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LETTERS TO THE EDITOR

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Understanding the structure of humpback whale songs (L)

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Structured sound sequences produced by humpback whales are described in the literature as hierarchically organized songs. Despite the prevalence of such descriptions, there is no direct evidence that humpback songs are hierarchically structured. It is suggested here that songs may instead be heterarchically structured, in which case traditional approaches to analyzing songs may obscure their organizational and acoustical features. An alternative framework for characterizing patterns within songs is presented, derived from models of humpback whale sound production, that characterizes rhythmic and sequential regularities in the sound sequences produced by singing whales in terms of interacting cycles of breathing and internal air recirculation.
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I. INTRODUCTION

Roughly 40 years ago Payne and McVay[1] described predictable patterns of sounds produced by humpback whales as "songs." They developed descriptors to analyze humpback whale songs in terms of tree-like levels progressively linking adjacent sound units: Song sessions consist of repeated songs, which consist of repeated cycles of themes, which consist of repeated phrases, which consist of repeated patterns of individual sounds (called units). Payne and Payne[2] later reported that singers from all locales almost always conformed to these "rules of song form," and suggested that songs were hierarchically structured because of syntax-like constraints on song production. This descriptive framework has since been widely used leading many researchers to suggest that the complex structure of humpback whale songs is one of its most universal and intriguing features.

In what sense could humpback whale songs be hierarchical? All hierarchies contain elements in one level that are embedded in higher levels. The higher levels create the contextual interpretation of the elements. For example, in sentences, certain words become subjects, verbs, and objects within one hierarchy although the same words would have another interpretation in a different hierarchy. Consequently, sentences such as "they are flying planes," can be interpreted in multiple ways. Similarly, certain musical tones become the musical center (i.e., the tonic) in one hierarchy, but are merely ornamental notes in another. The usefulness of such hierarchical descriptions rests on their ability to capture the processes that producers and listeners use when constructing and interpreting a sound sequence.[3]

We do not believe that characterizing whale songs as hierarchical meets this condition. Whale researchers describe humpback whale songs as hierarchical because the regular patterns within songs are generally consistent with the hierarchical framework proposed by Payne and McVay.[1] However, the fact that hierarchical descriptors can be useful for analyzing variations in humpback whale songs provides *no evidence* that the sound sequences being analyzed are hierarchical in either production or perception. Watches provide a simple way of hierarchically classifying time but this does not provide evidence that time itself is hierarchically structured. More generally, evidence of higher order structure in sound sequences does not provide evidence of hierarchical organization.[4] Consequently, the recent information theoretic analyses of songs by Suzuki and colleagues[5] also provide no evidence that songs are hierarchical. In the case of birdsong, bioacousticians generally focus less on theoretical definitions and instead use behavioral, physiological, or acoustic data to support claims that birdsong is hierarchical.[6] None of these approaches can be applied to singing whales, leaving acoustic analyses as the only viable approach to clarifying how whale songs are structured.

II. ANALYZING STRUCTURE IN WHALE SONGS

Unlike most songbirds, humpback whales do not use a fixed repertoire of sounds, phrases, themes, or songs, but instead gradually modify the sounds and sound patterns that

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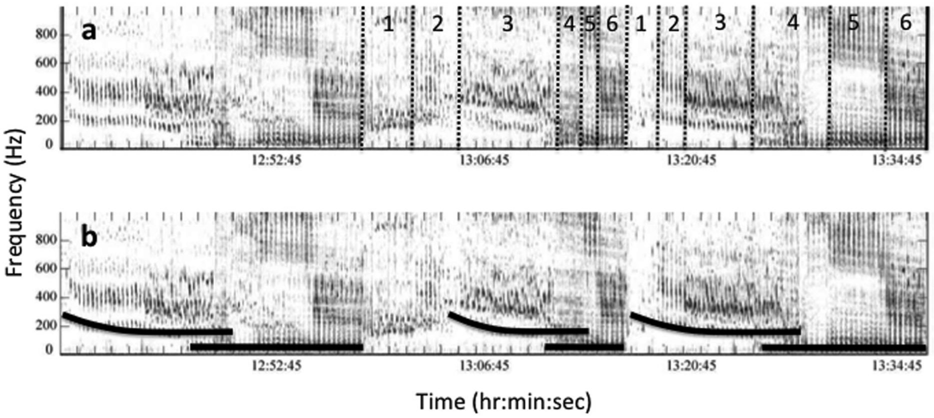

