Introduction

D. Lehmann

Zurich, Switzerland

The description of the conditions which limit a certain function can help to outline its mechanisms. Limits to conventional learning appear to be set by sleep - in spite of many commercial companies which make money on the opposite assumption. Or, is it indeed a contradictory assumption that one can learn during sleep? Is there possibly a type of learning, poorly tested by common experimental procedures, and related to the acquisition of material in early childhood, which is camouflaged later by apparent amnesia? Learning per se still is understood poorly, and there are many open questions to this theme. Some have been brought up in this symposium. The papers read during this symposium present the problems of learning in relation to sleep from different angles - from electroneurophysiology and experimental animal physiology to pathological physiology and psychiatry. It is realized that important aspects are left out, e.g. such as biochemistry and membrane physiology. However, we hope that our multi-faceted overview will be a useful résumé, and that it will serve as stimulus for future work.

A. Invited Papers

Information Processing during Sleep

H. L. Williams

Minneapolis, Minn., USA

Several current models of human information processing posit a sequence of distinct stages which link input to output [e.g., Atkinson and Shiffrin, 1968; Glanzer, 1971]. Thus, an item of information first goes
through preliminary processing at a sensory-perceptual level. Encoding and simple categorizing operations, which involve storage of information over very short periods of time, occur during this stimulus pre-processing stage [Sperling, 1960]. Then the item, or information about the item, enters a short-term, limited capacity buffer memory (STM) where it resides for varying periods of time depending on experimental conditions. If the item is not displaced from STM by new items coming in (and thereby lost from the system), it can be registered in long-term memory (LTM). The accuracy, strength and permanence of the record in LTM probably depends on a ‘consolidation’ process which lasts for at least several minutes, and possibly several hours. If consolidation is blocked, the item may fade from LTM. If consolidation does occur the item may, nevertheless, be inaccessible to interrogation. If retrieval is achieved, the final stage is response selection and execution.

What mechanisms of information processing normally available to the waking subject remain intact during sleep? It is useful to consider this question in relation to the sequential stage model just described.

Stimulus Pre-processing

Sensory Thresholds and Transmission

In general, with neutral stimuli such as clicks, flashes, electric shocks and the like, the intensity required to elicit behavioral responding during sleep is higher than that needed for reliable responding during waking. This well-known fact has been taken as evidence that in sleep, either sensory thresholds are raised or conduction in afferent pathways is diminished. However, several investigators, recording various physiological and behavioral responses to sensory input, have concluded that neither psychophysical thresholds nor the information handling capacity of sensory systems is necessarily impaired during sleep, at least in man [for recent reviews, see Koella, 1967, 1969]. For example, Williams et al. [1964] found that in stages 1, 2 and 3 of human sleep, simple acoustic stimuli no more than 5 dB above waking sensation threshold could evoke reliable EEG, autonomic and behavioral responses. Slightly higher intensities were usually required for sleep stages 4 and REM. This study showed further that for all three response systems, the magnitude of the reaction was a monotonic function of stimulus intensity.
Thus, the frequent failure to awaken the sleeping human with sensory stimuli whose intensity is above waking sensation thresholds is probably not due to raised thresholds at the periphery or impaired sensory transmission. The phenomenon requires some other interpretation.

