lateral-field animals. We can speculate that this would cause their eyes to accommodate more and that accommodation might conceivably lead to changes in eye growth. Others have made similar speculations (*16*). Another possibility is that near objects cause increased convergence of the eyes. We have shown by recording eye movements that frontal-field birds make more divergent and convergent saccades than do normal birds, whereas lateral-field birds make fewer (*17*). One could imagine that increased convergence might affect ocular growth. Alternatively, retinal location may be an important variable. If the absence of objects in the lateral visual field either causes extreme accommodation or otherwise has a particular effect on eye growth, it would account for the similar degree of myopia in the frontal-field animals and in those monocularly deprived of form vision.

In normal animals, each of the dimensions of the eye that affect refraction shows substantial interindividual variation (*7*). If, at least in birds, myopia is caused by increased accommodation for close vision, this etiology could be a clue to a developmental feedback mechanism that normally assures that the eye grow toward correct refraction. Thus an animal that starts out somewhat hyperopic would tend to accommodate more than a normal animal, which might cause a pattern of ocular growth that would tend to decrease the hyperopia.

The effects of different visual experiences on neuronal connectivity in the brain are well established. Our results suggest that the morphology of the eye is influenced not only by the absence of visual experience but also by the nature of the specific visual experiences.

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9. The eyes of deeply anesthetized birds were photographed from above, oriented so that the optical axes were nearly horizontal. The pupil, which appeared in the photographs as a narrow ellipse, was superimposed on one of a set of standard ellipses, and the distance along the short axis of the ellipse from the center of the pupil to the corneal surface was measured. By knowing the ellipse shape that fit the pupil, we could calculate a trigonometric correction for the slight tilt of the eye. Although this technique ignores the distortion caused by viewing the pupil through the peripheral cornea, this error probably does not affect the relative differences between the experimental groups both because the peripheral corneal curvature was approximately the same in all groups and because the results obtained were similar to those obtained with other measurement techniques (Fig. 3).
10. The apparent slight hyperopia of the normal animals is probably in part a systematic error of retinoscopy of small eyes [M. Glickstein and M. Millodot, *Science* **168**, 605 (1970)]. Pigeons, however, are somewhat hyperopic in their lateral visual fields (*11*), where these measurements were made.
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17. J. Wallman, in preparation.
18. We thank C. Ledoux for assistance in all phases of the work, L. Blumenstein for help with the anatomical measurements; Dr. E. Giglio and the New York State College of Optometry for assistance with the ultrasound measurements, and D. Pratt for statistical assistance. Figure 1 was drawn by J. Fevoli. Supported by a City University of New York faculty research award program grant and a NIH biomedical sciences subgrant. J. Turkel was a National Eye Institute postdoctoral fellow.

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Ethology of Sleep Studied with Time-Lapse Photography: Postural Immobility and Sleep-Cycle Phase in Humans

Abstract. *Human sleep is characterized by episodes of immobility punctuated by major postural shifts. The organization of this motor activity was shown with a combination of photographic and electroencephalographic recording to be periodic and related to the electroencephalographic sleep cycle. The amount of immobility as measured photographically was positively related to subjective estimates of the goodness of sleep.*

Since the discovery of the mammalian sleep cycle, it has been known that major body movements occur predominantly before and after the periodically recurrent episodes of desynchronization of the electroencephalogram (EEG) and rapid eye movements (REM) (*1*). Direct observation, photography, and videotape analysis have shown that many of these phase-locked movements are postural shifts (*2*). Implications of this finding are (i) that the longest periods of postural immobility are associated with the non-REM (NREM) phase of the cycle and (ii) that inactivation of the motor apparatus is a phase-locked event. It follows that postural immobility, easily detectable in time-lapse photographic data, could by itself provide a simple quantitative read-out of the state of the brain oscillator controlling the REM-NREM sleep cycle. In addition, the total duration of immobility so measured might be correlated with objective or subjective estimates of sleep duration and thus serve as a simple but valid measure of sleep quantity or quality. If so, time-lapse photography might be a means of conducting field studies of sleep behavior that could be related to the findings of the sleep laboratory. Here we report the results of our first efforts to explore this possibility.

