

Dreams may be crucial in mammalian memory processing. Important information acquired while awake may be reprocessed during sleep

The Meaning of Dreams

By Jonathan Winson

Throughout history, human beings have sought to understand the meaning of dreams.

The ancient Egyptians believed dreams possessed oracular power—in the Bible, for example, Joseph’s elucidation of Pharaoh’s dream averted seven years of famine. Other cultures have interpreted dreams as inspirational, curative or alternative reality. During the past century, scientists have offered conflicting psychological and neuroscientific explanations for dreams. In 1900, with the publication of *The Interpretation of Dreams*, Sigmund Freud proposed that dreams were the “royal road” to the unconscious, that they revealed in disguised form the deepest elements of an individual’s inner life.

More recently, in contrast, dreams have been characterized as meaningless, the result of random nerve cell activity. Dreaming has also been viewed as the means by which the brain rids itself of unnecessary information—a process of “reverse learning,” or unlearning.

Based on recent findings in my own and other neuroscientific laboratories, I propose that dreams are indeed meaningful. Studies of the hippocampus (a brain structure crucial to memory), of rapid eye movement (REM) sleep and of a brain wave called theta rhythm suggest that dreaming reflects a pivotal aspect of the processing of memory. In particular, studies of theta rhythm in subprimate animals have provided an evolutionary clue to the meaning of dreams. They appear to be the nightly record of a basic mammalian memory process: the means by which animals form strategies for survival and evaluate current experience in light of those strategies. The existence of this process may explain the meaning of dreams in human beings.

Stages of Sleep and Dreaming

THE PHYSIOLOGY OF DREAMING was first understood in 1953, when researchers characterized the human sleep cycle. They found that sleep in humans is initiated by the hypnagogic

state, a period of several minutes when thoughts consist of fragmented images or minidramas. The hypnagogic state is followed by slow-wave sleep, so called because at that time the brain waves of the neocortex (the convoluted outer mantle of the brain) are low in frequency and large in amplitude. These signals are measured as electroencephalographic (EEG) recordings.

Researchers also discovered that a night’s sleep is punctuated by periods in which the EEG readings are irregular in frequency and low in amplitude—similar to those observed in awake individuals. These periods of mental activity are called REM sleep. Dreaming takes place solely during these periods. While in REM sleep, motor neurons are inhibited, preventing the body from moving freely but allowing extremities to remain slightly active. Eyes move rapidly in unison under closed lids, breathing becomes irregular, and heart rate increases.

The first REM stage of the night follows 90 minutes of slow-wave sleep and lasts for 10 minutes. The second and third REM periods follow shorter slow-wave sleep episodes but grow progressively longer themselves. The fourth and final REM interval lasts 20 to 30 minutes and is followed by awakening. If a dream is remembered at all, it is most often the one that occurred in this last phase of REM sleep.

This sleep cycle—alternating slow-wave and REM sleep—appears to be present in all placental and marsupial mammals. Mammals exhibit the various REM-associated characteristics observed in humans, including EEG readings similar to those of the awake state. Animals also dream. By destroying neurons in the brain stem that inhibit movement during sleep, researchers found that sleeping cats rose up and attacked or were startled by invisible objects—ostensibly images from dreams.

By studying nonprimate animals, scientists have discovered additional neurophysiological aspects of REM sleep. They de-



JACOB'S LADDER, painted in 1973 by Marc Chagall, depicts a biblical story. Jacob dreams of angels ascending to and descending from heaven on a ladder.

termined that neural control of this stage of the sleep cycle is centered in the brain stem (the brain region closest to the spinal cord) and that during REM sleep neural signals—called pontine-geniculate-occipital (PGO) cortex spikes—proceed from the brain stem to the center of visual processing, the visual cortex. Brain stem neurons also initiate a sinusoidal wave (one resembling a sine curve) in the hippocampus. This brain signal is called theta rhythm.

At least one animal experiences slow-wave but not REM sleep—and, consequently, does not exhibit theta rhythm when asleep. This animal is the echidna, or spiny anteater, an egg-laying mammal (called a monotreme) that provides some insight into the origin of dreaming. The absence of REM sleep in the echidna suggests that this stage of the sleep cycle evolved some 140 million years ago, when marsupials and placentals diverged from the monotreme line. (Monotremes were the first mammals to develop from reptiles.)

By all evolutionary criteria, the perpetuation of a complex brain process such as REM sleep indicates that it serves an important function for the survival of mammalian species. Understanding that function might reveal the meaning of dreams.

When Freud wrote *The Interpretation of Dreams*, the physiology of sleep was unknown. In light of the discovery of REM sleep, certain elements of his psychoanalytic theory were modified, and the stage was set for more neurologically based theories. Dreaming came to be understood as part of a biologically determined sleep cycle. Yet the central concept of Freud's theory—namely, the belief that dreams reveal a censored representation of our innermost unconscious feelings and concerns—continues to be used in psychoanalysis.

