

Control of Sequencing and Timing in Birdsong

Andrew Matheson

Supervisor: Dr. Jon Sakata

Behaviours consist of action sequences that are timed and coordinated very precisely. Coordinating the motor elements of a behaviour is vital for its correct production. Arguably, one of the most complex behaviours that animals engage in is vocal communication. The sequence in which vocalizations are produced is important for relaying the correct message and the timing of vocal elements can also impact how the information is received. Songbirds have emerged as an excellent model system for studying sequential vocal motor behaviours. Songbirds use their song when they interact with conspecifics and the temporal structure of their song is altered by social context and environment^{1,2,3,4}. Precisely sequenced and timed acoustic elements, known as syllables, make up the song of a songbird (Fig. 1A)^{2,5}. There are specialized circuits in the songbird brain that control the moment-by-moment production of song^{6,7,8}. These circuits are thought to be analogous to those controlling human speech and by analyzing the relationship between sequencing and timing in birdsong we can provide insight into mechanisms underlying speech and motor control⁹. The timing of motor actions and the sequencing of motor actions have previously been examined independently, but little is known about the degree to which motor sequencing and timing are related^{10,11,12,13}.

In this study we examined a day's worth of recorded songs of adult male Bengalese finches to assess the relationship between syllable sequencing and timing. Bengalese finches are an excellent species to examine this relationship in because they exhibit complex temporal organization of their song (Fig. 1A)^{14,15,16,17,18}. The songs of Bengalese finches are composed of syllables that are arranged in stereotyped sequences with variable sequencing across renditions of the song. When more than one transition is possible a given point in song, we refer to the stereotyped sequence leading up to the node of variability as a branch point (Fig. 1B)^{15,19,20}. The frequency at which a variable transitions were produced over the day dictated the transition probabilities for a given branch point. First we examined the relationship between transition probabilities and inter-syllable gaps, which are responsible for the changes in song timing^{16,21}. Once this was established we assessed how this relationship was sculpted or constrained by changes to sequencing and timing. We examined birds at two ages and two social contexts. The finches were housed alone and their song was recorded when they were young adults and older adults. When a female is placed with a male, the male produces a much less variable and faster song than when he sings alone¹. This female directed (FD) song is much like a performance while his undirected (UD) song is more like practice⁴. We analyzed the degree that long-term age-dependent and acute social context-dependent changes to syllable sequencing were related to the magnitude of age and context-dependent changes to inter syllable gap durations.

We assigned labels to song syllables in all conditions based on their acoustic features. Following amplitude based segmentation we measured gap durations from the offset of the branch point syllable to the onset of the subsequent syllable. As UD and FD song were collected on the same day the recording conditions between contexts did not differ. However, there could be changes in recording conditions between young adult and older adult time points. We designed an algorithm to extract the waveform on each rendition of a transition and compute the median envelope such that the downstream syllable in the branch point had the same peak

amplitude across conditions. A common threshold was used to compare gap durations for these normalized traces.

Using a mixed effect model with we found a significant negative correlation between transition probability and gap duration that was previously observed (Fig. 1C)²². Next we sought to determine if the age dependent changes in transition probabilities were systematically related to the age dependent changes in gap durations. Using a mixed effects model we found a significant negative relationship between the change in transition probabilities at branch points that occur with age, and the change in inter-syllable gap durations (Fig. 1D). This indicates that transitions which over time have increased probabilities demonstrate relatively larger decreases in gap duration than those transitions in which the probability decreases over time.

To date context dependent changes to timing have only been examined in stereotyped sequences. In both UD and FD song there was an inverse relationship between gap durations and transition probabilities. However, there was little evidence to indicate the magnitude of the context dependent changes in transition probabilities were related to the context dependent changes in gap durations (Fig. 1E). Although there is a decrease of gap durations in FD song that is independent of changes to transition probabilities.

