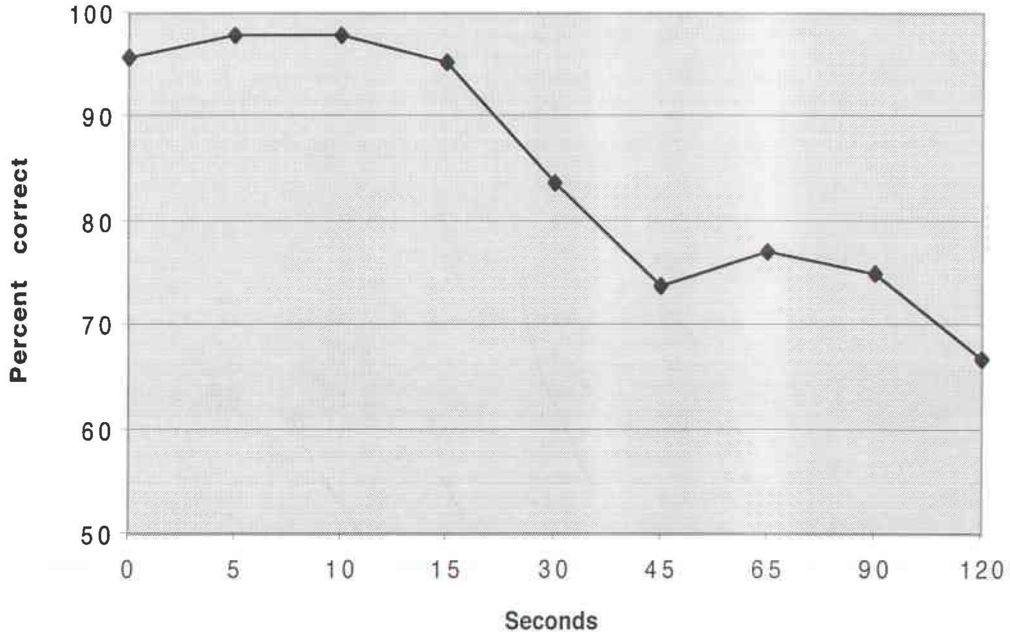


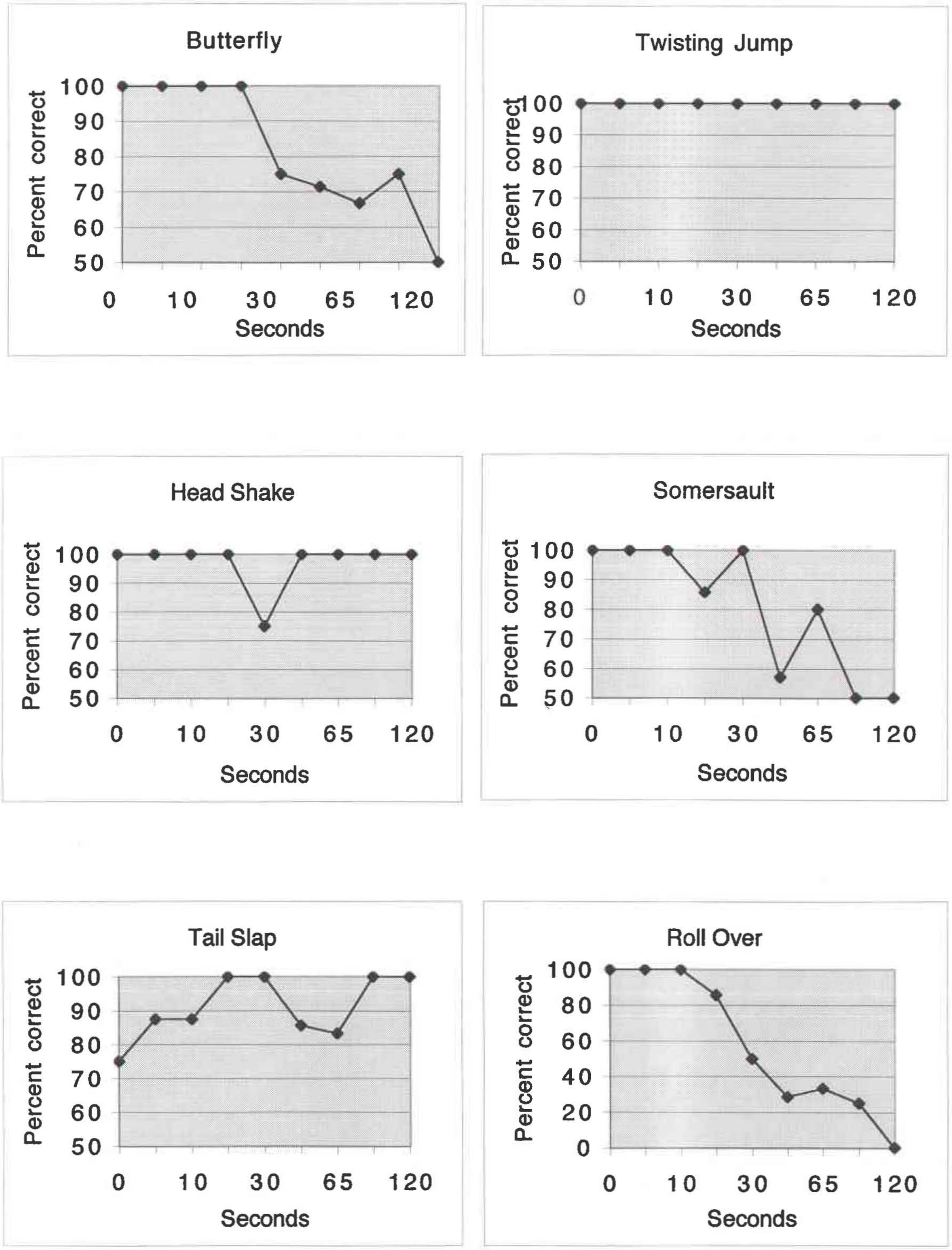
Figure 3. Overall repeat performance as a function of delay (seconds)



Her performance relative to each behavior was consistently high during Sets 1 and 2, ranging from 83-100% correct. During Delay Sets 3 and 4, there was a decreasing trend (42% and 25% correct, respectively) in Ake's repeat performance with the "roll-over" behavior which approached significance, F(3,20)=2.54, p <.1. Otherwise, her performance relative to behaviors remained high, continuing to range from 67-100% correct. If we consider Ake's performance across delays minus roll over trials, she performed correctly on 56 (93%) of 60 trials in Set 3, and on 53 (90%) of 59 repeat trials in Set 4 (see Figure 2).

