

# Novel sound production through contingency learning in the Pacific walrus (*Odobenus rosmarus divergens*)

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**Abstract** Walruses (*Odobenus rosmarus*) are highly vocal amphibious mammals with a range of anatomical specializations that can provide plasticity to their sound emissions. The objective of this descriptive study was to determine whether contingency learning could be used to increase variability and induce novelty in the acoustic behavior of walruses. The subjects were two twelve-year-old captive walruses, a male and a female that had previously been conditioned using food reinforcement to produce several specific sounds in response to different discriminative cues. In the current task, these individuals were encouraged to produce novel sounds and novel sound combinations in air by withholding reinforcement for sounds previously emitted in a given session and providing reinforcement only for qualitative differences in emitted sounds. Following training in air, the walruses were tested under water with the same reinforcement contingency. The subjects responded as they had done in air, by varying their underwater sound emissions until reinforcement was provided. Many of the sounds and sound combinations produced by the subjects during underwater testing were quite different

from those produced during training in air and those produced under water during baseline observations. Both the male and female spontaneously emitted knocks and soft bells which are components of the songs known to be emitted by mature male walruses during the breeding season. The finding that reinforced variability can induce creativity in sound production is consistent with recent experiments on budgerigar birds showing that vocal topographies, like motor responses, may be influenced by contingency learning.

**Keywords** Pacific walrus · *Odobenus rosmarus divergens* · Sound production · Vocal behavior · Vocal learning · Creativity

## Introduction

Novelty is fundamental to any theory of creativity, and has given rise to such psychological concepts as *generativity*, *emergence*, and *productivity* in studies of language acquisition and problem solving. Measuring creativity in humans frequently takes the form of requiring subjects to generate or produce as many variations as possible in the way that objects or language may be used. For example, a test subject might be required to list as many uses as they can think of for a particular item, produce an assortment of words that share a common meaning, or combine a set of basic shapes into as many recognizable figures as possible.

Laboratory tests given to a variety of nonhuman animals have shown that, like humans, many species are capable of showing the emergence of innovative behavior. For example, using domestic pigeons, Epstein (1987) demonstrated how individually trained behavioral repertoires can come together to generate new sequences of behaviors, which

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may have novel functions. Similarly, sea lions have been shown to be capable of solving original experimental problems by recombining previously learned associations between stimuli in conditional discrimination and reversal learning tasks (see, e.g., Schusterman and Kastak 1993, 1998; Reichmuth Kastak et al. 2001). Artificial language comprehension studies with dolphins (see, e.g., Herman et al. 1984) and California sea lions (see, e.g., Schusterman and Krieger 1984; Gisinier and Schusterman 1992) have shown that, subsequent to training to perform complex action sequences by responding to gestural cue sequences made up of modifiers, objects, and actions, these marine mammals can respond appropriately to novel instructions established from new combinations of the original cues. In a study of motor response patterns, Pryor et al. (1969) trained dolphins through selective reinforcement to do something different each day, and found that the dolphins spontaneously began performing innovative actions; that is, the dolphins acquired new response topographies based on a win-stay, lose-switch rule. In the vocal domain, Manabe et al. (1997) conducted experiments on the control of bird vocalizations using similar but more precise training and response measures than those used by Pryor and her co-workers with dolphins. In their study of budgerigar birds, food reinforcement was made contingent on each vocalization that differed reliably from the last one, two, or three vocalizations. These investigators found that their subjects developed a vocalization sequencing strategy based on innovative calls made up of elements of old call types. This brief survey of studies illustrates that many kinds of animals are capable of demonstrating creative or innovative behavior in a variety of experimental contexts.

The basis for creative behavior is flexibility or variability in responding. It is this variability that provides a basis for the modification of learned responses, facilitates the solving of never before encountered problems, and generates diverse or surprising behaviors that may have functional significance in certain situations. The role that reinforcement contingencies may play in increasing response variability has been experimentally addressed, primarily in paradigms which utilize changes in response rates or characteristics of motor responses (for review, see Neuringer 2004). The aforementioned study with budgerigars was the first to extend efforts based on reinforcing variability to the study of novel vocal behavior (Manabe et al. 1997). This approach has not yet been applied to experimental investigations of nonhuman mammals, whose vocalizations are widely considered to be more constrained with respect to voluntary control, structural plasticity, and capability for modification through learning than many birds (for review see Schusterman 2008).