Some theorists abandoned Freud altogether following the neurological discoveries. In 1977 J. Allan Hobson and Robert McCarley of Harvard Medical School proposed the “activation-synthesis” hypothesis. They suggested that dreaming consists of associations and memories elicited from the forebrain (the neocortex and associated structures) in response to random signals from the brain stem such as PGO spikes. Dreams were merely the “best fit” the forebrain could provide to this random bombardment from the brain stem. Although dreams might at times appear to have psychological content, their bizarreness was inherently meaningless.

The sense, or plot, of dreams resulted from order that was imposed on the chaos of neural signals, Hobson said. “That order is a function of our own personal view of the world, our remote memories,” he wrote. In other words, the individual's

emotional vocabulary could be relevant to dreams. In a further revision of the original hypothesis, Hobson also suggested that brain stem activation may serve merely to switch from one dream episode to another.

Reverse Learning

ALTHOUGH HOBSON and McCarley had presented an explanation of dream content, the basic function of REM sleep remained unknown. In 1983 Francis Crick of the Salk Institute for Biological Studies in San Diego and Graeme Mitchison of the University of Cambridge proposed the idea of reverse learning. Working from the Hobson-McCarley assumption of random neocortical bombard-

ment by PGO waves and their own knowledge of the behavior of stimulated neural networks, Crick and Mitchison postulated that a complex associational neural network such as the neocortex might become overloaded by vast amounts of incoming information. The neocortex could then develop false, or “parasitic,” thoughts that would jeopardize the true and orderly storage of memory.

According to their hypothesis, REM sleep served to erase these spurious associations on a regular basis. Random PGO waves impinged on the neocortex, resulting in erasure, or unlearning, of the false information. This process served an essential function: it allowed the orderly processing of memory. In humans, dreams

were a running record of these parasitic thoughts—material to be purged from memory. “We dream to forget,” Crick and Mitchison wrote.

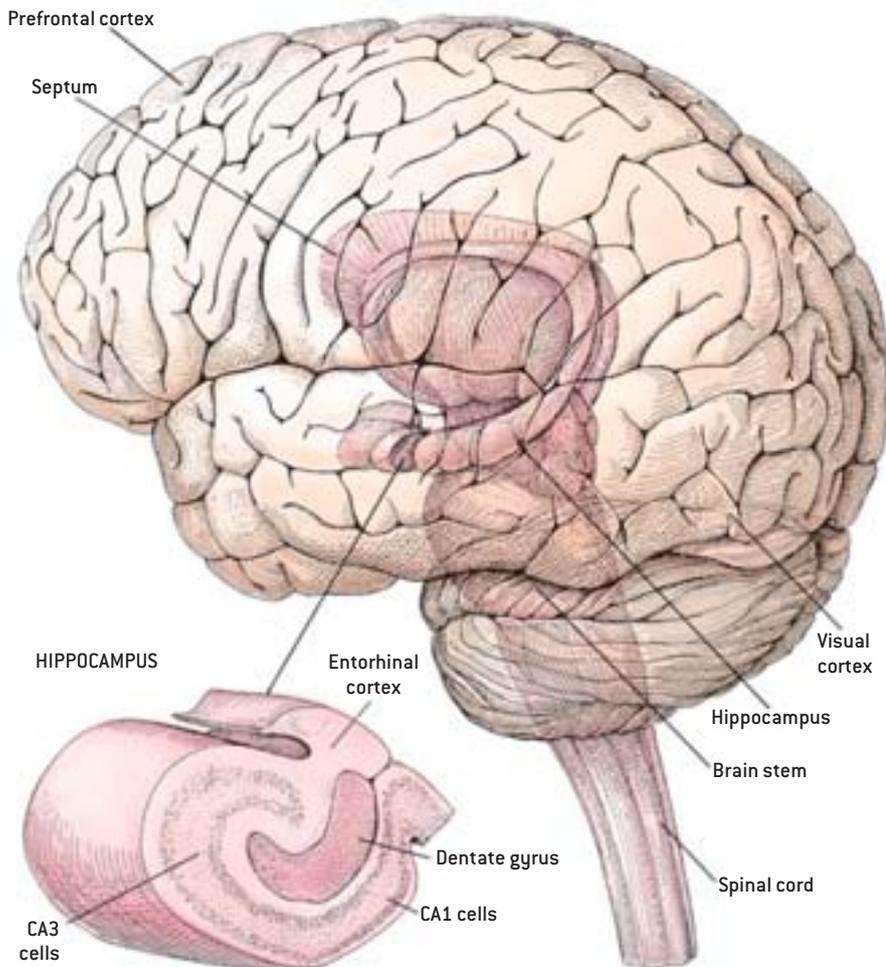
The two researchers proposed a revision in 1986. Erasure of parasitic thoughts accounted only for bizarre dream content. Nothing could be said about dream narrative. Furthermore, dreaming to forget, they said, was better expressed as dreaming to reduce fantasy or obsession.