This work lends insight to many models of song production in the songbird brain. It has been proposed that transition probabilities could be related to synaptic weights between populations of neurons that encode syllables²³. The difference in strength between two syllable populations could be realized as a difference in latency to produce the downstream syllable, and this is consistent with the inverse relationship we observe. The relationship between age dependent changes to transition probabilities and gap durations suggests that plasticity in sequencing is linked to plasticity in timing. The lack of relationship between context dependent changes to sequencing and timing suggests that acute control of syllable sequencing and timing is independent.

In summary, the relationship between sequencing and timing is complex, but it is clear the neuronal control of the two properties are intimately related. Further work is required to fully elucidate the neural mechanisms underlying sequence variability in vocal production, the precise timing of these elements, and how or if these properties are learned. Additional analyses could provide insight into speech and motor control properties and disorders.

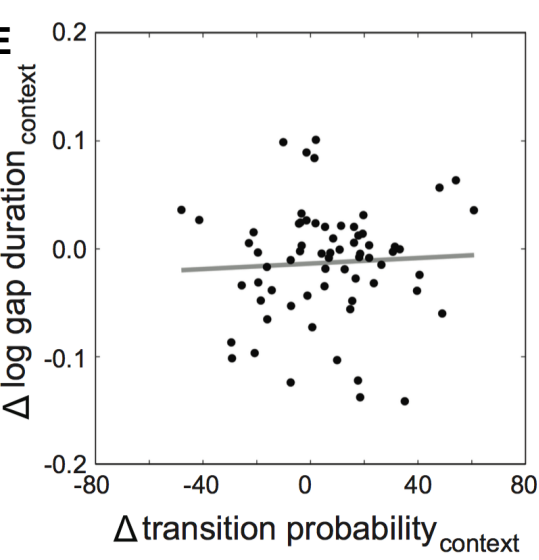
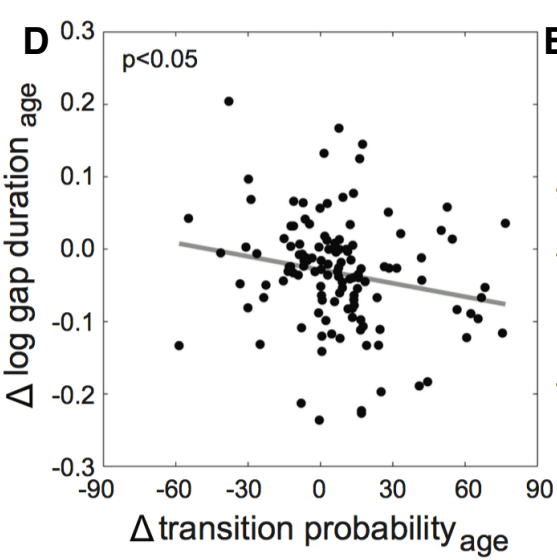
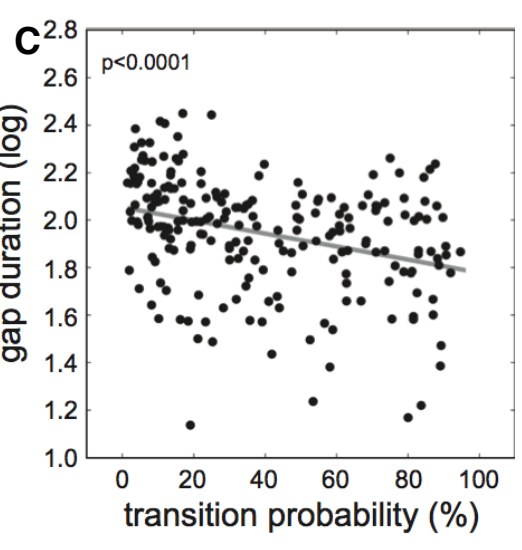
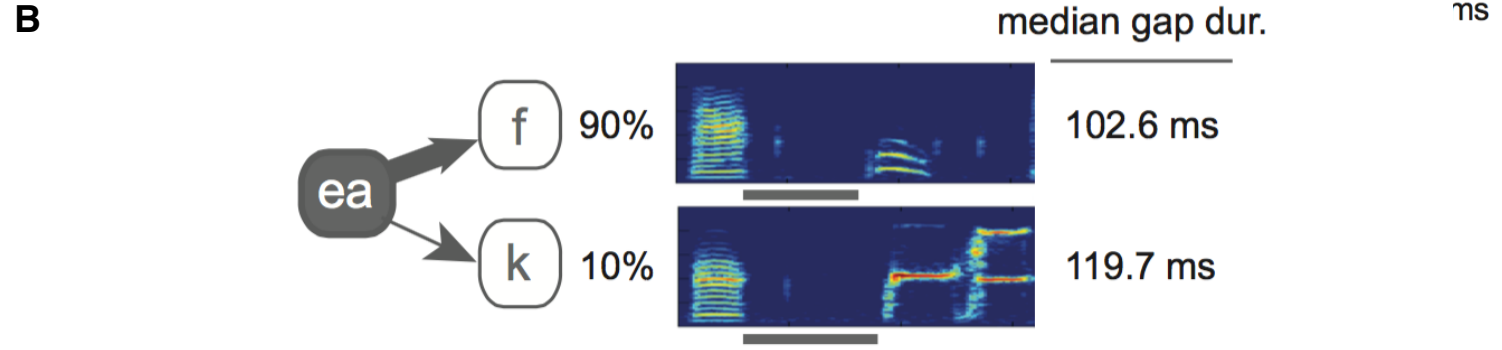
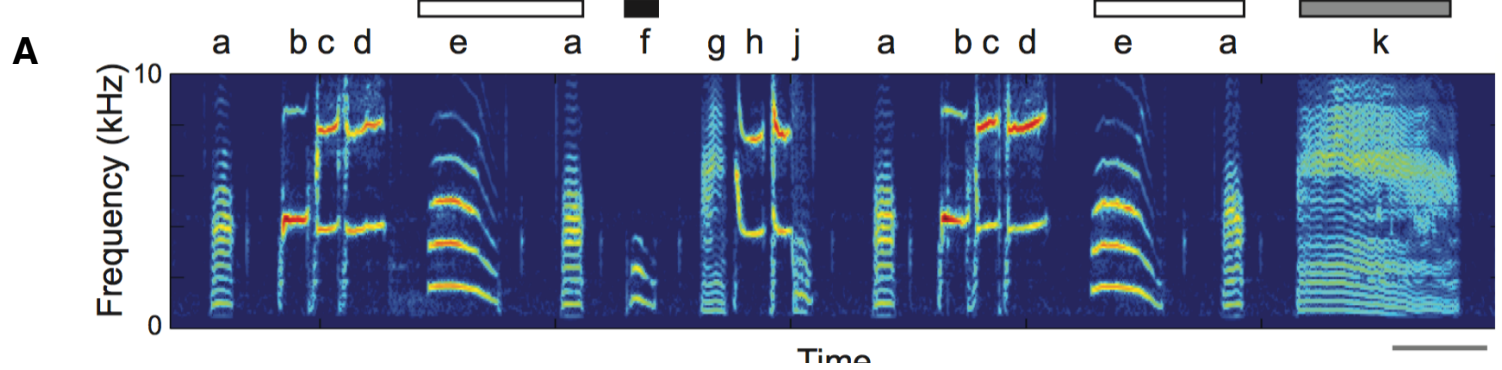