Observation of 50 individuals sleeping at home and being photographed at 15-minute intervals revealed epochs of apparent postural immobility lasting from 45 to 75 minutes and recurring with a periodicity of 75 to 120 minutes (*3*). We wished to determine the relationship of these epochs to the EEG sleep cycle and to verify the apparent absence of movement in the photographs by continuously monitoring muscle activity on the polygraph. The sleep of each of six subjects (three male and three female, between the ages of 20 and 30) was therefore recorded in the sleep laboratory for four consecutive nights with an electroencephalograph (Grass model 6). A camera (Zeiss Contarex) was mounted on the ceiling over the bed and connected to an electronic timer. The camera was housed in a Lucite box lined with polystyrene foam for sound attenuation. Black-and-white pictures (35mm) of the subject were taken automatically every 15 minutes throughout the night; a time ex-

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posure of 8 seconds and a 10-W nightlight plugged into a wall socket gave satisfactory photographic results with Tri-X film. The camera timer was connected to the polygraph so that each shutter activation pulse appeared on the recording, and a digital clock was placed next to the bed so that unequivocal matching of the polygraphic and photographic data could be made. No subject detected activation of the camera during a night's sleep.

The EEG recordings were scored according to the Kales-Rechtschaffen criteria for sleep stages (*4*). We use the terms NREM to refer to (synchronized) EEG stages I through IV and REM to (desynchronized) EEG stage I with rapid eye movements. Each EEG sleep cycle consisted of progressive EEG synchronization (descending NREM sleep) followed by progressive EEG desynchronization (ascending NREM sleep). A cycle was defined as the time between sleep onset and the end of the first REM period and, thereafter, between the ends of successive REM periods. We also recorded the electromyogram of the submental muscles and noted the magnitude and time of occurrence of movement artifacts in this and in the EEG channels (*2*). Postural immobility was quantified by examining the photographic contact sheet for each subject and identifying any adjacent photographs without evident movement of the trunk, head, or proximal limbs. Two consecutive photographs without any such movement were scored as one epoch (≥15 minutes) of consolidation (*5*). The electrographic data from each night of sleep were plotted on graph paper in the usual format for sleep stage display, and the episodes of postural immobility were shaded below (Fig. 1A).

A total of 147 episodes of immobility occurred during the study. The majority of these (61.2 percent) were two-frame epochs (≥15 minutes). A total of 57 prolonged episodes of immobility, three frames or longer, occurred. All but four of these began and ended in the same cycle. This striking evidence of the time-limited nature of postural immobility points to its coordination with the EEG cycle. Of the episodes of immobility, 54 began in descending stages II and III of NREM sleep; of these, 50 also ended in the same NREM sleep sequence; only four episodes were associated with the ascending NREM stages of the cycle. Of the 50 NREM episodes, 41 began in descending stages II or III and ended in stage IV; the nine others occurred in later-night cycles when only stage II was present. From this simple analysis, it appears that postural immobility as we define and measure it is related to the EEG sleep cycle and is associated mainly with the descending NREM phase of the cycle.

In order to further detail this phase relationship, sleep cycles were averaged by computing the percentage of time occupied by the sleep stages for each cycle that included immobility. Since many of the late-night cycles consisted only of stage II, only the first three cycles of each night were analyzed. Of the 41 early-night NREM episodes, 25 (or .6) were associated with prolonged (>30 minutes) periods of immobility. If time 0 marks the onset of stage II, the onsets of immobility for each episode were determined and plotted as the percentage of cycle completed (Fig. 1B). Most episodes (29, or .7) began in descending stage II. The end of epochs of immobility was similarly determined with time 0 designating the end of stage IV or of stage III if there was no stage IV. Some episodes ended in descending NREM stages, but the subsequent steeply rising curve indicates that the majority of episodes (27, or .7) ended in stage IV and ascending NREM stages III, II, and I, and an inflection point occurs at the onset of stage IV.