None of these hypotheses seems to explain adequately the function of dreaming. On the one hand, Freud’s theory lacked physiological evidence. (Although Freud had originally intended to describe the neurology of the unconscious and of dreams in his proposed “Project for a Scientific Psychology,” the undertaking was premature, and he limited himself to psychoanalysis.) On the other hand, despite revisions to incorporate elements of psychology, most of the later theories denied that dreams had meaning.

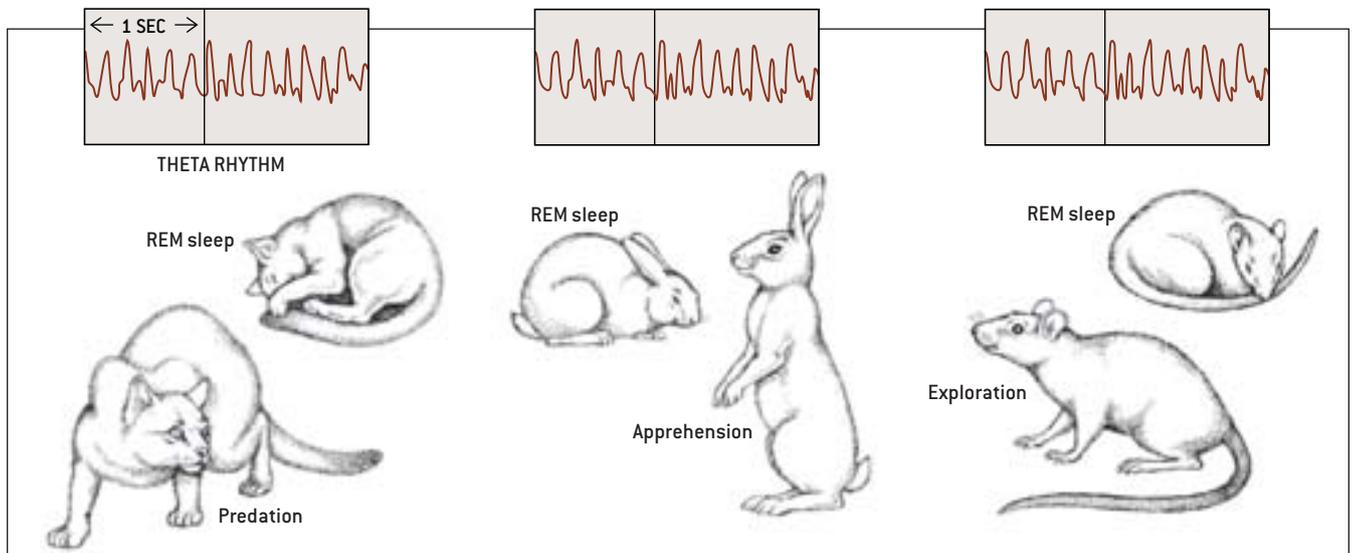
Exploring the neuroscientific aspects of REM sleep and of memory processing seemed to me to hold the greatest potential for understanding the meaning and function of dreams. The key to this research was theta rhythm.

Theta rhythm was discovered in 1954 in awake animals by John D. Green and Arnaldo A. Arduini of the University of California at Los Angeles. The researchers observed a regular sinusoidal signal of six cycles per second in the hippocampus of rabbits when the animals were apprehensive of stimuli in their environment. They named the signal theta rhythm after a previously discovered EEG component of the same frequency.

Theta rhythm was subsequently recorded in the tree shrew, mole, rat and cat. Although it was consistently observed in awake animals, theta rhythm was correlated with very different behaviors in each species. For example, in marked contrast to the rabbit, environmental stimuli did not induce theta rhythm in the rat. Rats demonstrated theta rhythm only during movement, typically when they explored. In 1969, however, Case H. Vanderwolf of the University of Western Ontario discovered there was one behavior during which the animals he studied,



ANATOMY OF THE BRAIN and cross section of the hippocampus show some of the regions involved in dreaming. In the hippocampus, incoming information is processed sequentially in the dentate gyrus and the CA3 and the CA1 pyramidal cells [so named for their triangular shape]. In nonprimate species, the theta rhythm brain wave is generated in the dentate gyrus and the CA1 cells.



THETA RHYTHM brain signal is present during different waking behaviors in different species. Each of these behaviors is pivotal to the animal's survival. In placental and marsupial animals, theta rhythm is present during rapid eye movement (REM) sleep.

including the rat, showed theta rhythm: REM sleep.

In 1972 I published a commentary pointing out that the different occurrences of theta rhythm could be understood in terms of animal behavior. Awake animals seemed to show theta rhythm when they were behaving in ways most crucial to their survival. In other words, theta rhythm appeared when they exhibited behavior that was not genetically encoded—such as feeding or sexual behavior—but rather a response to changing environmental information. Predatory behavior in the cat, prey behavior in the rabbit, and exploration in the rat are, respectively, most important to their survival. For example, a hungry rat will explore before it eats even if food is placed in front of it.

