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# Regularities in zebra finch song beyond the repeated motif

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ABSTRACT

The proliferation of birdsong research into the neural mechanisms of vocal learning is indebted to the remarkable stereotypy of the zebra finch's song motif. Motifs are composed of several syllables, which birds learn to produce in a fixed order. But at a higher level of organization—*the bout*—zebra finch song is no longer stereotyped. Song bouts include several repetitions of the motif, which are often linked by a variable number of short "connector" vocalizations. In this conceptual methods paper, we show that combinatorial analysis alone yields an incomplete description of this bout-level structure. In contrast, studying birdsong as a time-varying analog signal can reveal patterns of flexibility in the rhythmic organization of song bouts. Visualizing large song-samples in sorted raster plots shows that motifs are strung together via two distinct categories of connections: tight or loose. Loose connections allow considerable timing variation across renditions. Even among co-tutored birds that acquired similar motifs, we observe strong individual variability in rhythms and temporal plasticity of song bouts. These findings suggest that vocal flexibility could potentially allow individuals to express a variety of behavioral states through their songs, even in species that sing only a single stereotyped motif.

## 1. Introduction

Birdsong is among the most thoroughly studied vocal communication systems in non-human animals. However, relatively little is known about how the complex acoustic structure of birdsong might relate to specific social functions (cf. Todt and Naguib, 2000). Zebra finches are a predominant model system for studying vocal learning, due in part to the remarkable stereotypy of their songs. The male zebra finch typically produces renditions of his song 'motif' in bouts that begin with a series of introductory notes, followed by several renditions of the same motif. An individual song motif includes several 'syllables,' each with a distinct acoustic structure. Both the syllable types and their combinatorial order within the motif are highly stereotyped (Immelmann, 1969; Scharff and Nottebohm, 1991). Therefore, after hearing an adult zebra finch producing even a single song bout, one already knows much about his song structure, which remains stable over years. In other words, although a zebra finch often sings a lot (hundreds of motifs every day), his songs are nearly identical; it is as if the bird is always saying the same thing, again and again. To the extent that this picture is true, zebra finch song would seem unlikely to carry much dynamic information—for instance, to express the behavioral state of the bird, or to direct different intentions to other birds. This is puzzling, however, given that zebra finches are highly social, and appear to be communicating vocally much of the time (Elie and Theunissen, 2015).

In fact, we know that the zebra finch song motif is *not* entirely stereotyped, and *does* carry some information about behavioral state, as is observed in female-directed versus undirected singing. When a male zebra finch courts a female, he produces a dance, his motifs are sung slightly faster (Sossinka and Böhner, 1980), and syllable acoustic structure becomes more precise (Kao and Brainard, 2006). Female zebra finches can perceive these differences, and they typically prefer the female-directed version of the song (Woolley and Doupe, 2008). Still, the acoustic differences between female-directed and undirected songs are small, and some of these can be explained by involuntary changes in brain temperature (Aronov and Fee, 2012). In sum, only a restricted degree of plasticity has been found to exist in the mature zebra finch's song motif.

However, zebra finch song can *only* be considered stereotyped at the level of the motif, i.e., in repeating short sequences of syllables. The next level of song organization—the song bout—is not stereotyped: First, the number of motif renditions varies, typically ranging from two to ten motifs per bout. Second, song bouts often vary in the manner in which motifs are strung together. Fig. 1a presents five song bouts produced by one bird. As shown, the motifs are linked via a variable number of short vocalizations (Price, 1979); we call these "connectors." One approach for investigating the structure of song bouts would be to treat the song bout as a sequence of symbols and study its combinatorial structure. For example, the bout segments shown in Fig. 1a can be