Her overall performance ranged from 67-98% correct across delay intervals (see Figure 3). In general, the shorter the delay interval, the better Ake's performance. Table 3 shows the number of trials run per behavior and delay interval, and Ake's performance at each behavior and delay interval. Figure 4 graphically displays Ake's performance by behavior and delay interval. (Note that due to her poorer performance, the scale of the roll over graph is different than the scale of the other graphs.) Ake was most successful at repeating the twisting jump behavior at all delays. It is possible that jumps are easier to remember, than other types of behaviors. However, as only one aerial behavior was tested in this part of the experiment, it is difficult to make such a conclusion. It is also difficult to make comparisons between a dolphin's memory for its own behavior (of a particular type) and its memory for another dolphin's behavior. For example, Xitco (1988) only utilized one aerial behavior during his delayed imitation experiment: over. However, this behavior is done towards an object, and thus performance cannot be compared with Ake's repeat ability of aerial behaviors. In general, memory for each type of behavior (jumps, swims, and behaviors close to the training station) was very good.

Figure 4. Overall performance of each behavior at each delay interval



It is unclear why Ake's repeat performance with the roll over behavior declined significantly. Of interest were the behaviors offered in error. During delay Sets 1 and 2, Ake offered error behaviors that preserved the spinning element of the roll over behavior: spiral swim and pirouette. The spiral swim behavior consists of the dolphin spiraling while swimming underwater. The pirouette consists of the dolphin spinning while raising its body several feet out of the water. During delay Sets 3 and 4, Ake's roll over repeat errors increased in variety. She continued to offer pirouettes, but also offered head shaking, blowing bubbles, vertical somersault (one time), and no response. There were 23 additional repeat error responses to the other five behaviors in the set. As with roll over repeat errors, many of the other errors preserved key components of the behavior that should have been repeated. For example, Ake offered body wiggle as an error response to four of eight butterfly swim repeat trials. The body wiggle preserves the pec waving portion of the butterfly swim. Ake made an additional two butterfly swim repeat error responses; for each one, she waved a pec fin while swimming on her side. This response preserves not only the pec waving aspect of the butterfly swim, but also the swimming aspect; the only part of the behavior not replicated was the dolphin's orientation, which should have been ventral surface facing up (not to the side). In sum, 13 of the additional 23 repeat errors during this experiment replicated either the category of behavior to be repeated (like swims), or some aspect of the initial behavior (like spinning, for roll over), or both, just as in Experiment 1. This continues to be an important point, as the dolphin is retaining prominent elements of the behaviors to be repeated within her error responses.

Table 3. Number of correct trials/total number of trials conducted for each behavior at each delay interval.

Delay (sec)/ Behavior	0	5	10	15	30	45	65	90	120	Total
Butterfly swim	5/5	8/8	8/8	7/7	6/8	5/7	4/6	3/4	1/2	47/55
Twisting Jump	4/4	8/8	8/8	7/7	8/8	7/7	6/6	4/4	2/2	54/54
Head Shake	3/3	8/8	8/8	7/7	6/8	7/7	6/6	4/4	2/2	51/53
Tail Slap	3/4	7/8	7/8	7/7	9/9	6/7	5/6	4/4	2/2	50/55
Vertical Somersault	4/4	8/8	8/8	6/7	8/8	4/7	4/5	2/4	1/2	45/53
Roll Over	4/4	8/8	8/8	6/7	4/8	2/7	2/6	1/4	0/2	35/54
Total	23/24	47/48	47/48	40/42	41/49	31/42	27/35	18/24	8/12	282/324

During Part A, Ake was correct on 100 (99%) of 101 non-repeat trials. This performance level indicates she was attending to the instructions for B1 and B2 rather than relying on context or other cues to govern her repeating behavior.

Part B – Transfer Testing

In Part B, we tested the dolphin's ability to repeat self-performed behaviors after a delay interval, using five behaviors never previously repeated after a delay. This was a test of Ake's ability to transfer her delayed-repeat concept from familiar behaviors to behaviors novel to the delay task. As noted previously, we reserved five of the 11 behaviors (back dive, pirouette, blow bubbles, spit, and body wiggle) for first time exposure during this transfer test. We also removed the *roll over* behavior from the original set because of Ake's poor performance with this behavior during the last half of incremental delay testing.

Method. We selected five of the delay intervals previously tested: 30, 45, 65, 90, and 120 seconds. A balanced Latin-Square design was used to determine the order of each of the five transfer behaviors relative to the five delays. Transfer behaviors were probed with delays in a random and balanced fashion as determined by the Latin Square (i.e., delay intervals were assigned in a different and random order to each), in order to control for any effects of practice within the transfer test as well. For example, the first repeat trial tested with the back dive behavior was at a 45-sec delay. The first repeat trial tested with the blow bubbles behavior was at a 90-sec delay. Neither of these delay intervals are the shortest one tested in this part of the experiment.

Sessions were formatted similar to that of Part A. However, transfer trials were interposed between repeat and non-repeat trials using the five remaining behaviors from

Part A (now called baseline behaviors): twisting jump, somersault, head shake, tail slap, and butterfly swim. Baseline behavior trials using a sixth delay interval (10 sec) were interposed in a balanced fashion two to three times during each transfer session. This allowed baseline trials to be balanced by behavior and delay interval over the course of the test of each transfer behavior. Repeat trial density was again approximately 75%, and only one or two transfer trials were probed within each session. Trials were again run in blocks, and no more than one transfer trial was probed per block. All of the controls used during incremental delay testing were again in place for transfer testing.

Results and Discussion. Ake's performance with the baseline behavior repeat trials was near ceiling levels. She made only one error with the tail slap behavior at a 65-second delay. She was also 100% (55/55) correct on non-repeat performance during the transfer test.

Ake repeated three of the five transfer behaviors without error across all six of the delay intervals. These behaviors were: back dive, pirouette, and blow bubbles. She failed to repeat the other two behaviors, spit and body wiggle, at any delay interval. We again conservatively estimated chance performance at one correct repeat in six trials ($p=.166$), as there were six possible behaviors Ake could offer as correct responses to the repeat instruction during the test of each transfer behavior (five baseline behaviors plus one transfer behavior). Ake's repeat performance relative to each delay interval was statistically significant ($p<.05$), using the summed binomial test. That Ake was able to transfer to three previously untested behaviors, ordered using a Latin Square design, at all delay intervals without error discounts the likelihood of practice as an explanation for her delayed repeat ability. Clearly, Ake had no difficulty with the length of delay during this part of the experiment.

