Call Usage Learning in Gray Seals (*Halichoerus grypus*)

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Call usage learning can be demonstrated on 4 different levels: signaling on command, signaling and refraining from signaling on command, responding to a trained stimulus with a signal from a specific signal class, and responding to the playback of any untrained stimulus with one from the same signal class. Two young gray seals (*Halichoerus grypus*) were trained successfully to demonstrate the first 2 levels. They also learned to respond to 9 moan stimuli and 9 growl stimuli with vocalizations of the same class (Level 3). However, novel moan and growl stimuli tended to elicit growls. This casts doubt on the possibility that gray seals can reach the 4th level, but it demonstrates that they are capable of the first 3 levels of usage learning.

Contextual learning in animal calls is a form of social learning that yokes signals already present within an individual's repertoire to novel contexts based on experiences with how other individuals deploy these signals (Janik & Slater, 1997, 2000; Nelson & Marler, 1994). Janik and Slater (2000) further divided such contextual learning into comprehension and usage learning. The former occurs when an individual acts as a receiver, using experiences with the signal usage of others to extract a novel meaning from a signal. By contrast, usage learning of calls occurs when an individual learns to produce a signal from its existing repertoire in a novel context. Contextual learning in the vocal domain often represents an evolutionary compromise between an unlearned vocal repertoire broadly deployed in the correct circumstances for nearly immediate communication and one flexibly learned to account for unpredictable features of the environment that significantly impact on vocal usage (Seyfarth & Cheney, 1997).

Comprehension learning is widespread in the animal kingdom. For example, animals as different as Diana monkeys (*Cercopithecus diana;* Zuberbühler, 2000) and fatheaded minnows (*Pimephales promelas;* Mirza & Chivers, 2001) can learn to recognize signals from various predators or alarm signals produced by other species. Usage learning seems to be less common, but examples include vervet monkeys (*Cercopithecus aethiops*) and brown-headed cowbirds (*Molothrus ater*). Vervet monkeys exposed to

high rates of intergroup encounters used the associated "wrr" calls correctly earlier than infants without such experience (Hauser, 1989). Brown-headed cowbirds are brood parasites. During the breeding season, males sing relentlessly to females, maneuvering through literally thousands of songs. Females selectively prune and mold male song by performing abrupt wing strokes in response to certain components, a display that stimulates the males to sing these elements at a significantly elevated rate (West & King, 1988). Usage learning occurs rapidly under these circumstances, managed by a deadline imposed by reproductive necessity. Recently, Goldstein, King, and West (2003) demonstrated that human infant vocal production can be influenced in a similar way.

The demonstration of usage learning in animals can be divided into two different levels requiring different levels of complexity in the control over vocalizations. Janik and Slater (2000) distinguished between these, namely, learning to vocalize in an arbitrary context and learning to produce specific call types in response to specific stimuli. However, in an experimental demonstration, further steps can be identified. The first step consists of showing that an animal can vocalize in an arbitrary context, reliably producing a call when exposed to a particular stimulus. Success in this initial phase is encouraging, but it may be a by-product of the animal entering an excited motivational state in which the threshold for vocal activity has been lowered. A more convincing demonstration of usage learning therefore requires the subject to vocalize on one command and to remain silent on a different command. A more complicated level of usage learning requires an animal to produce different call types in response to distinct commands. This level requires an ability to differentiate among distinct components of the vocal repertoire and to produce them in particular contexts.

How do these levels differ in terms of behavioral control and processing? The first level involves a change of the motivational state of the animal, whereas the second requires control over motivation such that a vocalization is only emitted once a stimulus has been presented. The third level requires discriminating between different stimuli and having arbitrary control over different types of vocalizations rather than merely over the capacity to produce a vocalization. Beyond these levels, animals may be able to use generalization skills or even form broader mental concepts to respond to particular sets of stimuli. The use of novel stimuli can help in the recognition of patterns of generalization. For example,

an animal may either learn to respond to a single set of stimuli of a particular class in an identical fashion or learn to match any presented stimulus by producing a call of the same type as the stimulus. Whereas an animal generalizing between stimuli may be trained to respond to all growl stimuli by producing a growl (or any other vocalization type it is capable of producing), matching requires producing a call of the same type as the stimulus, independent of the call type to which this stimulus belongs. The present study is the first to investigate these different levels of usage learning systematically.

