

which can also be expressed as

$$v = \alpha t' \left(1 + \frac{\alpha^2 t'^2}{4c^2}\right)^{-1} \quad (8)$$

or

$$v = (2\alpha x)^{\frac{1}{2}} \left(1 + \frac{\alpha x}{2c^2}\right)^{\frac{1}{2}} \left(1 + \frac{\alpha x}{c^2}\right)^{-1} \quad (9)$$

It follows from Eq. 9 that the kinetic energy of the space ship relative to S is

$$E = m_0 c^2 \left[\left(1 - \frac{v^2}{c^2}\right)^{-\frac{1}{2}} - 1 \right] = m_0 \alpha x, \quad (10)$$

where m_0 is the rest mass of the space ship.

We shall denote the proper time of the observer in the space ship as τ , and find the relationship between t' and τ without involving the arguments of the general theory of relativity, which will also throw new light on the physical significance of the proper time.

It seems reasonable to assume that the most significant units of time for us are the periods of atoms we are made of. For, if the periods of atoms were to change, the rates of chemical reactions would also change, and the process of aging within our bodies would proceed at a different rate. Thus, in order to measure how much different observers have aged between two given events, each observer must assign the same value to the periods of atoms in his own frame of reference. For simplicity, let us confine our attention to the period of a hydrogen atom, which according to the semiclassical Bohr model is given in an inertial frame of reference by

$$T_0 = \frac{2\pi\hbar}{mc^2} \left(\frac{4\pi c\hbar}{e^2} \right)^2. \quad (11)$$

Now the basic equations of electrodynamics are invariant under the conformal transformations, but this invariance is obtained by assuming that the rest mass m of a particle transforms into a different rest mass m' . Therefore, to the occupant of the space ship the period of a hydrogen atom in the space ship is given by

$$T'_0 = \frac{2\pi\hbar}{m'c^2} \left(\frac{4\pi c\hbar}{e^2} \right)^2. \quad (12)$$

We must replace t' by a new time variable τ such that in terms of τ the period of the hydrogen atom in the space ship acquires the value shown in Eq. 11 for the occupant of the space ship. This can be achieved by defining τ by the relation

$$d\tau = \frac{m'}{m} dt'. \quad (13)$$

Since under the conformal transformations the rest mass transforms as (3)

$$m = m' (X'^2 + Y'^2 + Z'^2 - c^2 T'^2), \quad (14)$$

we obtain

$$d\tau = \frac{dt'}{X'^2 + Y'^2 + Z'^2 - c^2 T'^2} \quad (15)$$

or, putting $x' = y' = z' = 0$ for the space ship,

$$d\tau = \frac{dt'}{1 - \frac{\alpha^2 t'^2}{4c^2}}. \quad (16)$$

We can obtain a similar relation for the proper distance for the occupant of the space ship by requiring that each observer assign the same value to the Bohr radius of the hydrogen atom in his own frame of reference.

By integrating Eq. 16 we get

$$\frac{\alpha t'}{2c} = \tanh \frac{\alpha \tau}{2c}, \quad (17)$$

so that Eqs. 4, 5, and 8 can be expressed as

$$t = \frac{c}{\alpha} \sinh \frac{\alpha \tau}{c}, \quad (18)$$

$$x = \frac{c^2}{\alpha} \left(\cosh \frac{\alpha \tau}{c} - 1 \right), \quad (19)$$

$$v = c \tanh \frac{\alpha \tau}{c}, \quad (20)$$

which are identical with the usual relativistic results (8). Further, using Eqs. 4 and 8, we obtain from Eq. 16,

$$d\tau = \left(1 - \frac{v^2}{c^2}\right)^{\frac{1}{2}} dt, \quad (21)$$

which again is in agreement with the well-known result that the relationship between $d\tau$ and dt is the same as if the space ship were moving with a constant velocity v with respect to S .

