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A California Sea Lion (*Zalophus californianus*) Can Keep the Beat: Motor Entrainment to Rhythmic Auditory Stimuli in a Non Vocal Mimic

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Is the ability to entrain motor activity to a rhythmic auditory stimulus, that is “keep a beat,” dependent on neural adaptations supporting vocal mimicry? That is the premise of the vocal learning and synchronization hypothesis, recently advanced to explain the basis of this behavior (A. Patel, 2006, *Musical Rhythm, Linguistic Rhythm, and Human Evolution, Music Perception, 24*, 99–104). Prior to the current study, only vocal mimics, including humans, cockatoos, and budgerigars, have been shown to be capable of motoric entrainment. Here we demonstrate that a less vocally flexible animal, a California sea lion (*Zalophus californianus*), can learn to entrain head bobbing to an auditory rhythm meeting three criteria: a behavioral response that does not reproduce the stimulus; performance transfer to a range of novel tempos; and entrainment to complex, musical stimuli. These findings show that the capacity for entrainment of movement to rhythmic sounds does not depend on a capacity for vocal mimicry, and may be more widespread in the animal kingdom than previously hypothesized.

Keywords: sensorimotor synchronization, rhythmic entrainment, music cognition, sea lions

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Dancing to music is a human universal with no exact parallel elsewhere in the animal kingdom. Nevertheless, recent reports show components of this ability in other species. Notably, the ability to entrain (i.e., consistently beat-match) body movements to music or other rhythmic, auditory stimuli was first shown in a nonhuman by Patel, Iversen, Bregman, and Schulz (2009a), who

documented that a sulfur-crested cockatoo (*Cacatua galerita*) was able to bob his head in time to a Backstreet Boys song across a range of tempos. An African gray parrot (*Psittacus erithacus*) was also shown able to move in time to popular music (Schachner, Brady, Pepperberg, & Hauser, 2009), and subsequently budgerigars (*Melopsittacus undulatus*) were successfully trained to peck a target in time to an auditory-visual metronome-like stimulus (Hasegawa, Okanoya, Hasegawa, & Seki, 2011). All three species of birds show specialization for vocal learning, including vocal mimicry. Furthermore, a survey of an extensive public video database found no cases of beat keeping in non vocal mimics (Schachner et al., 2009).

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These findings have been used in support of the vocal learning and synchronization hypothesis (Patel, 2006; Patel et al., 2009a), which proposes that motoric entrainment to an auditory rhythm is a byproduct of neural adaptations allowing auditory-vocal mimicry, and therefore should be present only in species that perform such mimicry as part of their natural repertoire. This hypothesis has broad implications for our understanding of human music cognition, placing it in an evolutionary context and advancing a testable theory regarding the proximal mechanisms that support human response to rhythm. Furthermore, it has been proposed that nonhuman species with highly flexible vocal capabilities might serve as appropriate neural models for human rhythmic ability and related phenomena (Hasegawa et al., 2011; Patel, Iversen, Bregman, & Schulz, 2009b). However, with one exception, there have been no published experimental attempts to demonstrate entrainment to rhythm in non vocal mimics. Zarco, Merchant, Prado, and Mendez (2009) trained rhesus monkeys (*Macaca mullata*) to press a button in time to a rhythmic auditory stimulus. The monkeys learned this task and were able to press the button in time to the beat better than would be predicted by chance. However, the phase relationship of their tapping to the stimulus beat was more variable

than that generally demonstrated by humans, and the monkeys' taps tended to have a higher latency to the beat than demonstrated by humans in similar tasks. Although Hasegawa et al. (2011) cite these results as evidence that monkeys, as likely non vocal mimics, have great difficulty trying to synchronize behavior to rhythmic auditory stimuli, this particular study cannot be taken as strong evidence to that effect. The subjects were required to press the button in time to only four consecutive auditory beats, and a sequence of four presses was rewarded as long as the interval between each press was within $\pm 35\%$ of the stimulus interval. Thus, the increased variability and latency in button pushing by the monkeys could be because of the flexible performance criteria, as opposed to an inherent inability to precisely entrain to auditory stimuli. With broad performance criteria an animal could fall into a less cognitively taxing tone-response pattern even if capable of more synchronous entrainment.

In the present study, we sought to more rigorously test the proposition that a mammal without specialization for vocal mimicry could not learn to entrain motor behavior to a rhythmic auditory stimulus. Toward that end, we trained a California sea lion (*Zalophus californianus*) to move her head in time to an auditory beat and then tested her ability to entrain to a range of different tempos and stimulus types, up to and including music.

Sea lions are motivated, easily trained mammals that are amenable to voluntary participation in a variety of behavioral studies (see, e.g., Schusterman, 1981; Schusterman, Reichmuth Kastak, & Kastak, 2002). Important for our hypothesis, they demonstrate relatively limited vocal flexibility. While the species grouped under the designation "pinniped" are notable for a higher degree of plasticity in sound production than many terrestrial species (Schusterman, 2008), the sea lions and other Otariidae show less vocal flexibility than the true seals (Family Phocidae) and walruses (Family Odobenidae). While harbor seals (*Phoca vitulina*) have been shown to have some capability for vocal learning (Schusterman, 2008), including one known case of vocal mimicry (Ralls, Fiorelli, & Gish, 1985), and there are reports of vocal plasticity in walruses from field observations (Sjare, Stirling, & Spencer, 2003) and direct reinforcement training (Schusterman & Reichmuth, 2008), there is currently little evidence available for vocal flexibility in sea lions, despite decades of captive study (Janik & Slater, 1997). This is perhaps unsurprising because the Otariid clade has been separate from the true seals and walruses for at least 18 million years (Higdon, Bininda-Emonds, Beck, & Ferguson, 2007). Presently, the best available evidence suggests that sea lions have a relatively small acoustic repertoire (Peterson & Bartholomew, 1969). What evidence exists for plasticity is strictly related to bringing naturally occurring vocalizations under stimulus control (e.g., Schusterman & Feinstein, 1965), as opposed to plasticity in call type or mimicry per se. Sea lions' sister clades, the Phocids and the Odobenids, appear to possess more vocal flexibility, but even so, their capabilities inarguably pale next to the highly specialized vocal mimicry produced by parrots.

Because California sea lions probably do not possess neural specializations to support complex vocal learning, the ability of a sea lion subject to learn to entrain motor behavior to rhythmic auditory stimuli, and to transfer this ability to a range of complex stimuli, would challenge the current formulation of the vocal learning and synchronization hypothesis. This effort is in line with calls to broaden the search for species able to entrain, and to

document the conditions under which such a behavior might emerge (Patel et al., 2009b).

In the present study, we systematically documented the ability of a trained California sea lion to meet all three criteria stated under the vocal learning hypothesis: (a) the ability to entrain to rhythm cross-modally (in this case a nonauditory motor behavior to an auditory signal), (b) the ability to entrain to a range of different tempos, and (c) the ability to entrain to a tempo embedded in additional rhythmic or melodic elements. These criteria were specified in the vocal learning hypothesis to differentiate a flexible, voluntary beat-matching ability from the highly constrained entrainment found in fireflies, crickets, and frogs. Having met all three criteria, our subject might reasonably be assumed to have a rhythm-following capability in some ways qualitatively similar to that found in humans, or, at the least, categorically distinct from the automatic entrainment found in lower phyla.

Testing proceeded over six experiments, designed, respectively, to assess: (1) ability to learn to entrain to familiar stimuli; (2) ability to transfer entrainment to novel tempos without additional training; (3) whether beat-matching performance could be explained as a stimulus-response chain; (4) ability to transfer entrainment to complex, musical stimuli; (5) ability to entrain to novel tempos of a complex, musical stimulus; and (6) capability for sustained entrainment.

General Methods

Subject

Our subject for all six experiments was a healthy, female California sea lion identified as "Ronan" (NOA006602), who came into captivity at approximately 1 year of age following repeated stranding events. She was housed at Long Marine Laboratory at the University of California Santa Cruz, where she was trained using operant conditioning methods based on positive (fish) reinforcement for participation in research and husbandry activities. Ronan had previously participated in three experiments—delayed alternation in a T maze, simple visual discrimination learning, and psychophysical auditory testing—but prior to the current study had not been exposed to complex auditory stimuli or music. Ronan was 3 years of age when training for this study began in July 2011, and four when testing finished in November 2012. For the duration of the study, she was fed between 6.8 kg and 8.1 kg of freshly thawed, cut herring and capelin daily and maintained at a healthy weight of approximately 60 kg. Her diet was not constrained for experimental purposes. During training and testing, Ronan completed between one and two experimental sessions per day, 2 or 3 days per week.

Apparatus

Initial training was conducted in various locations within the subject's living areas. All testing in Experiments 2–5 was conducted in just one of these areas, the haulout deck of a 2.25m square pool. The experimental setup consisted of a simple 1.1 m \times 1.5 m painted wood panel mounted vertically in the doorway leading to the enclosure containing the haulout deck and pool. A 0.8 m \times 0.3 m wooden flipper station was placed on the deck on the pool side of the panel, far enough from the panel to allow

Ronan to place her flippers flat on the station while facing the wooden panel and freely move her head and torso up and down without being impeded. During training and testing, an assistant sat quietly on the opposite side of the panel from Ronan, outside of her enclosure and her view. The assistant was responsible for dispensing Ronan's fish reward through a small hole in the apparatus, as prompted by an experimenter. The experimenter observed the session in real time from behind a blind located ~2 m from Ronan, perpendicular to her right side. A Sony HD DCR-SR68 Handycam was mounted in the enclosure to record each training and testing session.

General Procedure

Training. The motor behavior used throughout this study was a continuous, up and down movement of the head and neck, referred to here as "bobbing." Ronan was initially trained through successive approximations and standard operant methods to bob in response to a visual discriminative stimulus. A criterion was set such that on each bob Ronan's head had to be displaced by ~10 cm or more. Behavioral control was established using a previously conditioned reinforcer (a brief whistle) immediately followed by fish that was hand-fed by the experimenter. Throughout training and testing, except where otherwise specified, fish reward following a continuous interval of bobbing consisted of one capelin. Sea lions have excellent voluntary neck control, and bobbing training progressed rapidly over the course of five to six sessions. Details on Ronan's training to produce bobbing in response to an auditory stimulus are discussed below in the method for Experiment 1.

