Anim Cogn (2002) 5 : 225–232
DOI 10.1007/s10071-002-0153-8

ORIGINAL ARTICLE

Colleen Reichmuth Kastak · Ronald J. Schusterman

Long-term memory for concepts in a California sea lion (*Zalophus californianus*)

Received: 31 May 2002 / Revised: 23 August 2002 / Accepted: 31 August 2002 / Published online: 12 October 2002

Abstract. An adult California sea lion (*Zalophus californianus*) with extensive experience in performing discrimination learning tasks was tested to evaluate her long-term memory for two previously learned concepts. An associative concept, that of equivalence classification, was retested after a retention interval of approximately 1 year. The sea lion had originally shown emergent equivalence classification with nonsimilarity-based classes of stimuli in a simple discrimination repeated-reversal procedure as well as in a matching-to-sample procedure. The 1-year memory test revealed no decrement in classification performance in either procedure. A relational concept, that of generalized identity matching, was retested after approximately 10 years. The sea lion had originally received trial-and-error exemplar training with identity matching-to-sample problems prior to transferring the concept to novel stimulus configurations. In the 10-year memory test, the sea lion immediately and reliably applied the previously established identity concept to familiar and novel sets of matching problems. These are the first reports of long-term conceptual memory in a nonprimate species. The experimental findings are consistent with a variety of observations of sea lions in natural settings, which indicate that natal sites, feeding areas, and individuals may be remembered over long periods of time.
Electronic Supplementary Material is available if you access this article at http://dx.doi.org/10.1007/s10071-002-0153-8. On that page (frame on the left side), a link takes you directly to the supplementary material.

Electronic Supplementary Material is available if you access this article at http://dx.doi.org/10.1007/s10071-002-0153-8. On that page (frame on the left side), a link takes you directly to the supplementary material.

C. Reichmuth Kastak (✉) · R.J. Schusterman
Long Marine Laboratory, University of California at Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060, USA
e-mail: coll@cats.ucsc.edu,
Tel.: +1-831-4593345, Fax: +1-831-4593383

Keywords Long-term memory · Concept formation · Identity · Equivalence · Sea lion

Introduction

Concept learning is perhaps the highest level of abstraction attained by nonhuman animals. Thus, substantial effort has been directed at investigating the experimental conditions under which concepts are developed and applied by animal subjects. In contrast to learning about the explicit relationships that exist between stimuli, responses, and outcomes, conceptual behavior involves learning about the general nature of entire groups of stimuli. Concepts are formed when experience with many problems of a given type allows new, similar problems to be solved more rapidly or without specific training. Such concept-governed or rule-governed problem solving is advantageous because it allows individuals to successfully cope with novel problems in the absence of specific prior experience.

Concept formation is typically studied under controlled conditions using discrimination training procedures and artificial stimuli. Subjects are given some amount of exemplar training with problems that are different with respect to particular stimulus configurations but similar with respect to their general properties. Following this training, conceptual behavior is demonstrated when a subject responds appropriately to new problems on the basis of these common properties. Concepts can be based on common perceptual properties, common relational properties, or common associational properties (Roberts 1998). Examples of perceptual concepts include categories such as “people,” “flowers,” and “trees,” in which application of the concept leads to the inclusion of novel exemplars that belong to the given category and the exclusion of novel exemplars that are not consistent with the given category (see, for example, Herrnstein and Loveland 1964). Relational concepts are based on common abstract relationships shared by sets of stimuli. For example, a generalized identity concept is shown by a subject that discriminates among novel sets of stimuli based on the perceptual "sameness" of identical stimuli; conversely, a generalized oddity concept is shown by a subject that discriminates among novel sets of stimuli based on their perceptual "difference" (see, for example, Oden et al. 1988). Finally, associative concepts are those in which stimuli are categorized on the basis of common associations with other stimuli, responses, or outcomes. For example, disparate arbitrary stimuli, such as A and C, may become related to one another through their common relationships with a given mediating stimulus, B. Although the stimuli in such associative categories are not perceptually similar, they are treated in a similar fashion, as demonstrated by a transfer of function among the stimuli in a given category (see, for example, Vaughan 1988).