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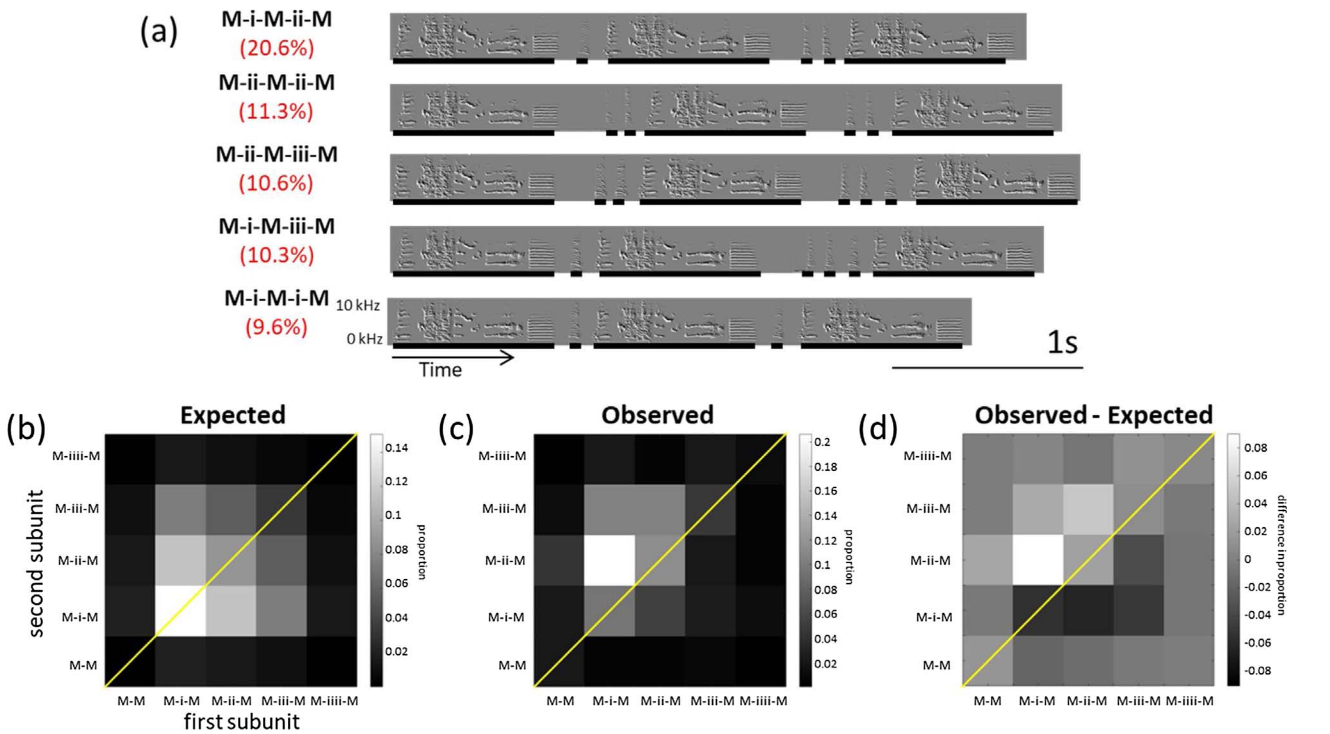


**Fig. 1.** Asymmetries in frequencies of motif connection type sequences. (a) Sonograms (*right*) and symbolic coding (*left*) of common patterns of motifs and connectors ('M' and 'i' respectively, indicated by black bars beneath the sonograms) in the song bouts of one bird. (b and c) Transition matrices of motif-connection types (number of connectors between motifs). Each cell presents the transition frequency for a sequence of two connection types (e.g., M-i-M-ii-M). (b) Bout sequence transitions expected on the basis of connection type frequency. (c) Observed transitions. The frequencies (% total) of the five brightest cells are given in (a). (d) Matrix showing the difference between observed and expected frequencies of bout sequences.

described as sequences of motifs ('M') and connectors ('i'): *M-i-M-ii-M*, etc. With this approach, one can estimate the transition probabilities between motifs and connectors within the bout.

First-order Markov Models have been shown to be useful for describing birdsong structure, although there is some debate about the appropriateness of such models (Kershenbaum et al., 2014). In canaries, for example, a recent study uncovered long-term temporal dependencies between phrases, unexplainable by simple 'bigram' Markov models (Markowitz et al., 2013). An entirely different approach is to investigate the song bout as an analog time-varying signal, focusing not on 'syntax' but on temporal regularities such as rhythms. Here, we compare the two approaches, considering transition probabilities between discrete types side by side with the continuous time structure of song bouts.

One may wonder whether it is even appropriate to treat the combinatorial (symbolic) and time-varying (analog) structure of birdsong as distinct levels of song organization. In linguistics, combinatorial structure (e.g., grammar, based on symbolic units) and temporal regularities (e.g., prosody, measured from the acoustic speech signal) are studied by different scientific communities, as they represent plausibly distinct features of language. In birdsong, however, we do not know if, or to what extent, song syntax and rhythms are independent levels of organization (Mol et al., in press). If these two levels are coupled, as our preliminary findings will suggest, then variability in song sequences could mirror adjustments of rhythms, serving, for example, to coordinate singing behaviors across individual birds. More generally, it might be essential to combine sequential analysis with investigation of temporal regularities in order to understand the communicative function of the song bout. In this conceptual paper we present methods for exploring zebra finch song bout structure, and preliminary findings that raise hypotheses for future research.

## 2. Methods and results

### 2.1. Animals

Birds in this study were adults, between 134 and 271 days post-hatch (dph). All experiments were approved by the Hunter College Institutional Animal Care and Use Committee.

### 2.2. Analysis of bout syntax

In order to first estimate the combinatorial structure of song bouts, we examined the transitions between song motifs within bouts. Fig. 1 presents such transitions in 289 song bouts produced by one adult zebra finch (270 dph) over the course of a day. In this bird's repertoire, motifs ('M') were in some cases linked directly to each other (*M-M*), but more often, motifs were strung together via short connector notes ('i'). Example sequences of motifs and connectors are shown in Fig. 1a. We categorize motif connections into distinct types based on the number of connectors: *M-M*, *M-i-M*, *M-ii-M*, etc. We then analyze sequences of connection types within a song bout. For example, at the pairwise (bigram) level, the sequence *M-i-M-ii-M* can be regarded as a transition from the *M-i-M* type to the *M-ii-M* type. Fig. 1b and c presents the expected and observed frequencies of pairwise transitions between connection types (within three-motif sequences). We see two effects: first, the frequencies of pairwise transitions between bout subunits showed a different distribution than expected from the frequency of connection types (Fig. 1d, $\chi^2$ (36, n = 407) = 209.62, $p < 0.001$). That is, there was an apparent rule-governed or 'syntactic' regularity in the transitions. Second, the pairwise transitions showed strong asymmetry: *M-i-M*, the most common subunit, was often followed by *M-ii-M* (*M-i-M-ii-M* frequency, 20.6%). However, the opposite transition, from *M-ii-M to* M-*i-M,* was rare (5.2%). This order-dependent asymmetry in the frequencies of transitions between shorter and longer connection-type subunits was stable across days and was statistically significant for this