Although studies in the wild broadly reveal the natural context in which learning is useful, research on captive animals can offer insight into their precise capabilities and behavioral flexibility. Early experiments investigating contextual learning in the vocal sphere sought to bring vocal behavior under operant control (Skinner, 1953) by reinforcing both vocal responses to unique stimuli and changes in vocalization rates in isolated animals. Positive results demonstrated that subjects had at least some degree of control over their vocal production and an ability to use their vocalizations in a novel context detached from social interactions (e.g., to avoid an electric shock stimulus or when viewing a colored light or a target of a particular size). This early experimental technique produced successful results with numerous avian and mammalian species (see, e.g., Burnstein & Wolff, 1967; Ginsburg, 1960; Krasner, 1958; Lal, 1967; Lane, 1960, 1961; Leander, Milan, Jasper, & Heaton, 1972; Molliver, 1963; Myers, Horel, & Pennypacker, 1965; Rheingold, Gewirtz, & Ross, 1959; Salzinger & Waller, 1962; Schusterman & Feinstein, 1965; Wilson, 1975; reviews in Adret, 1993; Janik & Slater, 2000). Most of these studies conclusively demonstrated the first two levels of usage learning.

Pinnipeds were the subject of this study. Because visual range is limited underwater, pinnipeds rely strongly on acoustic communication. Earlier studies demonstrated that some pinnipeds are capable of vocal usage and production learning. Schusterman and Feinstein (1965), for example, trained a generally nonvocal captive California sea lion (*Zalophus californianus*) to produce clicks underwater. Originally rewarding any vocalization, the experimenters gradually accepted only clicks produced in specific contexts. In particular, the subject was trained to click, causing a target that could be struck to receive food to be lowered into its pool. Furthermore, this sea lion managed to respond successfully to a discrimination exercise in which it clicked or remained silent in the presence of a large or small circular target, respectively. Ralls, Fiorelli, and Gish (1985) reported that harbor seals (*Phoca vitulina*) are able to mimic human speech, thus demonstrating a capability of vocal production learning. Thus, pinnipeds offer a compelling biological system in which to investigate learning behavior in the vocal domain.

We investigated whether two young captive gray seals (*Halichoerus grypus*) were able to use contextual learning to perform successfully in trained vocal tasks. Adults, juveniles, and pups produce distinct tonal and guttural vocalizations in air during breeding and lactation and underwater (Asselin, Hammill, & Barette, 1993; McCulloch, 1999). Although conflicting evidence has been reported regarding the ability of mothers to distinguish between the vocalizations of their pups (McCulloch & Boness, 2000; McCulloch, Pomeroy, & Slater, 1999), these pup calls appear to be stereotyped and individually distinctive (Caudron, Kondakov, &

Siryanov, 1998; McCulloch et al., 1999). This study investigated whether gray seals were capable of vocalizing and remaining silent on command and differentially producing moans and growls after they had heard playbacks of the same call type.

General Method

Training began on January 31, 2002, with two young gray seals (*Halichoerus grypus;* one male [Oscar] and one female [Kylie]) between 2 and 3 months of age at the time. After weaning at around 18 days of age, gray seals are solitary or associate with other seals of similar age (Bonner, 1972). Social learning seems unimportant in acquiring the skills needed at sea because the mothers and other adults leave the breeding colonies much earlier than their young and seal pups do not enter the water with their mothers before that time. Both experimental subjects were born in the wild on the Isle of May in the Firth of Forth, Scotland, and were subsequently transported to the captive research facility at the University of St. Andrews. A second female of the same age, a subadult female, and an adult female were housed there as well but were not involved in this study. All seals were fed herring daily with vitamin and iron supplements. The facility consisted of a large rectangular pool (42 m × 6 m × 2.5 m) and two circular pools (3 m and 5 m in diameter and 2 m deep).

During training procedures, the trainer depressed a clicker immediately after a correct response and before the food reward would be presented. After incorrect responses to training commands, the experimenter said "No" firmly and withdrew from the training area for 15–20 s.

Experiment 1: Usage Learning Levels 1 and 2

This first level examined whether Oscar and Kylie were capable of vocalizing only after observing a specific visual stimulus, withholding all vocal responses at other times.