Once meaningful concepts are established, it is important to understand how they are remembered over short and long time scales. A problem-solving strategy that is quickly forgotten does not provide much of a cognitive economy to an individual faced with problems that may be widely spaced in time. Despite several successful demonstrations of concept learning in animals, conceptual memory has not been well studied. To evaluate the extents and limits of conceptual behavior in animals, studies investigating short- and long-term memory for concepts are required. To date, a few studies, all with primates, have probed the long-term memory of individuals with previous histories of concept learning. These studies tested memory for various relational concepts. Johnson and Davis (1973) reported that eight rhesus monkeys (*Macaca mulatta*) who had developed oddity learning sets showed near-perfect retention when retested 7 years later on the same task. Burdyn et al. (1984) documented that three squirrel monkeys (*Samiri sciureus*) trained on an oddity concept also showed evidence of retention of the relational concept after over 2 years. Further, these investigators reported that one squirrel monkey, originally trained on a numerousness concept (two vs seven dots), and who received additional training on a relative numerosity task (quantities of "fewer," "intermediate," and "most"), showed excellent retention when retested on the two versus seven discrimination approximately 5 years later. Finally, Patterson and Tzeng (1979) retested four gorillas (*Gorilla gorilla gorilla*) that had previously demonstrated a win–stay, lose–shift strategy during training on a series of discrimination reversal problems. The gorillas showed performances comparable to their best prior performances when presented with similar problems after 2.5 years. From these few studies, it is clear that relational concepts can provide powerful problem-solving frameworks that can be remembered by individuals over very long periods of time.

Because reports of long-term conceptual memory in animals are rare, it has been suggested that investigators who have the opportunity to obtain such data should attempt to do so (Burdyn et al. 1984). In the present study, we investigated long-term memory for two different concepts in a single highly experienced California sea lion (*Zalophus californianus*) named Rio. We tested Rio's memory for an associative concept following 361 days (~1 year), and we also tested her memory for a relational concept after 3,673 days (~10 years). These memory tests constitute the first evaluations of long-term memory for concepts in a nonprimate species.

Experiment 1

The first concept considered was one of equivalence classification. Rio had recently demonstrated this associative concept, as described in detail in by Reichmuth Kastak et al. (2001). In this study, Rio formed two 10-member classes composed of visual stimuli that became associated through common functional and reinforcer relations. This was accomplished through the use of a simple discrimination repeated-reversal procedure. Categorization of the 20 stimuli into two classes was shown when Rio reversed her responses to all of the members of a class upon receiving feedback that the reinforcement contingencies for a single class member had been reversed. Following the formation of classes in this reversal procedure, Rio demonstrated transfer of the relations that emerged between class members to a matching-to-sample (MTS) procedure. Additional experimental phases showed that the classes that had formed also met the criteria of traditionally defined equivalence classes; that is, if a single class member was conditioned to a new stimulus, then relations between the new stimulus and the other members of the class emerged without further training. The training and testing required to establish these equivalence classes was extensive, and the entire experiment took Rio over 2.5 years to complete.

Following the termination of the classification experiments, Rio was not exposed to the stimuli, the apparatus, or either of the procedures for 361 days. The 20 stimuli were then reintroduced in the MTS procedure, immediately followed by the simple discrimination reversal procedure, to evaluate Rio's long-term memory for the equivalence relations that she had previously identified among the stimuli in each category.

Methods

Subject

Rio was born in captivity at Marine World, in Redwood City, California. Due to insufficient maternal care from her biological mother, she was transferred to Long Marine Laboratory at the University of California Santa Cruz when she was just a few days old, where she was raised by a human surrogate mother in the context of an imprinting study (Schusterman et al. 1992). As she matured, Rio acquired extensive experience in performing cognitive and psychophysical learning tasks (see Schusterman et al. 2002a, for a partial review); these included visual simple and conditional discrimination procedures similar to those used in the current study. The nature of Rio's lifelong participation in a behavioral research program provided the opportunity for the current tests to be conducted.

Rio was housed at Long Marine Laboratory in an outdoor enclosure that contained several saltwater pools and adjacent haul out areas. She was tested in an isolated section of the facility that contained a 7.5-m diameter pool and a deck where the experimental apparatus was placed. Rio was fed approximately 5 kg of freshly thawed cut herring and capelin each day, one half of which was typically consumed during experimental sessions. Rio was trained for research, as well as for a variety of examination and exercise behaviors, with standard operant conditioning procedures and fish reinforcement. Rio's memory for the previously established stimulus classes was tested in October 2000, when she was 15 years old.