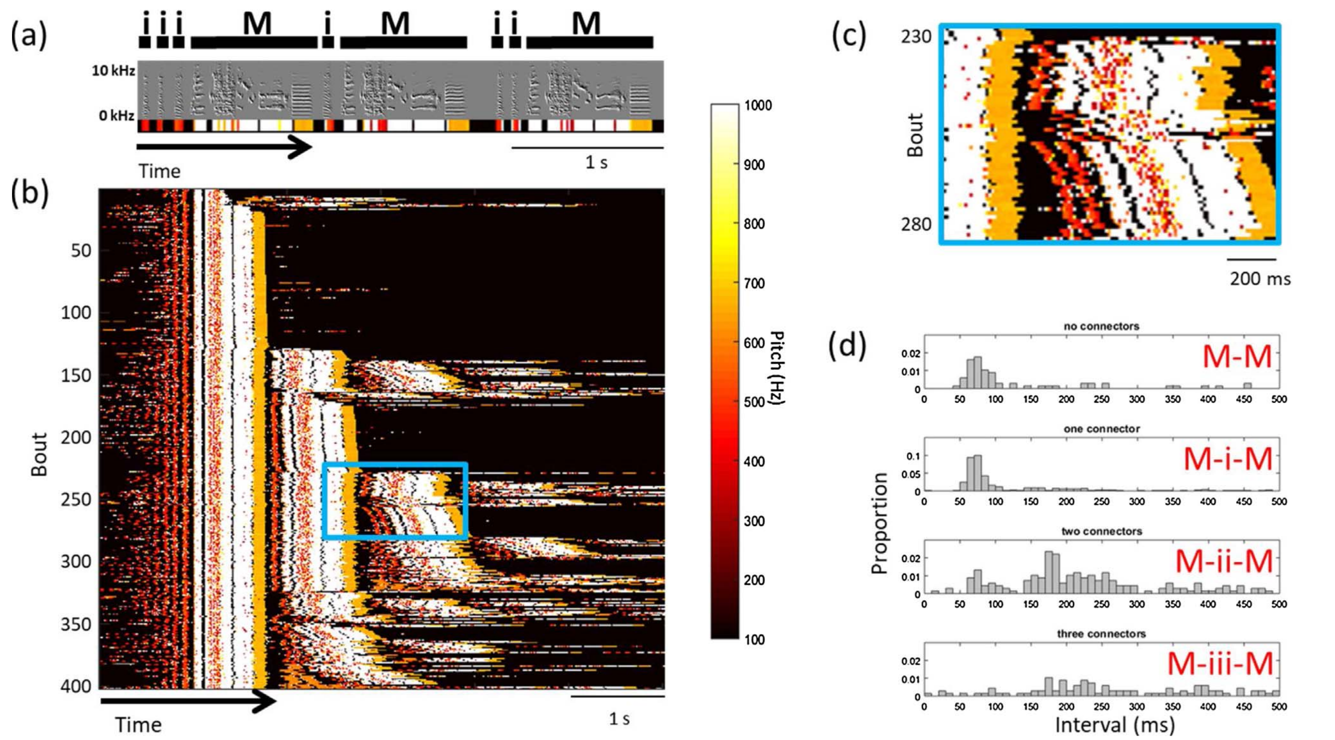


**Fig. 2.** Timing plasticity in song bouts. (a) Three representations of a song bout (same bird as in Fig. 1): *top*, symbolic string of motifs ('M') and connectors ('i'); *middle*, sonogram; *bottom*, millisecond-resolution pitch vector such as used to construct raster plots of large song samples. The color scheme used to represent 100–1000 Hz pitch values in (a–c) is indicated by the color bar. (b) Sorted raster plot of all the songs produced by this bird over two days, showing one bout per row. Bouts are aligned to the beginning of the first motif and sorted to reveal connection type and temporal jitter within motif/connector sequences. (c) Closer view of the area in (b) (blue box) showing greater relative plasticity when motifs were joined by two vs. one connector. (d) Histograms of the intervals separating motifs and subsequent song elements. Intervals in cases where motifs were linked by zero, one, two, or three connectors are shown in separate panels, with the y-axis indicating relative frequency with respect to all the motif transitions in the bird's repertoire. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bird ($\chi^2$ (20, n = 290) = 144.20, p < 0.001).

