

Cross-modal transitivity in a California sea lion (*Zalophus californianus*)

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Abstract The ability of an experimentally experienced female California sea lion to form transitive relations across sensory modalities was tested using a matching-to-sample procedure. The subject was trained by trial-and-error, using differential reinforcement, to relate an acoustic sample stimulus to one member from each of two previously established visual classes. Once the two auditory–visual relations were formed, she was tested to determine whether untrained transitive relations would emerge between each of the acoustic stimuli and the remaining stimuli of each 10-member visual class. During testing, the sea lion demonstrated immediate transfer by responding correctly on 89 % of the 18 novel transfer trials compared to 88 % on familiar baseline trials. We then repeated this training and transfer procedure twice more with new auditory–visual pairings with similar positive results. Finally, the six explicitly trained auditory–visual relations and the 56 derived auditory–visual relations were intermixed in a single session, and the subject’s performance remained stable at high levels. This sea lion’s transfer performance indicates that a nonhuman animal is capable of forming new associations through cross-modal transitivity.

Keywords Sea lion · Transitivity · Cognition · Cross-modal · Equivalence

Through the rules of logic, new relationships can emerge from prior knowledge, allowing us to act appropriately in novel situations. In particular, the rules of *transitive inference* and *associative transitivity* are often investigated in both human and nonhuman animals. For example, a test of transitive inference includes teaching a subject that $A > B$ and that $B > C$, and testing whether that subject can make a logical leap and infer that $A > C$. On the other hand, associative transitivity includes inferring a local connection between stimuli that is not necessarily based on a hierarchical schema. For example, if one has learned that item “A” is related to item “B” and then learns that item “B” is related to item “C,” then associative transitivity can be used to correctly and immediately relate “A” to “C” by the common relation with item “B”. In humans, associative transitivity has been demonstrated under controlled laboratory conditions both within the visual modality (Hayes et al. 1991; Schenk 1994; Sidman and Tailby 1982; Tomanari et al. 2006) and between the auditory and visual modalities (Brady and McLean 2000; Carr et al. 2000; Green 1990; Sidman 1971; Sidman and Tailby 1982; Sidman et al. 1986; Yamamoto 1990 as cited by Yamamoto 1994). Demonstration of this ability has been variable across animal species (see Zentall 1998). Rhesus monkeys (*Macaca mulatta*) and baboons (*Papio anubis*) failed to show transitivity within the visual modality (Sidman et al. 1982); however, other nonhuman primates including capuchin monkeys (*Cebus apella*) (D’Amato et al. 1985) and chimpanzees (*Pan troglodytes*) (Yamamoto and Asano 1995) have successfully demonstrated this skill. Studies investigating transitivity using visual stimuli with pigeons

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have been equivocal. For example, D'Amato et al. (1985) found transitive performances in one out of three pigeons, and Kuno et al. (1994) found only weak evidence for transitivity in an associative learning study. It has been suggested that conflicting results may be a function of the procedures and stimuli used in these types of transitivity experiments (D'Amato et al. 1985); however, there remains insufficient experimental evidence to assess methodological factors in performance.

The clearest demonstrations of associative transitivity in nonhuman mammals come from experimental laboratory studies of California sea lions (*Zalophus californianus*) performing problem-solving tasks in the visual domain. In a study of derived stimulus relations, Schusterman and Kastak (1993) demonstrated the emergence of transitive relations in a California sea lion named Rio, as one of three prerequisites for *equivalence* classification. Thirty, three-member equivalence classes, each consisting of visual shapes identified as "A", "B" and "C", were demonstrated by this sea lion when the logical relationships of reflexivity ($A \rightarrow A$, $B \rightarrow B$, and $C \rightarrow C$), transitivity ($A \rightarrow C$), and symmetry ($C \rightarrow A$) emerged without training in a predictable way on the basis of previously learned relations within each class ($A \rightarrow B$ and $B \rightarrow C$). In Schusterman and Kastak's (1993) study, the sea lion was tested using a matching-to-sample (MTS) procedure. In a MTS task, a given sample stimulus serves as a conditional cue for the selection of one of two simultaneously presented comparison stimuli. For example, a subject can learn that when shown the sample "square" to choose the comparison "circle", and not the "triangle", but when shown the sample "hexagon" to choose the comparison "triangle" rather than "circle". In this way, conditional discriminations, or *if...then* rules (i.e., if "square"...then "circle") can be established by MTS, and these learned associations can be used as the basis of future testing for emergent or logical relations. Rio's performances on such emergent matching tests with visual stimuli were similar to that of a child tested by Sidman (1971) on auditory-visual tests of reading comprehension and showed that a nonhuman animal was capable of the same sort of complex rule-based learning used by humans to solve novel problems.

Another demonstration of transitivity within the context of equivalence classification and class expansion comes from a second experiment with sea lion Rio and another sea lion named Rocky. In this experiment, the sea lions were tested to determine whether the association of a novel item with one member of an already established visual class would be sufficient to induce generalization to the remainder of the items in a class (Reichmuth Kastak et al. 2001). The methods were modeled after a study by Sidman and colleagues investigating what has been termed Vaughanian equivalence classification (see Sidman et al.

