may exist in an anatomically nondistinct form, its functional existence made evident only by removal and implantation experiments.

The application of high hydrostatic pressure to *Tigriopus* in the naupliar stages may be damaging a primordial organ or gland which is necessary for male differentiation. Without the influence of a male-determining structure the larvae become females. Evidence that the primary effect of pressure is not upon a biochemical product, such as a gonadotropin, but is on the site of production of a product, appears from the fact that pressurization occurred for only 2 hours. It seems reasonable to assume that any biochemical entity destroyed during this time could be resynthesized after depressurization.

The fact that the copepodid stage is insensitive to conversion may indicate maturation and insensitivity of the hypothetical androgenic gland. An alternative hypothesis is that pressure may be altering the function of genes responsible for male determination. Evidence for pressure-induced gene alteration has been reported in *Neurospora* by McElroy and de la Haba (*7*) and in *Serratia* by Palmer (*8*).

The exact mechanism of pressure-induced sex conversion may not be accessible to further study in *Tigriopus* because the small size of the larvae and adult restrict the precision of endocrinological experiments.

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Oxygen Consumption Rate and Electroencephalographic Stage of Sleep

Abstract. *In five male subjects, and a total of 15 man-nights, oxygen consumption rate ($\dot{V}_{O_2}$) was related to stage of sleep, as defined by electroencephalograms. Gross periodic variations which paralleled change in stage of sleep were discernible in analogue metabolic records. Computations revealed significant differences ($P < .01$) between all stages with $\dot{V}_{O_2}$ highest in stage I REM (dreaming sleep), least in stages III and IV (deep sleep), and intermediate in stage II (light sleep).*

Since the first report that visual dreams were accompanied by a low-voltage, fast electroencephalogram (EEG) and rapid eye movements (stage I REM) (*1*), a number of workers have studied the relationship between physiological indices and EEG stage of sleep. Kamiya noted that pulse and respiration were most rapid and irregular during stage I REM (*2*). Snyder *et al.* reported that blood pressure is higher and fluctuates more than in other stages of sleep (*3*). Evarts found cortical discharge rates to be highest during stage I REM sleep, almost approaching those of wakefulness (*4*).

Nocturnal patterns of gross energy expenditure have also been described, but thus far without reference to EEG recordings (*5–7*). The present study seeks to clarify the relationship between the rate of oxygen consumption ($\dot{V}_{O_2}$) during the night and the level of sleep as reflected by the EEG.

Determinations were made on five subjects for a total of 15 man-nights. The group comprised five males, ranging in age from 19 to 35, with a mean of 26 years. All subjects were caucasian and in good general health. Each reported to the laboratory at his usual bedtime for three consecutive nights, during which measurements were obtained under conditions of natural sleep. The subjects slept on a comfortable bed in a temperature-controlled metabolic chamber adjacent to the instrument laboratory. The EEG patterns were recorded from the right frontal and parietal areas by means of monopolar, silver-disc surface electrodes and a six-channel Grass Polygraph, model P7. Electrooculograms were similarly measured with electrodes placed at the outer canthus of each eye. Body movements were recorded by a transducer placed on the bedspring approximately at the level of the lumbar region of the body.

Respiratory exchange was measured continuously during sleep by means of an automatic gas analysis system similar to that described by Buskirk *et al.* (*7*). In this system the subject's head was enclosed in a specially constructed plastic hood, through which ambient air was drawn at a constant rate of 80 liter/min (approximately eight times ventilation volume). A sample of the mixture of ambient air and expired gases was diverted through paramagnetic and infrared gas analyzers for simultaneous analysis of oxygen and carbon dioxide content. The results of these analyses were converted into electrical outputs and written out to provide continuous and permanent analogue records. Values for rates of oxygen consumption were computed from the data by means of standard respiratory equations, after conversion

Table 1. Comparison of $\dot{V}_{O_2}$ in stages of sleep throughout the night (pooled data for 15 man-nights). Means are given with standard deviations. Only continuous stages lasting 15 minutes or more were used in this analysis. The fact that t is positive signifies that x is greater than y.

Stage of sleep			Mean $\dot{V}_{O_2}$ (cm³/min)		t value*	Level of significance
x	vs.	y	x	y		
I REM	vs.	II	228 ± 25	220 ± 27	3.82	$P < .01$
I REM	vs.	III + IV	228 ± 25	214 ± 26	6.64	$P < .001$
II	vs.	III + IV	220 ± 27	214 ± 26	3.09	$P < .01$

* The t-test was computed as follows (*13*): $t = (\bar{x}_1 - \bar{x}_2)/Sp[(1/N_1) + (1/N_2)]^{\frac{1}{2}}$, where: $Sp = [(N_1 - 1)S_1^2] + [(N_2 - 1)S_2^2]/(N_1 + N_2 - 2)$; $S_1^2 = \Sigma (x_{t_1} - \bar{x})^2/(N - 1)$; $\bar{x}_1$, $\bar{x}_2$ are means of sleep stages being compared; and N_1, N_2, are number of 5-minute observations taken in each stage. The significance levels quoted are for a two-tailed test.