Apparatus and stimuli

The visual two-choice MTS apparatus and the 20 stimuli used have been previously described by Reichmuth Kastak et al. (2001). The display comprised a set of three hinged plywood panels. At the center of each panel was an inset stimulus presentation box that was covered by a moveable opaque door. A T-bar station was positioned in front of the center (sample) box. The two side panels were angled in toward this station such that each side (comparison) box was equidistant to the station. The acoustic cues used during testing were played through a speaker that was positioned near the apparatus.

The stimuli used in the experiment were black-and-white patterns that were designed to be visually unique but roughly the same with respect to area and brightness. The 20 stimuli used were divided into two 10-member sets that were coded as letters (A–J) and numbers (1–10).

Original procedure

The details of the general procedure and controls used are reported in Reichmuth Kastak et al. (2001). In the original experiment, Rio demonstrated classification of the letter and number stimulus classes in two different procedures. The first was a two-choice simple discrimination repeated-reversal procedure, and the second was an MTS procedure. In both procedures, class-specific reinforcement (consisting of a particular tone and a specific fish type) was provided for correct responses and no correction procedures were used. Both experiments were run double blind (see Reichmuth Kastak et al. 2001).

During the simple discrimination experiment, Rio was presented with one to two daily sessions containing between 40 and 100 two-alternative forced-choice trials. To begin each trial, Rio approached the center of the apparatus and positioned her chin at the T-bar station. Once she was in position, the comparison stimuli were revealed in each of the side panels of the apparatus. Rio waited at the station until she was signaled by a release tone to make a response. She responded by moving from the station to touch one of the two stimuli with her nose. Selection of the stimulus designated as correct was marked by a particular tone that was followed by a piece of fish tossed from behind the apparatus. Selection of the stimulus designated as incorrect was marked by the verbal signal "no" and no fish reward was given. At the end of each trial, the two stimuli were covered and the next trial was prepared. The interval between trials was approximately 10 s.

The simple discriminations were structured so that the two stimuli presented on each trial were members of different stimulus sets. As a result, any stimulus assigned to the letter set could appear with any stimulus assigned to the number set on a given trial. The experimenter established the reinforcement contingencies so that responses to members of one set produced reinforcement while responses to members of the alternative set did not. The goal of the experiment was to determine if Rio could learn to classify the stimuli in each set based on their shared pattern and type of reinforcement. To this end, each time she was reliably selecting members of the set designated as positive, the reinforcement contingency was suddenly reversed: members of the previously positive set became negative and members of the previously negative set became positive. This series of reversals between the letter set and the number set continued until Rio showed evidence of stimulus classification. Rio demonstrated a class concept when, following feedback that a reversal had occurred for one member of a set, she immediately reversed her responses to the other members of that set (see video clip S1 in the electronic supplementary material).

Following the formation of classes in the simple discrimination procedure, Rio was presented with the same stimuli in conditional discrimination trials. The goal of this transfer experiment was to determine if Rio could apply knowledge about class membership to novel problems presented in an MTS procedure. In the conditional discrimination sessions, Rio was presented with a sample stimulus from one of the two sets. The comparison stimuli were one member of the letter set and one member of the number set. Rio was rewarded for choosing the comparison that shared class membership with the given sample. The trials operated in a similar fashion as the simple discrimination trials, except in this case, a sample stimulus was revealed in the center box 4 s prior to the exposure of the two comparison stimuli (see Reichmuth Kastak et al. 2001). Rio successfully passed this test when she immediately selected comparison stimuli that shared class membership with the sample, while avoiding comparison stimuli that were not related to the sample (see video clip S2 in the electronic supplementary material). Prior to the memory test, Rio was last exposed to the 20 stimuli in the two classification tasks in October 1999, when her performance in both procedures was maintained at virtually perfect levels.

Procedure for memory tests

Rio's memory tests were conducted in October 2000, 361 days after her last exposure to the apparatus, stimuli, and the two procedures. Rio's ability to remember how the stimuli were categorized was tested first in the MTS procedure and then in the simple discrimination procedure. This sequence was established because the MTS procedure, which evaluates classification within trials rather than between trials, provided the most rapid assessment of memory in the shortest number of non-duplicative trials. In this procedure, there was no possibility of within-test relearning of the categories. The first session conducted comprised 40 different conditional discrimination trials presented in an MTS procedure. The 40 trials presented were a subset of the 180 possible unique combinations of letters and numbers. On half of these trials, a stimulus from the letter set appeared in the sample box, another letter appeared as the positive comparison, and a number appeared as the negative comparison. On the 20 remaining trials, a number appeared as the sample, another number appeared as the positive comparison, and a letter appeared as the negative comparison. As in the original procedure (see Reichmuth Kastak et al. 2001), all trials were presented in a counterbalanced fashion and Rio was rewarded for matching within and not between stimulus classes. Rio's performance on this session was then compared to her performance on the last matching session that she completed the previous year.