1989; Vaughan 1988; see also Bhatt and Wasserman 1989; Lea 1984; Von Fersen and Lea 1990). The successful transfer performances demonstrated by Rio (Kastak and Schusterman 1994), and Rio and Rocky (Reichmuth Kastak et al. 2001), in these experiments supports the idea that logical inferences such as equivalence, and its prerequisites such as transitivity, are not language-dependent and may therefore be present in a variety of species (Schusterman and Kastak 1993; see also Sidman 2000). This view is consistent with the idea that these cognitive skills, and other forms of rule-governed behavior, have been subject to natural selection (Catania 1994). Therefore, it would not be surprising if the ability to apply a rule of logic, such as transitivity, is present in many species and is not a uniquely human characteristic.

As noted, there have been clear demonstrations of transitive performances within the visual modality in a few nonhuman species. However, animals live in a multi-modal world in which various sensory systems are utilized, raising the question of whether such relationships can emerge across, as well as within, sensory modalities. The ability to apply rules of logic across the senses was once thought to be unique to humans and based on language capabilities which connected words and their referents (Horne and Lowe 1996). Indeed, when humans were initially tested for associative transitivity using only visual stimuli, investigators were surprised by the positive results, as many had believed that the ability to perform auditory-visual associations of this nature probably depended on language specializations (Green 1990). More recent research has shown that humans are able to derive stimulus relations within as well as between various sensory modalities including auditory (Dube et al. 1993), visual and haptic (Belanich and Fields 1999; Easton et al. 1997; Ernst et al. 2007; O'Leary and Bush 1996; Reales and Ballesteros, 1999), and olfactory (Annett and Leslie 1995), demonstrating that the successful formation of logical inferences does not depend on the sensory modalities of the stimuli involved (Bush 1993).

Thus, studies of cross-modal performances in animals should reveal whether associative transitivity is a general phenomenon in animal learning that can be identified across different taxonomic classes, rather than a learning specialization. At present, an assortment of field observations, playback studies, and laboratory experiments suggest that some nonhuman mammals are able to form cross-modal categories and referential associations, allowing them to respond appropriately in a variety of novel situations (Lampe and Andre 2012; Schusterman et al. 2000). Further, research with some avian species, including budgerigars (*Melopsittacus undulatus*) and African gray parrots (*Psittacus erithacus*), has demonstrated emergent

associations among visual items mediated by common vocalizations (see Manabe et al. 1995; Pepperberg 2006).

Among nonhuman primates, several studies have provided evidence that many species can successfully recognize stimuli across the sensory modalities. For example, individuals of various species have performed successfully on a haptic–visual cross-modal recognition task, including chimpanzees (Davenport and Rogers 1970; Davenport et al. 1973), orangutans (*Pongo pygmaeus*) (Davenport and Rogers 1970; Davenport et al. 1973), rhesus monkeys (*M. mulatta*) (Weiskrantz and Cowey 1975), and pigtail monkeys (*Macaca nemestrina*) (Gunderson 1983; Gunderson et al. 1990). Also, auditory–visual matching has been demonstrated in capuchin monkeys (Evans et al. 2005) and rhesus monkeys (Ghazanfar and Logothetis 2003), with subjects successfully relating playbacks of vocalizations with images of the corresponding vocalizing monkeys.

A few studies have investigated the development of cross-modal associations in nonhuman primates by focusing on whether or not individuals can perform successfully on cross-modal MTS tasks in which the sample stimulus is presented in a different modality than that of the comparison choices. For example, Kojima et al. (2003) demonstrated that an experimentally experienced chimpanzee could correctly match the vocalizations of her troop members to pictures of those members without explicit training of these pairings. In addition, Bauer and Philip (1983) demonstrated that chimpanzees could perform the reverse task, matching facial images of familiar conspecifics to the auditory playbacks of their “pant-hoot” vocalizations. In a more complex cross-modal paradigm, Fouts et al. (1976) explicitly trained Pan, a chimpanzee, to relate ten gestural signs (from American Sign Language) to spoken English words. The objects that these words referred to were already familiar to the subject as they were found around his home. After direct training with verbal cues, the chimpanzee was able to spontaneously transfer the gestural signs to the physical objects, apparently through their common relation to the spoken words. Finally, following long-term participation in studies of referential communication, Kanzi, a bonobo (*Pan paniscus*), demonstrated the ability to correctly match spoken words to pictures of objects and also to correctly match spoken words to corresponding lexigrams (Savage-Rumbaugh et al. 1988).

These descriptions of emergent behavior in natural and laboratory settings support the idea that several nonhuman primates, and at least some other animal species, can form cross-modal representations. Therefore, to systematically explore the capability of animals to use transitive logic rules to spontaneously relate disparate stimuli across the auditory and visual modalities, in the absence of vocal labeling, we expanded upon past classification experiments

with a single sea lion subject that had an extensive history in associative learning paradigms. During the experiment, the subject learned to relate six different sounds with one member of each of two previously established visual classes. Once these auditory–visual relations were formed, she was tested to determine whether untrained transitive relations would emerge between each of the acoustic stimuli and the remaining members of each visual class. We proposed that, as with humans, the modalities of the stimuli would be irrelevant to the application of a transitive logic rule.