In the present study, we applied a contingency learning model based on reinforcing variability in the vocalizations

and other sound emissions of a nonhuman mammal not often tested in the laboratory, the walrus. Our primary objective was to determine whether variability in sound production by captive Pacific walruses (*Odobenus rosmarus divergens*) could be brought under operant control. We selected walruses as our study subjects for several reasons. Like other pinnipeds (seals and sea lions), walruses are amphibious diving mammals with exquisite breath control, and they emit sounds above as well as below the water's surface. They use more structures for producing sounds than any other pinniped and possibly any other mammal, including the larynx, specialized pharyngeal pouches, teeth, nose, mouth, lips, and a highly mobile tongue. These structures can take several different forms which enable walruses to emit a variety of sounds including whistles, grunts, moans, knocks, barks, burps, and gong-like sounds or bells (see Tyack and Miller 2002).

Walruses are highly social, highly vocal animals that are known to use their large repertoire of airborne sounds in several different contexts (Miller 1985). Their young have a protracted period of maturational dependency, with calves nursing for up to 3 years (Fay 1982). Thus, developing walruses have a significant portion of their lives that can be spent in optimal social learning situations; such extended periods for social learning might provide individuals with the opportunity for elaboration of sound-producing capability in communicative contexts. Complex acoustic behavior does appear to be critical to the reproductive success of mature walruses. During the breeding season, males position themselves under water near groups of females and their calves hauled out on the ice and produce loud, repetitive, highly stereotyped songs that commonly last more than 48 h (Sjare et al. 2003). These songs are made up of patterned sequences of pulses called knocks and taps which vary in length and are often punctuated by bell or gong sounds (Fay et al. 1981; Stirling et al. 1987). The structural complexity of these male walrus songs has been compared to that of humpback whales, and their sound production, like that of the whales, is thought to be the primary basis for intra- and/or inter-sexual selection (Sjare et al. 2003).

The songs emitted by mature male walruses during the breeding season have been recorded and described by a few investigators, despite the difficulties in accessing these animals in the unstable ice habitats of the High Arctic. Sjare and her colleagues (2003) identified four types of underwater song produced by adult male Atlantic walruses (*Odobenus rosmarus rosmarus*) during the breeding season. These include the “*coda song*” as described above, as well as three others. In what they call the “*diving vocalization song*” a few individuals emit long sequences of knocking and tapping, but without bell-knock codas while “*intermediate song*” is characterized by the individual switching back and forth between a coda song and a diving song.

Finally, there are “*aberrant songs*” featuring long periods of silence without a stereotyped pattern of a knocking and tapping, accompanied by frequent surface breaths and the emission of loud grunts and groans. To our knowledge, these four song types produced by mature male walrus include the entire repertoire of the underwater sounds reported thus far by field investigators for both the Atlantic and Pacific subspecies of walrus. To date, there have been no published descriptions of underwater vocalizations emitted by female walrus or juvenile walrus of either sex.

Prior to the current effort, our own recent research with four captive walrus had demonstrated that many naturally occurring airborne sounds could be selectively shaped and placed under the control of different discriminative stimuli (see Schusterman 2008). In order to elicit novel sounds from two of these walrus subjects during the present investigation, we first applied a reinforcement criterion which depended upon variability in aerial sound production. Once we had established consistently diverse and rapidly transitioning airborne sound production in our subjects, we transferred this procedure to water in order to determine whether innovative sound production by the walrus would continue to occur in this medium. The main purpose of this paper is to describe the emergence of untrained and highly variable sound emissions under water subsequent to in-air training for novel sound production.

## Methods

### Subjects

Two 12-year-old Pacific walrus participated in the current study. The male, Sivuqaq, and the female, Siku, had been orphaned in the wild near Gambel, Alaska in 1994 and had been reared in captivity from 2 weeks of age. The animals lived at Six Flags Marine World, in Vallejo, CA, in a salt water habitat with adjacent haul out areas. The living space was subdivided into separate areas with pools and/or deck spaces, which allowed individual animals to be trained and tested in isolation.