Starting on the following day, Rio was presented with the same 20 stimuli in the simple discrimination procedure. The simple discrimination procedure provided an additional and independent measure of stimulus classification. Although Rio could have potentially memorized the 180 different trial combinations used in the MTS procedure during the original experiment, performance on the simple discrimination trials following a reversal could not be controlled by rote memorization. Rather, performance on each trial could only be appropriately controlled by the outcome of the previous randomly selected trial. As in the original procedure, Rio was presented with one letter and one number on each trial, and trials were continued until Rio was reliably selecting only stimuli assigned to the set designated as positive by the experimenter. Each time Rio's performance stabilized at near-perfect levels (at least 10 consecutive correct trials), a reversal of reinforcement contingencies occurred. Reversals always occurred unpredictably within a session, that is, immediately following a series of correct responses to members of a given set. The first 10 trials following a reversal included only one presentation of each letter and each number. Ten reversals between the letter and the number sets were completed over five sessions that contained between 52 and 65 trials each. Each session lasted approximately 25 min. Only one session was completed per day, and the five sessions were spaced over a 3-week period; thus, there was little opportunity for within-test learning. Following the completion of the ten reversals that made up the memory test, Rio's performance on the first 10 trials of the ten reversals was compared to her performance on the first 10 trials of the last ten reversals that she had completed the previous year.

Results and discussion

In the MTS procedure, a class concept is demonstrated when the subject, given two alternatives from different sets, consistently chooses the alternative that belongs to the same class as the sample. Rio's performance in 1999 reflects such classificatory behavior; she made no errors on the last MTS session that she completed with the letter and number sets in 1999. Nearly a year later, without any exposure to the experimental situation, Rio's performance on a comparable session was also perfect, that is, she did not make a single error on the 40 unique problems presented in the memory test. Her performance was not different from that measured a year earlier (Fisher's exact test, $P>0.05$), and was much better than expected by chance (binomial test, $P<0.01$). It is unlikely that Rio remembered each of the individual problems presented in the memory test; rather, she likely remembered and applied the associative class concept that she had developed in the original experiment.

The hypothesis that Rio remembered the class concept rather than individual stimulus relations is also supported by Rio's performance in the simple discrimination repeated-reversal procedure. In this procedure, performance based on rote memory versus a class concept memory can be predicted. If Rio's performance is dependent on rote memory, then she should typically make errors on each of the first ten trials following a reversal. Her performance should only improve after she has received feedback about the change in reinforcement contingency applied to each stimulus in a given set. Such trial-and-error learning can be contrasted with performance based on a class concept. If Rio recognizes that the members of a stimulus set are related to one another, then a change in reinforcement applied to one member of a set should predict a change in reinforcement for the remaining members of the set. In this case, following a single error on the first trial of an unexpected reversal, performance should rise to near perfect levels. Rio's average performance following a reversal in 1999 shows strong evidence of class formation, as shown in Fig. 1. That is, following feedback that a reversal had occurred for one stimulus belonging to a given set, Rio consistently reversed her responses to the nine other members of that set. Rio's performance on the first trial of a reversal was predictably near zero; her performance on trials two through ten was predictably well above the 50% chance mark (Fig. 1). Statistical assessment of these data indicate that Rio's performance on the repeated-reversal memory test was not different from what it had been a year earlier (Friedman's $\chi^2_{(9)}=16.3$, $P>0.05$).

The results of the memory tests in both the MTS and simple discrimination reversal procedures provide strong evidence that equivalence classes can be remembered by a sea lion over an extended period of time. In each of the tests, a ceiling effect was evident; Rio's performance was at or near perfect prior to the cessation of testing, and her performance showed no decay when testing resumed nearly a year later. The findings support an earlier, shorter-term study by Schusterman and Kastak (1998), which showed