General method

The experimental design called for auditory–visual training followed by auditory–visual testing in a MTS procedure. The experiment was conducted in two parts with the first part including the acquisition of three pairs of new auditory–visual relations through explicit training, followed by assessment of spontaneous transfer of each pair to 18 potential auditory–visual relations through associative transitivity. In the final portion of the experiment, the six explicitly trained and the 54 derived auditory–visual relations were presented in an intermixed sequence in order to test the subject’s ability to perform successfully in a more cognitively demanding auditory–visual matching task. The general method for this study is provided in the following sections along with the procedural aspects specific to each part of the experiment.

Subject

One sea lion was tested in the current experiment. The subject was a 20-year-old female California sea lion named Rio (US National Marine Fisheries Service identification NOA0004827), who had been raised in a laboratory environment and had previous experience with a variety of operant learning tasks. For example, Rio had previously participated in a number of cognitive experiments using visual stimuli that were presented in a MTS paradigm, including investigations of learning by exclusion (Reichmuth Kastak and Schusterman 2002a; Schusterman et al. 1993), visual stimulus equivalence (Reichmuth Kastak et al. 2001; Schusterman and Kastak 1993), and generalized identity matching (Kastak and Schusterman 1994; Reichmuth Kastak and Schusterman 2002b). In addition to her experience with MTS tasks, Rio also had experience with two alternative forced choice discriminations. These included discrimination of visual stimuli on the basis of class membership (Reichmuth Kastak et al. 2001; Schusterman and Kastak 1998).

Prior to the present studies, Rio had no formal experience with cross-modal categorization. However, she had participated in a variety of psychoacoustic studies concerning hearing sensitivity and sound localization (Holt et al. 2004, 2005; Kastak et al. 2005, 2007; Southall et al. 2003).

Rio was housed at Long Marine Laboratory at the University of California Santa Cruz. Her habitat was outdoors in pools filled with free-flowing seawater. The pools were surrounded by adjacent haul out areas that allowed land access as well as a pathway between adjoining pools. Rio was fed between 5 and 7 kg of thawed cut herring and capelin each day, and approximately one-half of this diet was consumed during experimental sessions. She participated in two experimental sessions a day about 4 days each week from February 2004 to January 2005.

Apparatus

A two-choice visual MTS apparatus was used which allowed for the presentation of a sample stimulus from the center position and two comparison stimuli from either side. This was the same apparatus used by Rio in other MTS procedures involving visual stimuli (see Schusterman and Kastak 1993). During sessions, the apparatus was positioned on a shaded portion of the deck adjacent to one of the pools. For the present study, speakers were positioned over each of the three stimulus boxes to allow for the projection of amplified auditory stimuli. A separate speaker, positioned to the side of the apparatus, was used to provide auditory feedback following correct and incorrect responses as described below.

Stimuli

Visual

Twenty visual stimuli were used in the present experiment. They were black patterns painted onto the white backgrounds of 30 cm by 30 cm flat wooden squares. The patterns were chosen to be roughly equal in brightness and to be discriminable from each other (see Fig. 1). Rio had extensive prior experience with these stimuli, with which she had demonstrated visual equivalence classification using MTS and simple discrimination reversals (see Reichmuth Kastak and Schusterman 2002a; Reichmuth Kastak et al. 2001). The stimuli were divided into two 10-member classes coded as “Letters” (“A” through “J”) and “Numbers” (“1” through “10”). Rio was able to easily match these visual stimuli in 180 unique conditional discriminations on the basis of class membership because of their previous reinforcement history.

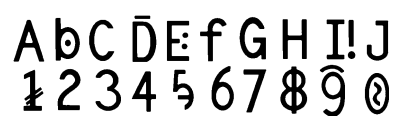


Fig. 1 Visual stimuli used in the experiment and originally described in Reichmuth Kastak et al. (2001). The ten stimuli in the top row comprise the “Letter” class (“A” through “J”) and the ten stimuli in the bottom row comprise the “Number” class (“1” through “10”)

Auditory

Three pairs of auditory stimuli were introduced in the present experiment (see Fig. 2). Each of these stimuli were configured to fall within the range of best hearing sensitivity for sea lions (see Moore and Schusterman 1976) as well as to be easily discriminable from one another. All auditory stimuli were 4 s in duration and had received sound pressure levels of approximately 68 dB re: 20 μ Pa. The six sounds used were descriptively identified and introduced to Rio in pairs: “Ring” and “Siren”, “Sweep” and “White”, and “Pulse” and “Tone” (Audio samples, Online Resources 1–6).