Testing. Ronan's testing proceeded over six distinct experiments (Table 1). Each testing session consisted of a number of presentations ("trials") of a continuous auditory stimulus. Each trial began when Ronan had placed her fore-flippers on the flipper station and was waiting calmly, and lasted until she met a criterion of either 20 or 60 consecutive, entrained head bobs as ascertained in real time by the experimenter. This point was marked by the whistle and quickly followed by a fish reward. Between each trial, Ronan returned to the pool for a brief period of time (<5 s), where she received a smaller fish reward (half capelin). Each experimental session consisted of between 10 and 25 successive trials. All human experimenters and assistants were out of sight during stimulus presentations. Stimuli were presented using an Advent AV570 amplified speaker, placed ~1.5 m in front of Ronan, and broadcasting signals at levels of ~80 dB. The stimuli in Experiments 1–3 were created using Audacity, an open-source audio editing program. The same program was used for the manipulation of the musical stimuli in Experiments 4–6.

Video and Audio Analysis

Throughout this series of experiments, our primary measure was the degree of concordance between the timing of Ronan's head bobs and the timing of the beat in the auditory stimuli. The timing of these were determined by video and audio analysis, respectively.

Video analysis. The time point of each of Ronan's head bobs on all analyzed trials was determined by frame-by-frame video analysis. The video was acquired in the standard 29.97 frames per second, but was de-interlaced¹ for analysis, allowing the bobbing

behavior to be functionally segmented into 59.94 individual time points per second. An observer determined the frame with the lowest head point for each bob (if Ronan's head was at its lowest point for more than one frame consecutively, the first of the lowest frames was selected as the relevant time point) and used the time point of that frame as the measure of the time point of that particular bob. On a test of interobserver reliability across 120 head bobs, 111 of the frames selected by both observers as representing the lowest point of a bob were identical. The other 9 were all within one frame of each other. Note that this means the two observers' matched observations fell within 17 ms of each other 100% of the time.

A measure of Cohen's kappa was calculated quantifying concordance between the two observers on each of the 3,914 frames over the 120 coded bobs. This high number of values was because each frame could, in essence, be coded as either the lowest, or not the lowest, point in Ronan's bobbing, allowing for possible disagreement on each individual frame. Kappa was calculated as 0.92, corresponding to very high interrater reliability (and still an underestimate of actual agreement given that all nine disagreements were within one frame of each other). Because of this high concordance, one observer coded all remaining trials.

Auditory analysis. The audio for each test trial was extracted from the video files and the timing of the beat placement was determined so that it could be compared with the timing of Ronan's bobbing for each respective trial. The time point of the first beat for all test trials was defined as the onset of the first beat's waveform as visually assessed in Audacity. Because the beats in the nonmusical auditory stimuli were explicitly designed to occur at a regular interval, the time points for all beats subsequent to the first in each trial using nonmusical stimuli were then determined as a function of stimulus tempo. The time points of the beats for the musical stimuli, "Down on the Corner" (Fogerty, 1969, track 1), "Everybody" (PoP & Martin, 1997, track 1), and "Boogie Wonderland" (Willis & Lind, 1979, track 5), were determined by a beat-tracking algorithm in the analysis program MATLAB (Ellis, 2007). These were then verified by examination of the waveforms: an experienced musician listened to the stimuli while observing the accompanying waveforms in Audacity in real time, and was able to identify the components that carried the beat (cowbell, hi-hat, bass drum, and snare drum in "Down on the Corner" (Fogerty, 1969, track 1); bass drum in "Boogie Wonderland" (Willis & Lind, 1979, track 5); and a combination of bass drum, snare drum, and bass guitar in "Everybody" (PoP & Martin, 1997, track 1). Because of the increased amplitude of these instruments on primary beats, it was then a simple matter to visually identify the onset of the beat in the waveform. For "Down on the Corner" (Fogerty, 1969, track 1), the automatically generated beat matched the manually selected beat, but for "Everybody" (PoP & Martin, 1997, track 1), and "Boogie Wonderland" (Willis & Lind,

¹ Standard modern video cameras take two lower-resolution images every 33.36 ms and interlace them into a single frame. When these images are then played back at the standard frame rate of 29.97 frames per second, the video stream is perceived as being twice the frame rate. By separating the two images ("de-interlacing"), the component images can be viewed in sequence, albeit with a sacrifice to visual resolution. In de-interlaced standard video, there is one frame for every 16.68 ms, or 59.97 frames per second, allowing a higher degree of temporal resolution in analysis.

Table 1
Stimulus Type, Stimulus Rate(s) in Beats per Minute (bpm), and Performance Criteria Expressed as Number of Beat-Matched Responses Required for Reinforcement for Each of the Six Experiments

Experiment	Stimulus type	Tempo (bpm)	Criterion
1	Frequency-modulated	80, 120	20
2	Frequency-modulated	72, 88, 96, 108, 132	20
3	Metronomic	120	20
4	“Everybody” and “Boogie Wonderland”	108.2 130	20
5	“Boogie Wonderland”	104, 117, 124, 137, 143	20
6	Frequency-Modulated and “Boogie Wonderland”	72, 80, 88, 96, 108, 120, 132 124, 130, 137	60

Note. Experiment 1 tested spontaneous entrainment and entrainment to two trained stimuli. Experiment 2 tested transfer of entrainment to five novel tempos. Experiment 3 tested ability to maintain entrainment to a stimulus with missing beats. Experiment 4 tested transfer of entrainment to two novel, musical stimuli. Experiment 5 tested transfer of entrainment to five novel tempos of a familiar musical stimulus. Experiment 6 tested sustained entrainment to familiar musical and nonmusical stimuli.

1979, track 5), the comparison showed that the algorithm-generated beats were placed between 20 and 30 ms ahead of the actual beat onset. In each of these cases, the beat pattern assigned by the algorithm was shifted the appropriate amount post hoc.

Statistical Analysis

Our primary statistical analysis was focused on Ronan’s criterial bob runs (either 20 or 60, depending on test trial). Justification for this decision is discussed below. In addition, we grouped criterial runs for each stimulus on which Ronan was tested. These numbered between one and seven, depending on the stimulus being tested—by grouping, we were able to present a more complete picture of Ronan’s performance. However, it is important to note that for all grouped test trial analyses that show statistically significant entrainment, analysis of the first test trial from those respective tests also shows statistically significant entrainment when analyzed alone, and, in many cases, synchronization. These data are presented in Supplementary Table S1, and are of potential interest because they highlight Ronan’s ability to spontaneously transfer entrainment ability to truly novel, previously unreinforced stimuli, without the possible benefit of learning from experience on the first test trial.

Circular statistics. As is common in studies examining rhythmic entrainment, we assigned our subject’s performance data to circular distributions. First, we computed the phase relation of each bob behavior to its closest auditory beat. In this type of circular distribution, each beat is surrounded by 360 degrees of temporal space, from -180 degrees (representing half the interbeat interval between the current and previous beat) to 180 degrees (half the interbeat interval between the current and following beat). Thus a bob that is exactly coincident with a beat would have a phase angle of 0 degrees. If the interbeat interval were 1000 ms, then a bob falling at 250 ms before the beat would have a phase angle of -90 degrees, and a bob falling at 125 ms after the beat would have a phase angle of 45 degrees, and so-forth. One can then compute a mean vector from the cumulative phase angles of bobs during a trial. The angle of this vector is the mean phase angle of all bobs from a particular trial, and will have a length between 0 and 1 —a vector length of 1 results from perfect concordance for all phase angles. With the mean vector length and number of observations, one can calculate the Rayleigh z statistic, which

allows one to compute the probability that a circular distribution is randomly distributed. A distribution very likely to be nonrandom suggests, in our case, that the period of the head bobs is contingent on the period of the auditory rhythm—in other words, entrained.

A more precise test we also use here is the Rayleigh’s test for uniformity versus specified mean angle (or the V Test [Zar, 1999]). The V Test produces the U statistic, a measure not just of concordance between phase angles, as with the z statistic, but also of how closely those phase angles lie to a preestablished phase-angle (in our case, 0 degrees, representing phase-locking, or synchronization). The z statistic can then be used to assess both entrainment and synchronization. In synchronized bobbing, each bob occurs on or very close to each auditory beat—it is important that it is possible to be entrained without being synchronized, but not possible to be synchronized without being entrained. If one sets the preferred angular direction at 0 degrees, statistical significance with the V Test indicates an entrained and synchronized response.

Visual representation of circular statistics. We represented these circular data using “rose plots” (Zar, 1999). Rose plots are circular histograms of phase angle data—we set each bin to encompass an angular range of 18 degrees (so 0 – 18 degrees, 18 – 36 degrees, etc.), with 20 bins in a circular distribution. The phase angles in each bin are combined into grouped vectors (the dark wedges extending from the center of each plot), and the area of each grouped vector is directly proportional to the number of observations within. Thus, the largest grouped vectors represent the most common phase angles in a data set. For illustrative purposes, we set the radial axis to range between zero and seven, this representing the square root of the number of observations in a potential grouped vector. However, as regards the computation of the Rayleigh z statistic and the V Test U statistic, the mean vector value was computed per standard between a minimum of zero and a maximum of one. Importantly, the length of the mean vector (represented by the black arrow) on the rose plots as printed is not representative of the actual mean vector length.

Justification for focusing analysis on criterial bobs. We elected to restrict our primary analysis to the criterial bobs from each test trial because we believe they are the best representation of Ronan’s actual ability to entrain—the generally small number of bobs prior to the beginning of the criterial chain of bobs on each trial, that is, the less entrained bobs, may occur as Ronan is

“finding the beat.” Humans also typically demonstrate a brief acquisition period while finding the beat (e.g., Smoll & Schutz, 1978), during which their movements are not precisely entrained.