It is also interesting to note that we can derive from Eq. 1 the relations

$$(X^2 + Y^2 + Z^2 - c^2 T^2) (X'^2 + Y'^2 + Z'^2 - c^2 T'^2) = 1 \quad (22)$$

and

$$\frac{dX^2 + dY^2 + dZ^2 - c^2 dT^2}{X^2 + Y^2 + Z^2 - c^2 T^2} = \frac{dX'^2 + dY'^2 + dZ'^2 - c^2 dT'^2}{X'^2 + Y'^2 + Z'^2 - c^2 T'^2} \quad (23)$$

whence it follows that

$$dx^2 + dy^2 + dz^2 - c^2 dt^2 = \frac{dx'^2 + dy'^2 + dz'^2 - c^2 dt'^2}{(X'^2 + Y'^2 + Z'^2 - c^2 T'^2)^2}. \quad (24)$$

According to the general theory of relativity, the above relation can be interpreted as meaning that while the metrical tensor has the Minkowskian

values in the frame of reference S , it has quite different values in the frame of reference S' . In particular, the g_{44} component of the metrical tensor in S' is

$$g_{44} = \frac{1}{(X'^2 + Y'^2 + Z'^2 - c^2 T'^2)^2}, \quad (25)$$

so that the proper time in S' is given by Eq. 26:

$$d\tau = (g_{44})^{\frac{1}{2}} dt' = \frac{dt'}{X'^2 + Y'^2 + Z'^2 - c^2 T'^2}, \quad (26)$$

which agrees with Eq. 15. Thus, the conformal transformations can be regarded as a special case of the general relativistic transformations of the space and time coordinates. We have also shown that the physical definition of proper time, in terms of atomic periods, is in complete agreement with the ideas of the general theory of relativity (9).

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8 May 1961

Persistence of a Photosynthetic Rhythm in Eucleated Acetabularia

Abstract. The unicellular alga *Acetabularia* was found to show a diurnal rhythm in photosynthesis. This rhythm continued for at least three cycles in constant light and temperature, and hence can be considered endogenous. Plants from which the nucleus had been removed by severing the basal rhizoids showed no modification in the photosynthetic rhythm over a number of cycles. The nucleus is, therefore, not immediately essential for the maintenance of rhythmicity in *Acetabularia*. Conversely, a mechanism for sustaining time-keeping must exist in the cytoplasm.

Endogenous diurnal rhythmicity, well known in a wide variety of multicellular plants and animals, has also been demonstrated in populations of unicellular organisms, for example, *Euglena* (1),

Gonyaulax (2), and *Paramecium* (3). With the additional observation that rhythms in photosynthesis and cell division persist in single isolated cells of *Gonyaulax* (4), it may be concluded that the mechanism of time-keeping can be contained within a single cell and does not require interactions with

other cells or tissues. The possibility that the control mechanism may be associated with specific subcellular components has been largely unexplored, although Ehret (5) found no evidence for involvement of the micronucleus in the control of time-keeping in *Paramecium*.

We have recently observed an endogenous diurnal rhythm in the photosynthesis of *Acetabularia*, thus making it possible to pursue studies of this problem with unusually favorable material. As shown by Hämmerling (6), this large unicellular alga contains a single nucleus which can readily be removed by severing the basal rhizoids. Enucleated plants can be maintained vegetatively for protracted periods and will grow and regenerate caps, while photosynthesis and respiration are unimpaired (7). Here we report evidence for the endogenous nature of the photosynthetic rhythm in *Acetabularia major* and preliminary studies on the rhythm in enucleated plants.

Juvenile and adult specimens of *Acetabularia major* (8) were collected from fringing reefs at Thursday Island, Queensland, Australia, and held for periods of up to 6 weeks in the laboratory (9). The plants were maintained in filtered sea water, which was renewed daily, and were exposed to subdued natural daylight. The photosynthetic rates were determined at high light intensities in natural sea water at 25°C; single plants with caps or groups of ten plants which had not yet formed caps were used in these measurements. Oxygen evolution was measured according to the microvolumetric method of Scholander *et al.* (10), but the potassium hydroxide cups were not used. Samples were illuminated from below with incandescent light of approximately saturating intensity (1500 ft-ca). The photosynthetic rates of the same samples were determined at noon and midnight on consecutive days over the experimental period. Between measurements, depending on the experiment, the plants were returned to the holding conditions described above, or they were maintained under constant conditions of temperature ($\pm 1^\circ\text{C}$) in the dark or in low-level illumination (30 ft-ca). In enucleation experiments, the bases of the plants were severed with a razor, either with or without a tie distal to the cut. In the case of the older plants with caps, the rates of photosynthesis were not significantly altered by the removal of the basal portions. Young plants, however,