Method

The procedure for this experiment developed gradually between January 31 and March 22, 2002. Training sessions occurred for each individual separately once per day, five to seven times each week, except for a gap from March 10–18, 2002. The training was conducted on land, with a gate separating the experimenter and seal as a safety precaution and to create a controlled experimental area (see Figure 1A). Initial sessions consisted of presenting a bicycle light and waiting for the seal to vocalize before offering a reward. The seals soon started to call incessantly regardless of whether the light was present. To increase attentiveness to the signals of the experimenter, stationing trials were introduced in which Oscar and Kylie were trained to respond to pointing gestures by touching their noses on
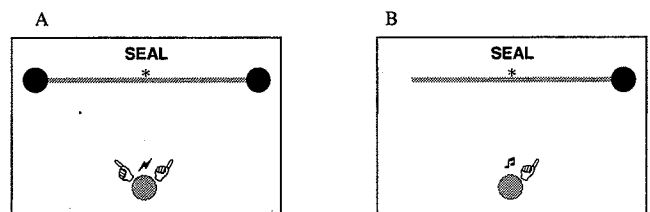

Figure 1. Overhead view of training. A: Experiment 1. The seal stationed behind the gate (gray line) on the Tupperware container (*) at the beginning of each trial. The experimenter (●) then directed the seal to station on either the left or the right shapes (here, ●) by pointing, represented by the two hands, or to vocalize by presenting the light (✗). B: Experiment 2. Pointing gestures were directed only to the right, and vocalizations were elicited with playbacks (♪) instead of a light.

wooden black circles and gray triangles, respectively. Vocalizing in response to these commands was considered incorrect. A Tupperware container was suspended from the middle of the gate, and the seals were rewarded for stationing on this container at the beginning of each trial. Once the subjects were performing successfully in these pointing trials, the light was reintroduced.

The eventual procedure consisted of isolating one individual on land, stating the subject's name, and waiting several seconds while he or she stationed on the Tupperware container without vocalizing. According to a predetermined randomized sequence that did not limit the maximum number of consecutive trials featuring the same command, the experimenter presented the light or pointed to the target object on the left or right. Because a fixed number of fish pieces were used for training, incorrect responses produced an increased number of trials in a particular session— Oscar: range of 19–44 trials with a mean ($\pm SD$) of 25.9 (± 6.9); Kylie: range of 19–34 trials with a mean ($\pm SD$) of 24.7 (± 4.8). Training sessions were recorded onto TDK SA90 audiotapes with a Sennheiser K6 microphone and a Marantz CP430 tape recorder (frequency response of the entire recording chain: 35–15000 Hz ± 3 dB). All vocalizations were subsequently digitized with Cool Edit Pro LE software at a sampling rate of 44100 Hz and 16-bit resolution using the Yamaha OPL3-SAx sound card of a Toshiba Satellite 320CDT.

Results

Training results are shown for Oscar and Kylie in Figure 2. The sessions depicted began on February 21, 2002, the first day when both pointing and vocalizing trials were introduced during the same training session, and ran until March 25, 2002. The number of pointing and vocalization trials varied between sessions according to the randomization schedule and the success of the seals (see above). The sessions with an overall success rate lower than that of the pointing and vocalization trials alone contained additional incorrect trials in which the seal had vocalized during the stationing phase.
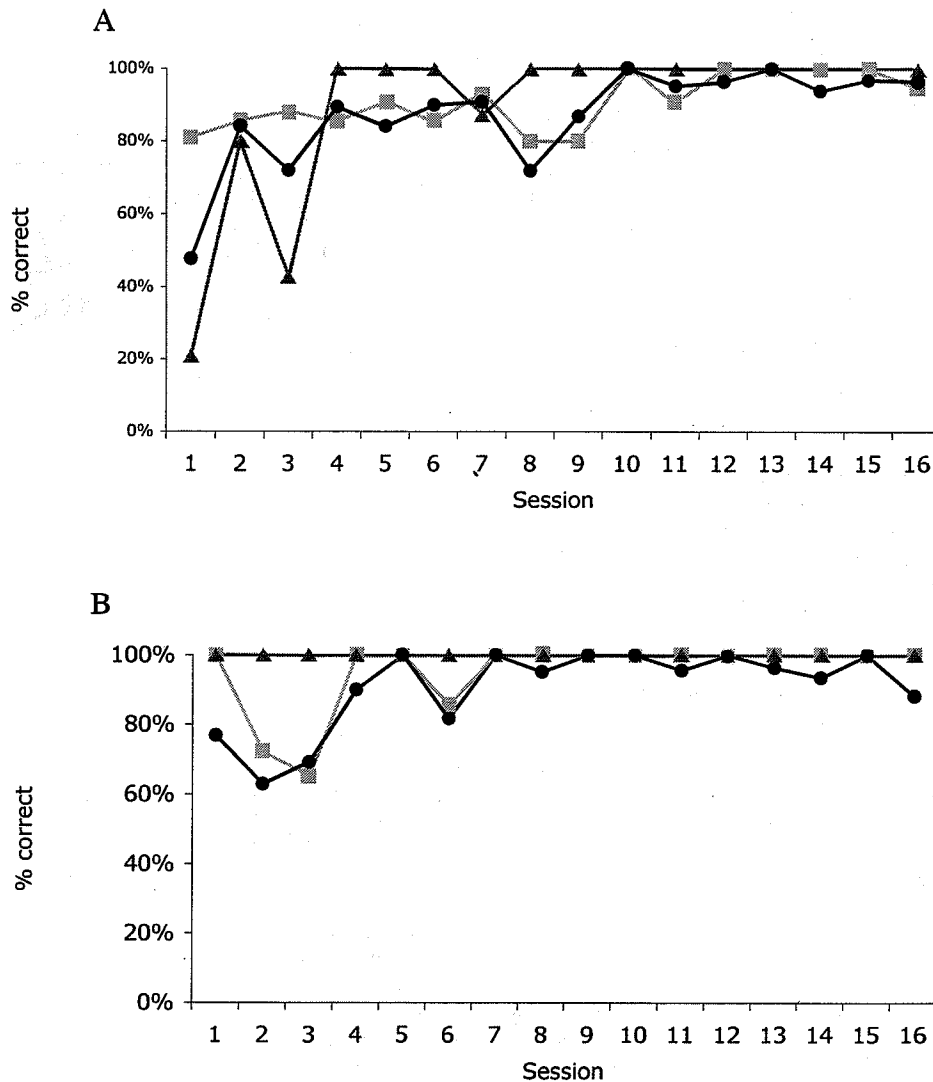

