SLEEP-DEPENDENT MODULATION OF BIRDSONG PRE-MOTOR PATTERNS AND A MODEL FOR OFFLINE PROCESSING OF SENSORY FEEDBACK

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ABSTRACT

In zebra finches, song learning and maintenance depend upon auditory feedback. The precise replay of pre-motor patterns during sleep has been observed in the song system nucleus RA, suggesting a role for sleep in consolidating information about singing. Here we show that RA single unit pre-motor patterns are often altered following sleep, but not during waking periods of comparable duration. We propose a model wherein this modulation results from sleep replay, mediated by an error-correction signal from the nucleus lMAN's projection to RA. We are currently investigating whether lMAN lesions abolish modulation of sleep-dependent changes to RA pre-motor patterns.

SUMMARY

In some species song maintenance in adult songbirds is dependent upon auditory feedback during singing. Neurons in the zebra finch song control nucleus robustus archistriatalis (RA) generate stereotyped, complex bursting patterns during song production; the timing and structure of these bursts show exquisite (<1 ms) temporal regulation. During sleep, song-related burst patterns are replayed both spontaneously and in response to song playback. This replay has been hypothesized to represent a mechanism whereby information regarding motor performance and auditory feedback from singing during the day is consolidated during sleep, potentially modulating pre-motor patterns in support of song maintenance.

We have recorded single units in RA during singing both preceding and following a period of sleep, finding sleep-dependent modulations of RA pre-motor patterns. While recording sessions of up to several hours show that burst patterns associated with specific song syllables remain consistent absent any intervening sleep, the bursts associated with the same syllables following sleep often have a subtly altered fine temporal structure and/or changes in the number of spikes. These changes are observed following brief (0.5-2 h) periods of sleep during the day, as well as following a full night of sleep; thus, this phenomenon is dependent upon sleep and is not a result of circadian patterns. Similar changes can occur in pre-motor patterns underlying distance calls, another type of learned vocalization. At 22 sites in 7 birds, we analyzed the number of spikes per burst associated with 78 different vocalizations (song syllables and distance calls). In 54 of 78 cases (from 20 of 22 sites), spike number per burst changed significantly ($p < 0.05$, unpaired t test). Note that this simple analysis fails to completely characterize the extent of the changes we observed, as it does not attempt to measure differences in fine temporal structure, yet it demonstrates the prevalence of pre-motor pattern modulation following sleep. The changes in patterns across episodes of sleep are unlikely to be the result of changes in motivational states because in all cases males sang directed songs towards females. Furthermore, the temporal "jitter" comparing comparable spikes (ie the 1st spike, 2nd spike, etc) appears similar before and after sleep, although as of this writing a formal analysis has not been completed. Rather than motivational effects, we

hypothesize that sleep-dependent modulation is driven by the same mechanisms underlying the sleep replay of pre-motor patterns.

The anatomy of the song control system, together with the replay and sleep-modulation phenomena, suggest a model for the control of motor plasticity using sleep-based processing of previously obtained auditory feedback. RA receives two primary sources of extrinsic input: a direct projection from the sensorimotor nucleus HVc, and indirect input from HVc through an anterior forebrain pathway (AFP) via the lateral magnocellular nucleus of the anterior neostriatum (lMAN). While only the direct projection from HVc is obligatory for song production, the input from lMAN is necessary for the vocal plasticity normally observed in song development in juveniles. Whereas lMAN lesions do not affect song in normal adults, such lesions have dramatic effects on the alteration of song in response to insult (e.g. deafening, syringeal nerve transection) in adults. In these cases, interestingly, lMAN lesions tend to reduce the degree of song modification that accompanies deafening or nerve sectioning. lMAN as well as HVc and the other nuclei of the AFP exhibit auditory responses highly tuned to the bird's own song which could provide the basis for an error signal used to evaluate auditory feedback.

In our proposed model, auditory feedback is processed via song-selective neurons in HVc and in the AFP. Information regarding the quality of song is encoded in song-selective responses, and is stored in the AFP. During sleep, this information is "read out" in the synchronized bursting activity of the song system as the predicted auditory feedback of replayed pre-motor patterns in HVc and RA. During this process, the intrinsic circuitry of RA is modulated by input from lMAN (which is largely mediated through NMDA receptors) in order to optimize the predicted auditory feedback. Sleep-based, "offline" processing may provide a solution to the problem of temporal credit assignment. Information regarding auditory feedback from a given song syllable can only arrive in HVc with a latency of ≥ 70 ms (ignoring auditory integration time which would increase the latency value) with respect to the initiation of the pre-motor program responsible for generating that syllable, by which time the motor program for generating following syllables may have already begun. Our model of offline processing suggests that the song system resolves the potential complications of temporal credit mismatch by synchronizing the generation of pre-motor patterns with the predicted auditory feedback directly corresponding to those patterns. Offline learning is not inconsistent with online learning – both processes could contribute to song development.

We hypothesize that the sleep-dependent changes in RA burst patterns are driven by the offline processing described in the model. A strong prediction of this hypothesis is that the lMAN-RA projection is necessary for the observed modulations in pre-motor patterns, and thus that lesions of lMAN should abolish these modulations. We are currently testing our hypothesis by recording the activity of single RA neurons before and after sleep in zebra finches following electrolytic lesions of lMAN. Thus far we have only preliminary results: two sites recorded from lMAN-lesioned birds showed no changes in pre-motor patterns following brief periods of sleep. This experiment provides an opportunity to study sleep-based mechansims of memory consolidation at the single-cell level.