Differential outcomes

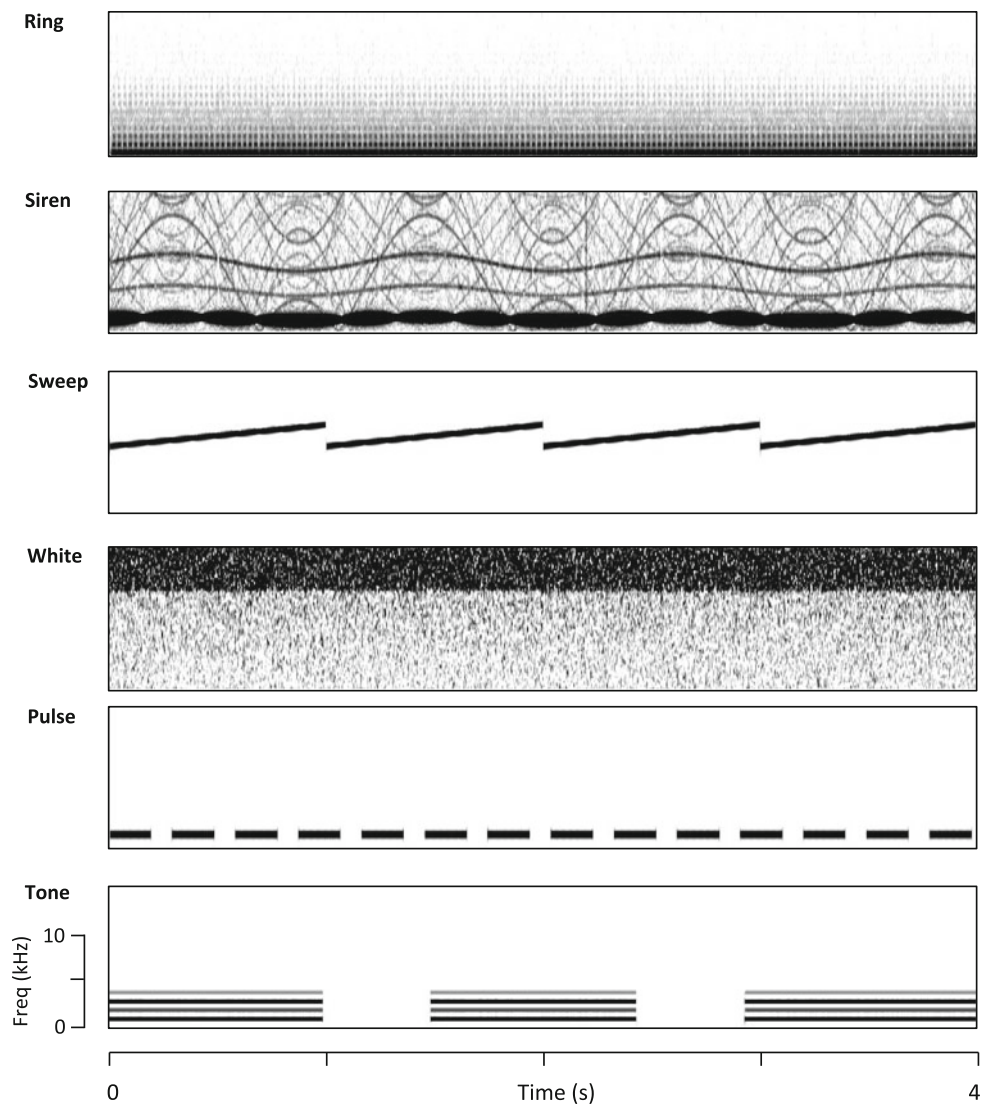
Rio had previously acquired these visual stimulus classes using differential outcomes with correct responses to the “Letter” class being reinforced with capelin fish and a corresponding 587-Hz-conditioned reinforcement tone, and correct responses to the “Number” class being reinforced with a herring fish and a corresponding 293-Hz-conditioned reinforcement tone (Reichmuth Kastak et al. 2001). These reinforcement contingencies remained in place throughout the present experiment.

General procedure

Experimental sessions were run following the same general methods as in past MTS work with Rio (see Kastak and Schusterman 1994; Reichmuth Kastak et al. 2001; Schusterman and Kastak 1993, 1998; Schusterman et al. 1993). The procedural aspects specific to an experimental section are explicitly discussed within that section.

At the start of each session, the subject entered the enclosure and was then cued by an assistant to position at a station in front of the apparatus. During experimental sessions, two assistants were seated behind the apparatus and were out of the subject’s view. For each trial, the assistants were instructed by headphones to place the visual stimuli into the appropriate stimulus boxes, which were concealed from the subject by sliding doors. The stimuli