Figure 2. Performance results for vocalizing on command. A: Oscar (February 21–March 25, 2002). B: Kylie (February 21–March 25, 2002). Success rates are displayed for pointing trials alone (▦), vocalization trials alone (▲), and all trials together (●).

The two seals quickly acquired proficiency in the tasks of vocalizing and remaining silent on command. Pointing trials consistently elicited appropriate responses from both seals across training sessions, an expected result because the vocalization task was reintroduced only after high success rates had been achieved on pointing trials alone. Oscar's success rate in the vocalization trials was considerably more variable than Kylie's immediately perfect performance partly because at first Oscar was arbitrarily held to a stricter training regime. In particular, movement toward one of the shapes when the light was presented was considered an incorrect response for Oscar but was initially ignored for Kylie. Overall, Oscar and Kylie both began to perform consistently at or above 80% at Session 4, except for one subsequent session with Oscar. Performance became nearly flawless for Oscar after Session 10 and for Kylie after Session 7. Of the 16 sessions displayed in Figure 2, Oscar performed with 100% accuracy in 2 of the trials and Kylie in 6 of the sessions.

Experiment 2: Usage Learning Level 3 and Beyond

In this experiment, we investigated the seals' ability to control the utterance of different sound types from their repertoire. This was achieved by training them to respond to moan or growl playbacks with vocalizations of the same category. We further tested whether our subjects would generalize this response to any moan or growl they heard or would learn each individual stimulus and the required response class separately.

Method

Playback stimuli. Playbacks were made from five moans and four growls produced by Oscar and four moans and five growls produced by Kylie during Experiment 1 and baseline vocal repertoire recording sessions made in nonexperimental contexts. Each seal was exposed only to the moans and growls he or she had produced him- or herself. These two categories of sounds are easily distinguished by ear and by visual inspection of spectrograms (see Figure 3). Moans are tonal and consist of a strong fundamental frequency below 1.5 kHz, with the most intense harmonics below 4 kHz and only weak sound energy above 5 kHz (see Figures 3A and 3B). Growls, however, are characterized by more broadband sound energy lacking harmonic structure, with a bandwidth that can extend as high as 15 or 20 kHz (see Figures 3C and 3D) but with most sound energy below 2 kHz. Whereas moans were used most frequently by the seals during nonexperimental feeding sessions and when they encountered the fences around their enclosure, growls were generally produced in aggressive interactions between seals.

All playbacks were standardized in amplitude and burned onto a compact disc in a random order, with each moan and growl appearing the same number of times. A Phillips CD player and a Teac PowerMax-500/B three-way-subwoofer system (frequency response: 40–18000 Hz ±4 dB) broadcast these vocalizations to the seals. The sessions were recorded with the same equipment described in Experiment 1. Each session was also monitored visually in the real-time spectrogram mode of Avisoft-SAS Lab Pro to facilitate distinguishing between moans and growls spectrographically.