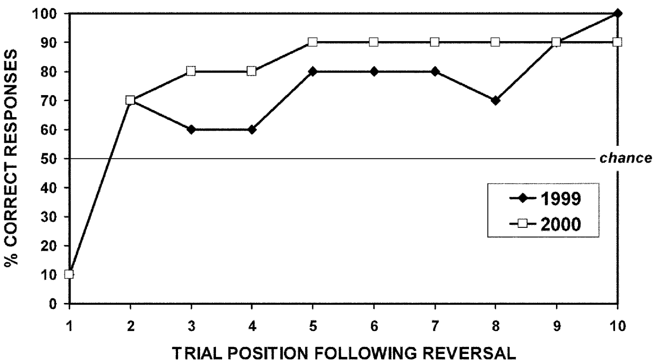

Fig. 1 Memory for the class concept was measured by the simple discrimination repeated-reversal procedure. Rio's performance on trials in positions 1–10 following each reversal is shown for the last ten reversals completed in 1999 and the first ten completed in 2000. Rio first experiences the reversal on the trial in position 1, when feedback is provided that a previously correct stimulus selection no longer produces reinforcement. The trials in positions 2–10 show Rio's responses to the remaining members of each stimulus class following this feedback

that the same sea lion remembered 30 three-member equivalence classes for at least 2 weeks. In this study, as well as in the current study, the subject applied the class structure that was established in one procedure to another. These findings clearly demonstrate the flexible and durable nature of the associative concepts formed by the sea lion.

Experiment 2

The second concept considered was one of generalized identity. Rio had previously demonstrated generalized identity matching as described in detail by Kastak and Schusterman (1994). In this study, Rio was trained on a two-choice, visual MTS task where the sample and positive comparison stimuli were perceptually identical. The negative comparison on each trial was perceptually different from the identity match. An exemplar training approach was used in an effort to establish a generalized identity concept. Following her trial-and-error acquisition of 60 different matching problems involving identical sets of sample and comparison stimuli, Rio showed strong evidence of relational concept formation. When presented with completely novel arrays of stimuli, she immediately related stimulus pairings on the basis of perceptual identity.

Following the completion of the identity matching experiments in May 1991, Rio continued to be trained on and tested in a variety of cognitive tasks. For the most part, these tasks involved arbitrary matching procedures. Thus, Rio received a great deal of experience in performing discriminations that involved perceptually dissimilar stimuli (i.e., neither comparison was identical to the sample) and no additional experience in performing discriminations that involved perceptually identical stimuli. The equivalence classification task described in the previous section (Reichmuth Kastak et al. 2001) is one of the non-similarity-based matching procedures that Rio participated in during this time. In June 2001, 3,673 days since completing her original demonstration of generalized identity matching, Rio's ability to relate stimuli on the basis of perceptual identity was retested.

Methods

Subject

Sea lion Rio was 6 years old when she completed the original identity matching experiment; she was 16 years old when her memory for the concept was retested.

Apparatus and stimuli

The physical dimensions of the apparatus were the same as those described in experiment 1. The stimuli used for the original experiment and for the memory test were 30×30-cm white squares that were painted with arbitrary black shapes. A total of 154 identical stimulus pairings were used in the memory test. The stimulus pairings were categorized on the basis of Rio's prior experience with them: 84 of the stimuli had been used in Rio's original identity matching experiment (see Kastak and Schusterman 1994) and 70 of the stimuli had never been exposed in the context of identity matching. Of these 70 stimuli, 28 had been used in a study involving arbitrary matching (see Schusterman and Kastak 1993), and 42 of the stimuli were completely novel. For labeling purposes, the stimulus types were coded as *identity*, *arbitrary*, and *novel*.

Original procedure

The details of the general procedure and controls used are reported in Kastak and Schusterman (1994). The MTS procedure used was the same as that described in the previous section; however, in this experiment, Rio was rewarded for selecting comparison stimuli that were perceptually identical to the sample while avoiding comparison stimuli that were perceptually different from the sample (see video clip S3 in the electronic supplementary material). Rio was presented with a series of identity matching problems. The problems were presented in pairs of novel identity matches to control for the possible effects of exclusion that may confound demonstrations of generalized identity matching (see Kastak and Schusterman 1992). For example, if the stimulus *triangle* appeared as the sample, then Rio was rewarded for choosing *triangle* and avoiding *hook*. Conversely, if *hook* appeared as the sample, then Rio was rewarded for choosing *hook* and avoiding *triangle*. All correct responses were marked by a tone that served as a conditioned reinforcer that was followed by a fish reward. No correction procedures were used. Each set of problems was repeated until Rio reached performance levels of 90% or better on two consecutive sessions. Each time Rio learned a new set of identity matching problems, two new identical stimulus pairings were introduced and then trained to criterion. After learning 60 such identity matching problems, Rio demonstrated the ability to relate 30 novel stimuli on the basis of perceptual identity without any stimulus-specific training. Through the exemplar training, Rio had formed a generalized identity concept that she could apply to any number of new problems. Rio completed the original identity matching experiment in May 1991.