Fig. 2 Spectrographic representations of the six auditory stimuli used in the experiment. Each stimulus was 4 s in duration. The stimuli were introduced in pairs and coded descriptively as “Ring” and “Siren”, “Sweep” and “White”, and “Pulse” and “Tone”. The auditory stimuli that were mapped to “Letters” were “Ring”, “Sweep”, and “Pulse”, while those mapped to “Numbers” were “Siren”, “White,” and “Tone”



were always placed into the boxes at the same time so that the subject could not be cued inadvertently. The instructions were given to the assistants by an experimenter who was located in a remote location and who observed the session in real time on closed-circuit video. All sessions were recorded and saved for video documentation. A trial began when the experimenter triggered the auditory sample stimulus. Two visual comparisons were revealed simultaneously at the onset of the auditory sample. A response by the subject was defined as moving from the center station to place her nose into a comparison stimulus box, and to hold the response for 1.5 s. This response criterion did not allow for ambiguous responses by the subject (i.e., she was explicitly correct or incorrect on each trial). Correct responses (selection of S+) were signaled to the subject by a 1-s tone that served as a conditioned reinforcer and was followed immediately by a piece of fish tossed directly over the center of the apparatus from behind. Differential

outcomes were used to reinforce correct responses to members of either class (see above). Incorrect responses (selection of S-) were not reinforced and instead were followed by a recorded vocal signal “no”. The comparison doors were closed simultaneously at the end of each trial.

Part 1

Auditory–visual training

Because Rio had a long history of visual–visual matching, and no prior experience with auditory–visual matching, she needed to be trained to attend to the auditory sample. To accomplish this, a fading procedure was used to establish auditory–visual matching performance (see e.g., Forestell and Herman 1988). Initially, a spatial cue was paired with the auditory stimuli presented to Rio, taking advantage of

the natural tendency of mammals to orient to the source of an auditory stimulus (Harrison and Beecher 1969).

The first training step was accomplished by mounting two speakers, spaced 90 cm apart, on the fence surrounding Rio's enclosure. Rio was positioned on the haul out area equidistant between the two speakers with a trainer located directly in front of her (on the opposite side of the fence). Rio was prompted with a pointing cue by the trainer to touch the speaker from which either of two auditory stimuli was projected, regardless of which stimulus it was. Her appropriate response was positively reinforced. In previous visual matching procedures, Rio had been trained to wait for a specific acoustic release sound to make her choice; this prompt was eventually faded back in and the gestural cue was faded out. When an auditory stimulus was projected from one of the speakers, Rio would remain still until the release cue was given. She would then move from the center position to touch one of the speakers for 1.5 s. The two auditory stimuli used for this training, coded as "*Ring*" and "*Siren*," were the same sounds that were used for Rio's first auditory–visual acquisition and subsequent transfer test. Therefore, differential outcomes were used to reinforce correct responses throughout training (i.e., correct responses to "*Ring*" were rewarded with capelin fish and the "*Letter*" reinforcement tone and correct responses to "*Siren*" were rewarded with herring fish and the "*Number*" reinforcement tone). Once Rio was reliably responding to the speaker that played the auditory cue, this situation was transferred to the MTS apparatus with a speaker placed over each comparison box and with the trainer removed from the testing environment.

Acquisition of auditory–visual discriminations

In the next training phase, the two auditory stimuli ("*Ring*" and "*Siren*") were each explicitly trained to an exemplar from each of Rio's visual equivalence classes ("*B*" and "*2*", respectively) using a spatial cue. The two speakers were located above the comparison doors, and the auditory cue was projected over the comparison box containing the correct visual stimulus choice. At the start of each trial, an auditory stimulus was projected, triggering the comparison doors to open, exposing the visual stimuli. After the auditory sample was played, a 2-s interval elapsed before Rio was prompted by the release cue to make her response. A response was defined as Rio moving from the center station to place her nose into a comparison stimulus box for 1.5 s to mark her choice. Each session included 40 intermixed trials and was counterbalanced for the correct stimulus appearing on the right or left, and with each visual comparison equally likely to be the correct or incorrect choice.

The spatial cue was removed after 11 sessions by taking away the speakers from above the two comparison doors

and instead projecting the auditory cue from a single speaker placed over the center sample box. This eliminated the directional cue that was previously available, and therefore, the only discriminative information that Rio was able to use to make a correct choice of the visual comparison was the spectral structure of the auditory sample. The sessions were run in exactly the same manner as the previous sessions except that the sample was projected from the speaker over the center sample box on each trial. As before, there was no visual sample presented and the center sample box door remained closed. These sessions were continued until Rio finally reached a criterion of 90 % correct responses or better on two consecutive sessions of 40 trials each, indicating she had learned the two auditory–visual discriminations: "*Ring*" → "*B*" and "*Siren*" → "*2*" (Video sample, Online Resource 7).

Transfer of auditory–visual discriminations

When Rio had acquired the auditory–visual discriminations with the first set of auditory stimuli ("*Ring*" and "*Siren*"), she was tested to evaluate spontaneous transfer of these discriminations to the rest of the previously established visual class members. The transfer test consisted of the auditory stimuli as possible samples and all of the remaining class members as possible comparison stimuli. Differential outcomes remained in place for the transfer test.

The test session began with the familiar auditory–visual (baseline) trials ("*Ring*" → "*B*" and "*Siren*" → "*2*") that were immediately followed by the transfer problems with additional baseline trials randomly intermixed. Of the 20 original visual stimuli, one exemplar from each 10-member class had been used during the training phases, which allowed for 18 novel transfer test trials (i.e., 18 unique "trial one" performances). To assess auditory–visual transfer, performance on the 18 novel test trials was compared to that on familiar baseline trials presented during the transfer test and also compared to performance expected by chance (50 %) (Video sample, Online Resource 8).