To obtain a single numerical estimate of the amount of immobility in a given nights sleep, a "consolidation index" was then computed for each night; this measure was simply the ratio of the number of immobile epochs to the total number of epochs asleep. Having observed the temporal association between immobility and descending stage of NREM sleep, we expected to find a high positive correlation between this value and the percentage of stages III and IV, but our data indicated no such correlation in the data from normal subjects ($\gamma = -.12$). Since all but one of our normal subjects were good sleepers (less than 15-minute latency to sleep onset and more than 7.0 hours duration), the weakness of correlation may be due to the lack of variability in the data as well as to the unreliability of the 15-minute interval method in measuring immobility absolutely.

With the goal of obtaining greater variability in these sleep variables and to test the possibility that the photographic method might be sensitive to a clinically important difference in those variables, we conducted a pilot study of six self-described poor sleepers (>30-minute latency to sleep onset, <6.5 hours total sleep, >5 awakenings per night). When the pooled data from the poor sleepers were compared with the age and sex-matched normal subjects, the consolidation index was less (.34) in the poor sleepers than in normal ones (.55). Subject mean values for the two groups did not overlap (Fig. 2) and the difference between the group means was significant (one-tailed t-test, $P < .005$). Thus, pho-

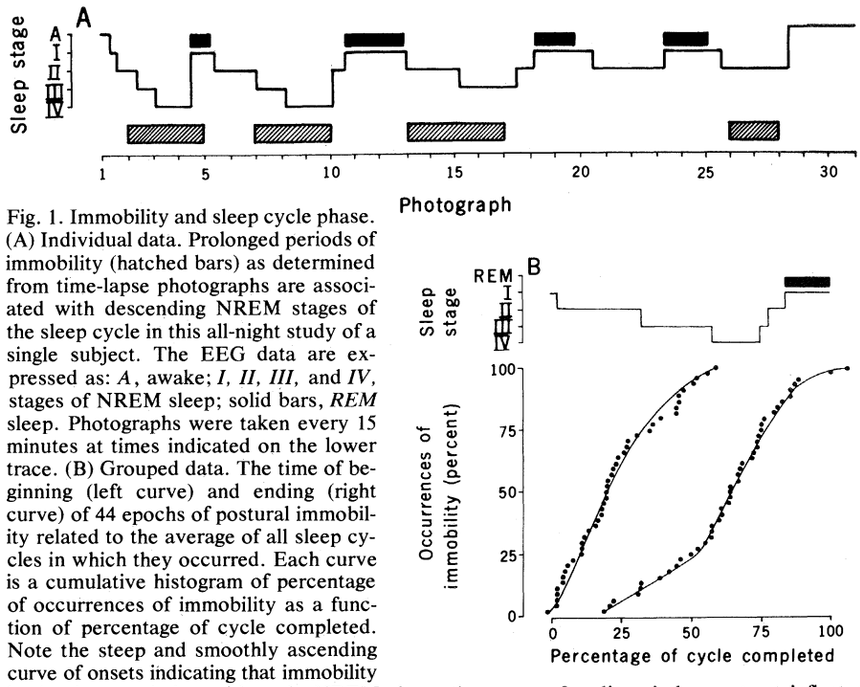

Fig. 1. Immobility and sleep cycle phase. (A) Individual data. Prolonged periods of immobility (hatched bars) as determined from time-lapse photographs are associated with descending NREM stages of the sleep cycle in this all-night study of a single subject. The EEG data are expressed as: *A*, awake; *I, II, III,* and *IV,* stages of NREM sleep; solid bars, *REM* sleep. Photographs were taken every 15 minutes at times indicated on the lower trace. (B) Grouped data. The time of beginning (left curve) and ending (right curve) of 44 epochs of postural immobility related to the average of all sleep cycles in which they occurred. Each curve is a cumulative histogram of percentage of occurrences of immobility as a function of percentage of cycle completed. Note the steep and smoothly ascending curve of onsets indicating that immobility begins in association with early NREM sleep; the curve of endings is by contrast inflected sharply at stage IV onset which indicates that the process controlling posture shifts is activated well before the end of NREM sleep (*8*).

tographically measured immobility not only temporally labels cycle phase but can also give a sensitive and clinically useful measure of sleep.