### 2.3. Temporal regularities beyond bout syntax

Why were song motifs of this one bird often linked together via a single connector and then two connectors, but rarely the other way around? Analysis at the level of the time course of the song bout provides additional information. Fig. 2 shows raster plots of the song bouts in this bird's full repertoire (as recorded on days 270 & 271 post-hatch), sorted by bout type and duration. A conservative 300-millisecond silence criterion was used to segment bouts (Okubo et al., 2015; Norton and Scharff, 2016). Pseudo-colors in Fig. 2a–c represent millisecond-resolution pitch changes within different syllables. Motifs appear as white and orange bands in the raster; connectors were lower in pitch, and stand out as red strips between motifs. As can be seen, when two motifs were joined via a single connector, the connection was very tight. However, when motifs were linked together by two connectors, the distribution of gaps was much more variable across renditions (Fig. 2c). Fig. 2d presents histograms of time intervals between the end of the previous motif and the onset of the first connector (or first motif element in cases where no connectors were present). As shown, for both *M-M* and *M-i-M* subunits, gaps were short and their distributions were narrow (Fig. 2d, *top two panels*). In contrast, when motifs were linked via two or three connectors (*M-ii-M*, *M-iii-M*), the time interval between the motif end and the next song element was much more variable (Fig. 2d, *bottom two panels*). We therefore call the single connector 'tight' and the double and triple connectors 'loose.' These categories of tight and loose connectors could suggest that zebra finches are capable of adjusting the time structure of their song bouts in an adaptive manner. Exhaustion, however, could also explain the asymmetries we observed in bout syntax. Indeed, in this bird's songs, once a bout became loose, it was unlikely to become tight again.

### 2.4. Diversity in bout structure repertoires across birds

We observed different patterns of tight and loose connectors across birds. Fig. 3 presents sorted raster plots of bout repertoires from eight additional birds that were raised together with a single tutor (as in Tchernichovski and Nottebohm, 1998). At the end of song development (134–145 dph), these birds had acquired fairly similar song motifs, but they varied considerably in how motifs were strung together. Comparing bout repertoires across birds (Fig. 3, different panels), raster plots appear 'step-like' in some birds (e.g., in bird p5) and gradated in others (e.g. in bird p2). At the combinatorial level of motif transitions, some birds (p5, p4, p1) produced primarily single connectors (*M-i-M*), others (p7, p2, p9) primarily two connectors (*M-ii-M*), and a third group produced both.

Single connectors were tight in all birds that produced them. In contrast, motifs strung together with two connectors tended to be loose – but to a variable extent across birds. For example, p7 and p9 both used two connectors exclusively, but for p7 motif connections were invariably tight (visible in the vertical columns in the raster), whereas p9 produced two acoustically-distinct types of double connectors, one loose and the other tight (with the first of the two connectors in the tight variant marked by a pitch down-sweep, Fig. 3).

Connectors were often acoustically distinct from introductory notes (which are used to introduce song bouts). Further, in several birds, the acoustic (spectral) structure of connectors varied across bout types. We therefore distinguish between connector type *(spectral)*, and connection type (the number of connectors between motifs). Pitch differences among connectors can be seen for example within the bouts of birds p9 and p6 (Fig. 3). Indeed, most birds possessed multiple acoustically-distinct connector types (Fig. 4, red clusters). In these eight birds, 13 out of 24 total connector types formed clusters that did not overlap with those of introductory notes (shown in blue, Fig. 4), and likewise 10 of