Of interest were her errors for each of the missed behaviors; for all spit errors she offered the head shake behavior, and for all body wiggle errors she offered a butterfly swim. Both of these default behaviors are baseline behaviors from the initial set used during incremental delay testing. In addition, each of the default behaviors preserved components of the behaviors that were to be repeated. For example, the spit behavior involves movement of the dolphin's head down (in order to fill the mouth with water) and then back up (to spit the water from the mouth into the air). In fact, in the previous experiment, we did see Ake offer a head nod behavior (moving the head up and down) twice in error for head shake repeat trials. The head shake behavior also involves movements of the head, from side to side. During informal training sessions, the dolphin occasionally offers up and down head movements when asked for side to side, or vice versa. Likewise, the body wiggle behavior requires the dolphin to wiggle both pectoral fins simultaneously from side to side. The butterfly swim is an extension of that behavior, requiring the dolphin to swim on her back while slapping both pecs on the water's surface. Again, these types of error responses (which preserve key components of the initial behaviors) are consistent with results from Experiment 1 and Part A of Experiment 2.

Part C - Postural Analysis

It is likely that, for some behaviors to be repeated in this experiment, Ake relied on her ability to adopt a particular posture during the delay interval. This posture could then serve as an associative stimulus once it came time to repeat the behavior. It is important to note that some postures may not have been salient to human observers.

Method. In order to determine if Ake was using postural coding as a memory strategy, we conducted a post-test video analysis of some trials. We selected all 30-sec delay trials in Part A of Experiment 2 for review. This delay interval was tested in each Delay Set of Experiment 2, and was sufficiently long enough to allow viewing of any posture or movement effected by Ake. Thus, we reviewed a total of 48 trials, eight each of the six behaviors tested in that experiment. We selected the following criteria for use in evaluating Ake's posture: head movement, pec movement, tail position, vertical angle, and vocalizations. These criteria were selected as they were the only postures or behaviors likely to be discernible by a human observer. For each trial, we evaluated whether head or pec movements occurred, and if so, characterized them. We noted whether Ake was upright on her tail during the delay interval, and if not, approximately how far off (in degrees) she was from vertical. We also listened for the presence or absence of vocalizations from Ake during the delay interval. We recorded all observations and grouped them by behavior. Due to the level of algae growth in the dolphins' habitat on certain days, and glare on the water's surface, it was difficult to evaluate all of these criteria on some trials.

Results and Discussion. Table 4 displays the number of trials where particular criteria could be observed occurring for each of the six behaviors as B1. Note that where the total for a given block is less than eight, that the corresponding criterion could not be evaluated for some of the trials. Vocalizations were present in 29 (60%) of the 48 trials reviewed, and Ake vocalized during at least three of the eight trials conducted for each behavior. Head movement was present in 40 (83%) of the 48 trials, and was present in at least five of the eight trials run for each behavior. In the majority (36/40) of the trials with head movement, the movement consisted of Ake nodding her head up and down. During seven of the eight head shake trials, head shaking (head moving from side to side) was also present. Shaking was not seen during trials with any other behavior as the B1. Pec movement could only be seen in five (10%) of the 48 trials reviewed. Four of the trials in which pec movement was observed during the delay interval had butterfly swim as the B1. The pec movement consisted of Ake lifting her pec fins up. Pec movement was not seen in 28 trials, and could not be verified in 15 trials. Ake's tail position could be determined in 25 (52%) of the 48 trials. In 19 of these trials, Ake was standing upright on her tail. Four of the trials when Ake's tail was not on the bottom were roll over trials, and Ake made errors on three of those four trials (i.e., if her tail position was a physical memory strategy, it did not prove to be a successful strategy). Ake had a curve in her body, or was off vertical by as much as 90 degrees, in 18 (38%) of the reviewed trials. Her body was curved in at least one trial for each behavior. Body curving or being off vertical was most prevalent during the delay interval of roll over trials (7/8). Again, however, Ake was least successful at repeating the roll over behavior; her posturing did not help her repeat that behavior. Ake's vertical position could not be verified in 16 of 48 trials.

The presence of a posture or movement during the delay interval only seemed evident for two of the six behaviors. Ake's lifting of her pec fins was clearly evident during the delay interval after her performance of the butterfly swim behavior; this behavior requires Ake to swim on her back at the surface and slap her pec fins on the

Table 4. Number of trials per each B1 with corresponding postures or behaviors occurring during the delay interval.

B1 Behavior	**Vocals**	**Head movement**	**Pec movement**	**Tail position off bottom**	**Vertical angle not 0**	**Number correct**
Butterfly Swim	4/8	5/8	4/6	0/5	1/5	6/8
Head Shake	6/8	7/8	0/6	0/4	1/5	6/8
Roll Over	3/8	7/8	0/6	4/4	7/7	4/8
Somersault	6/8	6/8	0/5	2/5	4/5	8/8
Twisting Jump	5/8	8/8	0/5	0/4	2/5	8/8
Tail Slap	5/8	7/8	1/5	0/3	3/5	8/8

water. Head shaking (essentially continuation of the behavior just performed) during the delay interval was clearly evident after performance of the head shake behavior. It is possible that other observed behaviors and postures were overlapping cues for several of the behaviors. For example, vocalizations were heard during delay intervals after each of the six behaviors. It is possible that Ake was repeating some sort of label of the behavior to be repeated, and she could use that strategy regardless of her previously performed behavior. If this labeling were in fact occurring, we would expect her vocalizations to be different depending on which behavior preceded the vocalization. However, as we did not perform acoustic recording or analysis, we cannot determine the character of Ake's vocalizations. It follows that the postures and movements observed during this experiment are representative of those present in trials (of different delays) that were not reviewed. Likewise, while several of these postures or movements could not be observed in particular trials (due to glare or algae growth), it seems reasonable that they may still have been occurring. And, although we were unable to observe other postures or movements coincident with other behaviors, they still could have been occurring.

Chapter 5
Experiment 3

During this experiment we introduced a distracter task during the delay interval. This task was intended to interfere with any mental or physical strategy Ake may have utilized during the delay interval to help her remember a behavior to be repeated. A mental strategy may involve some type of covert rehearsal or representation of the behavior just performed; a physical strategy may consist of a posture associated with the behavior just performed, or some type of associative response specific to that behavior (Lars-Goeran & Archer, 1985). A decrement in the dolphin's repeat ability following a distracter task would indicate the dolphin's reliance on such rehearsal methods as one strategy for performance of the repeat task.