### Background

Prior to the current investigation, Sivuqaq and Siku, along with two other female walrus, had participated in research on vocal conditioning using food reinforcement. This effort involved two components: establishing discriminative control over sound production and inhibition, and establishing discriminative control over the emission of structurally disparate sound types. The details of this study are described by Schusterman (2008). Through a process of selective reinforcement of natural sound emissions and

operant shaping techniques, reliable discriminative control of acoustic behavior was established in the subjects, with each individual acquiring a trained repertoire of specific sound types. The subjects were conditioned to emit these sounds in air in response to different verbal and gestural cues, and their trained repertoires included a range of acoustic emissions with different anatomical origins. The sounds included whistles, tonal bellows, growls, burps, sniffles, raspberries, and soft metallic sounds, among others. The walrus had not been conditioned to produce sound under water prior to the present study. However, the spontaneous underwater sounds produced by these individuals had been monitored over a period of several years prior to the present study (Quihuis, unpublished data). These observations revealed that all of the walrus vocalized under water, typically emitting relatively low amplitude buzzes and groans. On rare occasions as he approached sexual maturity, the male Sivuqaq emitted a very low intensity tapping sound coincident with the onset of the breeding season.

Sivuqaq and Siku were the two individuals selected for participation in the current study because they were the most spontaneously vocal individuals in the group and they had acquired the largest repertoires of conditioned sound types. At the start of this study, Sivuqaq could reliably differentiate between 10 different cues to emit 10 different sound types in air, and Siku could differentiate between eight different cues to emit eight different sound types in air.

The first step in the present study was to encourage creativity in the airborne sound emissions of Sivuqaq and Siku. In contrast to their previous training, which primarily used selective reinforcement to establish discriminative control over their production of highly stereotyped sound types, this effort relied on consistently reinforcing novelty or variability in sound production. The general procedure was roughly based on that first used by Pryor et al. (1969) to establish innovation in the motor behaviors of porpoises. Sessions involved a single subject and trainer working in an enclosed haul out area away from extraneous activity. This was the same area that had previously been used to condition the production of different sound types.

### Procedure

Each animal was given approximately 10 in-air training sessions over a 3-month period. Each session lasted between 15 and 30 min. At the start of a session, one of the subjects was brought into the enclosure. The first sound produced by the animal after entering the area was marked with a conditioned reinforcer (a verbal “okay” given by the trainer) that was followed by a fish reward. After this initial response, only acoustic responses judged by the trainer to be different from those preceding it were reinforced. The

trainer was instructed to reward the animal for obviously varying the form of the sound emitted rather than for subtle changes in sound level or duration. All other acoustic and motor responses produced by the subject were ignored. If the walrus ceased emitting sounds for an extended period, lost attention to the task, or became visibly frustrated, the trainer would occasionally prompt the animal with a verbal cue (“*give me a sound*”) paired with a slight hand gesture (two palms turned upwards). Sessions were ended when the rate of reinforcement began to slow significantly, and the walrus was rewarded for walking out of the enclosure and returning to its living space when cued to do so by the trainer.

Neither of the subjects had been conditioned using food reinforcement to emit sounds under water. However, both subjects had been trained to station at a large underwater window and orient to their trainer through the glass. After highly variable and rapidly transitioning acoustic responses had been established in air, the procedure was transferred to water without additional training. One or two relatively short (<15 min) underwater sessions were conducted with each subject. An underwater session began when the subject was called to the window by a cue from the trainer, given the “*give me a sound*” prompt through the glass, and rewarded for the first sound it emitted. Subsequently, the trainer used the verbal/visual “*give me a sound*” prompt to elicit variable sound production, provided some additional verbal feedback (“*good boy*” or “*good girl*”) for continued sound production, and selectively reinforced transitions between qualitatively different sounds. The sessions were intentionally kept brief and few in number to avoid the modification of particular sounds through inadvertent selective shaping.

Both the in-air and underwater sessions were typically conducted during morning hours when the walruses were active and eager to eat and interact with their trainer. The walruses typically consumed about a quarter of their daily diet during these sessions on the days they were conducted. Following the sessions, regardless of their performance on the task, the subjects received their full allotment of fish and shellfish throughout the remainder of the day.