Encoding of Sensory Stimuli

Koella [1969] pointed out that the arousal value of a stimulus depends on its quality as well as its strength. For example, weak stimuli that are novel or unexpected, are relevant to biological drives or have acquired significance (e.g., one’s own name, or the whimper of one’s child) can cause immediate awakening. Koella surmised, therefore, that during sleep, sensory analyzer mechanisms in the brain remain operative so that incoming signals can be categorized as ‘important’ or ‘unimportant’. The ‘watchpoint’ concept proposed by Soviet scientists is similar to Koella’s sensory analyzer [Svyadoschh, 1940]. There is now a great deal of evidence that in some stages of sleep, humans and animals can analyze and respond differentially to complex auditory stimuli. Moreover, as Svyadoschh [1940] asserted, the analyzer mechanism can be set prior to sleep. For example, differentiated responses acquired during waking to specific acoustic stimuli persist during sleep in both cats and humans [Buendia et al., 1964; Granda and Hammack, 1961; Williams et al., 1966]. Evidence is contradictory, however, as to whether behavioral responding can occur without associated EEG signs of arousal. Whereas, in cats, Buendia et al. [1964] found that discriminated motor responses were invariably preceded and accompanied by EEG desynchrony, Williams et al. [1966], reported that in humans many motor responses to designated auditory signals occurred without prior signs of awakening. Nevertheless, there seems to be no doubt that stimulus pre-processing and encoding phases can occur without prior awakening. Sleeping humans can follow instructions given prior to sleep to respond differentially to sounds, designated arbitrarily as ‘important’ or ‘unimportant’ [Zung and Wilson, 1961]. Moreover, during sleep human subjects can differentiate such complex auditory stimuli as spoken names [Oswald et al., 1960], sentences [Lehmann and Koukkou, 1971], or complex instructions [Evans et al., 1966]. Although differential physiological responses to simple stimulus parameters such as intensity occur in any stage of human sleep, it is difficult
during high-voltage S-sleep to elicit behavioral responses to any stimulus. For example, Williams et al. [1966], found instrumental motor responding only during stages 1, 2 and rapid eye movement sleep (REM), and Evans et al. [1966] were able to elicit more complex response sequences only during stage REM. The reasons for this difficulty are not known. The failure could be in the analyzer system, in the link between sensory and motor systems or in mechanisms which mediate the selection and execution of motor responses. For the latter possibility, Schicht et al. [1968] found that discriminated autonomic responses such as heart rate and peripheral vasoconstriction could be regularly elicited during extinction trials in stage 4 sleep. This finding, if confirmed, is evidence that signal analysis is still possible in high-voltage S-sleep and that previous failures to observe discrimination during stage 4 occurred because that state is not compatible with the execution of certain kinds of responses. Schicht et al. used simple acoustic stimuli, however, and other evidence suggests that more complex stimuli such as words may not be discriminated in stage 4. Working in the same laboratory, and using the same autonomic measures, Frazier et al. [1968] found differential responding to the subject’s own name in stage 2, but not in stages 3 or 4.

Results presented thus far indicate that instructions and items of information acquired prior to sleep remain in LTM. Furthermore, brain mechanisms must be available during sleep for transduction and transmission of acoustic information, interrogation of LTM, feature testing and classification. These encoding and categorizing operations take time, and therefore require a viable mechanism for short-term storage. Can information which enters STM during sleep be transferred to LTM and consolidated, thus becoming available for later recall? With a few exceptions, such as those of Beh and Barratt [1965], Weinberg [1966] and Evans et al. [1966], the majority of controlled studies appear to rule out sleep learning. Thus, unless transient waking (or EEG a-activity) occurred, information presented to the subject during EEG sleep was not recalled the next day [Simon and Emmons, 1955; Koukkou and Lehmann, 1968; Tani and Yoshii, 1970; Bruce et al, 1970]. Yet the early studies by Jenkins and Dallenbach [1924], confirmed recently by Ekstrand [1967], indicate that recall of verbal material is better after interpolated sleep than after interpolated waking. There is controversy, however, concerning the rôle of the various stages of sleep and of wakefulness in this process. Portnoff et al. [1966], presenting words to subjects awakened from non-REM sleep, found that subsequent morning recall was much better for subjects
kept briefly awake than for those who returned immediately to non-REM sleep. These investigators concluded that non-REM sleep inhibits consolidation, and that in the Jenkins and Dallenbach studies the material learned was probably consolidated prior to sleep onset.