Replication of auditory–visual acquisition and transfer

After assessing transfer of the first set of auditory stimuli from one exemplar of each visual class to the remaining members of each class, we sought to replicate our findings with two additional auditory stimulus pairs. Using trial-and-error training only (no spatial cues), Rio next acquired the auditory–visual discriminations "*Sweep*" → "*A*" and "*White*" → "*I*" and completed similar transfer testing to the remaining visual class members. She then replicated the procedure a final time with a third set of auditory

stimuli (“Pulse” and “Tone” mapped to “C” and “3,” respectively). The procedures for each cycle of acquisition and transfer testing are summarized in the left panels of Tables 1 and 2.

Part 2

In the first portion of the experiment, transfer was assessed from three pairs of auditory samples to 18 visual comparisons. Rio’s task had been to discriminate between two auditory samples (i.e., one set) during any given session. In other words, during a session, the auditory stimuli would be either Set 1 (“Ring” and “Siren”), Set 2 (“Sweep” and “White”), or Set 3 (“Pulse” and “Tone”). In Part 2, Rio was tested to see whether she would be able to complete the task successfully with the higher cognitive demand of all six auditory stimuli serving randomly as the sample within a single session.

The test session for Part 2 was structured so that any of the six auditory stimuli could serve as the sample and any of the 20 visual comparisons could serve as alternatives. This resulted in a session of 60 trials and was the first time that trials from each of the three transfer tests had been intermixed. The session therefore included one exposure out of each of the six directly trained auditory–visual comparisons and the 54 unique transfer problems that had been presented in the test phases of Part 1.

Results

The acquisition of the auditory–visual relations that were explicitly trained with each pair of auditory stimuli, and subsequent transfer of emergent auditory–visual relations, are depicted in Fig. 3. The corresponding performance data are provided in the right panels of Tables 1 and 2. The

results were verified by an observer (blind to the experimental conditions) who reviewed the video of each test session; the scores of this observer were in full agreement with the real-time scores of the experimenter.

Part 1

Acquisition

Rio successfully acquired the six auditory–visual pairings established in Part 1 with a minimum of 64 and a maximum of 279 errors to criterion. It is important to note that the performance data for the first pair of auditory–visual discriminations included sessions with the spatial cue—as well as those without it—as it is assumed that Rio had begun to learn the association between the stimuli as well as the procedural task during this training phase (Video sample, Online Resource 7).

Transfer test 1

Rio responded correctly on 89 % (16/18) of the novel transfer trials and 88 % (or 14/16) on familiar baseline trials (Video sample, Online Resource 8). The two errors made within the 18 novel transfer trials occurred on trials 4 and 13 with one error to the “Letter” class and one to the “Number” class. Rio’s performance on these transfer trials did not differ from her performance on familiar baseline trials ($P > 0.05$; Fisher’s exact test) and was much better than that would be predicted by chance (two tailed binomial test, $P < 0.001$).

Transfer test 2

Rio responded correctly on 100 % (18/18) of novel transfer trials and 100 % (10/10) of familiar baseline trials. Her

Table 1 Six auditory–visual conditional discriminations established by explicit training

Auditory–visual acquisition							
Procedure				Performance			
	Auditory sample	Visual S+	Visual S–	Errors	Total errors	Total trials	Total sessions
Set 1	Ring	B	2	135	228	1,199	24
	Siren	2	B	93			
Set 2	Sweep	A	1	279	469	1,874	38
	White	1	A	190			
Set 3	Pulse	C	3	80	144	1,027	10
	Tone	3	C	64			

The left panel (procedure) shows the trial configuration (auditory sample, correct visual comparison, and incorrect visual comparison) for each stimulus set. The right panel (performance) shows the number of corresponding errors, total trials presented, and total number of sessions prior to criteria performance on two consecutive sessions

Table 2 Fifty-four auditory–visual conditional discriminations derived from six explicitly trained relations

		Auditory–visual transfer			Performance		
		Procedure					
		Auditory sample	Visual S+	Visual S–	Baseline	Test	Total
Set 1	Ring		A C D E F G H I J	1 3 4 5 6 7 8 9 0	14/16	16/18	30/34
	Siren		1 3 4 5 6 7 8 9 0	A C D E F G H I J			
Set 2	Sweep		B C D E F G H I J	2 3 4 5 6 7 8 9 0	10/10	18/18	28/28
	White		2 3 4 5 6 7 8 9 0	B C D E F G H I J			
Set 3	Pulse		A B D E F G H I J	1 2 4 5 6 7 8 9 0	9/10	16/18	25/28
	Tone		1 2 4 5 6 7 8 9 0	A B D E F G H I J			

The left panel (procedure) shows the 18 transfer trial configurations (auditory sample, possible correct visual comparisons, and possible incorrect visual comparisons) for each stimulus set. The right panel (performance) shows the number of correct responses/trials presented for the directly trained (baseline) trials, the novel transfer trials, and overall performance