Method. It was important to select a distracter task stringent enough to disrupt rehearsal or postural coding, and yet one that the dolphin could not interpret as a behavior to be repeated. It did not seem feasible to select another regularly performed behavior from the dolphin's everyday repertoire. Paddle pressing is a task not typically requested with other behaviors during the course of a "play" training session with the dolphins; rather, it is most often used as a response option during research paradigms. Thus, it typically is not used in the same contexts as other, routine dolphin behaviors (like jumps and swims). Theoretically, had we asked the dolphin for such a behavior during the delay interval, after the performance of the official B1, this behavior could have, in the dolphin's mind, become a "new" B1 to be repeated upon termination of the delay interval. In order to avoid this problem, we needed to select a distracter task different enough from everyday dolphin behaviors under stimulus control. We selected paddle pressing as the distracter task. Ake had extensive experience with paddle pressing in other contexts (see Herman & Forestell, 1985), and within four sessions, we introduced her to the additional requirement of paddle pressing during the delay. This paddle pressing required significant enough movement on Ake's part to be incompatible with movements or postures she might otherwise choose to adopt during the delay interval, and thus seemed highly likely to interfere with postural coding. It is also possible that the task was incompatible with mental memory strategies. Paddles consisted of a PVC frame that could be mounted over the tank wall at the specified distance from the trainer. A PVC pipe with rubber tubing extended out and down a few inches over the water; a correct paddle response required the dolphin to touch the extended pipe with her rostrum.

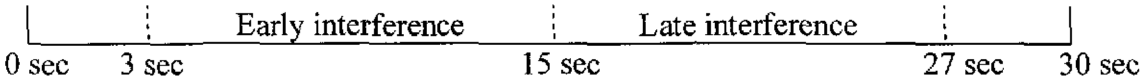
There were eight sessions, counterbalanced AABBBBAA between control sessions (designated "A," with no paddle pressing during the delay interval) and test sessions (designated "B," with paddle pressing during the delay interval). Counterbalancing monitored for effects of paddle pressing on the dolphin's global repeat ability. We standardized the delay interval across all sessions at 30-sec. The set of behaviors tested included the five remaining behaviors from the incremental delay set testing (butterfly swim, vertical somersault, tail slap, head shake, and twisting jump) and the three transfer behaviors with which Ake was successful (pirouette, blow bubbles, and back dive). Paddles were introduced at the beginning of a test session, and were located one each to the dolphin's left and right, approximately 122cm from the center of the training station. Paddles were present regardless of the type of session (control or test); no paddle pressing was required during control sessions.

Sessions consisted of 16 trials, eight repeat and eight non-repeat. Each of the eight behaviors was repeated once per session, and served as the B1 and B2 for non-repeat trials once each per session. Trials were divided into four blocks, with a two-minute break between blocks and a 30 second inter-trial interval.

The temporal location of the paddle-pressing task within the delay interval was manipulated, such that paddle pressing fell either early or late within the total delay interval (see Figure 5). We modified our computer program to prompt the trainer to instruct the dolphin to press paddles beginning at either three seconds (early interference) or fifteen seconds (late interference) into the delay interval. At the prompt, the trainer would use the indicative (pointing) gesture (Herman, et al, 1999) to prompt Ake to touch either the left or right side paddle with her rostrum. Pointing was always done cross-body, to make it as distinct as possible from regular gestural instructions. The trainer would indicate for Ake to touch a second paddle (again, either to the left or right) as soon as she touched, and then removed, her rostrum from the first paddle. This continued until the computer indicated the end of the pressing interval. Regardless of the timing of the start prompt, the computer would cue for the end of the paddle pressing interval twelve seconds after the start prompt. At that time, the trainer would prompt the dolphin to adopt the pay attention posture for the remainder of the delay interval.

During the majority (50/60) of 12-sec paddle pressing intervals, Ake performed three paddle presses. During seven of the intervals she performed four paddle presses; during three of the intervals she performed only two paddle presses. The direction of paddle presses was balanced across trials.

Figure 5. Temporal location (either early or late) of paddle pressing distracter task within 30-second delay interval



Results and Discussion. Chance performance during this experiment was considered, conservatively, to be one correct response in eight trials ($p=.125$), as there were eight behaviors to be repeated. Ake's performance was near ceiling levels during the first two control sessions (14/15 trials, 93.3%, correct). Yet, she performed correctly on only 9 (29%) of 31 repeat trials during which interference occurred. This was a significant drop in repeat performance, χ^2 (1, n=31) = 10.9, $p<.05$ (see Figure 6). However, this performance was still significantly greater than would be expected by chance ($p<.05$), using the summed binomial test. In the figure, the first three comparisons (column pairs) are of Ake's repeat and non-repeat performance before the distracter task, during the distracter task, and after the distracter task, respectively. The latter two comparisons are of Ake's repeat and non-repeat performance during trials with early and late interference respectively. Ake's overall repeat performance, both with and without interference, was statistically significantly greater than would be expected by chance, $p<.05$ (summed binomial test).

There was no significant effect of location of interference, either early or late, within the delay interval on repeat performance, χ^2 (1, n=31) = .0261, $p>.5$. Ake correctly performed 4 (25%) of 16 repeat trials containing early interference. She correctly performed 5 (33.3%) of 15 repeat trials containing late interference. Had we seen a significant difference in repeat performance relative to the location of interference, we may have inferred things about Ake's encoding strategies. For example, had we seen a significant decline in performance during trials with early interference, we may have concluded that this location of interference disrupted Ake's prospective coding. In this case, however, we can draw no such conclusion.

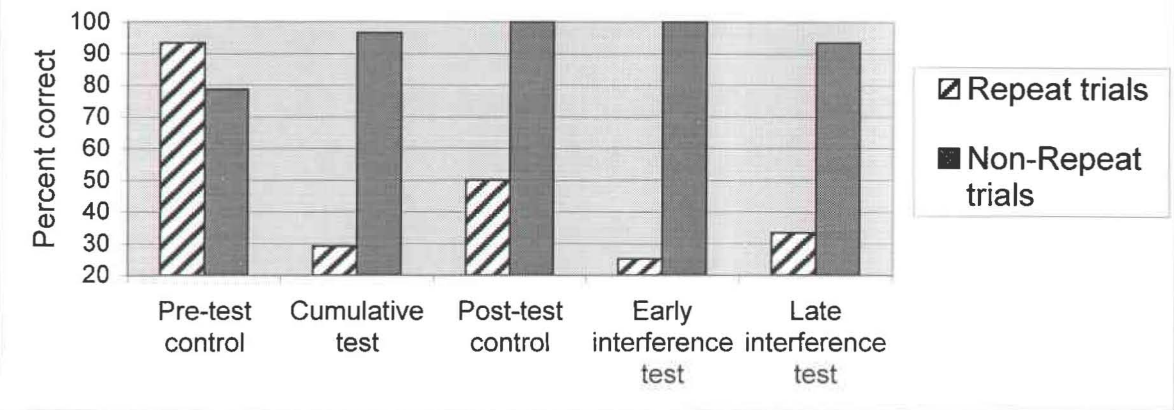


Figure 6. Interference test performance

Five of the 22 repeat error trials (23%) were ones during which Ake performed four paddle presses during the delay interval. However, there was only a trend towards a significant effect (χ^2 (2, n=60) = 5.22, p<.1) of number of paddle presses on Ake's performance. Ten of the 22 repeat errors (45%) were on trials involving behaviors from the transfer test. It is possible that Ake's performance on these trials was lower during the distracter task because she had had less experience with repeating these behaviors after a delay interval. Thus, perhaps her strategies for remembering these behaviors were less well developed. Had we continued to run this experiment for a longer period of time, we might have seen an improvement in Ake's repeat performance with these behaviors.

