EVOLUTION OF VOCAL COMPLEXITY: A PEAK-SHIFT AND EPIGENETICS ACCOUNT

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Peak-shift is a phenomenon in which perceptual preference moves exceeding the original preference. Peak-shift occurs in two steps. First, the animal learns discrimination between two stimuli differing in one dimension. Next, when exposed with multiple stimuli including even exaggerated trait, the animal would prefer that over the original. Here we used two experiments that showed peak shift of preference for song complexity did occur in female birds and the trait to express song complexity might be inherited in male birds through epigenetic and genetic modifications. First, we trained female Bengalese finches to discriminate among different songs that differ number of trill repetitions. After training, birds preferred stimuli with longer repetitions than the original. Second, we measured the degree of methylation in one of the song control nuclei in male finches. Methylation was negatively correlated with a measure of song complexity. Together, given a set of genes that controls epigenetics of androgen receptor methylation in males, peak-shift to prefer complex songs in females would advance evolution of song complexity.

1. Introduction

Evolution of signal complexity requires two sets of account. First, the receiver animal develops preference for more complex trait than the sender animal was generally given. Second, the sender develops a tendency to enable to learn more complex signals, and this tendency should be inherited by some means.

Bengalese finches are domesticated strain of the white-rumped munia that was imported from China to Japan about 260 years ago. The bird was used as fostering parents for other species of birds because they had stronger parental behavior. Although there is no record on the selection of song complexity, domesticated Bengalese finches sing phonologically and sequentially complex songs than wild white-rumped munias (Okanoya, 2004).

One of the complexities is the number of trills in the song. Bengalese finch songs include more occurrences of repeated signals than the munias, and when it occurs the number of repetition is higher than the munias. Here we showed an evidence of behavioral peak-shift in Bengalese finch songs. We then show an evidence that song complexity and androgen methylation correlates. Together, we provide a tractable hypothesis on the evolution of song complexity.

2. Peak-shift for song complexity in Bengalese finches

Bengalese finch songs often contain trilled syllables. On average, Bengalese finch songs contain 1.9 trilled syllables in one song while it is 0.8 in munias. The number of repetitions is on average 6.7 in Bengalese and 3.6 in munias. These differences are significant, and we hypothesized the difference came about by the process of peak-shift (Terrace, 1968). We prepared two songs differing only in the trill repetition numbers (6 and 10). We trained female Bengalese finches by operant conditioning with food reinforcement to peck the response key when the song with 10 repetition of trills was played, while retain from responding when the trill repetition was 6. After discrimination learning was complete, we tested using stimuli whose trill number ranged from 5 to 11. Result showed more response to the stimulus with 11 repetitions, indicating peak shift occurred in this task (Caspani *et al*, in press).

3. Song complexity and de-methylation of a vocal control area.

In search of neural correlates of song complexity, we measured song complexity as a coefficient of variation in inter-syllable-interval in Bengalese and munias. Expression of androgen receptor correlated significantly with the song complexity. Bengalese and munias showed highly significant difference both in the level of receptor expression and the song complexity. Furthermore, androgen receptor expression was negatively correlated with methylation at the receptor coding site (Wada *et al*, 2013). Results suggest that when learning complex songs, methylation should be lower at the coding site, or alternatively, less methylation enables learning of a complex song.

4. Integrating results in into hypothesis

We showed behaviorally that the preference for trill repetition number may increase via peak-shift within the life of individual (Caspani *et al*, in press). We showed at molecular level that song complexity and level of methylation negatively correlated (Wada *et al*, in press).

Taken together, the following scenario could be drawn. Preference for song complexity develops in individual females. Learning of more complex songs in males induces less methylation at the androgen receptor coding site. Assuming that there is a set of genes responsible to modulate the tendency of methylation in Area X, and also assuming that complex song is more preferred by females, this tendency should be enhanced through generations. As a result, learning of more complex songs might became possible in Bengalese finches.

This is not at all a Lamarckian scenario of inheritance of acquired traits, but totally within the framework of Darwinian evolution. We only assumed diversity in methylation tendency that is partially heritable in the male population. We do not need to assume inheritance of preference for song complexity in females.

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References

Caspani, G., Fujii G. T., Mizuhara, T., & Gillman, R. T. (in press). Biased learning of sexual signals by female Bengalese Finches. *Ornithological Science*.

Okanoya, K. (2004). Song syntax in Bengalese finches: proximate and ultimate analyses. *Advances in the Study of Behavior*, 34, 297-346.

Wada, K., Hayase, S., Imai, R., Mori, C., Kobayashi, M., Liu, W. C., Takahasi, M. & Okanoya, K. (2013). Differential androgen receptor expression and DNA methylation state in striatum song nucleus Area X between wild and domesticated songbird strains. *European Journal of Neuroscience*, 38, 2600-2610.

Terrace, H. S. (1968). Discrimination learning, the peak shift, and behavioral contrast. *Journal of the Experimental Analysis of Behavior*, 11, 727-741.