To test whether individuals would generalize their responses to any moan or growl vocalization, we introduced novel stimuli of each category once the first phase of Experiment 2 had been completed. Examples of the novel moans and novel growls introduced subsequently in the experiment (see *Procedure,* below) are depicted in Figures 3B and 3D. These novel sounds were recorded as responses to the original playbacks and were selected to be as similar in duration to the initial set of playback stimuli as
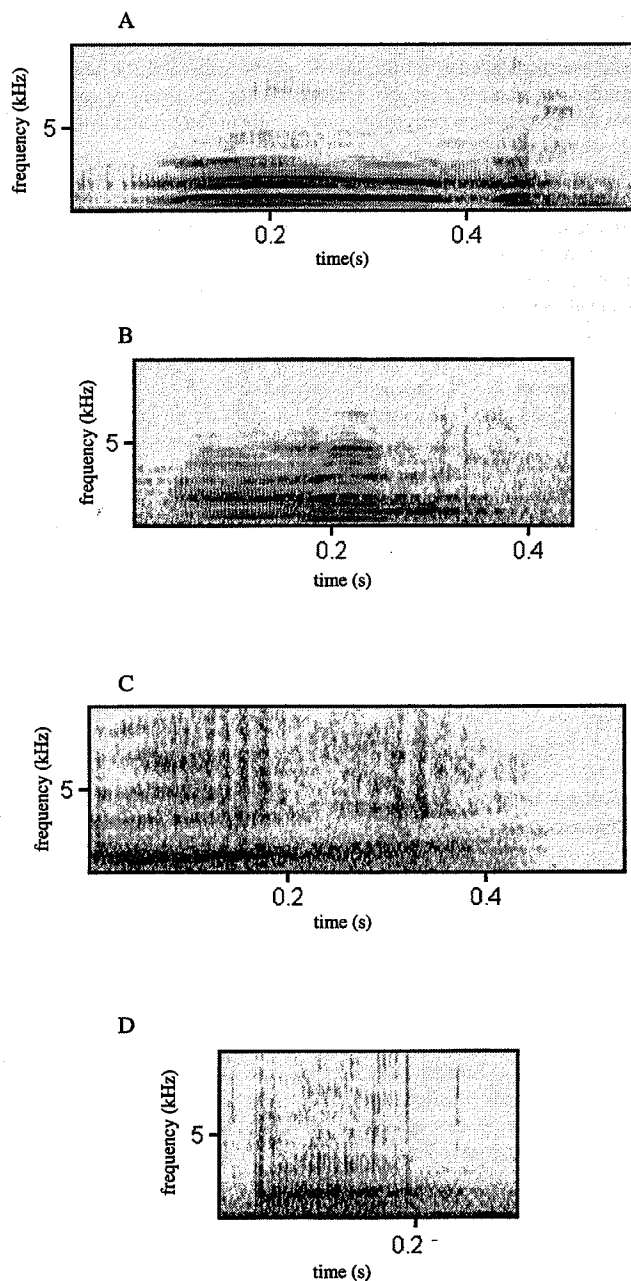

Figure 3. Sample spectrograms of playback stimuli. A: Trained moan from Oscar. B: Novel moan from Oscar. C: Trained growl from Kylie. D: Novel growl from Kylie.

possible (see Table 1) and distinguishable aurally and spectrographically. These calls were produced by the seals themselves so we knew that they had been heard before at least once and were therefore not entirely novel to the seals. Amplitude was again standardized, and new compact discs were burned in which every fourth trial introduced one of these novel playback stimuli. The three intervening trials played the same moans and growls between which the seals had been trained to differentiate. The order was randomized, and two of these sequences of 48 playbacks were generated and used in alternate training sessions. Table 1 lists the quantity and average duration of all playback stimuli.

Table 1

Quantitative Description of Acoustic Features of Training and Novel Playback Stimuli

Stimulus	Oscar	Kylie
Training moans		
Quantity	5	4
Average duration (± SD)	1.5 (± 0.9)	0.7 (± 0.2)
Training growls		
Quantity	4	5
Average duration (± SD)	2.6 (± 1.2)	0.5 (± 0.2)
Novel moans		
Quantity	6	6
Average duration (± SD)	0.4 (± 0.1)	0.4 (± 0.0)
Novel growls		
Quantity	6	6
Average duration (± SD)	0.7 (± 0.1)	0.3 (± 0.1)

Note. Duration is expressed in seconds.