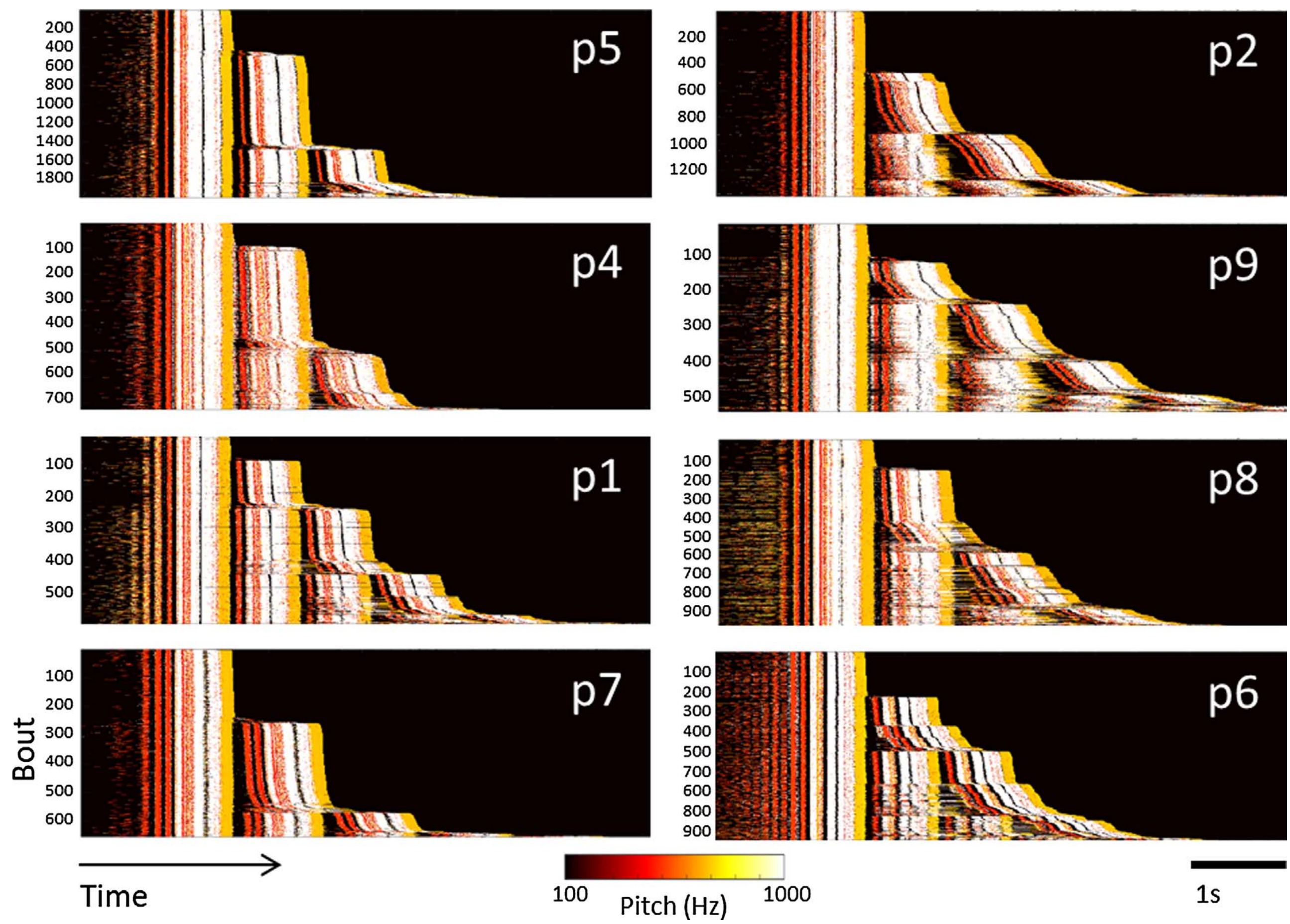


**Fig. 3.** Variability in bout repertoire across birds is associated with motif connection type. Individual panels present sorted bout raster plots showing all songs produced in a single day by eight different birds (ages 134–145 dph) that were raised together with the same tutor. Bouts are aligned to the onset of the first motif, and colors indicate pitch. Bird identity is included in the upper right corner of each panel. Birds on the left (p5, p4, p1, and p7) exhibited little variability in the timing of their motifs, as seen in the vertical columns in the raster plots, whereas birds on the right showed greater variability. (For interpretation of the references to colour in the text, the reader is referred to the web version of this article.)

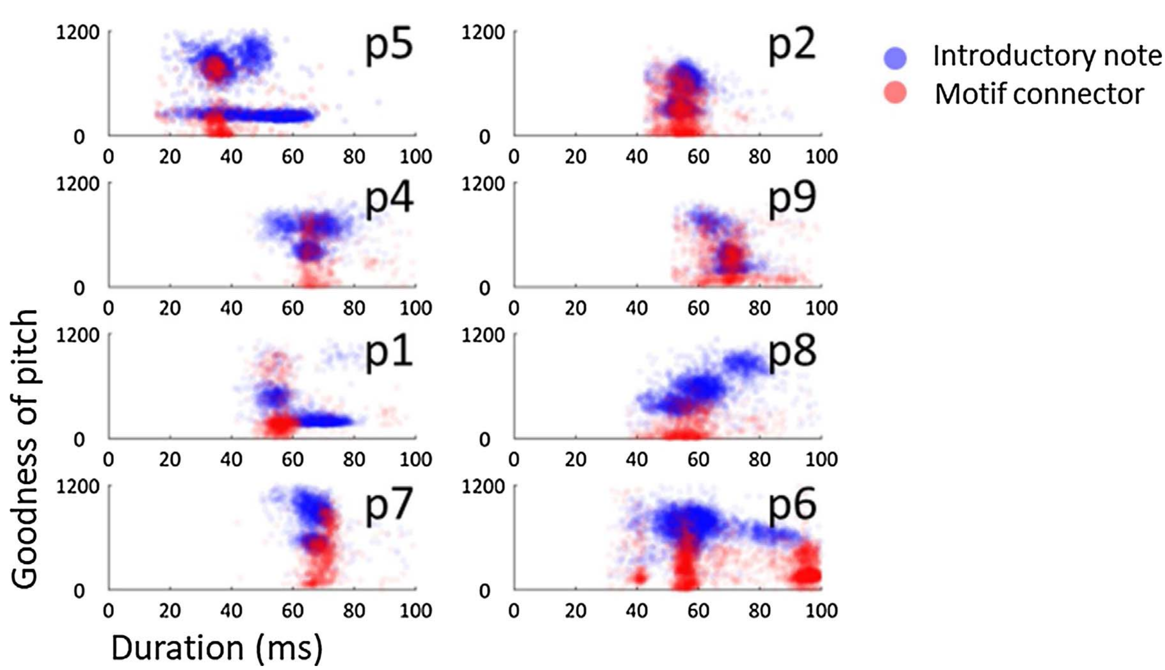


**Fig. 4.** Structural differences between motif connectors and introductory notes. Individual panels present scatter plots showing duration vs. goodness of pitch (an estimate of harmonic pitch periodicity (Tchernichovski et al., 2000) for both introductory notes and connectors, for each of the birds shown in Fig. 3. The opacity for all scatter plot data points is set at 5% to indicate density. Individual panels are labeled by bird identity, follow the same order as Fig. 3. (For interpretation of the references to colour in the text, the reader is referred to the web version of this article.)