Judging from a recent comment by F. Rubin [1970], Soviet scientists concerned with sleep learning would probably disagree with the conclusion that non-REM sleep inhibits consolidation. Their state of ‘hypnopedic sleep’ is like the Dement and Kleitman stage 1, where speech signals evoke intermittent alpha activity against a background of relatively low-voltage, mixed frequency electroencephalogram ‘...’ The purpose of further repetitions during the fluctuation of drowsiness and light sleep is the consolidation of the ... training material which is also aided by the sleep which follows this process’ [Rubin, 1970]. However, as was pointed out by Portnoff et al. [1960], non-REM sleep might have two effects on memory. That is, if it occurs after consolidation is more or less complete, it may reduce retroactive interference and thus help conserve the stored information. If it occurs immediately after the learning experience, it may block the consolidation process before the memory has attained stability.

There are several lines of evidence which imply that REM sleep is compatible with, possibly even necessary for, consolidation of memories in LTM. Among these are the following: (1) specific deprivation of stage REM apparently interferes with consolidation of material learned prior to sleep [Empson and Clarke, 1970], and (2) complex instructions administered during one REM episode are remembered and correctly executed during later REM periods of the same night, during REM periods of succeeding nights and even in REM-period tests conducted 5 months later [Evans et al., 1966]. On the other hand, Evans et al. found no systematic evidence of recall either during interpolated non-REM sleep or wakefulness.

The Evans et al. study [1966], if replicated in other laboratories, is direct evidence that all stages of information processing can be accomplished during stage REM. The study also raises some interesting possibilities for future research in this field. Firstly, the results resemble the dissociation phenomena found in state-dependent learning experiments. That is, a behavior that is learned when a subject is drugged often fails to appear during subsequent nondrug test trials, although it reappears whenever the drug is readministered. Conversely, if information is acquired in a nondrugged state, it may not be retrievable during the drugged state [see Overton, 1972, for a recent review]. No current attempt to explain the dissociation phenomena associated with change of state is completely satisfactory, but questions
regarding the status of information which a subject cannot recall should be raised in every memory situation in which retrieval is less than perfect with conventional tests.

Aids to Sleep Learning

Are there techniques to enhance the acquisition of information during sleep and its accurate retrieval upon awakening? Several interesting possibilities include: (1) the use of subjects with special aptitude; (2) the use of special preparatory instructions and training materials which ‘set’ the subject to process specific forms of input; (3) the use of special stimuli, modified for sleep learning, and (4) the use of methods, recently described in the literature on verbal learning, for aiding retrieval of previously unrecalled information.

Subject Selection

The first study by Orne’s group [Cobb et al., 1965] on performance during stage REM used two groups, one of which was composed of highly hypnotizable subjects. All 4 subjects in the latter group acquired the designated behavior whereas none of the 4 low-hypnotizable subjects did so.

Presleep Set

Orne’s group [Evans et al., 1966] examined the value of hypnotic suggestion administered prior to sleep for setting the subject to remember events which would occur during REM sleep. ‘One subject who responded to most suggestions during both the first and second nights, and who had complete amnesia while awake, ... was hypnotized deeply before sleeping; during this time it was suggested that he would recall all that was said to him during that evening. While asleep, he responded to old and new suggestions, and later, when awakened, recall for that evening’s procedure was complete.’ [Evans et al., 1966, p. 2]. Svyadoshch [1940] also reported that hypnosis was a useful adjunct to sleep learning. It is of course possible that hypnosis is not necessary, that simple instructions to remember would suffice. Bliznichenko, the leading Soviet exponent of sleep learning, does not use presleep hypnotic suggestion. He does give the subject brief practice on the material to be learned prior to sleep onset. He has devoted considerable
effort to the construction of stimuli which he believes have optimal acoustic characteristics for sleep learning [Bliznichenko, 1964].