Procedure. This phase began on March 26, 2002, and was conducted indoors to protect the electronic equipment from inclement weather and to reduce ambient noise. The generic setup was similar to Experiment 1 (see Figure 1B). The experimenter stood centrally before the seal, and several pointing trials to the right during each session were maintained. In this experiment, we replaced the light stimulus with playbacks of seal sounds. Strict rewarding for similarity between stimulus and response began on April 19, 2002. Similarity was assessed ad hoc by Ari D. Shapiro, who then gave or withheld the reward. The playback sequences containing the novel moans and growls described above were introduced on May 14, 2002, for Oscar and on June 19, 2002, for Kylie. The two sequences were alternated five times each. All sessions were recorded on audiotape, and a subset of 100 seal responses (Oscar: 23 moan trials and 22 growl trials; Kylie: 27 moan trials and 28 growl trials) was assessed independently by Vincent M. Janik to confirm that rewards were given or withheld appropriately. Observer agreement in this assessment was 97%.

Results

Figures 4A–4D present the performance results for Oscar and Kylie, respectively, for the trained playback stimuli alone during the novel playback sessions. These figures show the trials judged to be correct and incorrect within each session. It is evident that both Oscar and Kylie were capable of producing moans when hearing moans and growls when hearing growls in response to the stimuli on which they had been trained. Oscar achieved proficiency by Session 23, whereas Kylie required a total of 47 sessions. Vocal responses to the novel playbacks used in the last 10 sessions are shown in Figures 4E–4H. Oscar and Kylie responded to the first novel moan and the first novel growl playbacks by growling.

In the last 10 sessions, Oscar performed significantly above chance in response to the trained set of moan and growl stimuli combined (see Figures 4A and 4B), $\chi^2(1, N = 358) = 275.4, p < .001$. Oscar also responded to all novel playback stimuli in the first of these sessions significantly better than if he were moaning or growling randomly (see Figures 4E and 4F), $\chi^2(1, N = 12) = 8.33, p < .01$. Although his success in this and the last sessions was strikingly high, however, his performance oscillated over the interim. Similarly, Kylie responded at above-chance levels to the trained set of moans and growls together during the sessions in which novel stimuli were introduced (see Figures 4C and 4D),

$\chi^2(1, N = 360) = 288.0, p < .001$. However, she growled in response to the majority of the novel stimuli (see Figures 4G and 4H): 56 of 60 novel moan playbacks and 60 of 60 novel growl playbacks. Kylie's responses to the novel playbacks in the first of these 10 sessions did not differ from random, $\chi^2(1, N = 12) = 0.33, p = .57$. Because Oscar and Kylie were rewarded for responding correctly to novel stimuli, it would be misleading to compare their performance across all 10 sessions with that expected if they were moaning and growling randomly. In sum, both Oscar and Kylie had developed an ability to respond differentially to moans and growls in the trials presenting the trained stimuli, performing consistently above chance levels. Minor deviations from flawless performance (1–4 trials) transiently affected the moaning and growling results during the 10 experimental sessions, but consistent drops in performance were not observed. The novel stimuli, however, produced a different performance pattern with substantial, persistent dips in correct responses to one or both vocalization categories.

Discussion

Two young captive gray seals were trained in Experiment 1 to vocalize only when presented with a light and to remain silent and move in the direction indicated by a pointing experimenter to laterally positioned target objects. All categories of vocalization were rewarded in response to the light in this first part of the experiment because the primary objective was to control the timing and context of vocal production in these seals. The vocal behavior of the two seals was thus under operant control because it could be managed by a stimulus and released according to a schedule of differential reinforcement (Ginsburg, 1960). These gray seals demonstrated usage learning because this training procedure required them to produce vocal signals already within their repertoire in a novel context (Janik & Slater, 2000). The seals achieved the first two levels of usage learning, namely, vocalizing on command and differentially responding to discrete stimuli by either vocalizing or remaining silent.

Once these gray seals were responding successfully to a single visual cue, new signals were introduced to determine the sophistication of their ability to control vocal production. In this second phase of the training procedure, the seals learned to respond to nine playbacks of their own moans and growls by producing vocalizations of the same type. The seals did not need to attend to the specific playback stimuli during the initial sessions to respond correctly because only a single vocal category was being played and rewarded. Once the frequency of alternation between moans and growls increased, however, a new response strategy was required that involved listening to the stimulus before vocalizing. This transition emerged rapidly, with an abrupt shift from mediocre to nearly flawless performance.