FIG. 1. Spectrogram of singing by a humpback whale. (a) Traditional hierarchical descriptions require partitioning recordings into discrete sequences of numbered themes. (b) Acoustic trajectories alternatively suggest that sequences are progressively modulated over time in ways that can be quite stereotyped. Periodic bouts of decreasing frequency modulation may reflect the dive cycle of a singer. Adapted from Ref. 7, Fig. 3.

they produce within sequences each year. As a result, a necessary first step in traditional analyses of song structure is to identify the regularities within a recording and then to label repeated patterns as songs, themes, or phrases.[7]

Analyses of songs in terms of such groupings can increase our understanding of the singing behavior of humpback whales independently of whether the songs are hierarchically structured. Regardless, descriptions of song structure solely in terms of unit sequences suffer from two critical shortcomings. First, the partitioning of sequences is inherently ambiguous. For example, Fig. 1 shows the types of periodic acoustic regularities that initially led researchers to describe humpback whale vocalizations as songs. Unlike the songs of humans and most songbirds, humpback whale songs have no clear beginning. Instead, a position in the sequence must be arbitrarily chosen as the start of the “first” theme (designated numerically). How dissimilar two pattern sequences must be to qualify as different themes is subjectively determined. Consequently, the number of theme designations for identical recordings may vary across investigators.[8]

Just as hierarchical descriptors partition song sessions into discrete songs and songs into discrete themes, they also divide themes into sets of discrete phrases. Again, there are no clear acoustical features that identify where one phrase ends and another begins; what counts as a phrase for songs from a given year is typically decided based on subjective criteria that may vary across investigators. Figure 2 shows examples of sound patterns typical of those that would traditionally be classified as phrases. The patterns contain several acoustic regularities, including repetitions of similar units and similar patterns of timing across units. The hierarchical framework provides little guidance as to whether these patterns should be classified as instances of a single phrase type or of two different phrase types. Furthermore, without additional information it is impossible to determine whether Fig. 2 shows two different phrases containing six and eight units, respectively, or four phrases containing three or four units.

Second, because the hierarchical approach to partitioning songs emphasizes uniformity within themes, dissimilarities across themes, the prevalence of particular themes, and the order in which themes are produced, it obscures acoustic features that may be important to understanding the structure and function of songs. Returning to Fig. 2, regardless of how these patterns are classified, they show several acoustic regularities that traditional analyses are likely to miss, including the consistency of pattern timing despite changes in the number of constituent units and the consistency of spectral shifts despite large differences in the forms of individual units.

Furthermore, as Fig. 1(b) illustrates, such properties can be highly stereotyped across song repetitions. In this particular example, spectral energy peaks near two frequencies (90 and 180 Hz) alternate throughout the recording. The timing of spectral shifts in these bands is nearly identical for two of the three cycles shown; the remaining cycle appears to contain a time-compressed version of this same spectrotemporal pattern. Such stereotypy suggests that the acoustic properties of at least a subset of sounds within this sequence are being gradually modulated across the entire song cycle. The regularly spaced vertical striations in this spectrogram further indicate that some units were produced at a consistent pace for over an hour. Analyses that focus on identifying structure in sequences of symbolically notated units[5] are incapable of

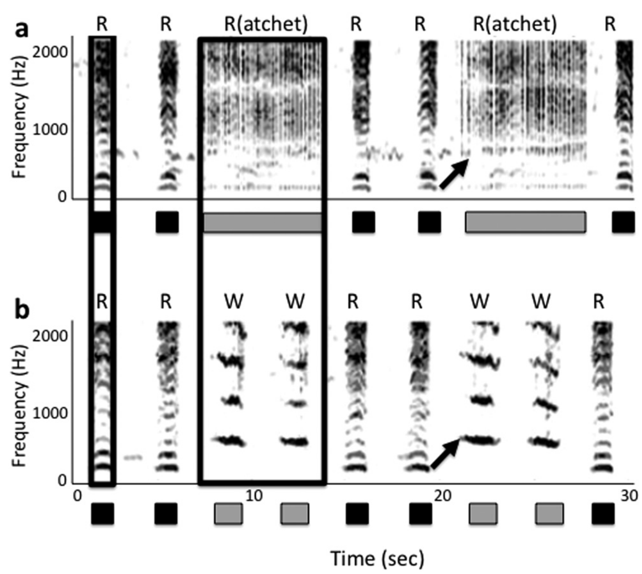

FIG. 2. Spectrogram of repeated patterns produced by a singing humpback. (a) Traditional hierarchical descriptions of phrases focus on identifying patterns of symbolically notated unit types. (b) Sound patterns containing different numbers and types of units may nevertheless share acoustic properties related to the timing and spectral features of units [compare (a) vs (b)]. Vertical rectangles show that relative timing is maintained, and arrows show that relative changes in frequency are stable, despite changes in the constituent units. Such regularities may reflect the constraints of bidirectional sound production. Black squares and gray rectangles denote possible egressive and ingressive units, respectively. Adapted from Ref. 10, Fig. 2.