Procedure for memory test

Rio's memory for the identity concept was tested in June 2001. Between May 1991 and June 2001 Rio was not exposed to any identity matching procedures. Prior to the test, Rio was performing arbitrary MTS sessions regularly, thus, she was familiar with the apparatus as well as the general MTS procedure. The aim of the memory test was to determine if Rio would spontaneously relate stimuli on the basis of perceptual identity in the absence of any exemplar training.

The memory test was conducted over 11 sessions that were completed during 5 days of testing. One or two 42-trial sessions were run each day. Each session typically lasted about 20 min and there was a short break (lasting 5–15 min) between consecutive sessions. Each session was divided into 7 consecutive 6-trial blocks, for a total of 77 blocks in the complete test. Prior to testing, the 154 stimuli to be used were randomly placed into pairs within each category of stimulus type (identity, arbitrary, or novel). Thus, there were 77 sets of identity matching problems, and each of these sets was presented in a single block of 6 trials. As described earlier, a set of problems might consist of the identity match between *triangle* and *triangle* (and not *hook*) and the identity match between *hook* and *hook* (and not *triangle*). Each of the two problems in a set appeared three times in a block of 6 trials, in a varied order and balanced for the placement of the correct choice (i.e., there were no positional cues or sequence cues that could influence the subject's responding). There were 42 blocks containing stimulus sets from the identity category, 14 from the arbitrary category, and 21 from the novel category; the 77 blocks were presented in a randomized order during the 11 test sessions.

As in the original identity matching experiment, Rio was rewarded on each trial for selecting the comparison stimulus that was perceptually identical to the sample while avoiding the comparison stimulus that was perceptually different from the sample. Every correct trial was marked by a conditioned reinforcer (an acoustic tone) that was immediately followed by a biological reinforcer (a capelin fish) tossed from behind the apparatus. Incorrect responses were not reinforced. Regardless of Rio's performance with each set of problems, she continued on to the next block of trials.

Three examples of each of the 154 identity matching problems were presented during the memory test based on the design of the experiment. However, only performance on the very first exposure of each of the 154 problems was considered in the analysis of Rio's performance. This trial-1 performance measure was used to evaluate whether a generalized identity concept had been applied. Rio's performance on the first exposure of each of the 154 identity matching problems presented during the 2001 memory test was compared to her performance on the 30 novel identity matching problems that were presented during her 1991 demonstration of generalized identity matching. The original report of the 1991 data (see Kastak and Schusterman 1994) did not specify Rio's performance on each of the 30 unique test trials; rather, only the first novel trial of each of the 15 stimulus pairs was reported. To compare Rio's previous performance with her current one, we reanalyzed the original data from 1991 to include all 30 novel transfer trials presented during testing.

Rio's trial-1 matching performance in the memory test was also evaluated to determine if her performance varied on the basis of her prior experience with the stimuli. Performance on the identity problems was compared between the three categories of stimuli used (those that had been previously exposed in identity matching problems, those that had been previously exposed in arbitrary matching problems, and those that were completely novel to the subject). Subsequently, the three stimulus categories were pooled into two more general stimulus categories: those that had previously been presented in the context of identity matching (that is, familiar transfer problems), and those that had never been presented in the context of identity matching (that is, novel transfer problems).

Results and discussion

In 1991, following exemplar training with 60 identical stimulus pairings, Rio responded correctly to 83% of trials (25 of 30) involving novel stimuli by using a generalized identity concept (Fig. 2). In 2001, without additional exemplar training, Rio responded correctly on 67% of identity matching problems (103 of 154). These performances, separated by 10 years, are not significantly different from one another (Fisher's exact test, $P>0.05$), and both performances are significantly better than would be expected by chance (binomial tests, $P<0.01$). Rio's performance in the memory test was further broken down by stimulus type (Fig. 2). Rio performed best on the problems that involved stimuli with a history of arbitrary matching, but her performances between the three stimulus categories were not significantly different (Fisher's exact tests, $P>0.05$). When these trials were pooled as either familiar or novel transfer problems, Rio made 65% (55 of 84) correct responses on familiar transfer problems, and she made 68% (48 of 70) correct responses on novel transfer problems. These scores are not different from one another (Fisher's exact test, $P>0.05$) and both are much better than would be predicted by chance (binomial tests, $P<0.01$).