Role of Theta Rhythm

FURTHERMORE, because the hippocampus is involved in memory processing, the presence of theta rhythm during REM sleep in that region of the brain might be related to that activity. I suggested that the theta rhythm reflected a neural process whereby information essential to the survival of a species—gathered during the day—was reprocessed into memory during REM sleep.

In 1974, by recording signals from the hippocampus of freely moving rats and rabbits, I found the source from

which theta rhythm was generated in the hippocampus. Together with the neocortex, the hippocampus is believed to provide the neural basis for memory storage. The hippocampus (from the Greek word for “seahorse,” which it resembles in shape) is a sequential structure composed of three types of neurons. Information from all sensory and associational areas of the neocortex converges in a region called the entorhinal cortex; from there it is transmitted to the three successive neuronal populations of the hippocampus. The signal arrives first at the granule cells of the dentate gyrus, then at the CA3 pyramidal cells (so called because of their triangular shape) and finally at the pyramidal cells of CA1. After information is processed by this trio of cells, it is retransmitted to the entorhinal cortex and then back to the neocortex.

My studies showed that theta rhythm was produced in two regions within the hippocampus: the dentate gyrus and the CA1 neurons. The rhythms in these two areas were synchronous. Subsequently,

James B. Ranck, Jr., of the State University of New York Downstate Medical Center and his then co-worker Susan Mitchell identified a third synchronous generator in the entorhinal cortex, and Robert Verdes of Wayne State University discovered the brain stem neurons that control theta rhythm. These neurons transmit signals to the septum (a forebrain structure) that activate theta rhythm in the hippocampus and the entorhinal cortex. Thus, the brain stem activates the hippocampus and the neocortex—the core memory system of the brain.

To determine the relation between theta rhythm and memory, I made a lesion in the rat septum. Rats that had previously learned, using spatial cues, to locate a particular position in a maze were no longer able to do so after their septums were disabled. Without theta rhythm, spatial memory was destroyed.

Studies of the cellular changes that bring about memory illustrated the role of theta rhythm. In particular, the discovery in 1973 of long-term potentiation

THE AUTHOR

JONATHAN WINSON started his career as an aeronautical engineer, graduating with an engineering degree from the California Institute of Technology in 1946. He completed his Ph.D. in mathematics at Columbia University and then turned to business for 15 years. Because of his long-standing interest in neuroscience, Winson then began research at the Rockefeller University on memory processing. In 1979 he became associate professor there and continued his work as professor emeritus, retiring in 1996. His research was supported by the National Institute of Mental Health, the National Science Foundation and the Harry F. Guggenheim Foundation.

(LTP)—a change in neural behavior that reflects previous activity—showed the means by which memory might be encoded. Timothy V. P. Bliss and A. R. Gardner-Medwin of the National Institute of Medical Research in London and Terje Lømo of the University of Oslo found changes in nerve cells that had been intensely stimulated with electrical pulses.

Long-Term Memory Storage

EARLIER STUDIES had shown that if one stimulated the pathway from the entorhinal cortex to the granule cells of the hippocampus, the response of these cells could be measured with a recording electrode. Using this technique, Bliss and his colleagues measured the normal response to a single electrical pulse. Then they applied a long series of high-

Unlike other neuronal receptors, NMDA possesses an additional property. If a further activation of glutamate occurs while the granule cell is depolarized, a second channel opens up, allowing an influx of calcium. Calcium is thought to act as a second messenger, initiating a cascade of intracellular events that culminates in long-lasting synaptic changes—or LTP. (The description given here has been necessarily simplified. LTP is the subject of extensive ongoing investigation.)

Because the tetanic impulses applied by Bliss and his colleagues did not occur naturally in the brain, the question remained as to how LTP was achieved under normal circumstances. In 1986 John Larson and Gary S. Lynch of the University of California at Irvine and Gregory Rose and Thomas V. Dunwiddie of the University of Colorado at Denver sug-

the rat is synchronized with theta rhythm, as is the twitching of whiskers) and other sensory information converge on the entorhinal cortex and the hippocampus. There they are partitioned into 200-millisecond “bites” by theta rhythm. The NMDA receptors, acting in conjunction with theta rhythm, allow for long-term storage of this information.

A similar process occurs during REM sleep. Although there is no incoming information or movement during REM sleep, the neocortical-hippocampal network is once again paced by theta rhythm. Theta rhythm might produce long-lasting changes in memory.

Storing Spatial Memory

THE RESULTS OF ONE of my further experiments served to show that spatial memory was indeed being stored in the



In a series of experiments, a coherent picture of MEMORY PROCESSING began to emerge.

frequency signals—called tetanic pulses—to this pathway. After the train of tetanic stimuli, a single electrical pulse caused much greater firing in the granule cells than had been observed prior to the experiment. The heightened effect persisted for as long as three days. This phenomenon of LTP was precisely the kind of increase in neuronal strength that could be capable of sustaining memory. LTP is now considered a model for learning and memory.

