Chapter

6

Introduction/Defining Sleep

Jerome M. Siegel

A relative seemed to fall asleep at a family gathering, with eyes closed, immobile, and conspicuous uninterrupted snoring. When he was elbowed "awake," he vigorously denied having been asleep. He then proceeded to recite, verbatim, conversations taking place right up to the point he was so rudely "awakened." Clearly it was incorrect to say he was asleep, even though a superficial evaluation might conclude otherwise. Conversely, it is common to fall asleep while watching TV, while a passenger on a long trip, or in a boring situation and to be unaware of this. When told you were asleep, you may deny it, but when quizzed about what you were watching or listening to, there is an undeniable gap in what you remember.

Sleep has historically been distinguished from waking by five criteria: (1) reduced motor activity, (2) decreased response to stimulation, (3) stereotypic postures (e.g., in humans, lying down with eyes closed), (4) relatively easy reversibility (distinguishing it from coma, hibernation, and estivation),[1] (5) homeostatic regulation (i.e., sleep deprivation is followed by sleep rebound). A frequently unstated, but central, attribute of sleep is (6) loss of consciousness of the environment.

It is important to appreciate that these are not binary criteria. At what point is motor activity, responsiveness, or reversibility considered to be reduced? What defines "loss of consciousness"? Is "rebound" always present after reduced sleep and equal to the amount of sleep lost?

How often are these criteria for defining and measuring sleep rigorously applied? In human studies the answer is "rarely." In animal studies the answer is "almost never."

A common practice in studies of mammals is to use electroencephalographic (EEG) activity as the only criterion of sleep, because it appears to correspond to sleep in humans. But this is also not a binary characteristic. Are alpha waves sufficient? Delta waves? Of what signal-to-noise ratio and at what sites within the brain? Clearly EEG is not "sleep determinative" in the case of rapid eye movement (REM) sleep in which the EEG is low-voltage "activated," as in waking, while the behavior is clearly sleep.

Contrary to some folk wisdom, humans are not completely inactive during sleep or even during "deep sleep." Movement is required in both sleep and waking, as is apparent in quadriplegics who cannot move. If they are not moved frequently during sleep and waking periods, bedsores will develop with eventual dire consequences, so nursing care or specially designed beds that frequently change pressure points are necessary. Movement during "sleep" is present even in smaller animals.

While inactivity is relatively easy to document with motion detectors or video, elevated arousal threshold is more difficult to define and measure. Arousal is not simply a response to an intense stimulus. You may not awaken to a thunderstorm, but you may awaken to your baby's faint cries. It is likely that nonhuman animals are similarly able to process sensory inputs during sleep and awaken only to the most salient patterns of noise, light, smell, and so on.

Elevated arousal thresholds must be species specific. If lions and giraffes, which live in the same African ecosystems, had equally elevated sleep arousal thresholds, giraffes would not exist. Adult giraffes must never be as deeply asleep as their predators. Giraffes not only sleep less deeply, but they also sleep less than 4 hours per day, based on observational studies in zoos, making them one of the shortest-sleeping species.[2] Immature giraffes, elephants, and other newborns appear to sleep relatively deeply and longer than adult members of their species, but they are always close enough to their mothers to be defended from predators. Conversely, lions and other predators can benefit from the reduced energy consumption accompanying sleep[3] with greatly elevated arousal thresholds. Individual humans and animals may sleep more or less deeply (i.e., have different arousal thresholds), depending on the sleep environment,[4] their age,[5] and other characteristics.

It has been supposed that lost sleep creates a "sleep debt" that is repaid in a sleep rebound. But in fact rebound is always substantially less than the amount of lost sleep. One of the best-documented periods of human sleep deprivation was an 11-day period of total sleep self-deprivation. This translates to

about 80 hours of sleep loss. Day one of recovery sleep produced 14.7 hours of sleep (1.8 hours of REM and 1.9 hours of deep, "stage 4" sleep). Sleep duration was 10.4 hours on the second day and 9.1 hours on the third day. When the next recording was made, 1 week later, the subject had just 7 hours of sleep.[6] In contrast, the major effect of total sleep deprivation in the rat for 11 to 32 days was a striking rebound of REM, not non-REM, sleep.[7] The argument can be made that rebound sleep, although shorter in duration than the sleep "debt," is more "intense," with higher voltage EEG or more rapid eye movements. But since there is no agreement on exactly what the underlying metric of sleep is, the intensity of recovery sleep is difficult to quantify.

Small cetacean (dolphins and whales) marine mammals, such as Commerson's dolphin,[8] are in continuous motion from the moment they are born until the end of their lives. A study of dolphins and of killer whales[9] found similar continuous motion both in calves and in their mothers for weeks to months after birth. During this period, the calves swim in tight formation with their mothers. In the wild, these are times of migration and high danger, and both mother and calf must remain alert. One can assume that brain motor and sensory systems are functioning at high levels, just the opposite of the behavioral definitions of sleep listed previously. Inactive behavior gradually returns to the adult pattern, with no evidence of rebound beyond baseline adult levels. Migrating birds greatly reduce sleep during migration periods without obvious deficits or rebounds.[10,11] Similarly it has been shown that, in certain birds, success in mating behavior is inversely correlated with sleep time during the 3-week mating period.[12,13]

Cetaceans show sleeplike high-voltage EEG in only one hemisphere at a time. Bilateral high-voltage EEG is never seen.[14-19] Cetaceans never show REM sleep. A study that attempted unihemispheric sleep deprivation produced an unclear outcome. A rebound specific to the hemisphere that triggered the deprivation procedure was not seen. Instead the dolphins showed highly asymmetric unihemispheric EEG patterns that were not clearly related to the prior deprivation procedures.[20]

CLINICAL PEARLS

It is frequently said that "all animals sleep" or "all animals with nervous systems sleep." This is incorrect, unless one adopts an extremely fluid definition of sleep.[3] When one makes a statement about sleep in animals, the message transmitted is that these animals sleep "like we do." This implies a period of inactivity, of substantially reduced consciousness and responsiveness, and with homeostatic regulation. Each of these criteria requires further data. These issues get even more difficult when one is studying "sleep" in insects such as drosophila, fish, amphibia, reptiles, or birds. Are we conflating changes in activity with changes in sleep? Without rigorous application of the sleep definition, we need to be more careful with claims of sleep, sleep duration, and sleep depth. We might also profitably highlight quantitative and qualitative individual and species differences in waking versus rest versus sleep patterns and how these may be evolutionarily adaptive.

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