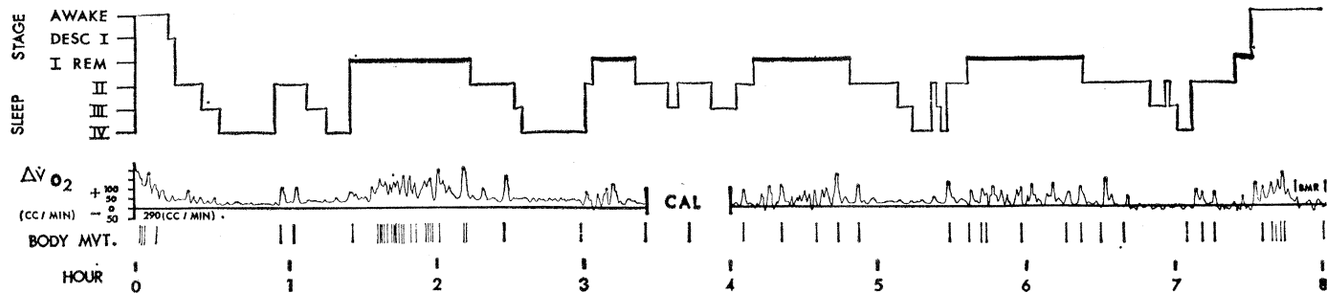

Fig. 1. Changes in oxygen consumption ($\Delta\dot{V}_{O_2}$) during a typical night for one subject. Values for oxygen are in cubic centimeters per minute relative to a reference line that represents the basal oxygen consumption level of 290 cm^3/min (41.27 kcal m^{-2} $hour^{-1}$) for this individual. This slightly raised basal $\dot{V}_{O_2}$ reflects the relatively elevated overall level of metabolism during the previous night. Stage of sleep and body movements are also represented. *CAL* marks the instrument calibration period, during which time the subject continued to sleep uninterrupted.

of the analogue to digital data, and correction to standard conditions of temperature, pressure, and saturation. For purposes of statistical analysis, the metabolic data of a given night were treated as a series of consecutive 5-minute segments, for each of which the average $\dot{V}_{O_2}$ value (oxygen consumption in cubic centimeters per minute) was calculated. The EEG records were scored for stage of sleep and matched by time with the respective metabolic values. The EEG was also treated as a series of 5-minute epochs, each scored according to the stage predominating at the beginning of the period. If more than two different stages occurred within a 5-minute interval, the segment was scored as a blank and was not used.

The criteria for EEG scoring were those of Dement and Kleitman (*8*), and Dement (*9*). According to these, stage I REM consists of low-voltage, fast activity accompanied by rapid eye movements; stage II is characterized by the presence of spindles and "K" complexes on a low-voltage background; in stage III, high-voltage, slow waves appear, with some spindling superimposed; in stage IV the high-voltage delta waves predominate; descending stage I is stage I without REM's, and occurs while falling asleep (for example, after a body movement or period of wakefulness); and body movements are considered brief episodes of waking. For statistical reasons, only stages lasting at least 15 minutes (thereby providing a minimum of three values for $\dot{V}_{O_2}$) were used for the metabolic comparisons. To conserve the data, stages III and IV were grouped together.

Averaged across all nights, the proportions of time in each stage of sleep were: stage I REM, 26 percent; stage II, 40 percent; stages III and IV, 30 percent; and descending stage I, 4 percent. These values were within the ranges reported elsewhere in the literature (*10*), with slight differences probably attributable to the system of scoring in sections of 5 minutes and elimination of periods with several transitions, usually at the expense of stage II.

Figure 1 is a typical metabolic record of moment to moment relative changes in $\dot{V}_{O_2}$ during sleep. Transient shifts and cyclical variations in $\dot{V}_{O_2}$ are clearly discernible. The stage of sleep is also plotted in the figure, and it is evident that changes in stage of sleep are accompanied by variations in the pattern of oxygen metabolism.

The nature and direction of these variations are summarized in Table 1, which compares mean values for oxygen consumption in all subjects according to the stage of sleep. Significant differences ($P < .01$) were found between all stages, with the highest rate of oxygen consumption during stage I REM, the least in stages III and IV, and intermediate levels during stage II; $\dot{V}_{O_2}$ was found to be greater during periods of wakefulness than in any stage of sleep.

Table 2. Comparison of $\dot{V}_{O_2}$ in contiguous stages of sleep (pooled data for 15 man-nights). Means are given with standard deviations. Only continuous stages lasting 15 minutes or more were used in this analysis, and arrows indicate direction of change. A positive t signifies that x is greater than y; a negative t, that y is greater than x. The t-test was computed as in Table 1. N.S., not significant.