LTP is achieved by the activity of the NMDA (*N*-methyl-D-aspartate) receptor. This molecule is embedded in the dendrites of the granule cells and the CA1 cells of the hippocampus as well as in neurons throughout the neocortex. Like other neuronal receptors, the NMDA receptor is activated by a neurotransmitter—glutamate in this case. Glutamate momentarily opens a non-NMDA channel in the granule cell dendrite, allowing sodium from the extracellular space to flow into the neuron. This influx causes the granule cell to become depolarized. If the depolarization is sufficient, the granule cell fires, transmitting information to other nerve cells.

gested that the occurrence of LTP in the hippocampus was linked to theta rhythm. They applied a small number of electrical pulses to CA1 cells in the rat hippocampus and produced LTP, but only when the pulses were separated by the normal time that elapses between two theta waves—approximately 200 milliseconds. Theta rhythm is apparently the natural means by which the NMDA receptor is activated in neurons in the hippocampus.

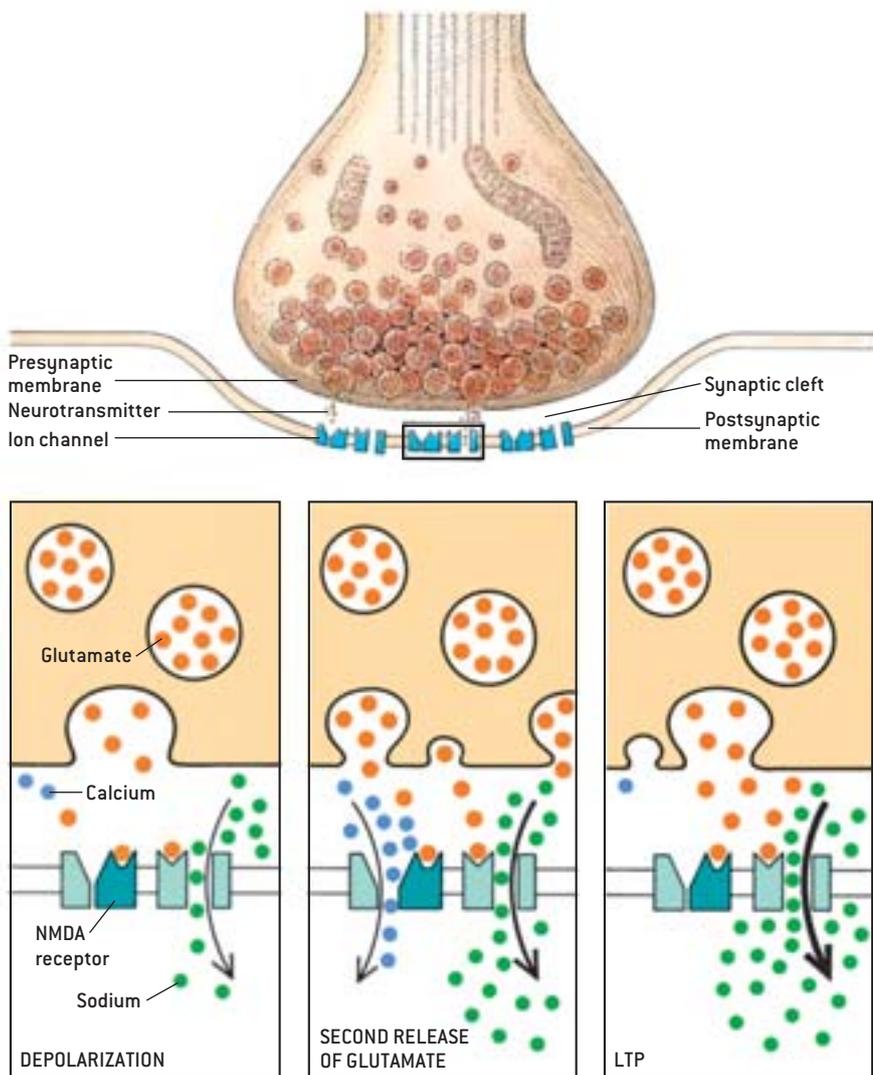
Work in my laboratory at the Rockefeller University duplicated Larson and Lynch's CA1 findings, but this time in the hippocampal granule cells. Constantine Pavlides, Yoram J. Greenstein and I then demonstrated that LTP was dependent on the presence and phase of theta rhythm. If electrical pulses were applied to the cells at the peak of the theta wave, LTP was induced. But if the same pulse were applied at the trough of the waves—or when theta rhythm was absent—LTP was not induced.

A coherent picture of memory processing was emerging. As a rat explores, for example, brain stem neurons activate theta rhythm. Olfactory input (which in

rat hippocampus during sleep. John O'Keefe and Jonathan O. Dostrovsky of University College London had demonstrated that individual CA1 neurons in the rat hippocampus fired when the awake animal moved to a particular location—namely, the neuron's place field. The implication of this finding was that the CA1 neuron fired to map the environment, thereby committing it to memory.