detecting acoustic regularities in the rhythm, timing, or spectral properties of sound production that may occur independently of the types of units being produced. Such regularities can provide important clues about how humpback whales perceive, produce, and modulate songs.[9,10]

III. MODELING NON-HIERARCHICAL STRUCTURE IN SONGS

The hierarchical framework is a descriptive model of a humpback whale song. This model names salient elements of songs and provides an interpretation of resulting song structure. However, when subjectively salient features are chosen to be consistent with a pre-existing theoretical framework, it becomes difficult to distinguish structure in the sequences from structure imposed by the methods. The hypothesis that humpback whale songs are hierarchically structured has never been empirically tested, and it is not clear how it could be. Moreover, this hypothesis does not explain any of the regularities present within songs, it does not make any novel predictions about how songs should vary within or across individuals, years, or geographic locations, nor does it explain how whales detect and incorporate changes in their evolving songs. Below, we describe an alternative, non-hierarchical model of humpback whale song structure that is explanatory rather than descriptive and that makes testable predictions.

The model assumes that basic physical constraints on sound production lead to acoustic regularities within songs by restricting when certain sounds or sound patterns can be produced. Specifically, two interacting physiological cycles are hypothesized to contribute to the sequential structure observed within humpback whale songs: The dive cycle and internal recirculation of air during sound production. In this framework, the apparent hierarchical structure within humpback whale songs is a consequence of production constraints rather than syntactic rules.

Singing humpback whales often spend long periods ($\sim$10 to 20 min) submerged,[11] intermittently rising to the surface briefly to breathe before diving again. As illustrated in Fig. 1, singers do not stop singing when they surface. Nevertheless, it is sometimes possible to acoustically detect when a singer is surfacing because sounds produced near the surface tend to be quieter due to greater propagation loss. Furthermore, in some seasons certain acoustic features within songs consistently occur when a singer is surfacing.[2,12] The diving cycle associated with breathing can potentially impact song structure in at least three ways. First, changes in the depth of the singer can lead to changes in the volume and pressure of internal air cavities, which can in turn affect sound generation.[13] Second, as the time a singer spends underwater increases, respiratory processes will lead to changes in the proportions of internal gases, which can affect the resonance frequencies of air cavities. Finally, sounds or sound patterns may vary in terms of their energetic demands, such that the number of times each sound pattern is produced may partly determine how long a singer can remain submerged.

Singers make sounds while submerged without producing any bubbles that would indicate air is leaving their bodies. This suggests that humpback whales recirculate air internally as they sing. Singers can potentially produce "egressive" sounds as air flows from the lungs, and "ingressive" sounds as air flows into the lungs. Bidirectional sound production could constrain the structural features of songs in two ways. First, the acoustic qualities of egressive sounds usually differ systematically from those of ingressive sounds.[14] Consequently, bidirectional phonation automatically leads to the cyclical production of contrasting sound types. Production of certain sounds may only be possible during specific phases of the recirculatory cycle. Second, because airflow in one direction precludes airflow in the other, vocal processes associated with airflow in each direction will be interdependent and coordinated, potentially constraining the duration, form, and rhythmic timing of sound patterns.

Together these two cycles of diving and recirculatory sound production can account for several regularities within songs. For example, the recurring shifts in overall song frequency content shown in Fig. 1 may reflect dive-cycle dependent changes in sound production. Specifically, as the ratio of carbon dioxide to oxygen gradually increases within a submerged singer, the frequencies with peak energy should drop. This is because sound velocity in oxygen is higher than in carbon dioxide; as oxygen is depleted, sound velocity will decrease, which will in turn lower the resonant frequencies of gas-filled cavities involved in sound production.[15] Also, when a singer surfaces the change in depth and the influx of oxygen should lead to a rapid shift in spectral energy. Both of these features are evident in Fig. 1(b). Stereotypical ordering of themes may thus partially reflect acoustic regularities caused by the diving cycles of singers. Deviations from typical theme sequences are associated with surfacing,[12] as would be expected if dive cycles directly impact the ordering of sound patterns within songs.