### Equipment

Aerial and underwater sounds were recorded during all sessions. Aerial sounds were collected with using a Neumann 82i condenser shotgun microphone with a Stewart Electronics BPS-1 power supply, which was connected to a SONY DC-8 DAT recorder with a sampling rate of 44.1 kHz (maximum recording frequency of 22 kHz). The microphone was typically positioned 1–2 m from the vocalizing animal. Underwater sounds were obtained with an ITC 1042 hydrophone. The hydrophone was positioned in a

“listening port” built into the side of the tank, where the hydrophone was protected from damage by the animals. The listening port was located next to the window where the underwater sessions were conducted, so that the receiver was approximately 2 m from the animal and 1 m below the surface of the water. The underwater sounds were passed through a Reson VP1000 voltage preamplifier to the same DAT recording device. In-air speakers were used so that the trainer could monitor, in real time, the underwater sounds being produced by an animal. The record levels used in air and under water were not altered during testing, therefore, the relative amplitude of the different sounds that were recorded were comparable within a given medium. In addition to audio recordings, video recordings were also obtained for some sessions.

### Analysis

The aerial sounds emitted by Sivuqaq and Siku during training sessions were recorded and described but were not spectrographically analyzed for the purposes of the present study. The underwater sounds obtained from Sivuqaq and Siku during testing sessions were transformed into spectrograms using Avisoft SASLab Pro (v. 4.39, © Avisoft Bioacoustics, Berlin, Germany). These spectrograms and the corresponding audio files were used to identify discrete sounds and combinations of sound types. The underwater sounds emitted by a given subject were qualitatively compared to those emitted in air during training, to those produced spontaneously during underwater baseline conditions, and to those previously reported in the literature by field investigators.

## Results

### In-air training

Both subjects were consistently vocal during the training sessions in which variations and novelty in airborne vocalizations were reinforced. A win-stay lose-shift pattern of responses was evident from both animals early in training. After the initial vocalization was marked for reinforcement, the subjects typically repeated a similar response several times. When this response was not reinforced, the subjects often showed signs of mild frustration and then eventually shifted their acoustic response to either a different sound from their trained repertoire or a loud or harsh vocalization that likely arose from frustration at non-reinforcement. As training progressed and the subjects gained more experience with the contingency of novelty or change in sound production, variability in the structure of the sound emissions increased and the number of responses made prior to

shifting to a different sound type decreased. Sounds that had been previously reinforced were repeated with elaborations of pitch changes and contour changes, such as upsweeps and downsweeps. Sounds such as moans and whinnies that had been heard in social contexts, but that had not been brought under stimulus control, emerged. Non-social sounds such as sneezes and lip smacking were emitted. Several novel sound emissions emerged during training that had not been heard before in either spontaneous or operant contexts. Many of these were combinations or blends of individual sounds that had been reinforced earlier in the session or in earlier sessions. Several of the responses emitted by the subjects were novel relative to the spontaneous and conditioned repertoires of the subjects; some of these were similar to those reported for wild walruses, such as a gonging sound emitted by the male that was accompanied by inflation of the pharyngeal pouches.

The airborne sounds produced by the subjects during training were highly graded with the animals generally transitioning almost continuously between variations of sounds and sound types (see S3). It was notable that a variety of different structures were used to these emit sounds. The sounds appeared to be generated by the changing the shape of the nose, mouth, lips, tongue, and chest and the force with which air was moved through these structures as well as the larynx. The expulsion of air was visible from the nose, mouth, or both during many of these responses. At least one response, the whistle, was produced upon inhalation as well as exhalation.

#### Underwater testing

When the walruses were tested under water, a variety of sound types and sound combinations were produced. Examples of the responses are shown as spectrograms in Figs. 1 and 2, with corresponding audio files provided as S1 and S2. The male, Sivuqaq, emitted a few underwater sounds that had been previously heard during baseline observations, descriptively coded as glubs, buzzes and moans (Fig. 1a). He also produced a range of relatively high amplitude sound types that had either not been heard before, or had been heard only on rare occasions, including chugging sounds, sharp knocks (Fig. 1b), rasps (Fig. 1c) and bell-like sounds. These sounds were combined into many different structural configurations, such as moans overlaid with knocks (Fig. 1d) or soft bells (Fig. 1e) or both (Fig. 1f). The female, Siku, also produced many different underwater sounds and sound combinations. These included repetitive glubs (Fig. 2a), rasps (Fig. 2b), soft chuffs (Fig. 2c), burps, moans, and soft bells (first and last halves of Fig. 2d). She combined many of these and other sounds into combinations and series that also included occasional knocks (Fig. 2e).