In 1989 Pavlides and I located two CA1 neurons in the rat hippocampus that had different place fields. We recorded from both cells simultaneously. After determining the normal firing rates in awake and asleep animals, we positioned a rat in the place field of one of the neurons. The neuron fired vigorously, mapping that location. The second cell fired only sporadically because it was not coding space. We continued recording from the two pairs of neurons as the rat moved about and then entered several sleep cycles. Six pairs of neurons were studied in this manner.

We found that neurons that had coded space fired at a normal rate as the animal moved about prior to sleep. In sleep, however, they fired at a significantly high-



NMDA RECEPTOR activation induces long-term potentiation (LTP), a model for memory. The release of the neurotransmitter glutamate (left panel) opens a non-NMDA (N-methyl-D-aspartate) receptor channel, allowing the influx of sodium, which depolarizes the neuron. If a further release of glutamate occurs while the cell is depolarized (center panel), the NMDA receptor opens a second channel, which allows calcium to flow in, leading to LTP. LTP occurs as a result of increased sodium through the non-NMDA channel (right panel) and the subsequent greater depolarization of the cell.

er rate than their previous sleeping baseline. There was no such increase in firing rate during sleep in neurons that had not mapped space. This experiment suggested that the reprocessing or strengthening of information encoded when the animal was awake occurred in sleep at the level of individual neurons.

Bruce L. McNaughton and his colleagues at the University of Arizona have developed a technique for simultaneously recording from a large number of neurons in the hippocampus that map locations. Their technique allows definitive patterns of firing to be identified. In animal studies, they found that ensembles of place-field

neurons that code space in the waking state reprocess information during slow-wave sleep and then in REM sleep. These results suggest that sleep processing of memory may have two stages—a preliminary stage in slow-wave sleep and a later phase in REM sleep, when dreaming occurs.

Evolution of REM Sleep

EVIDENCE THAT theta rhythm encodes memories during REM sleep may be derived not only from neuroscientific studies but also from evolution. The emergence of a neural mechanism to process memory in REM sleep suggests differences in brain anatomy between mam-

mals that have that aspect of the sleep cycle and those that do not. And in fact, such differences clearly exist between the echidna and the marsupials and placentals.

The echidna has a large convoluted prefrontal cortex, larger in relation to the rest of the brain than that of any other mammal, even humans. I believe it needed this huge prefrontal cortex to perform a dual function: to react to incoming information in an appropriate manner based on past experience and to evaluate and store new information to aid in future survival. Without theta rhythm during REM sleep, the echidna would not be able to process information while it slept. (The echidna does, however, show theta rhythm when foraging for food.) For higher capabilities to develop, the prefrontal cortex would have to become increasingly large—beyond the capacity of the skull—unless another brain mechanism evolved.

REM sleep could have provided this new mechanism, allowing memory processing to occur “off-line.” Coincident with the apparent development of REM sleep in marsupial and placental mammals was a remarkable neuroanatomical change: the prefrontal cortex was dramatically reduced in size. Far less prefrontal cortex was required to process information. That area of the brain could develop to provide advanced perceptual abilities in higher species.

The nature of REM sleep supports this evolutionary argument. During the day, animals gather information that involves locomotion and eye movement. The reprocessing of this information during REM sleep would not be easily separated from the locomotion related to the experience—such disassociation might be expecting too great a revision of brain circuitry. So to maintain sleep, locomotion had to be suppressed by inhibiting motor neurons. Suppressing eye movement was unnecessary because this activity does not disturb sleep.

Eye movement potentials, similar to PGO spikes, accompany rapid eye movement in the waking state and also during REM sleep. The function of these signals has not yet been established, but they may serve to alert the visual cortex to in-

coming information when the animal is awake and may reflect the reprocessing of this information during REM sleep. In any case, PGO spikes do not disturb sleep and do not have to be suppressed—unlike motor neurons.

Strategy for Survival

WITH THE EVOLUTION of REM sleep, each species could process the information most important for its survival, such as the location of food or the means of predation or escape—those activities during which theta rhythm is present. In REM sleep this information may be accessed again and integrated with past experience to provide an ongoing strategy for behavior. Although theta rhythm has not yet been demon-

strate an individual's strategy for survival. The subjects of dreams are broad-ranging and complex, incorporating self-image, fears, insecurities, strengths, grandiose ideas, sexual orientation, desire, jealousy and love.

Dreams clearly have a deep psychological core. This observation has been reported by psychoanalysts since Freud and is strikingly illustrated by the work of Rosalind Cartwright of Rush-Presbyterian–St. Luke's Hospital in Chicago. Cartwright studied a series of 90 subjects who were undergoing marital separation and divorce. All the subjects were clinically evaluated and psychologically tested to ascertain their attitudes and responses to their personal crisis. Cartwright's subjects were also awakened

and conditions are strongly biased toward early childhood experience.