22 introductory note types were unique to the starts of bouts.

In sum, we see that, within a bird, song bouts may vary not only in their durations, but also in their fine time structure. One component of this variability is that bout vocabulary often consists of more than one type of motif connection (due to varying numbers of connectors and/or variable connector types). The second component of the variability is the temporal jitter in the timing of the connectors themselves. As a result, song bout repertoires vary strongly across birds and some birds sing with less predictability than others. To the extent to which this variability is under voluntary control, possessing a variety of options for constructing song bouts could allow a bird to adapt his singing behavior based on context or feedback from a social partner. While it is beyond the scope of this study to explicitly test if loose (or tight) motif connections serve a social function, using an example will outline methods for exploring song bout plasticity in social scenarios.

### 2.5. Evidence for song plasticity during singing interactions

We selected one bird with rigid song bouts and another bird with high temporal variability (p5 and p6 from the group shown in Fig. 3). We placed them together for several days and monitored their singing interactions. Fig. 5 presents a snapshot of the pair's singing interactions during two consecutive days. These birds, which had shared a tutor, possessed similar motifs but dissimilar bout structure repertoires. Bird p5′s singing style consisted of stereotyped bouts of 1–3 motifs, predominantly separated by a single connector with only tight connections between motifs (left raster plot and motif/connector histogram, Fig. 5a). Bird p6, by contrast, produced song bouts with greater temporal variability and including both tight and loose motif connections (Fig. 5a, *right*). Both birds sang a lot (p5: 3928 motifs in two days, p6: 2790 motifs) but relatively rarely ( ~ 11% of all bouts) at the same time. When their songs did overlap, however, there was a clear asymmetry in the tendencies of the two birds to co-sing (see examples in Fig. 5b).

Fig. 5c shows a raster view of all the overlapping songs. For each bird, we sorted the bouts anchored to the onset of the partner's bouts (Fig. 5c, left and right panels respectively). As indicated by the horizontal black demarcation lines, bird p5, who performed exclusively tight motif connections (blue), tended to initiate singing, while bird p6, who performed both tight and loose motif connection (red), tended to join in. Note that the slope of the raster (marked 1, 2 & 3 in Fig. 5c, *left*) represents the likelihood of joining. We can see that p6's singing likelihood increased steeply with the bout onset of p5 and declined rapidly after the end of p5's first motif. This indicates that p6 tended to join (co-sing) during p5's first motif. Irregularities in the timing of p6's subsequent motifs (Fig. 5c, *left*) also suggest preferred bout patterns, perhaps related to the predictable time structure in the songs of p5 (Fig. 5c, *right*). Specifically, during the tightest co-singing episodes (section #2 in Fig. 5c, *left*), we can see that many of p6's second motifs within a bout begin near the offset of p5's second motif, or the onset of p5's third motif; the variation in gap duration visible between p6's first and second motifs is due to the use of variable connection types. These motif latency dynamics were observed on each of the two days (Fig. 5d), and histograms of relative bout onsets (Fig. 5e) clearly distinguish p6, whose songs were more plastic, as the 'answering bird' (positive latency) relative to p5 (negative latency). Given that this pair of birds developed their songs together, it is an intriguing question whether the establishment of bout structure repertoires might be related to patterns of social interaction.

## 3. Discussion

The song bout is the first timescale at which zebra finch song is not stereotyped, making it a logical place to investigate potential communicational aspects of singing behavior. Here, we have taken an early step toward characterizing the variability that exists in the structure and timing of zebra finch song performances.

Behaviorally, we have long known from Price (1979) and others that the song bout is an important level of song organization. For example, the courtship dance is organized at the level of the song bout (Williams, 2001; Ullrich et al., 2016). Studies of the neuronal coding of birdsong, however, have focused mostly on the hierarchical coding of syllable timing and acoustic structure in the premotor nuclei HVC and RA (e.g., Yu and Margoliash, 1996; Hahnloser et al., 2002). Still, there is some evidence for bout-level neural coding in the premotor song system. Williams and Vicario (1993) observed "superbursting" upstream of HVC in the thalamic nucleus Uva at the termination of song bouts. Chi and Margoliash (2001) reported changes in intra-syllable RA burst intervals as a function of motif position within the bout. And recently, Okubo et al. (2015) found a subset of HVC projection neurons that are active exclusively at bout onsets. How does the songbird brain gate which bout variant is produced from a repertoire of possible types, and what determines the timing of motifs (tight vs. loose connections)?