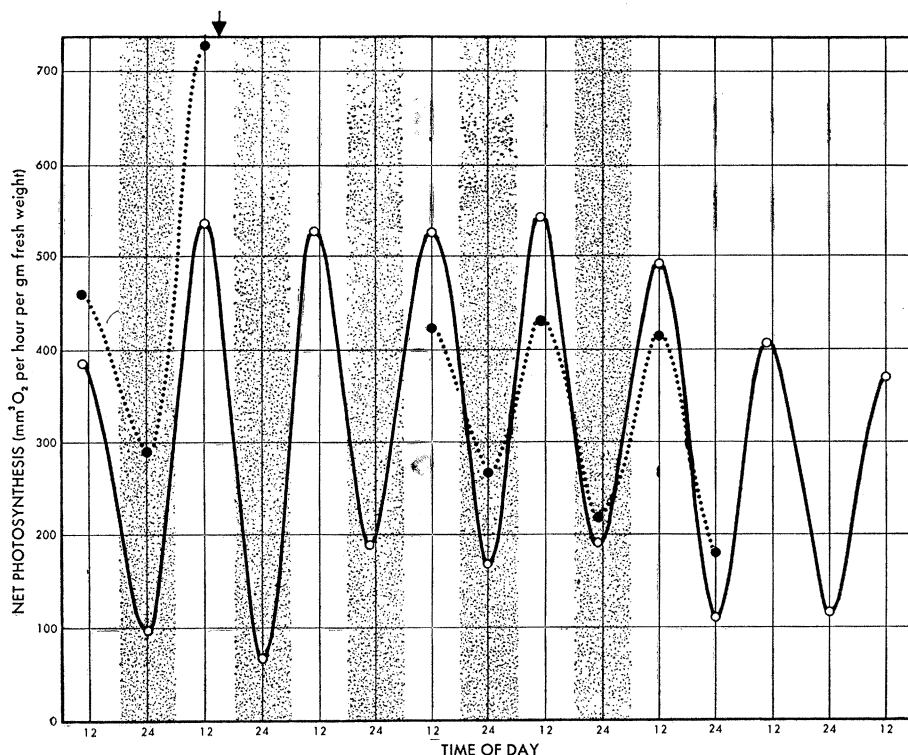


Fig. 1. Diurnal rhythm in photosynthesis in *Acetabularia major*. Plants were maintained in natural light during the first 5 days of the experiment, and then in continuous light (30 ft-ca) for the remainder. Night is indicated by a shaded bar. The oxygen evolution of a group of ten juvenile plants without caps (dotted line and solid circles) and of one plant with a cap (solid line and open circles) is shown before and after the removal of the nucleus. The time at which the base of the plants was removed is indicated by an arrow at top of figure. Net oxygen evolution was measured over a 30-min period at saturating light intensity (1500 ft-ca) and 25°C.

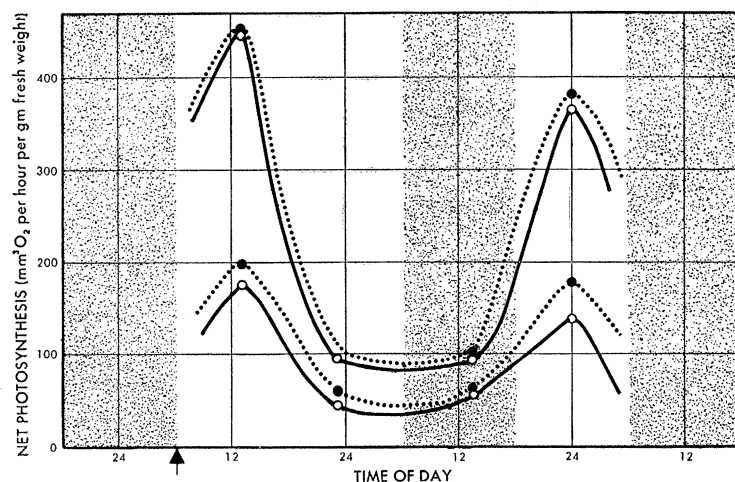


Fig. 2. Resetting the diurnal rhythm of photosynthesis in *Acetabularia crenulata*. During pretreatment, plants with nuclei (solid line and open circles) and plants without nuclei (dotted line and solid circles) were maintained under conditions similar to those described for Fig. 1. The regular light-dark schedule was then inverted (arrow on the abscissa) by interposition of a double light period. In both groups of plants this resulted in resetting of the photosynthetic rhythm so that the maximum occurred during the following light period. The two upper curves represent measurements for single plants with large caps, and each of the two lower curves represent measurements for five juvenile plants with small caps. Photosynthesis was measured as in Fig. 1.

showed a slight initial reduction in the photosynthetic rate, possibly because of damage to the fragile upper portions at the time of cutting. Localization of the nucleus in the rhizoidal part of the plant is well established for other species of *Acetabularia* (*A. mediterranea* and *A. crenulata*) (11). A similar position for the nucleus in *A. major* was indicated in specimens stained with Feulgen's reagent or methyl green-pyronin (12).