Figure 2 illustrates how recirculatory sound production could lead to repeating patterns within dive cycles. The "RRR(atchet)" pattern can be interpreted as two egressive sounds followed by an ingressive sound (or vice versa). "RRWW" corresponds to the same pattern but with a faster inspiration rate; faster air flow causes slow-repetition-rate pulse trains to transform into tonal sounds by increasing the vibratory rate of sound producing membranes to the point where pulse interval and pulse duration are comparable.[15] Rhythmic repetition of this three or four sound pattern may thus reflect the periodic shunting of air to and from the lungs. The relatively stable timing across such repeating patterns, despite changes in the number and types of units within the patterns, is indicative of physical constraints related to cyclical features of air recirculation. In Fig. 2, the admittedly speculative description of particular sounds as being egressive or ingressive reflects the fact that ingressive sounds often are more variable and contain spectral energy at higher frequencies.[14] Identifying how humpback whales produce different sounds can clarify how internal air recirculation may contribute to both unit and song structure.

These two physiological cycles are interactive because changes in internal and external conditions throughout a dive cycle can potentially impact a singer's ability to effectively control sound production within recirculatory cycles, and the difficulty of producing different acoustic features may impact when a singer will need to surface to breathe. Processes in which two or more physiological cycles interact to dynamically generate structured patterns can be described as *heterarchical*.[16] In heterarchical processes, there is neither a fixed order of precedence that determines sequential structure nor a simple set of rules that predicts how structure within a sequence will change over time.

One advantage of the heterarchical model of song structure described above is that it can be empirically tested. For instance, the model predicts that rhythmic patterns within sound sequences can be directly related to movements of air within a singer's body, and that the qualities of sounds within patterns will be correlated with the direction of internal airflow. Because gases within the lungs are the most acoustically reflective features of a submerged whale, the internal movements of air within a singer can potentially be monitored either remotely, using high-frequency sonar, or cutaneously using ultrasound. The model also predicts that sequential structure should be evident not only in the qualities of sounds but also in the rhythms of sound production[17] and in transitions across sounds.[9] Furthermore, the model predicts that the sequence of acoustic features within songs will be correlated with a singer's depth and surfacing patterns,[12] a prediction that can be tested using data from either tags or critter cams.

Another advantage of this non-hierarchical model is that it explains several properties of song structure that hierarchical descriptions have not. First, information theoretic analyses have identified two periodic cycles within song sessions: One spanning 6 to 8 units; the other spanning 200 to 400 units.[5] The heterarchical model identifies these periodicities as a consequence of the recirculatory cycle and dive cycle, respectively. Second, humpback songs are dynamic along multiple time scales, evolving within individual sessions and across years. The heterarchical model explains the capacity of singers to simultaneously preserve and yet continuously transform these sequences by identifying physiological constraints on sound production. In particular, this model suggests that certain patterns can only be produced at certain times within a dive cycle or recirculatory cycle, and that the modifiability of a sound or pattern depends both on how it is produced and when. In the heterarchical model, shifts in song structure only require minor adjustments to vocal gestures, and changes in song structure across years reflect the same processes that lead to changes across hours. Third, singers often produce sound patterns in highly regular orders.[2] In the heterarchical model, song consistency reflects physiological factors rather than syntactic rules of sequence construction. For example, the consistency of sequences over time is predicted to reflect the consistency of singer depth and surfacing intervals. Finally, as illustrated in Fig. 1, the heterarchical model explains the periodic, gradual modulation of sound frequency content over time as resulting from physiological processes associated with diving and long duration submersion.

Future computational analyses of acoustic regularities within humpback whale sound sequences, as well as experimental studies of how these features correlate with singer's movements, may provide new insights not only into how humpback whale vocalizations are structured, but also into how different sound production mechanisms contribute to their structure. We are not merely proposing that the heterarchical model described above supplements the traditional hierarchical framework by suggesting mechanisms to explain the sequencing of units within songs. Instead, we are proposing that the heterarchical model should supersede the hierarchical framework as the working model for understanding humpback whale song structure. This alternative perspective suggests several new questions that researchers could explore, including: Are some patterns within songs easier for singers to modify than others? Might a singer surface or change depth to modulate the sequence of sound patterns being produced? To what extent are the rhythmic features of songs a consequence of physiological versus functional constraints? Is it possible that the temporal dynamics of songs could reveal the swimming patterns and behavioral strategies of singers? Answering such questions can potentially move us closer to discovering how humpback whales make use of the acoustic structure within songs.

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