Rajan and Doupe (2013) showed that song-system neurons (including HVC interneurons and Area X projections) encode the serial position of introductory notes, which accelerate and converge on a stereotyped acoustic state, signaling readiness to begin singing. They also found that the number of introductory notes is correlated with the time elapsed since the end of the previous song motif, when considering intervals up to one second—i.e., including what we here refer to here as "connectors." Mechanistically, how does initiating a song bout differ from initiating a motif within a bout? Given our finding that motif connectors are often acoustically distinct from introductory notes, it could make sense to repeat the study by Rajan and Doupe (2013), distinguishing between different introductory note and connector types. Perhaps the acoustic differences we observed could be explained by the brain's varying "readiness" to produce sequences of stereotyped learned vocalizations (motifs) as a function of whether the bird is already in a singing "state."

We hope that future studies will soon reveal which brain areas regulate song bout plasticity. Sossinka and Böhner (1980) first dichotomized female-directed and undirected song on behavioral grounds, showing that the courtship context was associated with more introductory notes, shorter motif duration, more motifs per bout, and greater sequential stereotypy. The observed context-dependent shifts in these song features were interpreted to reflect the importance of joint stimulus- and motivational control in "releasing" singing behavior of variable intensity. This phenomenon has since been substantiated across multiple mechanistic levels (Walters et al., 1991; Hessler and Doupe, 1999; Jarvis et al., 1998). Kao and Brainard (2006) further demonstrated that anterior forebrain pathway (AFP) lesions abolish syllable-level acoustic feature variability found to accompany undirected song, although there was no effect found on the bout structure differences in the two types of song. It may be that temporal jitter in motif connections is also mediated by the AFP, while choice of bout 'vocabulary' (i.e., connector type) is controlled elsewhere. Zebra finches sometimes acquire multiple motif variants by adding or deleting song syllables (Sturdy et al., 1999; rare examples of truncated motifs are visible in Fig. 2b and c above); how motif variants contribute to bout structure variability and whether their expression is related to behavioral state is an additional topic for future investigation.

At the functional level, an in-depth characterization of singing behavior in social context, including tracking the production of tight and loose motif connections, is needed in order to explore the possible role of bout structure and plasticity in expressing behavioral state and coordinating behaviors. In many passerine species, song serves at least two social functions: courtship display, and male-male territorial defense (Kroodsma, 2005). However, there is no evidence for territorial singing in zebra finches (Zann, 1996). Although attacks and fighting are not unusual in captive settings, singing behavior does not appear to be associated with agonistic interactions in the lab or in the wild (Evans, 1970; Caryl, 1975; Immelmann, 1969). The primary biological function of the zebra finch's song is thought to be sexual, playing an important