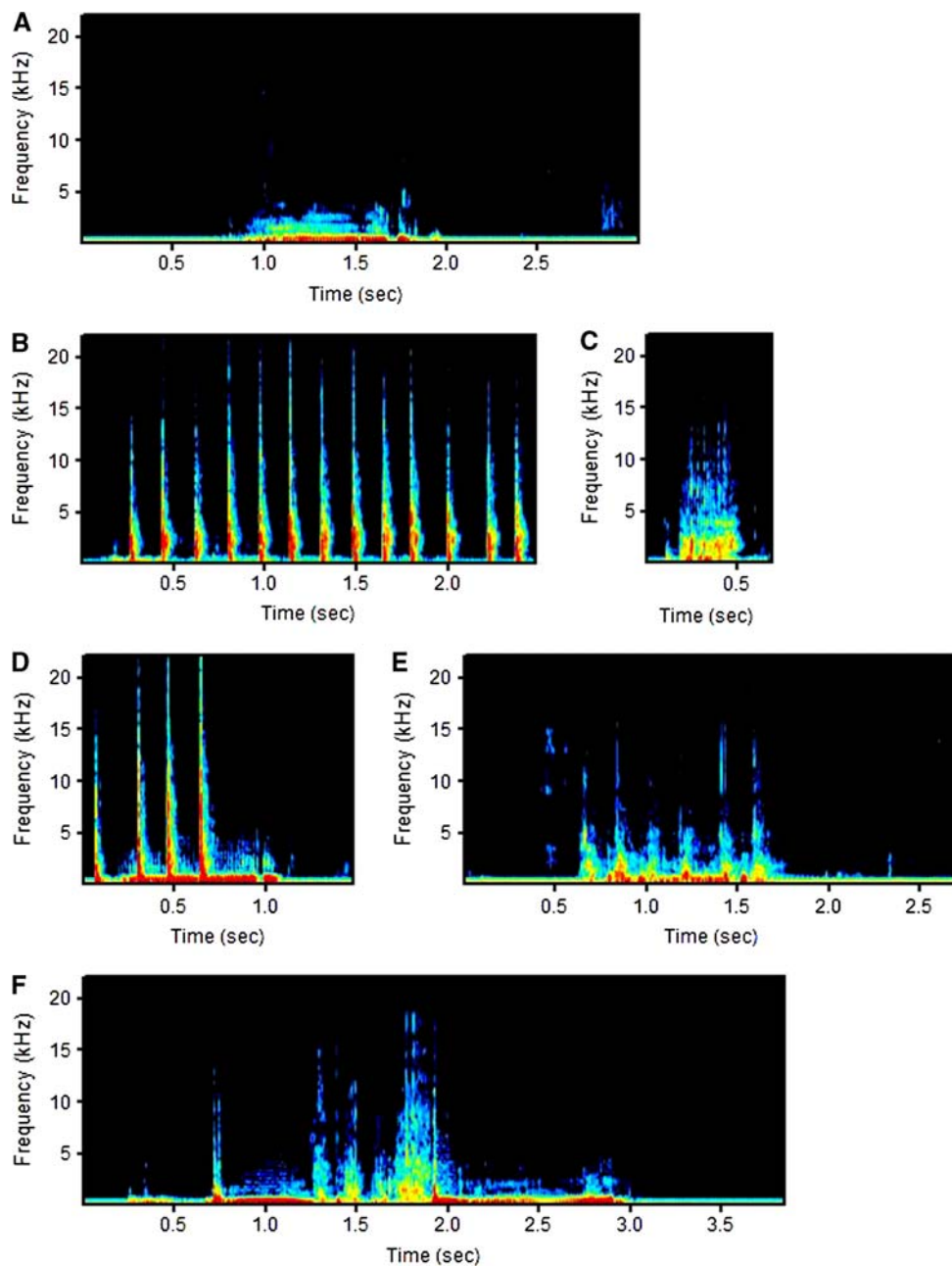
When the subjects were emitting underwater sounds in front of the observation window, it was noted that many of their sounds were produced without the expulsion of air. In particular, the male walrus while emitting a loud series of knocks at a rapid rate ( $\sim 6/s$ ), turned to show his profile, making it obvious that his mouth was opening and closing in time with the knocks, without releasing bubbles (see “Discussion”). Whether the knocks were produced by the sharp clacking or striking together of the teeth, or by breaking a powerful vacuum in the mouth by moving the tongue against the roof or back of the mouth, could not be determined. One of the pharyngeal pouches was inflated coincident to a portion of this response, as it was during the emission of the metallic sounds produced by both walruses.