Ake performed only 8 (50%) of 16 repeat trials correctly during the last two control sessions. This was a significant decrease in repeat session performance from the first two control sessions, χ^2 (1, n=31) = 7.06, p<.01. This may indicate that the interference may have actually affected Ake's conceptual understanding of the task as a whole, instead of simply making the task more difficult.

Because Ake's repeat performance with distraction was significantly worse than her repeat performance without distraction, we can infer that the distracter task disrupted Ake's memory strategies. It seems likely that the paddle pressing distracter task disrupted not only Ake's use of physical memory strategies, like postural coding and behavioral continuation, but also her use of mental strategies, like rehearsal and representation. In addition, it is likely the task disrupted any kinesthetic coding upon which she was relying. The act of paddle pressing would have potentially created new and different physical sensations, which would have replaced those left over from the B1 just performed. Overall, the paddle pressing distraction had a significant effect on Ake's repeat ability compared to the control condition, but not a large enough effect that she remembered nothing (i.e., less than chance performance).

Interestingly, Ake's repeat errors during the distracter task seemed largely to consist of default responses: head shake and twisting jump. She offered the head shake behavior as an error response in 17 of the 22 incorrect trials, and the twisting jump behavior in 4 of the 22 trials. In some cases these repeat error responses preserved components of the initial behavior performed. For example, a twisting jump behavior error following the performance of a back dive preserves the aerial component of the initial behavior. Likewise, a head shake error response following a blow bubbles preserves the head motion component. There were three behaviors Ake never correctly repeated during the distracter task: butterfly swim, back dive, and blow bubbles. Two of these, back dive and blow bubbles, were transfer behaviors. It is possible these were more difficult to repeat after distraction because Ake had less experience repeating them overall.

During the two control sessions after the distracter test, Ake made eight repeat errors. Two of these errors, offering back swim for a back dive repeat, still retain an element of the behavior to be repeated. The back swim behavior requires the dolphin to swim around underwater with her ventral surface up; the back dive behavior requires the same ventral up orientation. Ake's six remaining error responses during the late control sessions did not seem to preserve elements or behavioral categories of the behaviors that should have been repeated.

In the various imitative capacities they have demonstrated, dolphins may rely on mental representations or kinesthetic/proprioceptive feedback (Herman, 2002), or other strategies like postural coding or behavioral continuation (Mercado et al, 1998). Herman, Morrel-Samuels, and Brown (1989) tested the dolphin's delayed mimicry ability after a delay interval, and required the dolphin to perform a distracter behavior (another behavior under stimulus control) during the delay, in order to prevent the dolphin from postural coding or behavioral continuation. The dolphin was still able to successfully mimic behaviors, which the authors interpreted to mean that she was relying on mental representation, and not alternative explanations, in order to correctly mimic behavior. According to that explanation, it follows Ake must not have been relying on mental representations in order to repeat herself; had she been relying on such representations, we would have expected her repeat performance during the distracter task to be better. However, the actual data from that presentation were unavailable at this writing. Thus, it is unclear what length delays were used with distraction, which behaviors were successfully mimicked, and exactly how many behaviors were mimicked. It is unclear whether there was any drop in the dolphin's mimicry performance, even though she was still able to successfully mimic behaviors after distraction. Ake was also still able to repeat behaviors after distraction, albeit not as well.

However, there are alternate explanations. From the review of Ake's posture and movement during the delay interval, it is apparent that some posturing is occurring. However, it is also clear that strategies (even physical ones) on which the dolphin may be relying may not be readily apparent to the human eye. It is likely the dolphin relies on a variety, or combination, of strategies, in order to successfully repeat previously performed behaviors. Some behaviors to be repeated lend themselves more to one strategy or another. For example, memory for a jump lends itself much more to the mental representation strategy, while memory for shaking one's head lends itself to behavioral continuation. So it seems possible that depending on how the dolphin is conceptualizing the repeat task, the distracter task may have effects on several of the strategies employed. In addition, the distracter task, which obviously could have disrupted the dolphin's physical memory strategies, could also very well have disrupted her mental strategies. The task did require Ake to attend to and process additional gestural instructions. It should be noted that Ake never touched a paddle in error (i.e., touching the paddle to her right when she was directed to touch the one to her left), and she never offered a paddle press as a response to a repeat instruction. In an auditory memory interference task, distraction in the auditory modality was also disruptive to the dolphin's memory ability (Herman, 1975). That study did not test the effects of visual interference on auditory memory, although anecdotally, it reported that visual events, which happened accidentally during the course of some trials, did not disrupt the dolphin's auditory memory performance. Comparisons have also been drawn with primate studies (Worsham & D'Amato, 1973), which found that extraneous visual stimuli disrupted monkeys' memory for visual items. The current study found that physical activity was disruptive to the dolphin's memory for motor behavior. It is also possible that the physical task may have been disruptive to mental strategies used to remember behavior.

Also, curiously, Ake could be heard vocalizing during the delay interval of many different trials in Experiment 2. Unfortunately, we did not record or analyze these whistles, and thus cannot determine their significance, if any. These vocalizations could simply have been superstitious behaviors, ones that arose coincident with Ake receiving reinforcement. Ake may have continued to vocalize frequently during delay intervals in an attempt to get reinforced, even though reinforcement was not contingent upon her vocalizing. It is also possible that Ake used whistles as a sort of acoustic cue; potentially she was vocally rehearsing her own "label" of her most recent behavior aloud, as a reminder during the delay interval. Likewise, it is also plausible that there was something inherent in the distracter task we selected which disrupted the dolphin's conceptualization of the repeat task itself. Also, it is possible, but not mandatory, that the dolphin uses different strategies depending on the type of imitative task (for example, self- vs. social-imitation).