The results show that Rio remembered and applied a generalized identity concept during the memory test. Her

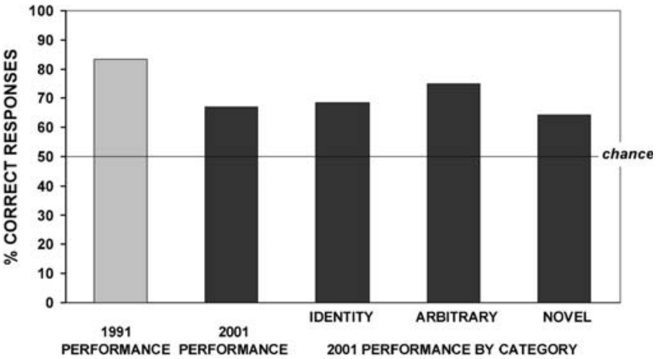

Fig. 2 Memory for the generalized identity concept was evaluated by comparing Rio's performance with 30 novel stimulus pairings in 1991 to her performance with 154 different identity matching problems in 2001. Performance in 2001 is further broken down into three trial categories: those involving stimuli that had been previously exposed in an identity matching task (*n*=84), those involving stimuli that had been previously exposed in an arbitrary matching task (*n*=28), and those that were completely novel (*n*=42)

consistent overall performance on the first exposure of each matching problem indicates successful transfer of the relational concept that she established 10 years earlier. Notably, Rio's prior experience with the subset of familiar stimuli presented did not influence her performance. She reliably matched stimuli on the basis of perceptual identity whether or not she had previously done so. Interestingly, Rio performed best when the stimuli that were presented had a prior experimental history in an arbitrary matching task. Of all the stimuli used in the current experiment, these were the most familiar to Rio, and it is likely that Rio's recognition of the stimuli was enhanced by her prior experience. One might have expected Rio's transfer performance to be poorest with these stimuli because they had been previously related in a task inconsistent with identity matching. However, in the absence of an appropriate previously trained arbitrary match, Rio apparently applied an identity strategy to these problems without interference. The results of this memory test demonstrate that Rio did not rely on her memory for specific stimulus relations, but rather, on her memory for a general relational rule, that is, the identity concept. The 10-year retention interval demonstrated in this experiment is the longest reported for any nonhuman subject.

General discussion

Both of the studies reported in the current paper add to the limited available information on long-term memory for concepts in nonhuman animals. The current studies show that a California sea lion can remember abstract problem-solving strategies for at least 1 and up to 10 or more years. The durability of the concepts formed by a single, highly-trained, captive sea lion reflects the cognitive potential of the species to remember and apply previously established behavioral rules when encountering novel experimental or environmental problems.

The experimental findings are consistent with accumulating laboratory and field observations made with sea lions and related taxa that reveal long-term memory for biologically significant experiences, locations, and individuals. In earlier research, we have found that sea lion Rio recognized the voice of her surrogate mother for at least 2 months following their separation (Schusterman et al. 1992). Furthermore, in an arbitrary matching procedure, Rio remembered a series of explicitly trained conditional discriminations for at least 1 year (E. Cenami Spada, July 1994, personal communication). Finally, as described earlier, Rio remembered another associative concept, the categorization of 30 three-member equivalence classes, for at least 2 weeks (Schusterman and Kastak 1998). Observations of sea lions in natural settings indicate that natal sites, breeding territories, traditional feeding areas, and individuals may be remembered over long periods of time. For example, several studies have demonstrated mutual individual recognition between female sea lions and their offspring during the period of maternal dependence (see, for example, Trillmich 1981). Recently, Insley (2000) extended this finding by showing that free-ranging northern fur seals (*Callorhinus ursinus*) are capable of recognizing their mothers' vocalizations for 4 or more years following the presumed termination of the mother–pup bond. Additionally, observations of male Steller sea lions (*Eumetopias jubatus*) suggest that territorial males may categorize their rivals as familiar "neighbors" or novel "intruders" and that they remember these designations over multiple breeding seasons (see Gisiner 1985, as discussed in Schusterman et al. 2002b). On the basis of these and other laboratory and field data, it is evident that sea lions and fur seals rely on long-term memory in a variety of social and ecological problem-solving contexts. The 10-year retention interval documented in the current study shows that these memories may extend over a significant portion of an individual's lifetime.

