Encyclopedia of Sleep and Dreams: The Evolution, Function, Nature, and Mysteries of Slumber
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Sleep and Bird Songs
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Songbirds are the only terrestrial animals other than humans that learn extensive and complex vocalizations as juveniles. Numerous parallels between vocal learning in songbirds and human infants have led to the use of the songbird as a model system for studying the development and neural basis of vocalization. Songbirds display REM sleep, non-REM intermediate sleep comparable to mammalian Stages 1 and 2, and high-amplitude slow-wave sleep (SWS),| also called deep sleep or non-REM Stage 3. Focused research on the relationship between sleep and bird song began in the late 1990s on the zebra finch (*Taeniopygia guttata*), and has led to the first discovery of a connection between sleep and vocal learning

Research on the interaction between sleep and bird-song learning is a model for integrating behavioral and neurobiological studies. A major result of this research is that juvenile zebra finches appear to replay songs they are learning during sleep, which aids the learning process and may be a mechanism underlying memory consolidation. The behavioral research consistent with this off-line processing hypothesis includes the finding that songs produced after sleep in juvenile zebra finches are different from songs produced the previous afternoon during the period when the birds are undergoing rapid learning, and that the magnitude of this difference predicts the accuracy of the final (crystallized) song. This difference is actually that songs in the morning are more primitive and unstructured; however, this change is not due to a lack of practice overnight, nor is it something that happens in the morning per se (a circadian phenomenon), and adult birds do not exhibit it. The probable reason for the temporary deterioration is that songs are replaying in the bird brain during sleep without the auditory feedback that happens when a bird is awake, so the song has drifted in the same way that the song of a deafened bird does. Nevertheless, this replay during sleep benefits memory formation, and the subsequent plasticity in the morning might provide raw material to then focus the song through daytime singing, facilitating more accurate copying in the end. Thus it is not simply sleep, but the interaction between sleep and subsequent practice, which enhances vocal learning in juvenile birds. A related behavioral finding is that at the very beginning of tutoring the songs of zebra finches do not display learning that same day but rather the next morning, suggesting that neural networks might change overnight in line with the previous day’s experiences.

Additional evidence for the function of sleep in bird-song learning comes from neurophysiological studies. During sleep, the neural firing in the HVC nucleus (an

important source of singing motor commands) in juveniles is lower than in adults and increases as song structure improves through development. Moreover, gene expression, a marker of neuronal activity, increases during sleep in a region that stores the target song the bird is learning, supporting the idea of off-line processing.

In the robust nucleus of the archistriatum (RA), a target of the HVC, burst patterns during singing are associated with specific elements of a song. Perhaps most importantly for the off-line processing hypothesis, identical burst patterns are found during sleep in the absence of singing, perhaps indicating song replay. RA bursts during sleep emerge only after exposure to a tutor (training) song and are less structured than in sleeping adults. Features of bursting are more similar among juveniles exposed to the same tutor than across different tutors, suggesting that the sleep bursts are specific to the vocalizations currently being learned. Lastly, both the HVC and RA in juveniles and adults respond preferentially to playback of their own song only during sleep, indicating a special role of sleep in the learning or maintenance of song production.

A role of sleep in perceptual learning has also been shown in the European starling (*Sturnus vulgaris*). A study testing the ability of starlings to distinguish between two novel songs showed that auditory discrimination in starlings was superior immediately after waking and remained stable throughout the day. These results, together with similar results in young chickens with respect to visual images, suggest that the benefit of sleep may not be specific to song motor learning, but may serve memory consolidation more generally.

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