A marked diurnal periodicity in photosynthesis was observed in both juvenile and capped plants maintained in natural light. In both cases the maximum rates occurred at about local noon and were approximately five times greater than the night values. Representative data are presented in Fig. 1 without correction for respiration. Measurements of respiratory rates (in the presence of potassium hydroxide) at noon and at night, however, gave values of only 6 and 8 percent, respectively, of the noon rates of net photosynthetic oxygen production.

The endogenous nature of this rhythm was established by observations that, at constant temperature, the photosynthetic rhythm persisted for at least several days in plants maintained in continuous light of low intensity (Fig. 1) and for one cycle when the plants were maintained in darkness. After enucleation, the rhythm in photosynthesis continued unaltered both in juvenile plants and in those with caps (Fig. 1). This was true of plants maintained either in alternating light and darkness or in constant light.

In a recent extension of these studies to *Acetabularia crenulata*, collected from the Florida Keys, a similar situation was observed. Enucleated plants showed a persistence of the endogenous photosynthetic rhythm characteristic of intact plants. In addition, it was found that the rhythm of enucleated, as well as intact, plants could be reset by inversion of an artificial light-dark schedule (Fig. 2).

These results lead to the conclusion that the nucleus is not required for the immediate maintenance of time-keeping in *Acetabularia*. In this organism, processes in the cytoplasm are able to control both the period and the phase of the endogenous diurnal rhythm in photosynthesis (13).

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Effect of Ribonuclease on Retention of Conditioned Response in Regenerated Planarians

Abstract. Conditioned planarians were transected and allowed to regenerate in a ribonuclease solution or in pond water. Heads which had regenerated in ribonuclease displayed a retention level equal to that of head and tail sections which had regenerated in pond water. However, tails regenerated in ribonuclease performed randomly although they could be retrained to criterion.

Various data suggest that the neurophysiological mechanism of memory consists of two classes of process: (i) a short-term process, perhaps consisting of reverberatory electrical activity, and (ii) a long-term process, by which neural excitability patterns are maintained by some sort of structural alteration. As radio isotope exchange data on brain compounds have accumulated, it has become apparent that these compounds seem to be characterized by rather rapid rates of turnover. In order to reconcile the persistence of memory with this lability of brain chemistry, it seems logical to search for a substance capable of maintaining a structural modification by imposing an experientially specified configuration on molecules being built in neural tissue. Imposition of the additional requirement that this substance be cytoplasmic in locus directs

attention to ribonucleic acid (RNA). Essentially similar conclusions have been suggested in theoretical speculations by von Foerster (1) and Hydén (2).

Some experimental data seem compatible with this suggestion. Brattgård (3) has demonstrated a relationship between RNA synthesis and stimulation in retinal ganglion cells. Morrell (4) has demonstrated histochemically an increase in RNA concentration which is a result of prior excitation. Kreps (5) has reported differentially increased turnover of RNA in the cortical receiving area of the conditioned stimulus after elaboration of conditioned responses in the dog. In earlier work, John, Wenzel and Tschirgi (6) observed that injection of ribonuclease solution into the lateral ventricle of cats interfered with performance of pattern discrimination for food but not with a conditioned avoidance response to visual or auditory stimuli. The anatomical and chemical complexity of the preparation posed formidable obstacles to the gathering of control data necessary for unambiguous interpretation of these results. Rather than attempt to cope with these complexities, it seems desirable to devise a simpler preparation.

Recent research on the planarian has demonstrated that this comparatively simple organism is capable of learning both a classical conditioned response and a T-maze (7-9). Of particular relevance to our present concern was the finding that when cut in half and allowed to regenerate, both the head and tail sections display equal savings scores in both types of situations (8). Since there is cephalad dominance in these animals, the tail sections have in some manner apparently transmitted the effects of learning experience to the regenerated anterior portion. Experiments in our own laboratory, with the classical conditioned response, have confirmed the above findings (10). These various considerations suggested to us the possibility that RNA might play a role in the transmission of an acquired structural configuration from the trained portion to the regenerating tissue. Conditioned tails, regenerating in the presence of ribonuclease, might be expected to produce anterior portions with a depleted or altered RNA structure, perhaps due to influences exerted at the regenerating interface. Such an organism might then have a naive dominant head. Conversely, since trained heads have only a nondominant tail to re-