#### Discussion

The persistence of the walruses in continuing to emit aerial acoustic responses even after previously reinforced responses were no longer rewarded is likely due in part to their prior training history that established discriminative control over different sound types. This training was conducted by the same trainer in the same area, and these contextual cues, along with the “*give me a sound*” prompt likely kept the acoustic responses from extinguishing altogether under low reward conditions. The walruses sometimes offered a vocalization from their trained repertoire when a repeated vocalization was not reinforced, and these sounds were selected for reinforcement the first time they were produced in a given session. The animals were also rewarded for making significant variations or elaborations on repeated sounds. Further, since certain harsh vocalizations tended to occur as the animals became frustrated—sounds that had not been previously conditioned—these responses provided additional opportunities to activate the reinforcement contingency for variability in acoustic emissions. The observation that frustration contributed to response variability is consistent with the emergence of the first “creative” motor responses described by Pryor et al. (1969). Some of the original responses emitted by captive porpoises when reinforcement for repeated behaviors was withheld were those associated with frustration (e.g., breaching, porpoising out of the water, tail slapping). The continued exposure of the walruses to the reinforcement contingency that depended on variability in responses eventually resulted in highly graded, highly variable sound emissions which featured novel sounds as well as novel sound combinations and sequences.

Several investigators have considered how the contingency of reinforced variability may lead to diverse or creative responding. For example, Manabe and colleagues (1997), Shahan and Chase (2002), and Neuringer (2004) all

**Fig. 1** Spectrograms of six different types and blends of types of underwater sounds emitted by the 12-year-old male Pacific walrus Sivuqaq at Six Flags Marine World in Vallejo, California. The acoustic emissions were produced in response to a discriminative stimulus signaling the walrus to vary its sound production. The sounds are descriptively labeled as **a** “moan” **b** “knocks” **c** “rasp” **d** “knocks/moan” **e** “soft bells/moan” and **f** “knock/soft bells/moan”