Chapter 6
General Discussion

The current study. Ake demonstrated the ability to repeat a variety of different types of behaviors (swims, jumps, and close to station behaviors) after delay intervals ranging from zero seconds to as long as two minutes (the longest delay tested). She successfully repeated all but two behaviors multiple times at a variety of delay intervals, and repeated several behaviors without error at multiple delay intervals. Ake also demonstrated the ability to spontaneously repeat three of five behaviors never previously tested after a delay interval. Clearly, memory for salient features of behaviors were important to Ake's ability to do the delayed repeat task.

Imitation studies with the dolphins have shown that while demonstrations of a given behavior to be copied may vary, the dolphin is still able to determine the critical components of the behavior and replicate those components (Herman, 2002). In many cases, Ake's performance of B1 in a repeat trial was much less well developed than her subsequent performance of B2. For example, for many initial twisting jumps, Ake jumped out of the water only as much as was necessary in order to lift her peduncle out and slap it on the water's surface. It is possible that Ake carried out only the most salient parts of a behavior initially, since those were the most important to remember if asked to repeat. Or, it is possible that Ake exerted the least amount of effort possible for B1, since her performance of B1 never directly resulted in Ake receiving a fish reward. If correct, Ake received a whistle reward for performance of B1, and only received a fish (or several) after correct performance of B2. Her B2 performances typically were much more robust than their B1 counterparts.

Also of interest was Ake's lack of emotional responding (e.g., jaw clapping, etc.) during trials with the longest delay intervals. Such emotional responding, and its correlation with poorer performance, has been noted in other short-term memory studies (D'Amato 1973; Herman & Gordon, 1974). Perhaps Ake's mood was better maintained by the pro-ration of fish reward relative to the amount of time she was required to wait. Thus, a longer delay interval resulted in a higher payoff.

The nature of our dolphin memory task is such that the "remember" rule is evident to the dolphin via the task context. This can be thought of as an explicit instruction to remember, which may encourage to the dolphin to undertake active strategies for remembering. This study attempted to better identify strategies Ake may have used to remember a previously performed behavior after a delay interval. While it is possible Ake was simply randomly responding to the repeat instruction, this seems highly unlikely. Her performance at all delay intervals was significantly greater than would be expected if she were guessing, and her error responses included behaviors not actually being tested in this study, in addition to some of those that were included. Also, the use of specific, non-repeat, gestural instructions for B2 insured Ake was actually attending to the repeat instruction, when given.

More likely, Ake was relying on one or more of a variety of different physical, mental, and acoustic strategies to help her remember her previously performed behavior. We utilized the delay interval between Ake's initial demonstration of the behavior, and the time she was asked to recall it, to help us identify possible memory strategies. Some researchers propose human action memory (called subject-performed tasks, SPTs) is in fact a verbal memory task that is facilitated by action. They suggest the performance mode of recall is but one of many strategies which helps a subject encode an item (Kormi-Nouri & Nilsson, 2001). Others suggest that obvious motor output is responsible for high memory performance of action memory tasks (Engelkamp & Zimmer, 2001). They propose that the performance of an action to be remembered provides motor information that becomes part of the memory trace. Any of these theories could apply to dolphin action memory as well.

In past repeat work (Mercado et al, 1998), the lack of a standardized delay interval could have allowed the dolphins simply to continue performing the first behavior (when possible), until they either received a reward or a second instruction for a different behavior. In the current study, the delay interval, especially lengthy ones, made it more difficult for Ake to utilize this strategy. And, this strategy does not lend itself to all behaviors; for example, it was not possible for Ake to perform repeated twisting jumps during a delay interval. However, we did see evidence that Ake utilized this strategy for remembering at least one behavior, head shake. Our postural analysis revealed head shaking during the delay interval of the majority of trials where head shake was the behavior to be remembered. This shaking was not present during the delay interval of any of the other reviewed trials. There was also evidence of pec movement during half of the delay intervals of trials where butterfly swim was the behavior to be remembered. This pec movement was seen in only one other, non-butterfly swim trial. While it would have been impossible for Ake to continue doing the actual swim during the delay interval, it was possible for her to continue to move her pec fins. A key component of the butterfly swim is slapping the pec fins on the surface of the water. Thus, the pec movement behavior during the delay interval may have been a continuation of a key component of the behavior to be remembered.

Interestingly, many of Ake's error responses consisted of partial replications of the behaviors that were to be remembered. These could be considered partial self-imitations. It is not uncommon for partial replications to be offered in many other types of imitation (Whiten & Ham, 1992). In many cases, certain prominent features of the initial behavior are retained in the replication. For example, several of Ake's roll over repeat errors preserved the spinning element of the behavior. In addition, Ake offered wiggling of her pec fins in error to butterfly repeat trials. Especially interesting was Ake's failure to repeat the body wiggle behavior in the transfer test (Ake offered butterfly swim as the error response for each body wiggle repeat trial). During delay testing, pec movement may have been a memory strategy to help Ake remember the butterfly swim behavior. It follows then, that performance of that same behavior as the behavior to be remembered, rather than as a memory strategy for a different behavior, could have proved confusing to Ake, and resulted in her errors during the transfer test.

Ake's errors also shed light on whether she was remembering the gesture of the behavior to be performed, or the behavior itself. Were Ake recalling the gesture of the behavior to be remembered, then we might expect her to offer behaviors in error whose gestural instructions are similar to the behavior she should have performed. Were Ake recalling the actual behavior to be performed, we might expect her to offer behaviors in error whose features are similar to the behavior she should have performed. For example, Ake made six tail slap repeat errors during Experiment 2. For three of these errors she offered a headstand behavior (rostrum to the tank bottom, tail in the air); for the other three errors, she offered twisting jumps. Each of these error behaviors preserves features of the behavior she should have offered, tail slap. The headstand behavior, like the tail slap, requires Ake to curl her body forward in order to adopt the correct position. Specifically, the headstand requires her to curl all the way to the bottom, while the tail slap requires her to curl until her body is horizontal or further relative to the water's surface, in order to be able to slap her tail on the water. Likewise, the twisting jump preserves the slapping component of the behavior; in the twisting jump, the dolphin slaps her peduncle and tail sideways on the water's surface as she re-enters after a jump. A past study (Shyan, 1985) has shown that the dolphin attends to arm movement and hand position as key features of gestural instructions. The gestural instruction for tail slap consists of essentially pretending to slap a table's surface with the palm of your hand, fingers together. The slapping motion occurs forward and slightly to the side of the body, at hip level. The gesture for headstand consists of placing forearms together in front of the torso, touching lengthwise from elbow to wrist, and pointed to the sky. Hands are apart and facing palms up. The resulting form of the arms and hands should resemble a dolphin's peduncle and tail in the air. Lastly, the gestural instruction for twisting jump is done to the side of the body. The elbow is pointed out to the right and down, and the forearm and fist are pointed to the sky. The forearm and then fist are then rotated clockwise around in a circle two times. The gestural instructions for these three behaviors are largely dissimilar, in terms of their movement, use of one or both hands and arms, and location relative to the signer's body. However, both of the error responses described have features similar to those of the behavior Ake should have performed.