Postural immobility generally begins in descending stage II and ends in stage III or stage IV, just prior to the ascending limb of the EEG sleep cycle. That is to say, time-lapse photographs taken at 15-minute intervals can detect a motor correlate of the progressive EEG synchronization of NREM sleep. Immobility may therefore reflect some fundamental process of the brain during sleep, which simultaneously and similarly "deactivates" both the cerebral cortex and the motor apparatus. Major postural shifts begin quite early in stage IV, that is, well before cortical activation is evident in the EEG. This apparent dissociation of motoric and EEG activity may be related to certain sleep "pathologies" such as somnambulism and enuresis, which have been characterized as disorders of arousal because they represent motor behavior in the absence of EEG activation and conscious awareness (*6*). It is also possible that this surprisingly early occurrence of movement is related to early activation of reticular brainstem neurons, which, in the cat, anticipates REM sleep by 5 minutes (*7*). (This phase lead of 15 percent is comparable to the inflection point in the human data of Fig. 1B.)

Even though the duration of immobility is underestimated by our 15-minute-interval technique, it can both approximate the time of occurrence of NREM sleep and be correlated with subjective estimates of goodness of sleep. Although the photographic technique cannot possibly duplicate the detailed and precise data of the sleep laboratory, we believe that a greater knowledge of the characteristics of immobility may enable us to obtain useful data about a night's sleep with a single roll of film. This technique is inexpensive and simple to apply. The data are rapidly and reliably scored. Thus, widespread and extended field uses of the procedure are feasible.

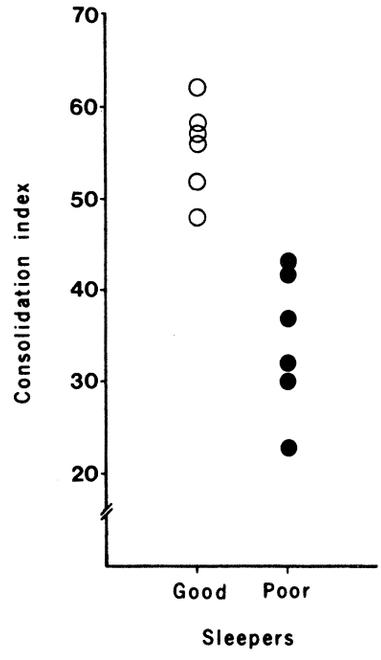

Fig. 2. The immobility indices of six "good" and six "poor" sleepers. The consolidation index is the percent of adjacent frames showing no major posture shifts. Good sleepers spend more time immobile than poor sleepers. There is no overlap in the subject means and the group means differ significantly.

Since it is now possible to record quantifiable aspects of a subject's sleep in the comfort of the home rather than in the sleep laboratory, the behavioral scope of sleep research could be broadened to include person-to-person, behavior-to-behavior, and species-to-species interactions. Our anecdotal home studies have already revealed quantifiable interactions between the sleep of man and wife, between their presleep activity and subsequent sleep, and between their sleep and that of their pets (*3*). We also foresee use of the method in documenting the most common of all sleep complaints, insomnia. In sum, we see the technique as opening the way to an ethology of human sleep behavior that could provide new insights into the behavioral, functional, and clinical significance of the sleep cycle.

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5. As a check on the reliability of the method, all photographic records were scored by two observers; interrater agreement was +.97. As a check on the sensitivity of the method we have also performed two studies with 7.5- and 4-minute intervals; decreasing the interval duration increases the number of movements detected and lengthens the absolute duration of the periods of nonmovement, but it reveals no previously undetected posture shifts within the epochs of immobility. While admittedly insensitive as an absolute measure, the 15-minute-interval data give a valid relative index of immobility, cycle phase, and sleep duration.
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8. To derive this graph, 44 EEG cycles were normalized by setting their total duration equal to 100 percent. We then expressed the time of each stage transition relative to the total duration of the cycle in which it occurred, summed all times, and divided the total by 44. To derive the curve of onset of immobility, the time at which the photographic data indicated the onset of a period of immobility was expressed relative to the time of occurrence of the transition from stage I to stage II in the cycle in which it occurred. To derive the curve of the end of immobility, the time at which the photographic data indicated that a period of immobility had ended was expressed relative to the time of occurrence of the transition from stage IV to stage III in the cycle in which it occurred.
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