We justified this approach statistically by using a Monte Carlo simulation to test for the likelihood of Ronan’s reaching 20 consecutive criterial bobs in as few total bobs as it took her on her worst successful test trial (111, also her longest trial overall, including unsuccessful trials, on all of which she quit prior to reaching this many bobs), assuming the timing of each head bob was random within the constraints of her actual bobbing rates on test trials. The likelihood was $p < .00001$ that this would have occurred on any particular trial (see Supplementary Method). Across all testing, Ronan successfully achieved criterion on 72 out of 82 test trials, with a mean of 15.7 bobs prior to the beginning of the criterial runs. In brief, the likelihood of Ronan’s achieving by chance so many criterial strings of bobs across so many test trials with so few precriterial bobs is vanishingly small, justifying our focusing analysis on criterial runs, similar to windowed analyses used in prior research examining entrainment in nonhumans (e.g., Patel et al., 2009a).

It is important that we also used circular statistics to analyze all test trials with all bobs present, including the noncriterial bobs preceding the 20 (or 60) consecutive criterial bobs. These data can be found in Supplementary Table S1, and it is notable that in every test in which Ronan was able to reach 20 criterial bobs, and these were statistically entrained, the entire trial, analyzed with precriterial bobs, was also found to be statistically entrained. This is in part because her accuracy is so high on the criterial runs, but is also because of her frequently entraining, albeit for fewer than 20 consecutive bobs, during precriterial performance. In addition, on a number of trials in which Ronan was not able to meet the 20 bob criterion, her overall performance was still significantly entrained, highlighting the stringency of our criterion. In other words, we could have confidently reported either value, entrainment for all bobs on test trials or just for criterial bobs, in the body of this paper, but, again, judged the criterial performance to be most emblematic of Ronan’s best capability.

One further statistical approach was used to assess rate fluctuation in Ronan’s performance. For test trials on which Ronan’s criterion was 60 consecutive, entrained bobs, we generated time-course plots. In these, the x -axis represents the progression of time, and the y -axis represents instantaneous tempo. The instantaneous tempo is calculated by taking the duration between the current and most recent bob, then dividing 60 by that number. That produces the tempo in beats per minute (bpm) of those two bobs. Each one of Ronan’s bobs (except for the first, which has no preceding bob) can then be plotted sequentially in terms of rate—this allows one to see how Ronan’s bob rate changes over the duration of a trial. One can further use linear regression to examine the slope of her continuous bob rate. If Ronan’s rate holds steady around a particular tempo, the slope of the time course plot should be very close to zero.

Experiment 1

In this experiment, we first probed Ronan for a spontaneous capability to entrain, prior to reinforcing her for matching the period of her head bobbing to the period of the auditory stimulus. We then attempted to explicitly train her to reliably produce 20

consecutive, entrained bobs with two separate training stimuli. Our goals here were first to assess whether this sea lion would spontaneously entrain motor behavior to a rhythmic stimulus, and, if she did not, to determine whether she could learn to entrain motoric behavior to a familiar stimulus with explicit reinforcement training.

Method

Once Ronan had learned to bob her head continuously during presentation of a visual discriminative stimulus, as described in the General Methods, she was trained during July 2011 to bob continuously during presentation of a rhythmic auditory stimulus, which was introduced over the course of two to three training sessions. This initial auditory stimulus (here referred to as the “frequency-modulated” stimulus) consisted of a metronomic track with regularly repeating 10 ms “clicks.” Each click comprised two overlaid pure tones at 659 Hz and 1319 Hz, and clicks were presented at 120 bpm. The click track was accompanied by a continuous pure tone that oscillated in frequency sinusoidally. The tone was centered at 1047 Hz and oscillated between 800 Hz and 1300 Hz at the same rate as the repetition of clicks. The frequency oscillation was created using a custom plugin for Audacity. The stimulus was designed to provide both intermittent (click) and continuous (tonal oscillations) information at the set rate.

After the auditory stimulus was faded in, the visual discriminative stimulus was faded out over successive approximations until Ronan would reliably bob her head only when, and as long as, the auditory stimulus was presented, for up to 10 seconds, and could do so prompted only by a stationary hand signal, as opposed to the moving hand used in initial training. During this time, the experimenter made no effort to reinforce Ronan for bobbing in time to the tempo of the auditory stimulus, using instead preset durational criteria for continuous bobbing to determine reinforcement points.

After this training, we assessed Ronan’s performance to determine whether she was spontaneously keeping the beat. As for all subsequent tests, we assessed Ronan’s bobbing both for entrainment (i.e., matching her bob rate to the period of the auditory stimulus) and for synchronization (i.e., producing each bob coterminously with the beat). The test was the first trial in which she reliably bobbed continually during the stimulus prompted only by a stationary hand signal. Unlike all subsequent tests, the trainer was in view for this trial, standing approximately two meters in front of Ronan, who was stationed in front of a chain-link fence rather than the painted wooden panel used in later testing. The experimenter was in view because we could not be certain, prior to the session, that Ronan no longer needed visual prompting to bob.

Ronan subsequently began explicit training for matching her bobbing rate to the stimulus rate. During this training, a second stimulus, identical to the first frequency-modulated stimulus but at 80 bpm, was introduced. The purpose of introducing a second stimulus early in training was to promote rate flexibility. During this initial training phase, trials with these two stimulus types were randomly intermixed in each session. Ronan was reinforced on each trial when her instantaneous rate of bobbing (as tracked in real time by an assistant using an application for the Apple iPhone called “BPM Graph,” v1.00) remained within ~ 10 – 15 bpm of the current auditory stimulus’ rate for more than two consecutive beats. Perhaps predictably, given that Ronan was being selectively

reinforced for changing her bobbing speed between 80 and 120 bpm trials, within a few sessions Ronan was changing bobbing speed rapidly during each trial. Also during this training phase, the experimenter began conducting sessions from behind a visual barrier, such that Ronan had no visual access to any person during sessions. All subsequent training and testing was conducted under the same rigorous experimental controls.

Because Ronan did not appear to be progressing toward entrainment after approximately 30 training sessions focused on rate matching, we changed our training approach. In the next phase of training, which occurred during December 2011 and January 2012, the 80 and 120 bpm frequency-modulated stimuli were presented only in separate sessions. In addition, Ronan was reinforced not for rate matching, but for beat matching, that is, apparent synchronization of her head movement to the beats in the auditory stimulus. This was accomplished through real-time judgment by the hidden experimenter, who visually scanned for behavior where the lowest point on Ronan's head's trajectory matched very closely the beat in the auditory stimulus. Because the speed of Ronan's bobbing was quite variable during trials at this time, it was relatively easy to identify and reinforce such concurrences. At first, Ronan was reinforced for any single head bob that was synchronized with a beat in the auditory stimulus, and then the number of matched (or "criterial") consecutive beats required for reinforcement was gradually increased until Ronan could reliably produce 20 criterial bobs at both 80 and 120 bpm.

On each trial, Ronan began bobbing at the onset of the auditory stimulus and was allowed to continue until she met criterion. She could, however, meet the criterion only if she produced only one bob per beat—that is, the count of entrained bobs in a particular trial was restarted at zero if she inserted an extra head bob between two otherwise entrained bobs. On any particular trial, Ronan typically produced fewer than 20 nonentrained bobs before beginning to bob in time with the auditory stimulus on the way to meeting the reinforcement criterion of 20 consecutive entrained bobs. This was likely because of our only increasing the number of criterial bobs required for reinforcement incrementally and after she could reliably meet the current criterion.

Once Ronan was apparently able to reliably entrain for 20 consecutive beats to both the 120 bpm and 80 bpm stimuli, she began receiving mixed training sessions containing trials with both stimulus tempos. After approximately 25 additional training sessions, she was reliably able to meet criterion on both 80 and 120 bpm trials in mixed sessions. At this point we assessed her performance statistically. We treated as the test the first two trials at each rate immediately following the first mixed session in which she met the 20-bob criterion quickly and reliably across both tempos on every trial. The two test trials at each tempo were combined for analysis—as for other tests, analysis of individual trials can be found in Supplementary Table S1. It was the strong impression of the experimenter at that point that Ronan was successfully entraining to both the 80 and 120 bpm stimuli—these tests served as statistical confirmation.

Results and Discussion

Ronan did not spontaneously entrain her head bobbing to the rhythmic stimuli prior to explicit training for beat matching. On her first posttraining exposure to the 120 bpm frequency-

modulated stimulus, Ronan's bobbing rate was 160.7 bpm with a mean vector angle of -113.2 degrees (Figure 1A). Ronan was not entrained to this stimulus (Rayleigh Test: $z_{20} = 0.02$, $p > .05$). This should not, however, be taken as strong proof of a general inability in sea lions to spontaneously entrain to a rhythmic auditory stimulus—our training approach, the particular auditory stimulus, or the bobbing behavior selected for Ronan to perform, could all have been confounding factors.

Ronan was able to entrain to both practice stimuli following explicit training. Ronan's cumulative mean bob rate in her 80 bpm test trials was 80.3 bpm with a mean vector angle of -118.3 degrees (Figure 1B). Ronan did not synchronize to this stimulus (V Test: $u_{40} = -3.9$, $p > .25$) but did entrain (Rayleigh Test: $z_{40} = 34.2$, $p < .001$). Ronan's cumulative mean bob rate in her 120 bpm test trials was 121.6 bpm with a mean vector angle of -49.5 degrees (Figure 1C). Ronan was synchronized and entrained with this stimulus (V Test: $u_{40} = 5.1$, $p < .001$). Ronan's mean number of precriterial bobs across these four test trials was 22.8.

These findings show that an animal without specialized adaptation for vocal learning or mimicry, a California sea lion, is able to learn to entrain a motoric behavior to regular rhythmic auditory stimuli. However, because of the training provided, we could not be certain that Ronan had not internalized two set rates of bobbing and was somehow able to deploy them correctly on perceiving the faster or slower stimulus rate, independent of an actual ability to flexibly entrain motor behavior to an auditory stimulus. Therefore, her performance was assessed with novel tempo transfer testing in Experiment 2.

Experiment 2

Following her successful acquisition of the two training tempos, and without further training, in February of 2012 we tested Ronan's ability to entrain to a range of novel tempos through a series of transfer tests. Ronan was tested on five frequency-modulated stimuli that were identical to the 80 and 120 bpm training stimuli except novel in rate. While performance with the 80 and 120 bpm frequency-modulated stimuli was assessed following explicit training at those rates, performance with the five novel stimulus tempos was assessed based on Ronan's first two exposures to each stimulus, with no prior training at the test rates.