Stage of sleep			Mean $\dot{V}_{O_2}$ (cm^3/min)		t value	Level of significance
x	→	y	x	y		
I REM	→	II	228 ± 24	217 ± 28	3.52	$P < .01$
I REM	→	III + IV	243 ± 13	216 ± 10	4.04	$P < .01$
II	→	I REM	214 ± 27	231 ± 31	−3.99	$P < .01$
II	→	III + IV	233 ± 31	221 ± 25	3.07	$P < .01$
III + IV	→	I REM	209 ± 19	229 ± 20	−6.67	$P < .001$
III + IV	→	II	223 ± 37	231 ± 33	−1.39	N.S.

Table 3. Frequency and direction of differences in $\dot{V}_{O_2}$ with change in stage of sleep (pooled data for 15 man-nights). Only continuous stages lasting 15 minutes or more were used in this analysis and arrows indicate that changes in both directions are counted.

Stages of sleep		Frequency of change			
x	y	$x < y$ significant	$x < y$ not significant	$x > y$ not significant	$x > y$ significant
I REM	↔ I	1	5	19	13
I REM	↔ III + IV	0	0	18	14
II	↔ III + IV	1	8	14	6

While statistically significant, the differences obtained among stages of sleep were relatively small from a physiologic standpoint. This apparent low order of change is probably due to the fact that shifts in metabolic level with variation in stage of sleep are superimposed upon the overall nightly trend in $\dot{V}_{O_2}$. Oxygen consumption rate decreases during the early hours of sleep and rises toward morning (*5, 7*). Comparison of stages that are averaged throughout the night might therefore be expected to minimize existing differences.

To take into account the changing slope of $\dot{V}_{O_2}$, contiguous sleep stages were compared. Thus, the difference in $\dot{V}_{O_2}$ between a given stage and that which immediately preceded or followed it could be obtained. The results of these comparisons are presented in Table 2. The data confirmed the findings in Table 1, and the differences were generally of greater magnitude. Indeed, there were significant differences even if only the last 5 minutes of a given stage were compared with the first 5 minutes of the next stage.

Thus, perusal of the analogues and computations derived from the data make it clear that differences in rate of oxygen metabolism parallel the level of sleep as defined by EEG. If one wishes to define level of sleep in terms of metabolic activity, then these data confirm the equivalence of depth of sleep and EEG stage.

The differences reported have been calculated from pooled data on all subjects. While these differences generally held for each individual, not every shift within a given night was of significant proportions. Table 3 shows the frequency with which significant and nonsignificant changes in $\dot{V}_{O_2}$ occurred with a transition in stage of sleep. A number of factors may bear upon the large number of changes which do not reach the level of significance, and the occasional change in the direction opposite to that expected. An increasing number of body movements before a REM period (*11*) could at times obscure differences by increasing oxygen utilization prior to the change in stage. Acting in the opposite direction, periods of apnea during stage I REM (*12*) could also be responsible for the occasional lack of significant differences. Interindividual variation in patterns of metabolism during sleep (*5*) might also contribute to the lack of uniformity in results.

It could conceivably be argued that body movements throughout the night are responsible for all differences in $\dot{V}_{O_2}$ observed. While the relationship between physical activity and other variables during sleep is indeed little understood, it is our impression that such activity has not significantly affected the data. Major body movement artifact has been avoided by omitting sections in which more than two changes in stage occur, for example, awake going to descending I and then stage II. Additional bases for this impression are that differential variations with stage of sleep have been reported for other physiologic parameters when episodes of body movement were removed from comparisons (*3*), and that gross cyclical changes in $\dot{V}_{O_2}$ were noted in REM sleep when little evidence of body movement was present (see Fig. 1).

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Detection Thresholds as a Function of Interval Separation between Two Successive Targets

Abstract. *Detection thresholds for two successive targets varied systematically with the interval between the two pulses. At intervals of 10 to 30 milliseconds, and again at 80 to 200 milliseconds, the threshold was lowered as compared to that for a single target, while at a separation of 50 to 60 milliseconds, the threshold was raised.*

The relative energy required to attain threshold when two successive light flashes are used has been shown to be equivalent to that necessary for one light flash provided that (i) the integral, intensity × time, is the same for two as for one light flash and (ii) that the flashes occur within a certain critical period. These factors are embodied in Bloch's Law which states that for short pulses of light the Bunsen-Roscoe law of photochemistry applies to the human visual system (*1*). The changes in target detectability when the separation of two stimuli exceeds the critical period are presented in this report. The available evidence is conflicting. On the one hand, Davy (*2*) reported that threshold energy rises when two flashes are separated by intervals greater than the critical duration and, at a temporal separation of 0.5 sec, it is the same for each of the two flashes as it is for one flash. On the other hand, Clark and Blackwell (*3*) have reported that double-pulse targets separated by intervals exceeding the critical duration are more detectable than are the corresponding single-pulse targets. We have attempted to determine, in greater detail, the functional relationship between target detectability and the temporal separation between two targets.

Four adult males served as subjects. All were personnel of the laboratories and had normal or corrected vision. The apparatus consisted of a two-field mixing tachistoscope providing a distal stimulus at a constant illumi-