My hypothesis also offers an explanation for the large amount of REM sleep in infants and children. Newborns spend eight hours a day in REM sleep. The sleep cycle is disorganized at this age. Sleep occurs in 50- to 60-minute bouts and begins with REM rather than with slow-wave sleep. By the age of two, REM sleep is reduced to three hours a day, and the adult pattern has been established. Thereafter, the time spent in REM sleep gradually diminishes to a little less than two hours.

REM sleep may perform a special function in infants. A leading theory proposes that it stimulates nerve growth. Whatever the purpose in infants may be, I suggest that at about the age of two,



Dreams MAY REFLECT a memory-processing mechanism inherited from LOWER SPECIES.

strated in primates, including humans, the brain signal provides a clue to the origin of dreaming in humans. Dreams may reflect a memory-processing mechanism inherited from lower species, in which information important for survival is reprocessed during REM sleep. This information may constitute the core of the unconscious.

Because animals do not possess language, the information they process during REM sleep is necessarily sensory. Consistent with our early mammalian origins, dreams in humans are sensory, primarily visual. Dreams do not take the form of verbal narration.

Also in keeping with the role REM sleep played in processing memories in animals, there is no functional necessity for this material to become conscious. Consciousness arose later in evolution in humans. But neither is there any reason for the material of dreams not to reach consciousness. Therefore, dreams can be remembered—most readily if awakening occurs during or shortly after a REM sleep period.

Consistent with evolution and evidence derived from neuroscience and reports of dreams, I suggest that dreams re-

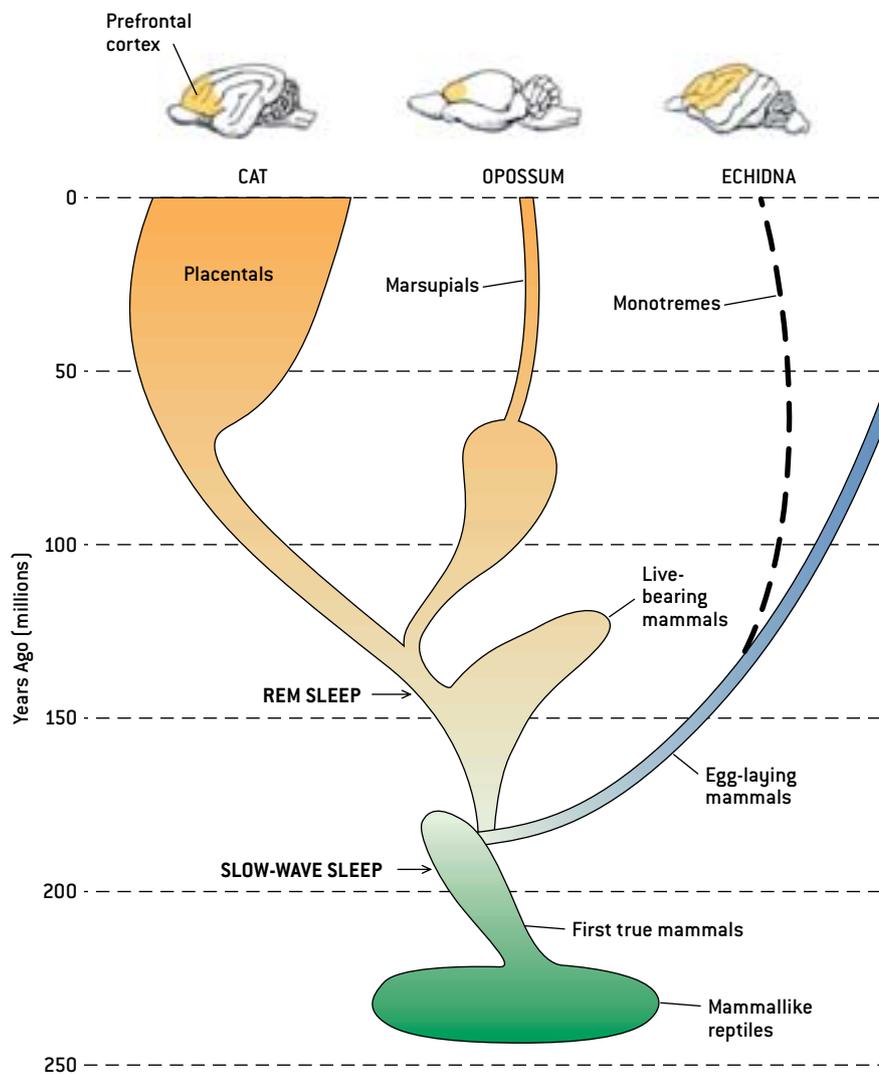
from REM sleep to report their dreams, which were then interpreted by the subjects themselves without questions that might have influenced their interpretation. In 70 of the individuals studied, the dream content conveyed the person's unconscious thoughts and was strongly correlated with the manner in which he or she was coping with the crisis while awake.