Method

Ronan was tested on her ability to generalize to five novel tempos of the frequency-modulated stimulus. These were (in order of presentation): 96 bpm (20% slower than 120 bpm and 20% faster than 80 bpm), 88 bpm (10% faster than 80 bpm), 108 bpm (10% slower than 120 bpm), 132 bpm (10% faster than 120 bpm), and 72 bpm (10% slower than 80 bpm). These five test sessions were conducted in succession, without practice sessions in between.

For each transfer test, Ronan received one 20-trial session with a 1:1 mixture of familiar 80 bpm and 120 bpm frequency-modulated stimuli, with a single novel exposure trial to the stimulus tempo being tested inserted randomly between Trials 1 and 10 and a second exposure trial to the same test stimulus between Trials 11 and 20. Both test trials with the novel stimulus tempo were grouped and analyzed together. Reinforcement on the novel

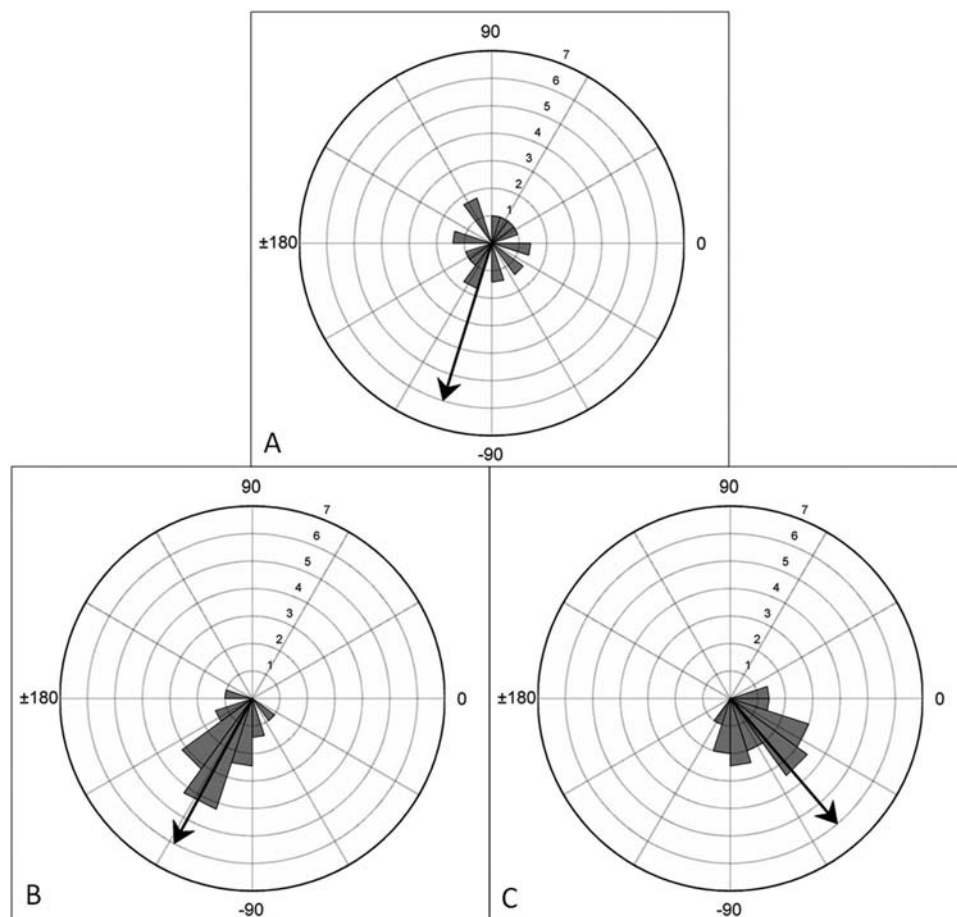


Figure 1. The angular distribution of Ronan's phase angles on her test for spontaneous entrainment to a frequency-modulated 120 beats per minute (bpm) stimulus (A), and her subsequent tests following training to the same 120 bpm stimulus (B) and a frequency-modulated 80 bpm stimulus (C). These tests were conducted in Experiment 1. Each phase angle represents the temporal relationship of a head bob and its closest beat in the auditory stimulus. Angles 0 to 180 degrees represent head bobs falling after the beat. Angles 0 to -180 degrees represent head bobs falling before the beat. The radial axis scale (1–7) corresponds to the square root of the count of each vector such that the area of each vector is proportional to the number of individual phase angles it contains. The arrow represents the direction of Ronan's mean vector, but is not representative of the mean vector length.

transfer trials was contingent on the same 20-beat criterion used throughout training and the majority of testing.

Results and Discussion

Ronan successfully entrained to all five novel tempos of the frequency-modulated stimulus (96 bpm, 108 bpm, 88 bpm, 132 bpm, and 72 bpm). Performance was calculated from the combination of both test trials for each stimulus. Specific values for individual trials are available in Supplemental Table S1.

Ronan's cumulative mean bob rate on her 96 bpm test trials was 96.8 bpm with a mean vector angle of -49.9 degrees (Figure 2A). Ronan's cumulative mean bob rate on her 108 bpm tests was 109.3 bpm with a mean vector angle of 3.5 degrees (Figure 2B). Ronan's cumulative mean bob rate on her 88 bpm test was 89.1 bpm with a mean vector angle of -35.3 degrees (Figure 2C). Ronan's cumulative mean bob rate on her 132 bpm test was 132.5 bpm with a mean vector angle of 40.3 degrees (Figure 2D). Ronan's cumulative

mean bob rate on her 72 bpm test was 73.3 bpm with a mean vector angle of -76.5 degrees (Figure 2E). Her behavioral response was synchronized (and thus by definition also entrained) with all of the novel tempos of the frequency-modulated stimulus (V Test: 96bpm: $u_{40} = 5.3$, 108 bpm: $u_{40} = 8.4$, 88 bpm: $u_{40} = 6.4$, 132 bpm: $u_{40} = 6.6$; all $p < .001$) except for the 72 bpm stimulus (V Test: $u_{40} = 1.6$, $p > .05$). She was, however, entrained to the 72 bpm stimulus (Rayleigh Test: $z_{40} = 22.9$, $p < .001$). Her mean number of pre-criterial bobs across these 10 test trials was 3.9.

Ronan's bobbing during test trials was clearly entrained to each respective novel stimulus rate, and was also synchronized to all test rates save 72 bpm. However, there was an evident phase/tempo relationship between the stimulus tempos and Ronan's respective bobbing rates. Specifically, Ronan tended to be behind the beat with faster stimuli and ahead of the beat with slower stimuli. Such a pattern is generally not seen in human subjects, who tend to more tightly synchronize across a rela-

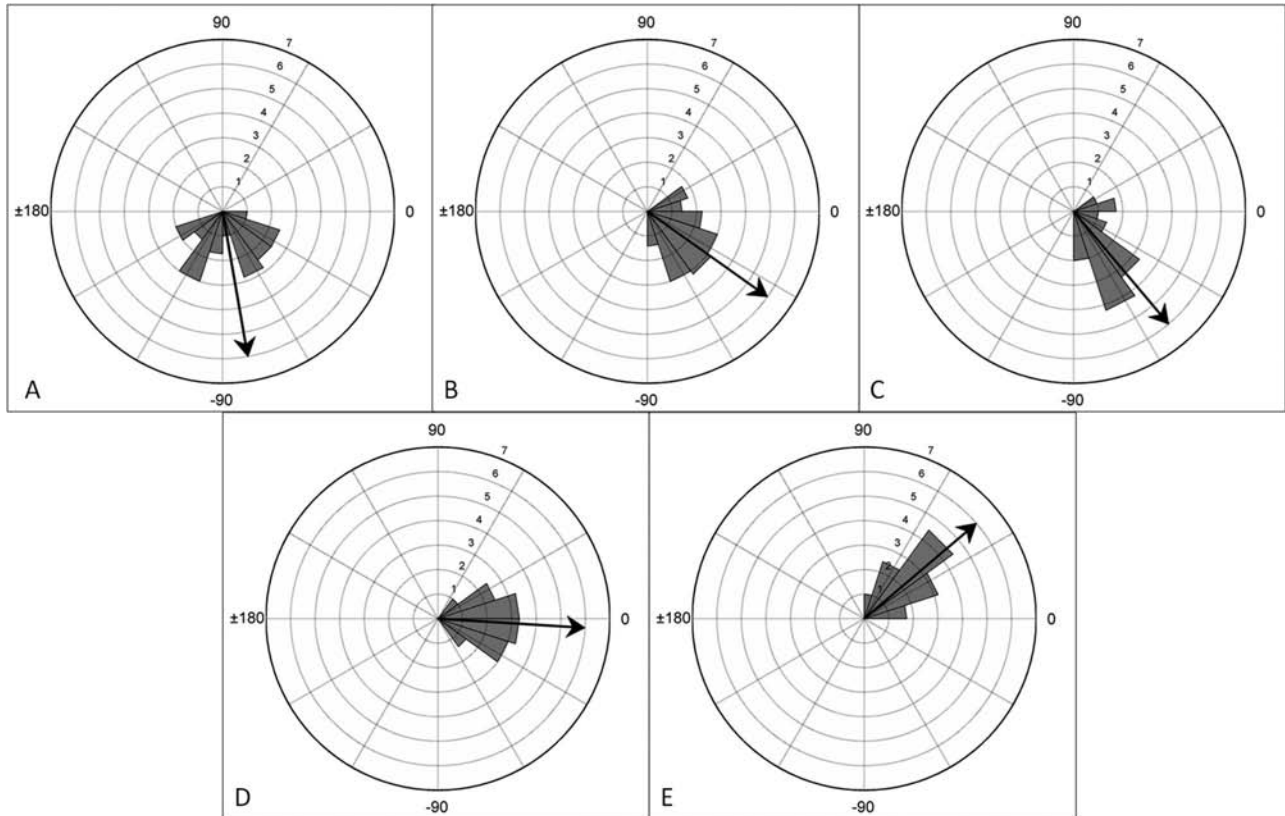


Figure 2. The cumulative angular distribution of Ronan's phase angles on her first two exposure trials to 5 frequency-modulated stimuli at the novel rates of (A) 72 beats per minute (bpm), (B) 88 bpm, (C) 96 bpm, (D) 108 bpm, and (E) 132 bpm. These tests made up Experiment 2.

tively wide range of rhythmic stimuli (Repp, 2005). Implications are explored in the General Discussion.