This is the case for other error responses as well. Thus, it seems likely she was remembering the behavior itself, and not the gestural instruction for the behavior.

The only other evidence of posturing occurred during roll over repeat trials. During the delay intervals of several of these trials, Ake's body was curved and her tail was not on the tank bottom. However, Ake was least successful at repeating the roll over behavior after a delay interval. Whether these postures were failed attempts at memory strategies, or whether they were coincidental, is questionable.

While it is clear that not all aspects of Ake's posture and movement may be apparent to a human observer, it is evident Ake did not rely solely on physical strategies to help her remember behaviors. Some behaviors, like aerial behaviors (e.g., twisting jump, back dive) simply do not lend themselves to behavior continuation during the delay interval, or to a postural code. It is possible Ake was relying on an acoustic type of cueing as well. As noted previously, SPTs in memory tests may actually be a verbal memory task. In other words, the stimulus code (its mental representation in memory, see Herman et al 1989) may not be the action itself but rather some verbal/linguistic label of the action. This may be the case for the dolphin as well, that in some way, part of the mental representation of the behavior to be remembered is the "label" assigned to that behavior. Whistling was present during the delay interval of 60% of the trials reviewed. Our study did not anticipate those vocalizations, so unfortunately did not record or analyze the vocalizations. They may simply have been superstitious behaviors. However, they may have served as some sort of vocal label of the behavior to be remembered.

Another explanation, not measurable in this study, was the presence of physical sensory cues to help Ake recall her previously performed behavior. It has been suggested that information from an initial sample stimulus may also be maintained kinesthetically, in a pattern of muscular tension, or by a particular body orientation (Grant, 1986). There is no doubt the performance of certain behaviors by the dolphin would result in lingering physical cues or sensations which could be discriminated, and could thus be used to help her recall past behavior. For example, the twisting jump requires the dolphin to slap her peduncle (tail stock) sideways on the surface of the water as she re-enters after a leap. This slapping of her body on the water must create a sensation on the side of the body that makes contact. Depending on the length of the delay, this sensation could still be present at the time Ake is asked to recall the behavior.

Ake could also have relied on location cues, or a form of stereotyped responding, to assist her memory. For example, Ake reliably seemed to perform twisting jump as the B1 at a specific location in the tank, to her left and a few feet back from station. If she consistently performed only that behavior in that way, then she could simplify her task. In essence, that location could become an associative stimulus for the twisting jump behavior; then all Ake would have to recall was the location, and the association would follow. In fact, she could have even simply kept her left eye trained on that location during the delay interval, to reduce the task even further. We did not measure eye gaze in this study.

Given that it was impractical, for some behaviors (e.g., back dive), for Ake to rely on the previously described strategies, it follows that in some cases she may have been relying on some form of internal representation of her past behavior. This study, in addition to the previous repeat studies (Mercado et al, 1998, 1999) confirms that dolphins must have flexible systems for encoding, representing, and identifying past actions. In general, the ability to imitate requires the dolphin to be able to represent sounds heard, behaviors observed, abstract representations of behaviors, and physical feedback from their own bodies (Herman, 2002).

Theoretical considerations. Many of the previously described strategies can be considered forms of rehearsal. Rehearsal has been defined as "the maintenance of a representation in short-term memory after the removal of a stimulus to be remembered" (Rilling & Nieworth, 1986). It may take place during and/or after the presentation of an initial stimulus, and may continue until a subsequent memory test. In humans and animals, one factor affecting rehearsal is the occurrence of a distracter task during the time when rehearsal might take place. Memory performance is worse when the distracter task interferes with the animal's ability to rehearse.

The delayed repeat task compels a variety of interpretations. The task may test the dolphin's proactive memory, memory for things in the future (Zimmer & Cohen, 2001), or retroactive memory, memory for things in the past (Roitblat, 1987). More specifically, upon performance of the B1 in a repeat trial (the dolphin does not know at that time whether or not she will have to repeat her behavior), the dolphin may enact strategies to rehearse the necessary information, in case it is needed in the future (prospection). Or, she may simply perform the B1 and incur the delay interval, and then, if necessary (i.e., if she is asked to repeat the behavior), access any available information about the behavior previously performed (retrospection). Were the dolphin relying on retrospection, we would not expect a decrement in performance after interference during the delay interval. In addition, we would not expect to see any forms of posturing, or behavioral continuation, during the delay interval. However, both of these did in fact occur, and suggest the repeat task is a prospective memory task. It is important to note, however, that one cannot assume the processes of prospection and retrospection are mutually exclusive (Kendrick & Rilling, 1986). One subject may employ multiple strategies within a given test session, even within a given trial.

There is conflicting evidence as to the relative strengths of prospective and retrospective memory coding (Wasserman, 1986). Superior performance on a simple delayed discrimination task (presumably involving prospective coding) compared to performance on a conditional delayed discrimination task (presumably involving retrospective coding) suggests prospective coding may offer more durable representations over time. Other researchers have suggested response instructions (generated by prospective coding) are better remembered than stimuli (recalled via retrospective coding), so prospective memory is more "robust" than retrospective memory (Honig & Dodd, 1986). According to them, a response instruction is generated early on in a trial using the information currently available and is remembered during the delay interval via prospective coding. Through retrospection, no response instruction is generated; rather, a response to the test stimulus is contingent upon information from the sample stimulus being still available in memory.

If an animal is relying on prospection to solve a memory task, sample exposure time should have little effect on performance. The sample must be present only long enough for the animal to create an anticipatory response to the stimulus (Wasserman, 1986). However, if retrospection is required, then a longer sample exposure time should yield a more salient sample representation in memory, due to rehearsal (Roberts & Grant, 1978a). This may be relevant to Ake's task. Do behaviors which require less time to perform (and thus result in a shorter "sample exposure time") allow her to develop a less salient representation than behaviors which take a longer time to perform, if she relies in any way on retrospective memory? Likewise, could smaller behaviors be more difficult to encode prospectively? The types of behaviors used in this study (jumps, swims, and close to station) could be categorized according to length of time to necessary to perform, with swims and jumps taking a longer amount of time, and close to station behaviors requiring little time. Curiously, the behaviors Ake had the most difficulty repeating after a delay in Experiment 2 were close to station behaviors: roll over, spit, and body wiggle. Ironically, given the nature of the repeat task, what would be rehearsed if the dolphin were prospecting, and what would be recalled if the dolphin were retrospecting, could be the same thing. This is different from an associative memory task, for example, where a pigeon could be required to peck one of two keys (i.e., red or green) depending on the behavior it had previously performed (i.e., scratch the ground or bob head, respectively). In this example, the information to be prospected (i.e., peck the green key) could be very different from the information to be recalled (i.e., did a head bob). This study attempted, in a minimal way, to address issues of prospection, particularly anticipatory behavior and postural coding. A future study might further examine just how prospection affects performance. Some ways this may occur are via facilitating initial encoding of stimuli, or reducing the rate of forgetting (Honig & Dodd, 1986).

