in Y_i at a small fixed distance from x_i we may write for the concentration $C_S(y_i)$ of S,

$$kCs\,(y_i) = \bar{R}\,(c_i) + \frac{U'}{(A)^{1/2}} \sum_{j \neq i} \frac{\bar{R}(c_j)\frac{A}{N}}{d(y_i,x_j)}$$

Finally, suppose that each cell c_i moves in the direction bringing $kC_S(y_i)$ closer to K. Now, since the distribution of $\bar{R}(c_i)$ converges to the original distribution $D(R(x))$ the cell structure will evolve in the direction of the organ shape provided a metastable impasse is not reached.

The application of the concept of an $r(x_i)$ code to embryology not only leads to the quantitative "field" theory sketched above but predicts as well the clumping seen during early stages of reorganization of experimentally dispersed embryonic tissues.

The neurophysiological application of the above ideas involves identifying the figure F with a subset of cells in a nucleus G and the rates of firing of the cells x_i with the values $r(x_i)$. Suppose the rate of firing of a cell is the sum of the values of its excitation and its inhibition if this sum is positive and zero if the sum is negative. Suppose all cells in the pattern F have excitation K and all other cells have zero excitation. Suppose that the inhibition of any cell x_i is equal to the sum of inhibitions from other cells x_j and that the inhibition I_{ij} of cell x_i by cell x_j is proportional to the rate of firing of x_j and inversely proportional to the distance $d(x_i,x_j)$ between the two cells. That is,

$$I_{ij} = -\left(W\frac{A}{N}\right)\frac{r(x_j)}{d(x_i,x_j)}.$$

If we let W, the distance coefficient of spread of inhibition, depend on the area A of F according to,

$$W = \frac{U}{A^{1/2}},$$

then we have,

$$r(x_i) = K + I_i$$
$$= K - \frac{U}{(A)^{1/2}} \sum_{j \neq i} \frac{r(x_j)\frac{A}{N}}{d(x_i,x_j)}.$$

Hence the rates of firing of cells of G are structurally determined by F according to Eq. 1. Then, if axon branches of the cells x_i of G constitute its efferent projection the distribution function $D(r(x_i))$ of the rates of firing of the efferent fibers of G is a relative invariant of the shape of the figure F with respect to size and position of F within G. It should be pointed out that since the information of such a signal is carried purely by the distribution function it is ideal for transmission of information over nonaddressed channels. A distribution type code and suitable decoding system have previously been suggested for the auditory system, but for this system the initial coding problem is much more straightforward (*1*). Finally, a spatial function much like the one defined in this report has been reported in the visual system of the horseshoe crab (*2*).

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Perturbations in Perigee Height of Vanguard I

Abstract. The effect of solar radiation pressure on the perigee height of satellite $1958\beta_2$ (Vanguard I) has been considered. Previous consideration of the effect of the third harmonic and the lunar and solar gravitational perturbations left an unexplained discrepancy between the observed and calculated values of perigee height. The inclusion of the effect of radiation pressure leads to close agreement between the orbit data and the theoretical results for Vanguard I.

We have extended the previously developed theory of gravitational perturbations to include the effects of solar radiation pressure (*1*, *2*). The theory leads to an analytical development of the long periodic perturbations in the orbital elements. The applications of the results of this theory to the Vanguard I satellite indicate that solar radiation pressure will produce a variation in the perigee height of this satellite with a period of ~850 days and an amplitude of 1 or 2 km. This effect accounts almost completely for the observed variations in perigee height when combined with the previously determined solar and lunar gravitational perturbations (*3*) and the effect of the third harmonic (*4*).

The results of the calculation for Vanguard I are shown in Fig. 1. The radiation pressure calculation was based on an estimated acceleration of 9.7×10^{-6} cm/sec^2, which is obtained by using the assumption of specular reflection, a solar constant of 2.0 cal/cm^2 per minute, an effective cross-sectional area of 308.4 cm^2, and a mass of 1456.7 gm. The effects of reradiated and reflected light and of shadowing by the earth were considered negligible in a first approximation.

The data for the perigee height of Vanguard I are indicated in Fig. 1 by circles. Curve A represents the results of the analytical development of solar and lunar perturbations acting on the satellite (*5*, *6*). It is seen that curve A departs from the observed values of perigee height by several kilometers over the course of two years.

Curve B contains the results of the present calculation in which solar radiation pressure is included. The agreement between curve B and the data is now within the scatter of the experimental points, with the exception of an oscillation of relatively short period which becomes noticeable in the second year of observation.