Experiment 3

At the completion of Experiment 2, we had assumed that Ronan's demonstrated ability to entrain could be explained by an ability to find and match the beat in an auditory stimulus. However, in the comparative literature on entrainment to auditory rhythm it has been argued that some cases of apparent entrainment might be more parsimoniously explained by a simple pattern of stimulus and response (Hasegawa et al., 2011; Patel et al., 2009a). For instance, one might argue that each of Ronan's head bobs was merely in response to the previous beat in the stimulus, and thus its coincidence with the following beat was incidental. To rule out this alternative explanation for her robust transfer performance, in June 2012 we tested Ronan with a series of stimuli with missing beats. Had each of Ronan's bobs been merely in response to the preceding beat, her performance should have been disrupted immediately following missing beats in the stimulus presentation.

Method

Ronan was presented with a single, mixed session of metronomic 120 bpm trials with no missing beats and metronomic 120 bpm trials

with a missing beat. The stimulus for this test session comprised only discrete clicks—we removed the oscillating tone so that Ronan's ability to keep the beat following dropped beats could not be supported by continuous auditory information. Twelve trials with one missing beat were mixed with eight trials without missing beats in an otherwise typical, 20-trial session. The arrangement of dropped-beat and no-dropped beat trials was semirandom. In addition, the placement of the missing beat in missing-beat trials was semirandom, such that Ronan would not be able to predict its occurrence.

To assess Ronan's performance on this session, we grouped phase angles of bobs falling immediately before and after the missing beats spread throughout the testing session. Both groups of phase angles were represented as circular distributions, and, to test for a difference between the before and after distributions, the Watson and Williams Two-Sample Mean Angle Test (Zar, 1999) was used. This is a circular test that assesses the probability that two sets of phase angles are drawn from the same population. We also assessed the cumulative phase angle distribution of the beats following the dropped beats for entrainment and synchronization using the Rayleigh and V tests.

Results and Discussion

Ronan did not cease bobbing following any of the missing beats during stimulus presentations. Ronan's cumulative mean vector angle for beats immediately preceding the missing beats was 37.8

degrees (Figure 3A). Her cumulative mean vector angle for beats immediately following the missing beats was 39.0 degrees (Figure 3B). There was no statistical difference between these two populations of phase angles (Watson and Williams Two-Sample Mean Angle Test: $F(1, 22) = 0.04, p > .05$). Furthermore, Ronan's cumulative bobs immediately following the missing beats were entrained and synchronized (V Test: $u_{12} = 3.9, p < .001$).

Viewed cumulatively, the phase angles of the bobs immediately following the 12 dropped beats were synchronized. Furthermore, there was no statistical difference between the phase angles of the 12 bobs immediately before and the 12 bobs immediately after the dropped beats. The resilience of Ronan's beat matching behavior to disruption by dropped beats provides strong evidence that Ronan was not merely initiating a delayed response to each beat. In conjunction with the results from Experiment 2, this performance suggests that Ronan has a flexible ability to entrain motor behavior to simple rhythmic auditory stimuli.

Experiment 4

To assess Ronan's ability to entrain to a tempo embedded in a complex, musical stimulus, Ronan was exposed to actual music during additional transfer trials conducted between April and August of 2012. There were two primary tests of entrainment to music, described below. These employed novel transfers to two pop songs: "Everybody," by The Backstreet Boys (PoP & Martin, 1997, track 1), the same song to which the first nonhuman animal had been shown to entrain (Patel et al., 2009a), and "Boogie Wonderland," by Earth Wind and Fire (Willis & Lind, 1979, track 5). To prepare Ronan for her attempted transfers to complex musical stimuli, we first exposed her to two nonmusical stimuli differing in type from the previous frequency-modulated stimuli, to make certain that her ability to entrain would generalize beyond the stimulus type she was trained on. She then received exemplar training with a simplified subsection of a third song, "Down on the Corner" (Fogerty, 1969, track 1).

Method

In preparation for musical transfer tests, Ronan was first exposed to two novel stimulus types. Both featured metronomic click tracks as in the frequency-modulated stimulus, but instead of a continuous tone changing in frequency, included either a continuous tone changing in amplitude or a back-beat mixed in with the primary beat. These stimuli were presented at rates that had not been previously used during the earlier experiments. Ronan proved able to entrain to both stimuli on her first exposures (Supplementary Table S1), so was moved on to musical exemplar training with "Down on the Corner" (Fogerty, 1969, track 1).

Initially, Ronan was assessed for spontaneous transfer to the complete version of "Down on the Corner" (Fogerty, 1969, track 1). Ronan did not entrain spontaneously, and was then trained on a simple subsection of the song for approximately 10 sessions. When she was able to reliably produce 20 consecutive, entrained bobs, and was able to transfer performance to novel tempos of this subsection (see Supplementary Table S1), she was judged ready for primary music testing.

Ronan's test exposure to "Everybody" (PoP & Martin, 1997, track 1) was to a 90-s, unaltered clip of the song at the native rate of 108.2 bpm, including vocals and transitions between verse, chorus, and bridge. Ronan's test exposure to "Boogie Wonderland" (Willis & Lind, 1979, track 5) was to a 45-s unaltered clip of the song, starting at the beginning. The tempo of "Everybody" (PoP & Martin, 1997, track 1) is very steady, fluctuating between 107 and 109 bpm, but "Boogie Wonderland" (Willis & Lind, 1979, track 5) does not have a steady tempo. The tempo in the latter song changes over the course of the selection we tested, ranging between 123 bpm and 138 bpm. The mean bpm of the section of the song we used is 130.

Musical transfer test sessions were structured differently than were prior test sessions with the frequency-modulated stimuli. Instead of embedding two test trials within a session of familiar stimuli, for musical transfers Ronan was repeatedly presented with the test stimulus. If she did not meet criterion during the length of

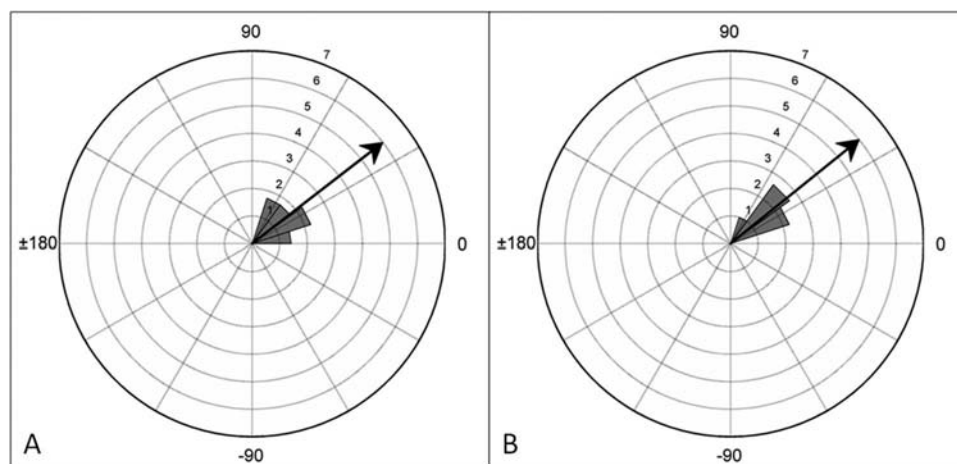


Figure 3. The angular distribution of Ronan's phase angles on beats preceding the missing beats (A) and beats following the missing beats (B) in a 120 beats per minute (bpm) stimulus with no tonal overlay and some missing beats. These tests made up Experiment 3.

the stimulus, she was not reinforced, but was instead cued to return to the water, then brought back to the station for another trial. If she failed to meet criterion on four trials within a session (these were not required to be consecutive), the session would be ended. For each song, to meet criterion during a test trial, a head bob had to come down very near the beat representing 4/4 time (i.e., she could not be reinforced for bobbing just on every other beat, or in counter phase).

Results and Discussion

Ronan succeeded in transferring to “Everybody” (PoP & Martin, 1997, track 1), meeting criterion on 7 of 11 trials. Her cumulative mean tempo was 109.4 bpm with a mean vector angle of 7.2 degrees (Figure 4A). Ronan was both entrained and synchronized to this stimulus (V Test: $u_{140} = 14.1, p < .001$).

Ronan succeeded in transferring to “Boogie Wonderland” (Willis & Lind, 1979, track 5), meeting criterion on five of five trials. Her mean tempo was 128.1 bpm with a mean vector angle of 43.7 degrees (Figure 4B). Ronan was both entrained and synchronized to this stimulus (V Test: $u_{100} = 7.1, p < .001$).

Without any prior exposure, training, or reinforcement on these complex, musical stimuli, Ronan was able to entrain and synchronize to the beat on both songs over the course of multiple trials.

After seven consecutive successful trials on “Everybody” (PoP & Martin, 1997, track 1) Ronan failed to meet criterion on her next four trials, and the session was ended. This does not, however, suggest that her ability to entrain was the product of chance—the mean number of beats prior to criterion on the seven successful trials was only 29.9. In addition, her phase angles across the seven trials ranged only from -10.5 degrees to 28.6 degrees, and were highly significant for synchronization when analyzed together, suggesting phase consistency across the seven successful trials. Anecdotally, Ronan seemed irritated or tired near the end of the session, quitting prior to the end of the stimulus on all four failed trials. Despite her high degree of success, we believe this was a difficult task and required physical and mental focus that could have waned across the course of a difficult and potentially con-

fusing session. Up to the point at which she ceased to entrain in this session, the number of bobs prior to the criterial runs was never higher than on the first trial, suggesting performance was not declining gradually across the course of the session, and further indicating that her sudden fall off in performance was because of factors aside from her core capability.