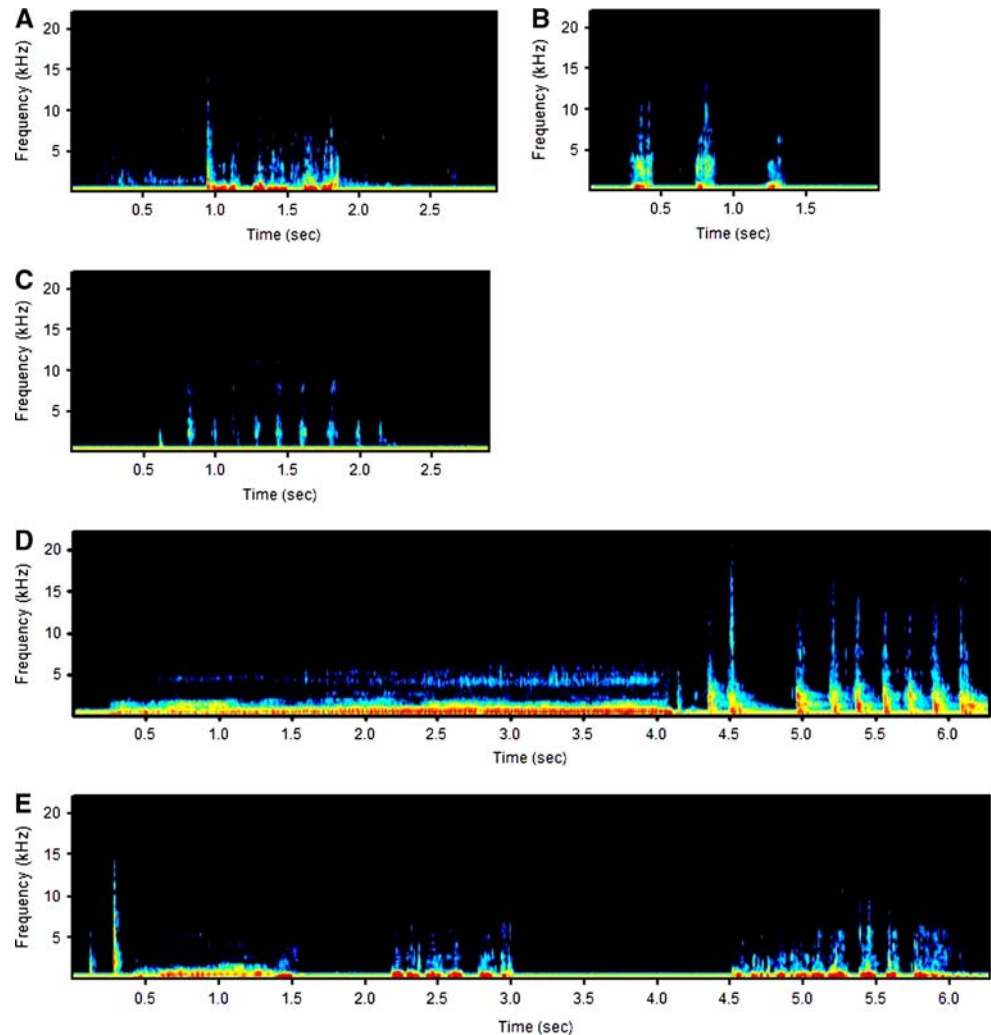
discussed how variable behavior may be brought under stimulus control in a manner similar to that of other response dimensions. The performances of the animals during the aerial portion of the current study support the notion that animals can “*learn to vary*” (Grunow and Neuringer 2002) or “*learn to try*” (Skinner 1953), even when the responses occur in the vocal rather than the motor domain. As they became more experienced in the task, the walrus often shifted their sound emissions quite rapidly, and appeared to vary their behavior in order to explore which sound(s) would be selected for reinforcement.

In addition to looking at how response variability may come under operant control, some investigators have also

considered how the reinforcement of variable responses in one setting may facilitate responding in another (see Neuringer 2004). In the current study, when the training procedure was transferred from air to water, the walrus emitted sounds that were quite different from many of those produced in air as well as from many of those produced underwater during baseline observations. As they had done in air, the animals shifted between sound types if a particular response was not selected for reinforcement. They also blended different sound types into novel combinations and sequences.

Some of the sounds emitted by the walrus underwater during testing were structurally similar to those recorded

**Fig. 2** Spectrograms of five different types and blends of types of underwater sounds emitted by the 12-year-old female Pacific walrus Siku at Six Flags Marine World in Vallejo, California. These acoustic emissions were made in response to a discriminative stimulus signaling the walrus to vary its sound production. The sounds are descriptively labeled as **a** “glubs” **b** “rasps” **c** “soft chuffs” **d** “moan/soft bells” and **e** “knock/moan/burp/soft bells”



from mature male walrus in the wild during periods of reproductive activity. For example, when the male walrus, Sivuqaq, was not rewarded for producing a chugging sound, he shifted to the knocking sound described earlier (see “Results”). Although he had rarely been observed to emit sounds of this nature before, the sharp knocking sound he emitted was similar in structure to the knocking and tapping elements of the coda displays that comprise walrus song. Sivuqaq’s knocks, which were correlated with movement of the mouth, were emitted at a rate of 5–6 pulses/s, with frequency composition from below 500 Hz to about 15 kHz. These knocking sounds appear to contain more energy at higher frequencies than the knocks described spectrographically for singing male walrus in breeding areas, although this difference may be due in part to the proximity of the receiver used for recording. At this point, it is impossible to say whether the knocking sounds made by Sivuqaq share a similar anatomical origin with those produced by wild walrus, but this observation may be helpful in evaluating competing theories to account for the production of these unusual sounds (Stirling and Sjare

1981). Sivuqaq also produced metallic sounds underwater, which were qualitatively similar to the bell components of male walrus song (Sjare et al. 2003). These sounds were comparable to those he had previously emitted in air under reinforcement conditions, but he had not been heard to emit such sounds in air or under water under baseline conditions prior to the current task. At times, Sivuqaq’s underwater bells were preceded by knocks and at other times they were not. In comparing his sound producing performance with that obtained in the field for Atlantic walrus, it is clear that his knocks and bells were not as organized as those produced by mature males during the breeding season, and therefore cannot be considered “songs”.