Although cognitive processes related to the acquisition, organization, and retention of information are currently being studied in a variety of animal species, the assessment of long-term memory has been limited by the longitudinal nature of the studies required. As investigators continue to make progress in describing the perceptual, relational, and associative concept-forming abilities of animals, longer-term studies will be useful in revealing the extents and limits of these skills. Such studies require established animal colonies in which experienced individuals can be tested and retested over various retention intervals. As we improve our understanding of the conceptual behavior of animals in controlled laboratory situations, it will become possible to obtain a better understanding of how animals use their long-term memory for biological activities that depend on generalized problem-solving strategies.

Acknowledgements This research was funded in part by Office of Naval Research grant N00014-02-1-0159 to Ronald J. Schusterman. Colleen Reichmuth Kastak was supported by Department of Defense Augmentation Award for Science and Engineering Research Training award N00014-98-1-0603 and a Graduate Assistance in Areas of National Need fellowship awarded by the Department of Ocean Sciences at UCSC. We thank David Kastak for encouraging us to carry out these experiments and for access to the original identity matching data. We thank Shannon Spillman for her significant contributions to experimental design, data collection, and data analysis. We also gratefully acknowledge the dedicated research team at the Pinniped Cognition and Sensory Systems Lab, which is based at Long Marine Laboratory in Santa Cruz, California. The animal care, training, and testing protocols used in these studies comply with the current laws of the United States of America that govern marine mammal research.

References

Burdyn LE Jr, Noble L, Shreves LE, Thomas RK (1984) Long-term memory for concepts by squirrel monkeys. Physiol Psychol 12:97–102

Gisiner RC (1985) Male territoriality and reproductive behavior in the Steller sea lion, *Eumetopias jubatus*. Unpublished PhD thesis, University of California Santa Cruz

Herrnstein RJ, Loveland DH (1964) Complex visual concept in the pigeon. Science 146:549–551

Insley SJ (2000) Long-term vocal recognition in the northern fur seal. Nature 406:404–405

Johnson CK, Davis RT (1973) Seven-year retention of oddity learning set in monkeys. Percept Motor Skills 37:920–922

Kastak D, Schusterman RJ (1992) Comparative cognition in marine mammals: a clarification on match-to-sample tests. Mar Mammal Sci 8:414–417

Kastak D, Schusterman RJ (1994) Transfer of visual identity matching-to-sample in two California sea lions (*Zalophus californianus*). Anim Learn Behav 22:427–435

Oden DL, Thompson RKR, Premack C (1988) Spontaneous transfer of matching by infant chimpanzees (*Pan troglodytes*). J Exp Psychol Anim Behav Process 14:140–145

Patterson RL, Tzeng OJL (1979) Long-term memory for abstract concepts in the lowland gorilla (*Gorilla g. gorilla*). Bull Psychon Soc 13:279–282

Reichmuth Kastak C, Schusterman RJ, Kastak D (2001) Equivalence classification by California sea lions using class-specific reinforcers. J Exp Anal Behav 76:131–158

Roberts WA (1998) Principles of animal cognition. McGraw-Hill, Boston

Schusterman RJ, Kastak D (1993) A California sea lion (*Zalophus californianus*) is capable of forming equivalence relations. Psychol Rec 43:823–839

Schusterman RJ, Kastak D (1998) Functional equivalence in a California sea lion: relevance to animal social and communicative interactions. Anim Behav 55:1087–1095

Schusterman RJ, Gisiner RC, Hanggi EB (1992) Imprinting and other aspects of pinniped/human interactions. In: Davis H, Balfour H (eds) The inevitable bond: examining scientist/animal interactions. Blackwell, London, pp 334–356

Schusterman RJ, Reichmuth Kastak C, Kastak D (2002a) The cognitive sea lion: meaning and memory in the lab and in nature. In: Bekoff M, Allen C, Burghardt G (eds) The cognitive animal: empirical and theoretical perspectives on animal cognition. MIT Press, Cambridge, Mass., pp 217–228

Schusterman RJ, Reichmuth Kastak C, Kastak D (2002b) Equivalence classification as an approach to social knowledge: from sea lions to simians. In: DeWaal FBM, Tyack PL (eds) Animal social complexity: intelligence, culture, and individualized societies. Harvard University Press, Cambridge, Mass. (in press)

Trillmich F (1981) Mutual mother-pup recognition in Galápagos fur seals and sea lions: cues used and functional significance. Behaviour 78:21–42

Vaughan W (1988) Formation of equivalence sets in pigeons. J Exp Psychol Anim Behav Process 14:36–42