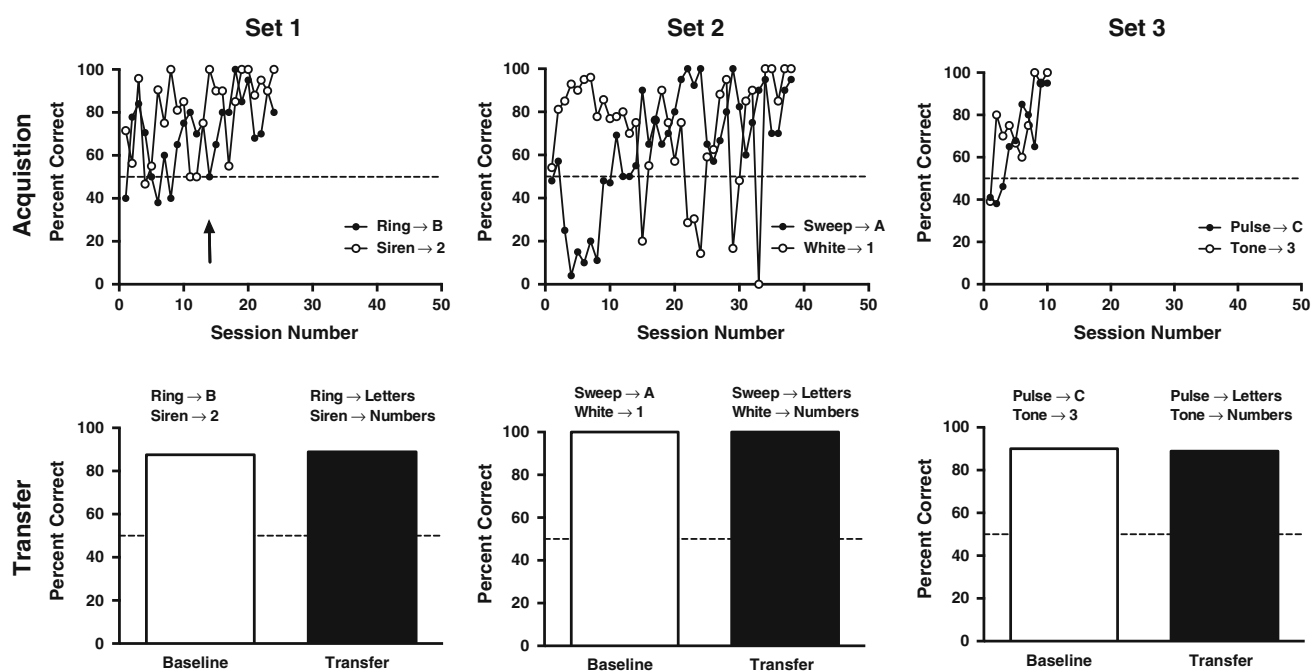


Fig. 3 The top row (from left to right) shows Rio's acquisition of three sets of explicitly trained auditory–visual discriminations. The plots illustrate performance on successive sessions to a criterion of 90 % correct responses (or higher) on two 40-trial sessions. In the top-left panel, the arrow indicates the point at which the spatial cue was removed from the training procedure. The bottom row (from left

to right) shows the auditory–visual transfer test performances corresponding to each set of auditory stimuli. They illustrate trial one performance on the 18 novel transfer trials compared to familiar baseline trials. In all cases, performance predicted by chance (50 %) is denoted by the dashed line

performance did not differ from her performance on baseline trials ($P > 0.05$, Fisher's exact test) and was much better than predicted by chance (two tailed binomial test, $P < 0.001$).

Transfer test 3

Rio responded correctly on 89 % (16/18) of novel transfer trials and 90 % (9/10) on familiar baseline trials. The two errors made within the transfer trials were on trials 8 and 18 with both errors to the “Letter” class. Her performance on

these test trials did not differ from her performance on baseline trials ($P > 0.05$, Fisher's exact test), and again, her performance far exceeded that predicted by chance (two tailed binomial test, $P < 0.001$).

Part 2

Rio responded correctly on 97 % (58/60) of the auditory–visual discrimination problems presented in the intermixed session with one error to the “Letter” class and one to the

“*Number*” class. Therefore, her performance did not decline on this session (with intermixed trials) relative to the earlier sessions she had completed with each set of auditory stimuli, demonstrating Rio’s ability to perform successfully on a session with a higher cognitive demand.

Discussion

We now have evidence that a sea lion is capable of using a logic rule of associative transitivity across sensory modalities to solve novel problems. After learning to relate acoustic samples to familiar visual stimuli, Rio showed immediate emergent transfer across preexisting classes of visual items.