The seals could have achieved this level of performance by using one of three strategies. First, they could have learned to respond uniquely to each of the nine specific playback stimuli, requiring nine separate associations to have been formed. Secondly, they may have learned to generalize between different samples of the same call class. According to this strategy, the seals could have learned to growl in response to a growl playback, for example. This requires only two associations, namely, to answer a growl with a growl and a moan with a moan and to generalize
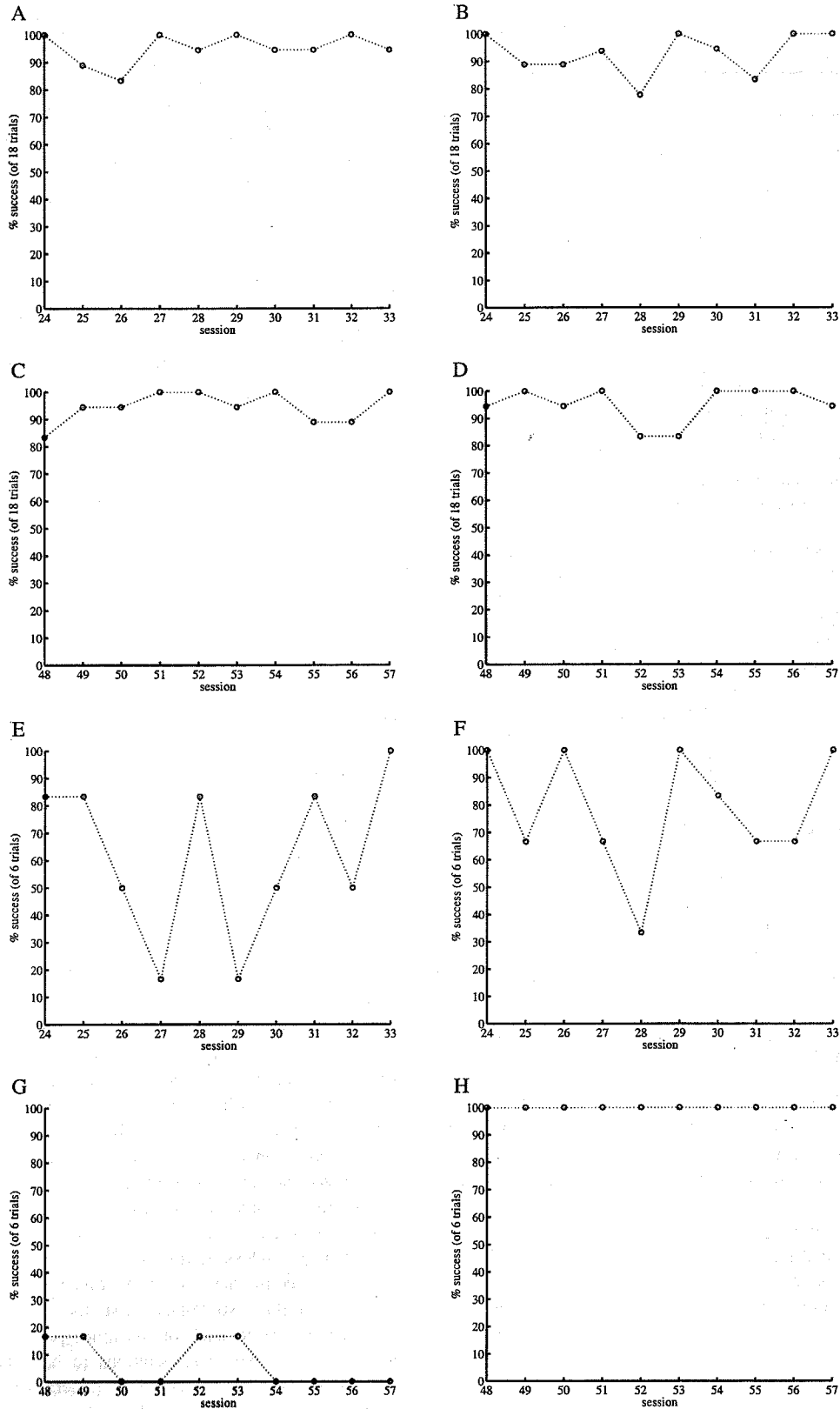
Figure 4. Results gathered during the final 10 sessions including the novel playbacks. The figure shows Oscar's performance results with familiar moan (A) and growl (B) stimuli to which he had been trained to respond by producing a sound of the same call class, Kylie's performance results with familiar moan (C) and growl (D) stimuli to which she had been trained to respond by producing a sound of the same call class, Oscar's performance results during the first 10 sessions involving novel moan (E) and growl (F) playbacks, and Kylie's performance results during the first 10 sessions involving novel moan (G) and growl (H) playbacks.

between stimuli of the same class at the perception level. If this were the correct explanation, it would have been as simple to have trained them to produce a moan in response to a growl stimulus. This sets the second explanation apart from the third, which assumes that the seals learned to match any auditory stimulus by producing a call of the same type as the stimulus no matter what call was presented. This strategy could be examined by presenting the seals with a stimulus from a third call class to determine whether they answer not with a moan or a growl but by producing a call from the same call class as the new stimulus.