Ronan’s performance to “Boogie Wonderland” (Willis & Lind, 1979, track 5) was perhaps even more impressive. Here the session was ended prior to Ronan’s producing any nonentrained trials so as to prestage frustration and negative conditioning with a stimulus planned for further testing (see Experiments 5 and 6). Given the substantial tempo change across the course of the stimulus, Ronan would not have been able to remain entrained by producing only a steady bob rate near the mean stimulus rate, but rather had to dynamically alter her bobbing tempo to stay in time with the changing song. Despite this, the mean number of precriterial bobs across these 5 trials was only 12.6, and aside from the first trial on which Ronan produced 28 precriterial bobs, she never produced more than four. Again, as with “Everybody” (PoP & Martin, 1997, track 1), the mean angles of Ronan’s criterial runs were grouped closely, ranging from 2.6 to 57.0 degrees with the exception of the first trial, on which her mean angle was 131.6 . In addition, the cumulative bobs were highly significant for synchronization when analyzed together.

Ability to find and keep the beat on two novel, quite different musical stimuli strongly suggests a flexible capability to entrain to complex stimuli. The data to this point clearly suggest Ronan was able to meet the three criteria specified by the vocal learning and synchronization hypothesis: a behavioral response in a different modality from the stimulus, ability to flexibly entrain to different rates, and ability to extract tempo from complex stimuli. Even so, our focus on transfer performance with novel stimuli could have underrepresented Ronan’s full rhythmic capability. As discussed earlier, learning likely plays a role in improving human entrainment capability, and these stimuli were the first nonsimplified songs to which Ronan had been exposed. In Experiment 5, we tested Ronan’s ability to transfer to novel tempos of “Boogie

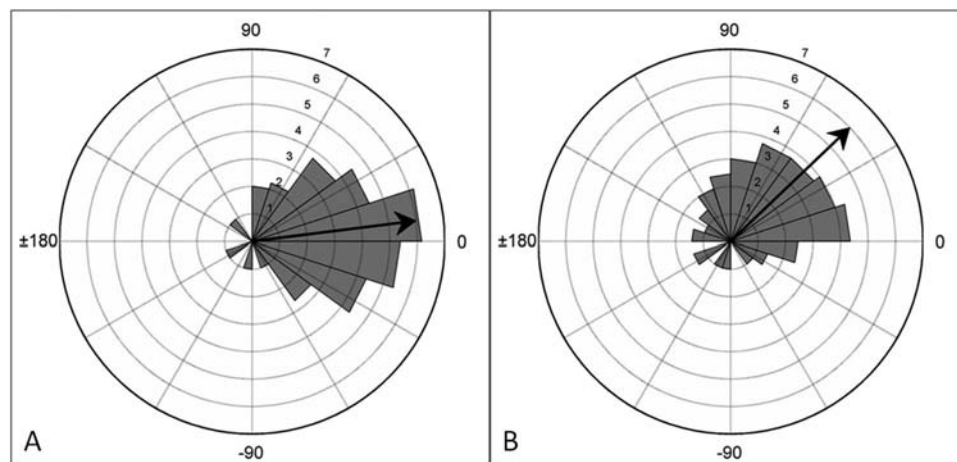


Figure 4. The angular distribution of Ronan’s phase angles on seven test trials of the song “Everybody” at the native rate of 108.2 beats per minute (bpm) (A) and five test trials of the song “Boogie Wonderland” at the native rate of 130 bpm (B). These tests made up Experiment 4.

Wonderland” (Willis & Lind, 1979, track 5) following further practice entraining to the native rate.

Experiment 5

Because we believed that Ronan’s ability to entrain to complex musical stimuli would likely improve with practice, and all prior exposures to nonsimplified musical stimuli had been conducted within one testing session per song, she received explicit training with the native format of “Boogie Wonderland” (Willis & Lind, 1979, track 5) throughout September 2012. Then, in October of 2012, we conducted a tempo transfer test with five novel tempos of “Boogie Wonderland” (Willis & Lind, 1979, track 5). These tempo transfer tests were conducted without any prior exposure to the song at any rate other than the native 130 bpm.

Method

Training with “Boogie Wonderland” (Willis & Lind, 1979, track 5) was similar in nature to Ronan’s initial training with the frequency-modulated stimuli. Although her performance at initial exposure to “Boogie Wonderland” (Willis & Lind, 1979, track 5) had been very strong, we began explicit training by reducing the number of criterial bobs required to receive reinforcement to five. This allowed the experimenter to reinforce her only for the most clearly synchronized sets of bobs without risking Ronan’s becoming frustrated. The reinforcement criterion was then approximated up to 20 over the course of approximately seven sessions, at which point Ronan received tempo transfer tests.

To test her ability to transfer performance on “Boogie Wonderland” to novel tempos, Ronan was exposed in one 24-trial session to 4 trials each of the song at the native rate (130 bpm) as well as versions of the song identical but for a shifted tempo: -20% (104

bpm), -10% (117 bpm), -5% (124 bpm), 5% (137 bpm), and 10% (143 bpm). Four trials were used instead of two, as in the test of the frequency-modulated tempo transfers, to provide more data in keeping with the more complex nature of the musical stimulus. We did not use a tempo shifted $+20\%$ because pilot work with metronomic stimuli indicated that Ronan could not reliably bob at a rate greater than 150 bpm. Trial order was semirandom, with no back-to-back presentations of any particular stimulus tempo.

Results and Discussion

Ronan successfully entrained to all five transfer tempos of “Boogie Wonderland” (104 bpm, 117 bpm, 124 bpm, 137 bpm, and 143 bpm). As with previous tests, performance was calculated from the combination of successful criterial runs at each tempo. Ronan met criterion on 14 of these 20 test trials: four trials at 137 bpm, three of four trials at 117, 124, and 143 bpm, and only one of four trials at 104 bpm. Her mean number of precriterial bobs across these 14 trials was 9.8.

Ronan’s mean bob rate on her successful 104 bpm test trial was 103.3 bpm with a mean vector angle of -57.3 degrees (Figure 5A). Ronan’s mean bpm was above 120 for the following three exposures at this stimulus rate, and none of these trials were significant for entrainment or synchronization individually. Ronan’s cumulative mean bob rate on her three successful 117 bpm test trials was 118.3 bpm with a mean vector angle of -30.5 degrees (Figure 5B). Ronan’s cumulative mean bob rate on her three successful 124 bpm test trials was 123.3 bpm with a mean vector angle of -20.1 degrees (Figure 5C). Ronan’s cumulative mean bob rate on her four successful 137 bpm test trials was 134.7 bpm with a mean vector angle of 11.2 degrees (Figure 5D). Ronan’s cumulative mean bob rate on her three successful 143 bpm test trials was 141.7 bpm with a mean vector angle of 82.5

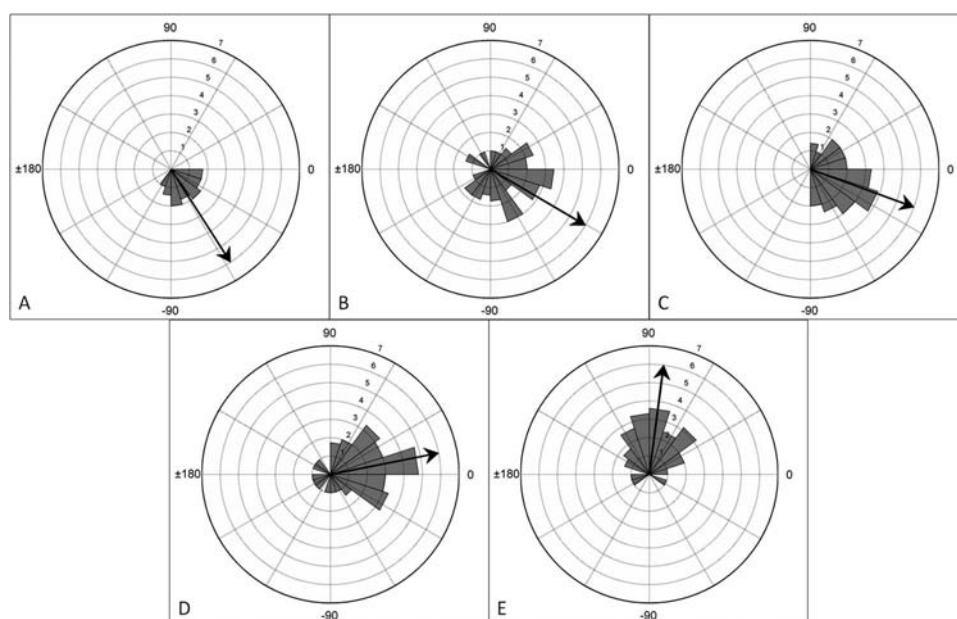


Figure 5. The cumulative angular distribution of Ronan’s phase angles on successful novel tempo transfer trials to “Boogie Wonderland” at 104 beats per minute (bpm) (A), 117 bpm (B), 124 bpm (C), 137 bpm (D), and 143 bpm (E). These tests made up Experiment 5.

degrees (Figure 5E). Ronan was synchronized on the successful 117, 124, and 137 bpm trials (V Test: 117bpm: $u_{60} = 4.3$, 124 bpm: $u_{60} = 7.1$, 137 bpm: $u_{80} = 9.1$, all $p < .001$) and not on the successful 104 and 143 bpm trials (V Test: 104 bpm $u_{20} = 0.9$, 143 bpm $u_{80} = 1.1$, both $p > .05$). She was, however, entrained on the successful 104 and 143 bpm test trials (Rayleigh Test: 104 bpm $z_{20} = 11.8$, $p < .01$, 143 bpm $z_{80} = 30.2$, $p < .001$).

Even if we included all test trials in the analysis for all five tempos, using the last 20 bobs from each of the noncriterial trials, Ronan's cumulative bobbing for each transfer tempo would be significant for entrainment. Notably, Ronan's combined performance, although still showing marginal entrainment, was by far the poorest for the 104 bpm stimulus. The experimenters noted, subjectively, that the "attack" of the drum and bass parts was much weaker in the 104 bpm version, likely because of distortion as a result of the lengthening of the waveforms in tempo shifting. This might have accounted for Ronan's relatively poor performance, as previous stimuli in this tempo range (e.g., 108 bpm frequency-modulated and "Everybody" (PoP & Martin, 1997, track 1) had presented little apparent difficulty for her.

Ronan's ability not only to find and keep the beat in a novel, complex musical stimulus, as in Experiment 4, but to maintain that capability across further training, and then successfully transfer to a range of novel stimulus rates, shows a truly flexible capability to entrain to a musical stimulus.