Figure 1: Plasticity and Control of Birdsong. (A) Spectrogram: a plot of frequency (y-axis) vs time (x-axis) where colour represents intensity. Depicts the acoustic elements in one young adult male Bengalese finch song where syllable labels, used for offline analysis, have been placed above to identify individual acoustic elements. The sequences 'bcd' and 'ghj' are stereotyped sequences. White bars indicate the branch point 'ea'. (B) Transitions: 'ea' is a branch point because transitions vary between 'the f' syllable 90% of the time and the 'k' syllable 10% of the time. Median gap durations vary for different transitions. (C) Sequence Tempo Relationships: Young adult transition probabilities for branchpoints vs gap durations (significant by mixed effect model), gap durations are shorter for higher probability transitions. (D) Age Changes: Age-dependent changes to transition probability are related to age-dependent changes in gap durations (significant by mixed effect model). Transitions where probability increased showed decreases in gap durations. (E) Context Changes: Context-dependent changes in transition probability were not related to context-dependent changes in gap durations (not significant by mixed effect model).

References:

1. **Sakata JT, Hampton CM, Brainard MS.** Social modulation of sequence and syllable variability in adult birdsong. *J Neurophysiol* 99: 1700–1711, 2008.
2. **Catchpole C, Slater PJB.** Birdsong: biological themes and variations. Cambridge, *Cambridge University Press*, 2008.
3. **Podos J, Lahti DC, Moseley DL.** Vocal performance and sensorimotor learning in songbirds. *Adv Study Behav* 40: 159–195, 2009.
4. **Sakata JT, Vehrencamp SL.** Integrating perspectives on vocal performance and consistency. *J Exp Biol* 215: 201–209, 2012.
5. **Doupe AJ, Kuhl PK.** Birdsong and human speech: common themes and mechanisms. *Annu Rev Neurosci* 22: 567–631, 1999.
6. **Mooney R.** Neural mechanisms for learned birdsong. *Learn Mem* 16: 655–669, 2009.
7. **Fee MS, Kozhevnikov AA, Hahnloser RH.** Neural mechanisms of vocal sequence generation in the songbird. *Ann NY Acad Sci* 1016: 153–170, 2004
8. **Brainard MS, Doupe AJ.** Translating birdsong: songbirds as a model for basic and applied medical research. *Annu Rev Neurosci* 36: 489–517, 2013.
9. **Hickok G, Poeppel D.** The cortical organization of speech processing. *Nat Rev Neurosci* 8: 393–402, 2007.
10. **Doya K.** Complementary roles of basal ganglia and cerebellum in learning and motor control. *Curt Opin Neurobiol* 10: 732–739, 2000.
11. **Houde JF, Jordan MI.** Sensorimotor adaptation in speech production. *Science* 279: 1213–1216, 1998.
12. **Shadmehr R, Krakauer JW.** A computational neuroanatomy for motor control. *Exp Brain Res* 185: 359–381, 2008.
13. **Wolpert DM, Doya K, Kawato M.** A unifying computational framework for motor control and social interaction. *Phil Trans R Soc Lond B* 358: 593–602, 2003.
14. **Okanoya K, Yamaguchi A.** Adult Bengalese finches (*Lonchura striata* var. *domestica*) require real time auditory feedback to produce normal song syntax. *J Neurobiol* 33: 343–356, 1997.
15. **Sakata JT, Brainard MS.** Real-time contributions of auditory feedback to avian vocal motor control. *J Neurosci* 26: 9619–9628, 2006.
16. **James LS, Sakata JT.** Vocal motor changes beyond the sensitive period for song plasticity. *J Neurophysiol* 112: 2040–2052, 2014.
17. **Heinig A, Pant S, Dunning J, Bass A, Coburn Z, Prather JF.** Male mate preference in mutual mate choice: finches modulate their songs across and within male-female interactions. *Animal Behaviour* 97: 1–12, 2014.
18. **Matheson LE, Sakata JT.** Catecholaminergic contributions to vocal communication signals. *Eur J Neurosci* 41: 1180–1194, 2015.
19. **Jin DZ.** Generating variable birdsong syllable sequences with branching chain networks in avian premotor nucleus HVC. *Phys Rev E Stat Nonlin Soft Matter Phys* 80: 051902, 2009.
20. **Warren TL, Charlesworth JD, Tumer EC, Brainard MS.** Variable sequencing is actively maintained in a well learned motor skill. *J Neurosci* 32: 15414–15425, 2012
21. **Glaze CM, Troyer TW.** Development of temporal structure in zebra finch song. *J Neurophysiol* 109: 1025–1035, 2013.
22. **Takahasi M, Yamada H, Okanoya K.** Statistical and prosodic cues for song segmentation learning by bengalese finches (*Lonchura striata* var. *domestica*). *Ethology* 116: 481–489, 2010.
23. **Jin DZ.** The Neural basis of birdsong syntax. In: Progress in cognitive science: from cellular mechanisms to computational theories, edited by Lu ZL, Luo Y. *Peking University Press*, 2013.