We tested these possibilities by presenting novel moan and growl stimuli to investigate how the seals responded. The seals did not perform consistently by producing a growl in response to a novel growl or a moan in response to a novel moan, which suggests that they had actually learned nine individual associations between the nine stimuli and the responses required for each one. Thus, these seals both failed to generalize between auditory stimuli belonging to the same class and to match their vocal response to the perceived call type. They did, however, learn to produce a particular call type in response to specific stimuli, clearly demonstrating a mastery of the third step of contextual learning in the vocal domain. Further studies are needed to evaluate the extent to which gray seals are able to generalize between stimuli or match playback stimuli.

Once the novel playbacks had been introduced, both seals continued to respond correctly to the moans and growls used as the original playback stimuli with only minor fluctuations in performance. Oscar's reactions to the novel stimuli were highly variable. Figures 4E and 4F do not resemble a learning curve or reflect an immediate ability to assign these new playbacks to the appropriate vocal category. His initial success should be evaluated cautiously because it broke down dramatically in subsequent sessions, suggesting that his early performance might have been random. Judging from Oscar's rapid learning of the nine training stimuli, it was possible that he had been trained within only 10 sessions to respond appropriately to the novel playbacks, accounting for his perfect performance in the final session (see Figures 4E and 4F). After a certain larger quantity of stimuli was introduced, generalization may have become an emergent strategy of the seals in this particular training regimen once the individual stimuli become too numerous to keep track of.

The results presented in Figures 4G and 4H show that Kylie growled in response to most of the novel stimuli (116 out of 120). This is in direct contrast to her nearly flawless performance during the trained moan and growl playback trials of the final 10 sessions (see Figures 4C and 4D). The longer period of time required to train Kylie initially may explain this discrepancy. She often responded to all playbacks in these early sessions by either only moaning or only growling until she learned to distinguish between the individual stimuli. The 10 sessions with the novel stimuli may have revealed a similar pattern.

Given Oscar's initial performance in Level 4 tests and the sample size of only 2 seals, we cannot conclude that grey seals are not able to generalize between stimuli. Other aspects could have made generalization difficult for the seals. The initial training with visual stimuli may have drawn attention away from the type of stimulus used and thus have led to a decreased probability of generalizing. However, we used acoustic stimuli excessively in Level 3 training, which makes this explanation less likely. Another factor that we cannot exclude completely is some degree of cuing by the experimenter. Although we tried to avoid any kind of cuing, it is difficult to reject categorically the possibility that the seal could have picked up on some subtle cue provided involuntarily. This is not a problem for the demonstration of Levels 1 to 3 because here the seals were required to produce sounds in response to a stimulus. If they had used some visual stimulus, we would still have demonstrated usage learning on these three levels, only not with the acoustic stimulus. However, it would pose a problem for the demonstration of Level 4, in which the seals were expected to generalize, because they would not have attended to the acoustic stimulus in previous training sessions. Finally, there is a small possibility that seals classified moans and growls differently from the human observer. This seems unlikely given the dramatic differences in the stimuli chosen and the low intrastimulus variability in key parameters. Nevertheless, it is possible that seals use different parameters that are less salient to humans. Currently, there are no data available on this aspect.

The area of pinniped acoustics would benefit greatly both from longitudinal examinations of the natural vocal development of these animals to determine how their repertoire emerges and from studies exploring how they use their vocalizations in the wild. The evidence for contextual learning in the gray seal presented here suggests the possibility of a more elaborate usage and deployment of the vocal repertoire than previously considered. Future work might focus on which acoustic features gray seals use to distinguish between original moan and growl playbacks as used in this study. Additional inquiry into the extent to which subadult and adult pinnipeds are capable of similar tasks would reveal whether vocal contextual learning is possible at any age or is restricted to a particular developmental period. Finally, it would be interesting to investigate whether gray seals are capable of production learning as demonstrated for harbor seals (Ralls et al., 1985). Our study has shown that young gray seals are capable of the first three levels of contextual usage learning, ultimately flexibly pairing classes of vocalizations already within their repertoire with specific contexts.

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