One of the more common sounds emitted by Sivuqaq under water was the low frequency moan. This sound usually lasted for over a second, and sometimes for several seconds. The moan produced by Sivuqaq was frequently combined with other sound types such as the knock and the gong. Indeed, sometimes the moan was produced simultaneously with the bell and the knock, and other times, the

moan either preceded or followed the bell and the knock as well as other sound types, such as glubs and rasps (which have also been described for a captive male walrus by Schevill et al. 1966). Clearly, many of these different sounds are related to different mechanisms for sound production, which can operate either successively in different sequences or simultaneously. This enables walruses to produce a blend of sounds, giving them an opportunity to vary their acoustic emissions over a wide range of sound types.

The female walrus, Siku, like the male Sivuqaq, shifted her underwater sound emissions from one sound type to another soon after we ceased reinforcing a repeated sound type. One of the most surprising things about her performance was the diversity of the sounds she emitted under conditions of reinforced variability. The underwater vocal behavior of wild female walruses has not been described, and preliminary observations of captive walruses suggest that females are not as acoustically active as males. However, Siku emitted series and combinations of underwater sounds that were as variable as Sivuqaq's, showing that female walruses have the capacity to be highly vocal under water. Further, Siku produced two sounds that appeared structurally similar to those acoustic elements of male walrus song, that is, relatively soft knocks and bells. We should note that Siku appears to have pharyngeal pouches, which she inflates like the male Sivuqaq, although to a lesser extent while emitting certain sounds. Fay (1960) has stated that these air sacs are found primarily in adult males that they are much less likely to be found in adult females, and that they are never found in immature walruses. Inflation of these air sacs takes place with air from the lungs, and although they are believed to function primarily in the production of male coda songs (particularly in enhancing the bell-like sound), the pouches can be inflated and used as buoys when a walrus rests or sleeps at the surface of the water. Thus, the observation that the female walrus Siku has pharyngeal pouches and can control them to produce some components of the male walrus coda song, while heretofore unreported for females, is perhaps not too surprising.

In a previous study (Schusterman 2008), we showed that Siku, as well as two other similarly aged female walruses, could produce loud tonal or harsh whistles in air, in the same manner as mature male walruses, who have been reported to whistle during the surfacing intervals of their aquatic displays (e.g., Fay et al. 1981; Miller 1985; Ray and Watkins 1975; Verboom and Kastelein 1995). Again, this finding indicates that potential sex differences in the sound production of walruses are not well understood, and the differences that do occur may be more the result of behavioral rather than structural or physiological factors.

The findings of the present study provide preliminary but compelling evidence that this highly vocal mammalian

species is capable of a significant degree of variability and flexibility in sound production, and that the acoustic emissions of walruses are susceptible to modification through contingency learning. The results complement earlier findings on discriminative control and selective shaping of certain call types by showing that variability in acoustic behavior can be brought under the control of reinforcing consequences. The extent to which wild walruses or other vocal mammals modify their acoustic communication as a result of social reinforcement is unknown. However, the findings presented here suggest that such learning about sound producing responses and associated consequences is possible. Perhaps it is the ability to perform flexibly when emitting sounds that accounts for the recent finding that mature Atlantic male walruses (*Odobenus rosmarus rosmarus*) breeding in the Canadian high Arctic sing all major song types, along with variations, and that some individuals change the percentage of song types and variations they sing from year to year (Sjare et al. 2003).

These observations with Pacific walruses show that reinforced variability of emitted responses can result in the expansion and diversification of response repertoires within the acoustic domain. While this effort may be the first to apply this method to the study of sound production in a mammal, the results are in keeping with recent findings showing that humans and many other animals can learn to vary their behavior under the control of reinforcing consequences, and that such variability can lead to innovative behavior. In general, exploring the extent to which contingency learning can impact acoustic behavior provides insight into the learning mechanisms underlying non-imitative social learning, or what Marler and Nelson (1993) have termed "action-based learning" in the study of animal communication.

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