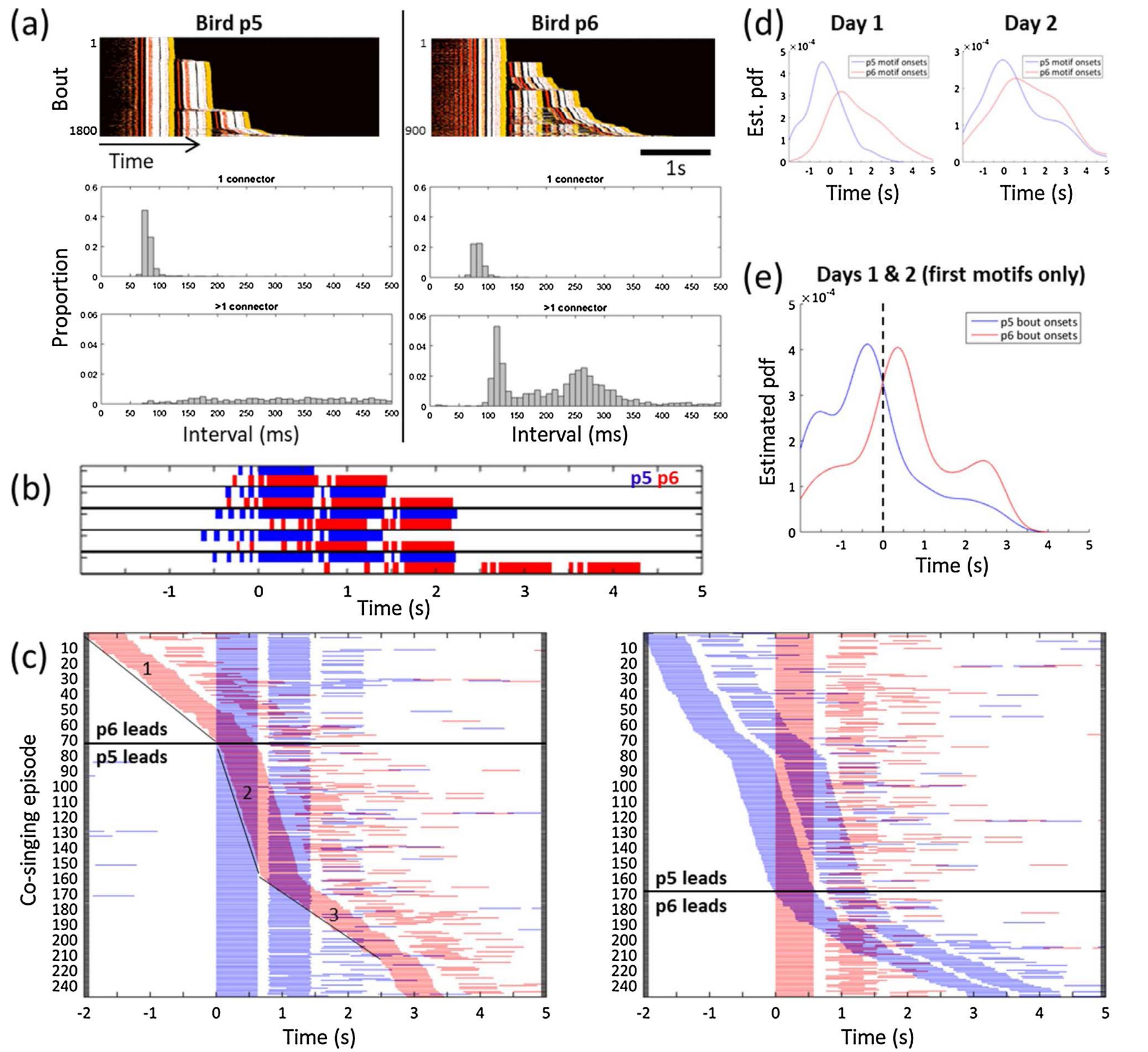


**Fig. 5.** Song flexibility at the bout structure level during singing interactions. (a) Solo song bout raster plots (*top*) and motif/connector interval histograms (*bottom*; see Fig. 2d) for p5 (*left*) and p6 (*right*), two birds raised in the same social group (Fig. 3). Intervals between motif offsets and subsequent connector onsets are plotted separately for motifs linked by a single vs. more than one connector (*M-i-M* vs. *M-ii-M*, *M-iii-M*, etc.). (b–d) Co-singing data for birds p5 (blue) and p6 (red). (b) Symbolic raster plot of five co-singing examples showing alignment of introductory notes, motifs and connectors. (c) Symbolic raster plots (motifs only) of all overlapping songs occurring over the course of two consecutive days, with the data sorted by the bout onset lag of either p6 (*left*) or p5 (*right*; same data). Horizontal black lines in both panels demarcate bouts initiated by one bird versus the other. Slopes of the numbered sections of the left raster are as follows: 1) −0.11, 2) −0.39, and 3) −0.09, indicating that the probability of p6 to join in was greatest during the first motif of p5. (d) Probability density estimates of each bird's motif onsets relative to the start of the partner's bout, plotted separately for the two days pooled together in (c). (e) Probability density estimates of the relative timing of each bird's bout onsets across both days. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

role in both courtship and pair-bond maintenance (zebra finches pair for life (Zann, 1996)). Somewhat mysteriously, then, wild male zebra finches spend proportionally more time singing when no females are present (Dunn and Zann, 1996). This "undirected" song is by no means all solitary, and singing in the presence of other males was once speculated to facilitate flock cohesion (Immelmann, 1968, 1969; Hall, 1962; Sossinka and Böhner, 1980; Tokarev et al., 2017). While Immelmann reported male zebra finches "singing in duos and trios" as early as 1968, we know of only one paper since then that mentioned male-male co-singing (Anisimov et al., 2014). The tight and loose song motif connections we observed could be involved in regulating such social functions.

In order to assess the potential for communication via bout structure variability, it will be important to test the influence of social partner behavior on the fine temporal structure of song bouts. Heinig et al. (2014) found that male Bengalese finch song syntax varied in the presence of different females. Might the analog methods we propose reveal a similar capacity for performance adaptation in the zebra finch on the level of timing? New wireless recording technology that enables source separation of the vocalizations of individual birds in social groups (Ter Maat et al., 2014; Anisimov et al., 2014) should be used in future systematic study of song plasticity. Such technology could also be used to probe whether bout structure is meaningful to the listener, for example by monitoring the timing of female calls during a potential male's song over the course of pair bonding. Another interesting angle would be to investigate the influence of the tutor's bout structure on song learning in the developing juvenile, given prior evidence that pupils copy "chunks" of syllables corresponding to occasional production breaks in the tutor's song (Williams and Staples, 1992).

At this point, we do not know if any of the bout structure features reported here are learned. What is the origin of bout structure diversity? Here we showed that birds that learned the same song together as a group can nevertheless develop divergent bout structure repertoires. We also showed preliminary evidence that relative bout plasticity is associated with individual differences in singing behavior during social interactions. What developmental processes generate such diversity and what is the time course of the emergence of bout-level structure in zebra finch song? Here we presented only snapshots of adult song repertoires; we do not know how age or experience may affect singing behavior in adulthood. Might learning *how* to sing be separate from learning *what* to sing? To investigate this possibility, it will be necessary to study song bout development longitudinally both during and beyond the sensitive period for song learning.

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