To this point, we strongly felt Ronan had demonstrated a capability for entrainment and synchronization at least on par with that demonstrated by any other nonhuman animal. Our Monte Carlo simulation justified focusing analysis on the criterial bob runs. In addition, every single trial in which Ronan met criterion was also significant for entrainment if analyzed using all bobs that occurred from the moment of stimulus onset (that is, both precriterial and criterial). One could, however, argue that Ronan's results were none-the-less being skewed positively by our ending each test trial at a point when Ronan was judged by the experimenter to be entrained. Doing so was necessary because of our training paradigm—Ronan was explicitly reinforced following consecutive, entrained bobs, so to end trials without this criterion could have led to the breakdown of her performance. Given the small number of precriterial bobs across all test trials, and her high success rate, it seems very unlikely that such a selection bias would meaningfully impact our measures of Ronan's performance. However, to definitively demonstrate that Ronan's performance was very unlikely to be explained as a function of fortunate rate drift, and to show that it was not being meaningfully inflated by our ending trials following only successful bobbing runs, Ronan was tested with a 60 consecutive beat criterion in Experiment 6.

Experiment 6

To look for drift in Ronan's bobbing, we retested her in November of 2012 on the seven frequency-modulated tempos previously used in testing, as well as on three tempos of "Boogie Wonderland" (Willis & Lind, 1979, track 5). These tests were conducted with a criterion of 60, instead of 20, consecutive, entrained bobs. In the case of the frequency-modulated and "Boogie Wonderland" (Willis & Lind, 1979, track 5) transfer tempos, Ronan had had extremely limited exposure (fewer than 10 trials) to any of these stimuli following initial transfer testing. The aim

during these tests was to determine if Ronan's motoric entrainment to simple and complex rhythmic stimuli could be accurately sustained over relatively long testing intervals.

Method

Ronan first received one week of training during which she was run to a 60-beat criterion on her two initial frequency-modulated training stimuli, 120 bpm and 80 bpm. The structure of these trials was identical to the previous 20-beat-criterion trials, in that Ronan was required to keep bobbing until producing 60 consecutive bobs that appeared entrained to the eye of the experimenter. The only change aside from the extended criterion was that she now received two capelin as reinforcement instead of one, as well as an extra capelin in the water in-between trials—reinforcement was increased because 60 consecutive bobs represented a potentially large increase in difficulty and physical cost on each trial.

We selected a 60-bob criterion as comfortably above Ronan's mean bobs per test trial (counting both precriterial and criterial bobs) to this point: 39.5. Ronan had had only five test trials to this point where she had bobbed 60 times or more, including criterial bobs. Four of these trials came on the "Boogie Wonderland" (Willis & Lind, 1979, track 5) tempo transfers.

When Ronan was reliably able to produce criterial runs of 60 consecutive bobs with the 80 and 120 bpm stimuli, we tested her on these and on the five frequency-modulated stimuli initially used in her tempo transfer testing: 72 bpm, 88 bpm, 96 bpm, 108 bpm, and 132 bpm. Ronan received these stimuli within one testing session that comprised two initial 20-beat-criterion trials, one at 120 bpm and one at 80 bpm, then two 60-beat-criterion trials, one each at 120 bpm and 80 bpm, followed by the five test trials, one each at the five transfer tempos.

To further assess her ability to maintain entrainment for longer durations, Ronan was subsequently exposed in 60-beat-criterion test trials to "Boogie Wonderland" (Willis & Lind, 1979, track 5) at the native rate of 130 bpm, as well as at 124 bpm and 137 bpm. Ronan had not previously received any practice with musical stimuli with a criterion of higher than 20 beats. In this test session, Ronan first received one warm-up trial each with the 120 bpm and 80 bpm stimuli with a 20-beat criterion. She then received three 60-beat test trials with the 130 bpm stimulus, and two each with the 124 bpm and 137 bpm stimuli. Each 60-beat-criterion trial was preceded by a trial at the same rate with a 20-beat criterion. The total number of trials was thus 16. Because we were interested in best capability, we elected to analyze the final 60-beat-criterion trial at each rate.

Results and Discussion

Ronan successfully entrained to all seven frequency-modulated stimuli, and was able to sustain this performance to produce 60 criterial bobs at each tempo. Her mean number of precriterial bobs on these trials was 5.7, and she had no more than 23 precriterial bobs on any of these seven trials. Three emblematic trials were selected for Figure 6, the 120 bpm trial, as well as one faster (132 bpm) and one slower (108 bpm) trial, demonstrating performance on her most practiced stimulus, as well as performance on less familiar stimuli, one faster and one slower.

Ronan's mean bob rate on her 120 bpm test was 120.7 bpm with a mean vector angle of 1.4 degrees (Figure 6B). Ronan's mean bob

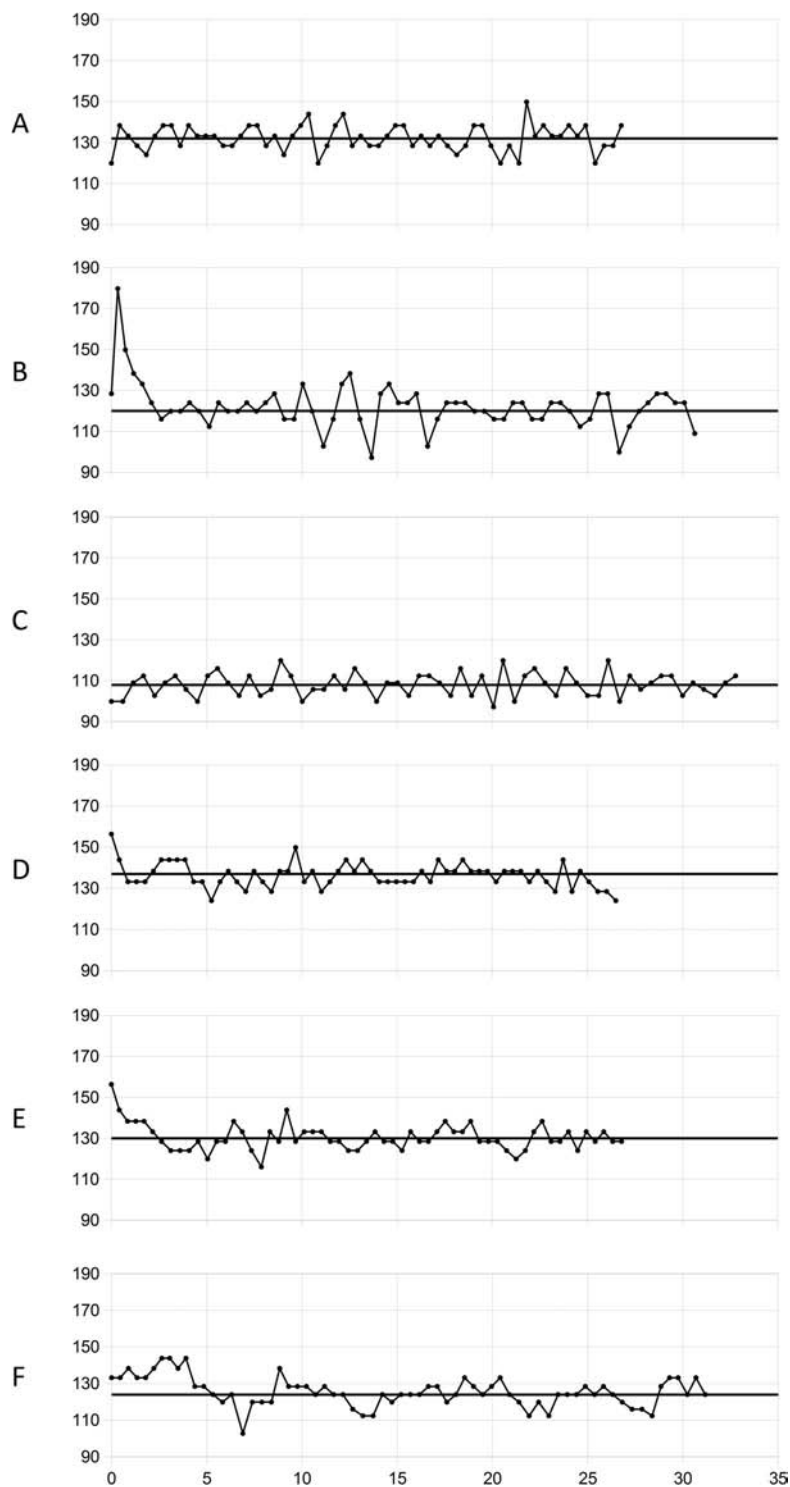


Figure 6. Time course plots showing the instantaneous tempo of Ronan's individual bobs on the y axis sequentially over time in seconds on the x axis, for 60-beat criterion trials of the frequency-modulated stimuli at 132 beats per minute (bpm) (A), 120 bpm (B), and 108 bpm (C); and for "Boogie Wonderland" at 137 bpm (D), 130 bpm (E), and 124 bpm (F). These plots represent entire trials, including both precriterial and criterial bobs. These tests were conducted in Experiment 6.

rate on her 80 bpm test was 80.6 bpm with a mean vector angle of -30.2 degrees. Ronan's mean bob rate on her 96 bpm test was 96.6 bpm with a mean vector angle of -11.6 . Ronan's mean bob rate on her 132 bpm test was 132.5 bpm with a mean vector angle of 40.3 degrees (Figure 6A). Ronan's mean bob rate on her 72 bpm test was 72.1 bpm with a mean vector angle of -62.7 degrees. Ronan's mean bob rate on her 88 bpm test was 88.2 bpm with a mean vector angle of -23.6 . Ronan's mean bob rate on her 108 bpm test was 108.3 bpm with a mean vector angle of -5.9 (Figure 6C). Unlike with her initial frequency-modulated tempo transfer test, Ronan was not just entrained but synchronized to all of these stimuli (V Test: 120 bpm: $u_{60} = 9.8$, 80 bpm: $u_{60} = 8.6$, 96 bpm: $u_{60} = 10.2$, 132 bpm: $u_{60} = 7.6$, 72 bpm: $u_{60} = 4.8$, 88 bpm: $u_{60} = 9.6$, 108 bpm: $u_{60} = 10.5$; all $p < .001$).