While Rio was an experimentally experienced animal with a special learning history, she had no prior experience with auditory–visual matching. In Part 1 of this experiment, she successfully acquired six auditory–visual conditional discriminations. She learned these discriminations relatively quickly, even in the absence of the spatial cues used in her initial training. Notably, Rio’s acquisition of the final training pair of new auditory–visual discriminations was more rapid than either prior acquisition. This improved efficiency in learning new auditory–visual relationships by trial-and-error suggests that she was “learning to learn” the cross-modal stimulus pairings (Harlow 1949). After explicit learning of each pair of auditory–visual discriminations, Rio’s transfer of these trained relations to other members of previously existing visual stimulus classes demonstrated cross-modal associative transitivity. Specifically, her strong and immediate transfer performance with each set of auditory stimuli suggests that once the initial auditory–visual pairings were established, the discriminative functions of the auditory stimuli transferred spontaneously to all remaining stimuli within the visual classes.

Rio’s performance in Part 2 demonstrated that she was able to perform successfully, and without decrement in performance, with the increased cognitive load of encountering all six auditory samples presented randomly within one session along with twenty different visual comparison stimuli. This further supports the idea that Rio formed cross-modal classes and developed logical emergent associations since she responded correctly on these trials regardless of the particular stimuli presented or the order in which they were presented. Thus, it is reasonable to conclude that the 10-member visual classes previously established by Rio were expanded to incorporate auditory cues using the MTS procedure, so that auditory cues that had been associated with any class member were ultimately associated with every class member.

These findings of associative transitivity with sea lion Rio address several interesting questions and also inspire

new ones. One unresolved issue stems from the observation that, on the basis of her performance, Rio apparently formed two large cross-modal equivalence classes in which the stimuli in the classes were treated as functionally interchangeable. However, transitivity is only one of three prerequisites for equivalence class formation (Sidman and Tailby 1982). As discussed earlier, Schusterman and Kastak (1993) reported successful transfer within the visual modality with Rio for all three prerequisites, and this work remains the most convincing experimental demonstration of equivalence class formation in a nonhuman animal. Future work with Rio will attempt to clarify whether or not she can form auditory–visual equivalence classes according to the same criteria. In order to formally demonstrate this type of equivalence classification, Rio would need to perform successfully on tests of transitivity (as she did in the current study) and also succeed on tests of identity matching of all stimuli (reflexivity) and the reversal of the presentation of the auditory and the visual stimuli (symmetry). This will require Rio to respond to auditory comparisons in addition to the visual comparisons used in the present experiments. Such a procedural change will require additional training before auditory–auditory and visual–auditory transfer can be experimentally evaluated.

We also must consider the potential effects of the differential outcomes that were used to reinforce correct responses throughout this experiment. Differential outcomes were originally used during the training of large visual stimulus sets with Rio as they have been shown to improve acquisition of new explicitly trained discriminations (Goeters et al. 1992; Overmier et al. 1971). Perhaps associating responses to each class with a different fish type, and its corresponding conditioned reinforcement tone, contributed to Rio’s success in the transfer tests that followed training by providing other common cues to mediate the emergent stimulus relations (see Sidman 2000 for a discussion of this issue). In other words, perhaps the demonstrated inferences are based in part on Rio learning that each class indicates a specific reinforcer. However, we have reason to believe that, even if the differential reinforcement facilitated learning, it was not a critical factor in her performance. This view is supported by Reichmuth Kastak et al. (2001), who experimentally evaluated the role of the reinforcer in visual class formation by sea lions, and by Schusterman and Kastak (1993), who showed that Rio was capable of forming equivalence relations within the visual modality in the absence of differential outcomes, indicating that class-specific reinforcement is not required to induce emergent stimulus associations such as the transitive relations demonstrated here.

The extent to which the present findings of cross-modal associative transitivity can be generalized to other sea lions is unclear as the experiment was conducted with a single,

experimentally experienced subject. Observations of wild sea lions illustrate that these animals are behaving in ways that appear to involve complex categorization, such as that seen with Rio, and we feel that it is reasonable to assume that work with other naïve subjects would result in similar findings. However, this study is an extension of Rio's past learning history and not only investigates cross-modal transitivity but does so in the context of previously acquired categories. Therefore, her past and current experience is inherently entangled. Nevertheless, the current data provide clear and compelling evidence that a sea lion can possess the ability to form logical inferences to solve novel problems across sensory modalities.

In summary, this sea lion subject demonstrated class expansion by logical inference across sensory modalities in a similar fashion to that observed in the context of within-modal transfer (Reichmuth Kastak and Schusterman 2002a; Reichmuth Kastak et al. 2001). This demonstration, in the absence of vocal labeling by the subject, suggests that the cognitive processes which enable the emergent association of perceptually different stimuli are fundamental and that linguistic ability is not necessary to support this capability as has been previously suggested (Devany et al. 1986; Dugdale and Lowe 1990; Hayes 1991; Horne and Lowe 1996). Applying a rule of transitivity enables individuals to make sensible inferences about their environment based on prior experience and to obtain a considerable degree of cognitive economy by being able to respond appropriately to novel situations. For species such as sea lions, this ability would be especially useful for predator recognition and avoidance, exploiting novel hunting scenarios (e.g., stealing from fisherman), and individual recognition (which is especially critical for mother–pup reunions on the rookeries). Therefore, it should not be surprising that this general cognitive principle may be adaptive and is not restricted to a single sensory modality or a specific taxonomic group.

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