Although the topic “chosen” for consideration during a night's sleep is unpredictable, certain of life's difficulties—as in the case of Cartwright's subjects—so engage psychological survival that they are selected for REM sleep processing. In the ordinary course of events, depending on the individual's personality, the themes of dreams may be freewheeling. Moreover, when joined with the intricate associations that are an intrinsic part of REM sleep processing, the dream's statement may be rather obscure.

Nevertheless, there is every reason to believe that the cognitive process that took place in Cartwright's subjects occurs in every individual. Interpretation of the coherent statement that is being made depends on the individual's tracing of relevant or similar events. These associa-

when the hippocampus, which continues to develop after birth, becomes functional, REM sleep takes on its interpretive memory function. The waking information to be integrated at this point in development constitutes the basic cognitive substrate for memory—the concept of the real world against which later experiences must be compared and interpreted. The organization in memory of this extensive infrastructure requires the additional REM sleep time.

For reasons he could not possibly have known, Freud set forth a profound truth in his work. There is an unconscious, and dreams are indeed the “royal road” to understanding it. The characteristics of the unconscious and associated processes of brain functioning, however, are very different from what Freud thought. Rather than being a cauldron of untamed passions and destructive wishes, I propose that the unconscious is a cohesive, continuously active mental structure that takes note of life's experiences and reacts according to its own scheme of interpretation. Dreams are not disguised as a consequence of repression. Their unusual character is a result of the complex associations that are culled from memory.



EVOLUTIONARY TREE shows the divergence of placentals and marsupials from monotremes. The echidna, which does not experience REM sleep, has a larger prefrontal cortex compared with the rest of its brain than does any mammal, even humans. It is larger than in similarly sized animals, including the opossum and the cat.

REM processing in lower species must be defined before the theory can be evaluated further. In addition, the Crick-Mitchison hypothesis as applied to the hippocampus would suggest that neurons fire randomly during REM sleep, providing reverse learning. Instead, in my experiment on the neurons that coded space, these neurons fired selectively, implying an orderly processing of memory.

Avi Karni and his colleagues at the Weizmann Institute of Science in Israel were able to show that memory processing occurs in humans during REM sleep. In their experiment, individuals learned to identify particular patterns on a screen. The memory of this skill improved after a night with REM sleep. When the subjects were deprived of REM sleep, memory consolidation did not occur. This study opens a promising field for exploration.

Perhaps of greatest interest is evidence supporting the role of REM sleep in memory processing that has emerged from molecular biology. Sidarta Ribeiro and his colleagues at the Rockefeller University have reported that the immediate early gene *zif-268* that is associated with learning is selectively upgraded during REM sleep in rats exposed to experience in a preceding waking period. Further understanding of the role of REM sleep may be expected from this area of research.

Research on REM sleep suggests that there is a biologically relevant reason for dreaming. The revised version of the Hobson-McCarley activation-synthesis hypothesis acknowledges the deep psychological core of dreams. In its present truncated form, the hypothesis of ran-

dom brain stem activation has little explanatory or predictive power.

The Crick-Mitchison hypothesis provides a function for REM sleep—reverse learning—but it does not apply to narrative, only to the bizarre elements of the dream. What this implies with regard to

MORE TO EXPLORE

Interspecies Differences in the Occurrence of Theta. Jonathan Winson in *Behavioral Biology*, Vol. 7, No. 4, pages 479–487; 1972.

Loss of Hippocampal Theta Rhythm Results in Spatial Memory Deficit in the Rat. Jonathan Winson in *Science*, Vol. 201, No. 435, pages 160–163; 1978.

Brain and Psyche: The Biology of the Unconscious. Jonathan Winson. Anchor Press, Doubleday, 1985.

Long-Term Potentiation in the Dentate Gyrus Is Induced Preferentially on the Positive Phase of Q-Rhythm. Constantine Pavlides, Yoram J. Greenstein, Mark Grudman and Jonathan Winson in *Brain Research*, Vol. 439, pages 383–387; 1988.

Influences of Hippocampal Place Cell Firing in the Awake State on the

Activity of These Cells during Subsequent Sleep Episodes. Constantine Pavlides and Jonathan Winson in *Journal of Neuroscience*, Vol. 9, No. 8, pages 2907–2918; August 1989.

Dependence on REM Sleep of Overnight Improvement of a Perceptual Skill. Avi Karni, David Tanne, Barton S. Rubenstein, Jean J. M. Askenasy and Dov Sagi in *Science*, Vol. 265, pages 679–682; July 29, 1994.

Reactivation of Hippocampal Ensemble Memories during Sleep. Matthew A. Wilson and Bruce L. McNaughton in *Science*, Vol. 265, pages 676–679; July 29, 1994.

Brain Gene Expression during REM Sleep Depends on Prior Waking Experience. Sidarta Ribeiro, Vikas Goyal, Claudio V. Mello and Constantine Pavlides in *Learning and Memory*, Vol. 6, pages 500–508; 1999.