We introduced a distracter task to measure the effect of interference on Ake's ability to remember a previously performed behavior. Two types of interference have typically been examined in memory research: proactive and retroactive. In proactive interference, information from a previous trial interferes with memory for a future trial. In retroactive interference, a stimulus presented after the information to be remembered, but before the memory test, interferes with the information to be remembered (Roitblat, 1987). Some researchers suggest the role of proactive interference has been largely underestimated in studies of animal short-term memory (Wright, Urcuioli, & Sands, 1986). These authors reference studies of "highly trained monkeys and dolphins," which seemed to show limited short-term memory capacities (chance performance after 1-2 minute delay intervals). In particular, they cite a cumulative effect of interference over time, as a result of a variety of factors including item repetition, insufficient inter-trial intervals, and small sample size. The current study controlled for several potential sources of proactive interference by having sufficiently long inter-trial intervals, a large sample set, and only minor repetition of behaviors within a test session. It also showed the dolphin could perform this short-term memory task at levels significantly greater than would be expected by chance at intervals as long as two minutes. One way to improve upon the current study would be to have sample items each appear only once during a given test session.

For the current study, we utilized a type of retroactive interference, in an attempt to disrupt Ake's encoding of the information to be remembered. The paddle pressing task clearly was disruptive enough to significantly decrease Ake's ability to remember a previously performed behavior after a delay interval. The task was such that it not only could have disrupted physical rehearsal strategies, but mental ones as well. However, it was not so difficult that Ake could not remember anything. If any of the body movements/positions occurring within the delay interval described previously were in fact attempts at memory strategies by Ake, then the physical act of repeatedly pressing paddles no doubt disrupted those strategies. Likewise, if mental rehearsal or representation was occurring, the task of correctly following indicative instructions was disruptive to mental memory strategies.

Past repeat work (Mercado et al, 1998, 1999) has shown that dolphins are able to recall a previously performed behavior by accessing a representation of that behavior from short-term memory. The current study tried to better ascertain upon which type of representation (mental or physical) the dolphin relies to carry out the repeat task. However, this may be a moot discussion, in light of the existence of mirror neurons (Arbib, 2002). These neurons, present in the monkey brain, are activated whether the monkey performs a particular action or observes another monkey performing the same action. This means that regardless of the type of representation used (mental or physical), the most very basic element that supports an animal's ability to replicate behavior lies at the neuronal level.

Imitation has been defined as "the process of accessing a mental representation of an experienced event to reproduce that event through one's own behavior" (Herman, 2002). In most cases, imitation has been thought of as one element of social behavior, where one animal perceives a behavioral event of another animal, and then reproduces that event itself. Both social and self-imitation require access to mental representations of behavior; in the former, representation is generated by watching another perform an action; in the latter, representation is generated from performing the action. However, even though the basis of an imitative ability in a species may be social; the expression of said ability may also occur in non-social contexts (Herman, 2002). This is the case in the delayed repeat paradigm. The current study of self-imitation is also an extension of past studies looking in part at aspects of dolphin self-awareness. The delayed repeat task can be considered a test of episodic memory, or memory of personal events (Kormi-Nouri & Nilsson, 2001). Episodic memory is characterized by several types of active knowledge: firsthand spatial and temporal knowledge, awareness of one's identity or existence, and a deliberate process of remembering and accessing information. Certainly the dolphin's excellent performance in the delayed repeat task provides support for the dolphin demonstrating aspects of self-awareness.

Ecological significance. The study of memory for behavior in animals compels the question of ecological significance. Laboratory tests of memory for actions in humans are artificial in many ways (Foley & Ratner, 2001). However, they still have real world implications. In humans, action memory has great significance ecologically. Memory for actions allows for successful day to day functioning and coordination of actions within one's environment. It may be said that human memory is specifically geared towards monitoring what was, and should be, done. Being able to "keep track," so to speak, gives one an advantage (Zimmer & Cohen, 2001). Some of the reasons memory for action is important to humans include: life management, sequential processes, prospective memory (memory of the plan of something to come), and successful interaction with one's environment (Zimmer & Cohen, 2001). Zimmer (2001) suggests "action memory is an evolutionary old memory performance (p.177)." Animals behave, and it may "enhance the success of an organism if the actions are remembered that were performed in reaction to a certain stimulus or to achieve a specific goal (p.177)." Wasserman (1986) notes that processes of prospection and retrospection may be integral to vital action patterns like locating food, courting mates, and escaping enemies. Future study of memory processes may very well shed further light on the ecology and evolution of complex cognitive capabilities (Wassserman, 1986). Also important to an animal is the ability to remember the corresponding outcomes or consequences of particular actions, in order to evaluate their usefulness in the future. In sum, an animal must remember what to do, and know when and when not to do it. (Zimmer & Cohen, 2001). It follows that the same might be true for dolphins.

Because dolphins, like humans, are highly social animals (Pryor & Norris, 1991), it is important that dolphins' have proficient action memory. For dolphins, the ability to remember, and replicate, past behavior may be critical. There may be benefits to being able to plan to perform certain actions, and to recall that certain actions have been performed (Wasserman, 1986). Prospective memory may allow an animal to direct its behavior and fulfill certain goals. Retrospective memory (the ability to remember finished activities) allows animals to avoid inefficient repetition. In dolphin societies, many activities frequently require coordinated actions among several individuals: foraging, predator defense, allo-parental care, and reproduction (Wells, 1991). The need for coordination in these types of activities may contribute to the need for an ability to self-imitate. An animal's first trial learning ability (or lack thereof) will have consequences in many areas necessary for survival. For example, if an animal is able to observe another animal's well-honed foraging strategy, replicate that strategy on the first attempt (imitation of other), and maintain the critical elements of that strategy on future attempts (self-imitation), then the food gathering process will have become as efficient as possible.

In conclusion, the current study has examined motor memory in the bottlenose dolphin. Variables, including delay intervals and a distracter task, were manipulated to examine effects on memory and memory strategies. Future work should further explore the role of distraction on animal motor memory, and how animals represent the identity, or salient features, of motor behaviors in memory.

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