Ronan was also able to successfully entrain to all three tempos of "Boogie Wonderland" (Willis & Lind, 1979, track 5) on each of the seven test trials. On her first two test trials she did not reach the 60 beat criterion, although her bobbing was synchronized, choosing instead to cease bobbing before the end of the stimulus. She reached the 60 beat criterion on each of the next five test trials. Performance on each of these seven trials (including those on which she quit) was highly statistically significant for synchronization (see Supplementary Table S1), but we focused analysis on the last trial for each tempo; on these trials her mean number of precriterial bobs was 3.0.

Ronan's mean bob rate on her 130 bpm test was 130.6 bpm with a mean vector angle of 0.9 degrees (Figure 6E). Ronan's mean bob rate on her 137 bpm test was 136.0 bpm with a mean vector angle of 43.5 (Figure 6F). Ronan's mean bob rate on her 124 bpm test was 124.5 bpm with a mean vector angle of -11.7 . Ronan was synchronized on all three of these trials (V Test: 130 bpm: $u_{60} = 9.3$, 137 bpm: $u_{60} = 6.5$, 124 bpm: $u_{60} = 7.8$; all $p < .001$).

It is clear from Figure 6 that Ronan's bobbing rates across these extended trial test sessions did not trend in a particular tempo direction, instead being grouped quite tightly around each stimulus rate. To statistically address the possibility of drift, we performed regression analysis of Ronan's instantaneous bob rate against time for each trial. The slope of none of these time-courses was significantly different than 0, strongly indicating no directional tempo bias in bob rate. (Regression: 132 bpm: slope = -0.4 , $R^2 = 0.1$; 120 bpm: slope = -0.3 , $R^2 = 0.1$; 108 bpm: slope = 0.0 , $R^2 = 0.0$; 137 bpm: slope = -0.2 , $R^2 = 0.1$; 130 bpm: slope = -0.2 , $R^2 = 0.0$; 124 bpm: slope = -0.3 , $R^2 = 0.1$; all $p > .05$).

Given that Ronan's bobbing rate was clearly not drifting on these extended test trials, but instead fluctuated tightly around the stimulus rate on each test trial, even when pushed to 60 consecutive entrained bobs, her ability to produce strings of criterial bobs is even less likely the product of some kind of random or semirandom drift. Furthermore, given this performance on trials with a consecutive bob criterion much higher than her mean number of total bobs per trial on previous test trials, it is untenable to explain away her performance on Experiments 2–5 as due merely to selection bias introduced by capping the majority of test trials at 20 consecutive entrained bobs. These findings are in keeping both with the results of our Monte Carlo simulation and with our analysis of Ronan's performance including precriterial bobs (see Supplementary Table S1). Once Ronan finds the beat, it appears that she reliably maintains behavior at that rate indefinitely, at least within the limits of her current training.

Interestingly, while the general trend of Ronan's phase/tempo relationship (ahead of the beat with slower tempos, behind the beat with faster tempos) held between the first frequency-modulated exposures in April 2012 and the 60-beat criterion follow-up in October 2012, she showed a marked tightening of phase angles in the later exposure, even for tempos she had not encountered regularly. Most notable was her improvement on her three most practiced stimuli. Her 120 bpm frequency modulated stimulus phase angle went from -49.5 degrees to 1.4 degrees. Her 80 bpm phase angle went from -118.3 degrees to -30.2 degrees, and her 130 bpm "Boogie Wonderland" mean phase angle went from 43.0 degrees over her initial five exposures to 0.9 degrees. These data suggest that practice markedly improves Ronan's capability to precisely synchronize.

In conjunction with the previous results, Ronan's ability to maintain synchronized bobbing behavior for up to 60 consecutive beats suggests a flexible, reliable, and broadly applicable capability for rhythmic entrainment and synchronization to a wide range of simple to complex stimuli.

General Discussion

According to the vocal learning and synchronization hypothesis, only species producing vocal mimicry should be capable of flexible entrainment (Patel et al., 2009a). The present results show, however, that a mammal unlikely to have adaptations supporting complex vocal learning or mimicry, a California sea lion, can learn to entrain and synchronize motoric behavior to an auditory beat. Furthermore, this ability was shown to transfer to novel tempos and novel stimuli, including music. Such an ability clearly meets the three criteria for flexible, human-like entrainment established under the vocal learning and synchronization hypothesis. The sea lion trained and tested in the present study was able to entrain a response that was in a different sensory modality than the signal, she was able to entrain to a wide range of novel tempos, and she was able to entrain to the beat from complex, musical stimuli.

While it is true that, aside from their distant phylogenetic connection to true seals, there is currently no reason to believe that sea lions are vocal mimics, it is of course possible that future studies may reveal that sea lions do possess the capacity for some degree of complex vocal learning. In light of such evidence, and no contrary evidence showing flexible entrainment in other vocally inflexible species, our current findings would have to be reinterpreted in support of the vocal learning hypothesis. However, until further evidence accumulates, the default assumption must be that the ability to learn beat-matching is not restricted to those species with a particular cognitive ability such as complex vocal learning or mimicry, and thus may be widespread in the animal kingdom.

The parsimony of this assumption is further supported by the ubiquity of neural timing mechanisms in animal brains. These operate across a wide range of durations and rates (Mauk & Buonomano, 2004; Buhusi & Meck, 2005), are essential for coordinating perception and action (Sumbre, Muto, Baier, & Poo, 2008), and can entrain to both endogenous and exogenous input (Treisman, Faulkner, & Naish, 1992; Schroeder & Lakatos, 2009; Meck, Penney, & Pouthas, 2008). Perhaps such timing mechanisms are recruited and flexibly deployed to support sensorimotor entrainment in some species. Indeed, there is some evidence for such an explanation of sensorimotor entrainment in humans (Will

& Berg, 2007; Jantzen, Steinberg, & Kelso, 2009). Given this, further exploration of the relation of these proximal mechanisms to sensorimotor entrainment in nonhuman animals is warranted.

In light of the experimental and anecdotal observations presently available, the question remains whether the capability of nonhumans to beat match is analogous to that found in humans. Some have suggested that a spontaneous capability for beat matching, without any prior training, may be most emblematic of human-like performance (Patel et al., 2009b). However, although humans are sensitive to beat from an early age (Drake, Jones, & Baruch, 2000), there is no strong scientific consensus that they spontaneously entrain without practice and social reinforcement. Indeed, there is evidence that the ability to tap in time to a rhythmic stimulus improves from toddlerhood to adulthood, indicating a potential role for learning during development (McAuley, Jones, Holub, Johnston, & Miller, 2006; Provasi & Bobin-Begue, 2003). In addition, without early exposure to certain types of nonisochronous rhythms, adults are unable to detect disruptions in such rhythms (Hannon & Trehub, 2005). The limited evidence for human-like entrainment in animals so far does not include any clear-cut cases of spontaneous entrainment. The animals shown capable of entrainment have either received explicit training as in our study and that of Hasegawa et al. (2011), or have long histories of human interaction that could have allowed for incidental social reinforcement of rhythmic behavior (Patel et al., 2009a; Schachner et al., 2009). Given the potential role of learning in human entrainment and the lack of unequivocal evidence of spontaneous entrainment in nonhumans, spontaneity may not bear strongly on the question of similarity of rhythmic capability in humans and nonhuman animals. The issue awaits further research.

Although the performance of the sea lion in the current study did parallel human capability in the flexibility and reliability of her phase-sensitive beat matching across a range of stimuli, there was one notable difference. While humans tend to produce quite uniform phase angles across different tempos (Repp, 2005), there was a directional relationship between Ronan's bobbing angles and respective stimulus tempos. Specifically, despite producing reliable phase angles within each stimulus presentation, Ronan was generally farther behind the beat for faster stimuli and farther ahead of the beat for slower stimuli (although, as noted in Experiment 6, Ronan's ability to precisely synchronize appeared to improve with repeated exposure to particular stimuli). The proximal explanation for this phenomenon is unclear. However, if Ronan's ability to entrain is because of some sort of neural oscillation mechanism with a preferred endogenous rate being driven by an external rhythm, one might expect just this sort of phase/tempo relationship (e.g., Corron, Blakely, & Pethel, 2005). It is also unclear how exactly Ronan's phase/tempo relationship compares to the performance of other animals, as appropriately detailed data have not been presented, but Hasegawa et al. (2011) did report that their budgerigars entrained with a phase angle farther ahead of the beat at slower tempos than at faster.

In summation, the sea lion in this study was able to entrain and synchronize across a wide range of different types of stimuli, including music, and a wide range of tempos. Following initial training with two simple tempos, she was able to entrain on her first and all subsequent exposures to the majority of stimuli tested, and maintained continuous entrainment when pushed from a 20- to a sustained 60-beat criterion. Alternative explanations for her

performance, such as a high degree of entrainment and synchronization by chance, or some type of simple, response-based performance, were empirically discounted. Therefore, the present results constitute strong evidence that entrainment—and within a broad tempo range, synchronization—is present in a mammal with apparently limited vocal flexibility. This indicates that previous assumptions (Patel et al., 2009a; Schachner et al., 2009b; Hasegawa et al., 2011) about the neural mechanisms and evolutionary pathways associated with human beat-matching need either to be substantiated by further empirical evidence or fundamentally rethought.

In addition to the value of our empirical results, the methods developed for this study may be of use to other comparative studies of sensory-motor synchronization. Several aspects of the approach applied were somewhat novel and of apparent utility. The motor behavior used for beat matching was appropriate for the sea lion subject; other animals might be more naturally inclined to perform different repetitive motions. The response itself was initially trained as a continuous behavior in the absence of acoustic cues—once established, explicit reinforcement for successive beat matching was used to bring the behavior into the same phase as the auditory training stimuli. This procedure may have prevented the behavior from developing as a reactive stimulus-response chain and facilitated the emergence of entrained behavior. Both the nature of the behavior itself and the gradual steps used to bring the behavior under the control of the stimulus beats were likely instrumental in supporting the eventual transfer performance of this individual. The application of relatively precise criteria for what constituted a “matched” beat also probably served to provide optimal instruction to the subject during training. Given the theoretical framework established for comparative analyses of beat matching capability (Patel et al., 2009b), and the findings within the current study, future studies may wish to focus both on a more diverse range of species and on specific factors implicated in the emergence of beat-keeping ability with explicit training. We believe the methods described here may serve as a useful map for such explorations.

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