Aided Retrieval

If information is actually in store but cannot be recalled in conventional tests, it is still possible to probe the subject’s memory regarding the nature and extent of that storage. One method is stimulated recall [Fox and Dahl, 1971] where prompters (moderate strength associates of the required responses) are used to evoke previously unrealled responses. Recognition tasks are another, and familiar, way to stimulate recall. However, it seems from studies by Bahrick [1969] and by Fox and Dahl that the loci of effect for the two methods, prompting and recognition, are different. Prompting appears quite specific for stimulating the selection of a correct response, whereas recognition techniques enhance the retrieval of associative links.

Summary

During human sleep, sensory thresholds are not markedly raised and transmission of sensory data to the brain is not grossly impaired. Moreover, in some stages of sleep, analyzer mechanisms continue to function so that signals can be processed, encoded, categorized and stored. Discriminated physiological and motor responses acquired prior to sleep can persist during sleep, and in some stages of sleep, instructions delivered during waking can be followed throughout the night. This indicates that the analyzer system has access to and can interrogate LTM.

However, the number and complexity of operations available to the signal analyzer may be a decreasing function of the period and amplitude of the background EEG. For example, during stage 4 sleep, the brain continues to respond differentially to physical parameters of stimuli, such as intensity, but specific motor responses to designated stimuli are difficult to elicit. The reasons for this difficulty are not yet understood. That is, the failure could be due to impairment of the analyzer system, of sensorimotor linkages or of mechanisms mediating the selection and execution of motor responses. The results of one recent study imply the latter explanation. Discriminated autonomic responses conditioned prior to sleep were regularly elicited during extinction trials in stage 4. Thus, stage 4 may be incompatible with certain classes of responding but not with the informational analysis of simple signals. On the other hand, more complex stimuli such as words may not be discriminated in stage 4. Frazier et al. [1968], using the same autonomic measures found differential responding to the subject’s own name in stage 2, but not in stages 3 or 4.
Stimulus pre-processing, interrogation of LTM, and selection of responses take time, and thus require the operation of STM. Does sleep impair the transfer of information from STM to LTM? The answer seems to be yes and no. At least two investigators, monitoring sleep with EEG, have reported that simple conditioned responses could be acquired and sustained during unbroken non-REM sleep. However, complex stimuli such as words and sentences are apparently retained for subsequent recall only if the a-rhythm is evoked during presentation of the message. Furthermore, the strength of consolidation is a positive function of the duration of the period of arousal induced by the message.

Stage REM, during which intermittent a-activity is usually seen, may be compatible with all stages of information processing. An exciting series of experiments in Martin Orne’s laboratory showed that during this stage the subject could be trained to execute complex motor responses to verbal signals, and that retention of this behavior could persist for at least 5 months. However, the responses could be elicited only in stage REM. During waking, the subjects had no recollection of the acquired skill, and the verbal signal did not elicit the designated response. This state-dependent effect is well known in drug experiments. Its presence here suggests that the frequent failure in well designed experiments to elicit recall of information presented during sleep may be due to impairment of retrieval operations rather than retention. If so, prompting and recognition techniques described in studies of verbal learning might be useful adjuncts to standard tests of retention. Finally, the experience of Orne’s laboratory, and of the Soviet investigators as well, suggests that sleep learning studies could be improved by (1) selecting subjects with high aptitude (e.g., hypnotizability), and (2) using techniques for ‘setting’ the subject to attend to, acquire and retain information during sleep.


Learning and EEG during Sleep in Humans

D. Lehmann and Martha Koukkou

Zurich, Switzerland

The scalp EEG pattern which exists shortly after the input of information into the central nervous system is a good predictor of the fate of the information. This implies that the functional state of the brain is sensitively expressed by the scalp EEG. If EEG slow-waves existed during the critical period, the fed-in information may lead to evoked responses, discrimination, logical decision, and even to motor reactions [e.g., Okuma et al., 1966; Williams et al., 1964, 1966; Zung and Wilson, 1966], but no permanent
Supported by NIH Grants NB 06038 and 1 R03 MH 18178-01.