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The Sleeping Bird Gets the Song. Focus on: “HVC Neural Sleep Activity Increases With Development and Parallels Nightly Changes in Song Behavior”

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What is sleep’s function? Despite different opinions, there is consensus that sleep is not a passive state but rather involves active changes in brain metabolism and neuronal activity including, in terrestrial animals, alternation between two sleep stages, rapid-eye movements (REM) and non-REM sleep (selected reviews: Markov and Goldman 2006; Siegel 2005). In adult human imaging and behavioral studies, sleep disruption affects cognitive and motor function (selected references: Kuriyama et al. 2004; Maquet 2001; Stricker et al. 2006). But does sleep affect a developing animal’s cognitive capacity? In this issue of *Journal of Neurophysiology* (p. 232–240), Crandall, Adam, Kinnischtzke, and Nick (2007) provide evidence that neural activity in sleeping juvenile songbirds parallels learning and may ultimately influence their “songsmanship.”

In humans and rodents, neural activity during sleep is postulated to reinforce motor skills and memory consolidation of waking experiences (selected reviews: Rauchs et al. 2005; Ribeiro and Nicolelis 2004). In the adult rat hippocampus, sleep activation patterns “replay” those during tasks performed while awake, a “nighttime rehearsal” that facilitates memory consolidation (Wilson and McNaughton 1994). Human developmental disorders marked by communication deficits, such as autism spectrum disorders and Down and Fragile X syndromes, are associated with decreased quality of sleep (reviewed in: Harvey and Kennedy 2002). REM specific sleep deficits in adulthood correlate with the degree of mental retardation in these disorders, suggesting that poor sleep worsens the cognitive phenotype, but compared with adult function, the role of sleep in developmental learning is less characterized. Now Crandall et al. (2007) use birdsong to link changes in neural activity during sleep to the gradual maturation of learned communication.

Songbirds, like humans but unlike traditional lab animals, learn their vocalizations while young and from interacting with adult tutor(s). After an early perceptual phase, birds and humans engage in sensorimotor learning when vocal output is actively shaped to mimic the tutor’s sounds. Neural substrates for song (Reiner et al. 2004) reside in two interconnected brain loops, each of which originates in a premotor-association cortex-like pallial region called HVC. Crandall et al. monitored activity in this region in young, sleeping birds. Some HVC neurons project to the robust nucleus of the arcopallium (RA), which controls hypoglossal motoneurons that innervate the song organ, the syrinx, and respiratory muscles. Activity in these HVC neurons thus commands the motor output of song. A second set of HVC neurons projects into the anterior fore-brain, forming a pallio-striatal-thalamic loop necessary for modifying song, most evident during song development but also during adult song maintenance (selected review: Doupe et al. 2005). Thus HVC neural activity is crucial to both song output and modification.

Clues that neural activity during sleep is important in adult song came from observations that RA neurons known to fire at precise moments during singing exhibit similar firing patterns during sleep (selected review: Margoliash 2005). RA-projecting neurons in HVC likely drive this night time activity because reversibly silencing HVC with lidocaine abolishes sleep bursts in RA, which recover after washout (Hahnloser et al. 2006). In one model, singing-related neural activation of song pathways during sleep includes rehearsal of the bird's own song, which then shapes motor output during wakefulness (Margoliash 2005). Such shaping could fine tune the relatively stable song of adult zebra finches but leaves open the question of what happens during development when young birds actively modify their songs.

A recent behavioral study showed that during rapid phases of learning in juvenile finches, song deteriorates during sleep, with recovery 2–3 h after the morning onset of singing (Derégnaucourt et al. 2005). A sensitive measure of song deterioration is the variability in entropy of individual song syllables. A syllable with high entropy is akin to white noise and lacks sound structure. Greater variance in entropy is indicative of more structure. The overnight loss of syllable structure/decrease in entropy variance (EV) is most evident during the sensorimotor phase of song learning. Strikingly, the magnitude of the song deterioration in juveniles positively correlates with the eventual replication of the tutor's song, meaning that juveniles with the largest decrease in overnight EV end up being the best learners. Whatever drives the overnight change in EV could ultimately influence the quality of learning.

Crandall et al. (2007) now provide electrophysiological correlates for these behavioral changes. This is a first of its kind longitudinal study to explore the role of neural activity during sleep in vocal learning using chronic population recordings in HVC that span late sensorimotor learning through adulthood. The authors show that during sleep, juveniles have a lower firing rate than adults and longer interspike intervals. HVC spike rate increases as development proceeds, coincident with the increase in song structure. On nights when HVC spiking activity is low, there is more overnight deterioration in song, reflective of the juvenile stage, but when nightly HVC spiking activity is high and similar to adult activity, song is stabilized. Curiously, overall activity decreases or remains the same across development, suggesting that juvenile HVC has greater levels of activity, potentially including synaptic potentials, and/or asynchronous firing that did not meet the strict criteria for spiking used here.

These findings reinforce the idea that sleep provides an opportunity for young songbirds to modify prior progress in learning, perhaps through asynchronous activity, ultimately improving song. Further, they suggest that during maturation, increased spiking activity stabilizes the maturing song. An alternative interpretation is that changes in nighttime activity are merely the consequence of learning the prior day. Although the data do not differentiate cause from consequence, they do chart the time course for age-dependent nightly changes in neuronal activity coincident with behavioral changes in song. This sets the stage for future experiments that will manipulate activity or perturb sleep to determine causality. Such studies in songbirds may, by analogy, inform the role of neural activity during sleep in the learning of human speech and other procedurally learned behaviors.

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