The data shown in Fig. 1 were obtained by removing the effect of the third harmonic from the published values of perigee height. Each published datum is a determination of the Vanguard orbit elements from Minitrack readings for a 7-day interval. It is important to note that these Vanguard elements are not osculating elements, but are constants of integration of the orbit theory used. That is, if all the

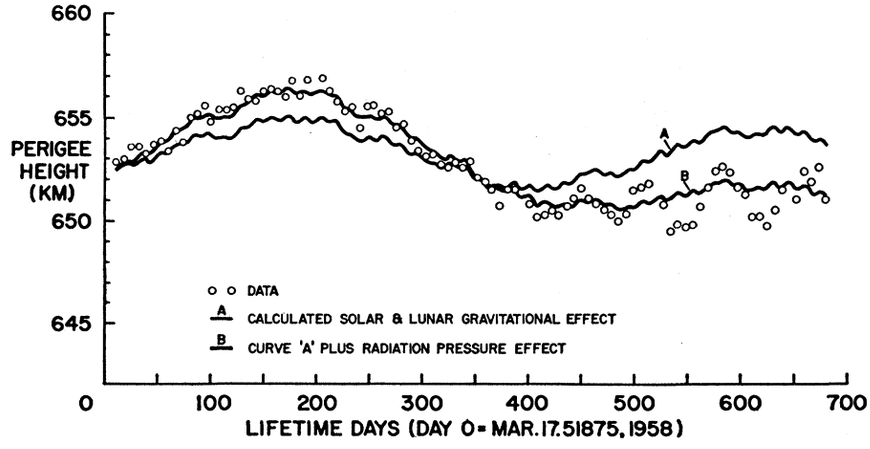

Fig. 1. Perturbations on perigee height of Vanguard I; the data are published orbital elements with the effect of the third harmonic removed.

forces acting on the satellite are represented in the program completely and accurately, these elements will remain constant. Hence, any variations which appear are the result of other forces such as atmospheric drag, inaccurate or neglected gravitational terms, and the radiation pressure considered in the present note.

It appears surprising at first that the effect of solar radiation on the satellite orbit should be comparable to that produced by the gravitational attraction of the sun, since the gravitational force of the sun is larger than the force of solar radiation by a factor of 10^5. However, the major part of the solar gravitational effect disappears because the earth undergoes approximately the same acceleration as the satellite; that is, the net effect of the geocentric solar gravitational force around a complete orbit is nearly zero. In the case of radiation pressure, the resultant acceleration of the earth is many orders of magnitude less than that of the satellite.

We have also applied this theory to the 100-foot balloon satellite which is planned for launching by the National Aeronautics and Space Administration as a communications experiment. This satellite represents a high ratio of area to mass, and is therefore one in which the effect of solar radiation pressure will be substantial. We find that for representative values of the orbit elements of the balloon satellite, solar radiation can in fact produce orbit perturbations on the order of hundreds of kilometers in a few months.

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2 March 1960

Virus Production by Subcultured Monkey-Kidney Cells

Abstract. Cultured monkey-kidney cells, like the rabbit cells previously studied, have a relatively high folic acid requirement for growth. Subcultures can be readily prepared if the medium is supplemented with a high level of the vitamin. The sensitivity of the resultant cells to poliovirus and the yields of virus obtainable with them are the same as with primary cultures.

Examination of primary cultures (*1*) from various rabbit organs revealed a common, relatively high folic acid requirement for growth, a property not shared with the permanently cultivable mammalian cells tested. Thus, with the primary cells, 10^{-3} to 2×10^{-3} μmole of folic acid per milliliter was needed to provide a maximum growth rate and yield, while a concentration about 1/100, or less, of the vitamin satisfied the cell lines (*2*). With high levels of folic acid, further cultivation of the primary rabbit cells became readily achievable for at least an additional six or eight doublings.

These observations suggested a possible application of some value to the virologist. While monkey-kidney cells cultured directly from the animal provide luxuriant growth, subcultures not initiated with extremely large inocula grow poorly, and they rarely, if ever, provide cells useful for virus studies. It was of interest, therefore, to determine whether the growth of subcultured monkey-kidney cells is enhanced by high levels of folic acid and whether the resultant cells can well support virus multiplication.

To test this, primary cultures of trypsin-dispersed monkey-kidney cells were prepared in a medium similar to that of Healy *et al.* (*3*), containing 15 percent of beef serum. Subcultures were prepared with populations which allowed about a sixfold increase in cell numbers, and growth and virus studies were made with the various cultures.

The growth response of the monkey-kidney cells to a high level of folic acid was similar to that of the rabbit cultures. With no further supplementation of the medium (1.4×10^{-5} μmole of folate per milliliter), growth of the subcultured primary cells occurred initially with a doubling time of about 36 hours but ceased before a confluent sheet was made. Replacement of the medium with fresh medium did not stimulate further growth. On the other hand, in the same medium supplemented with folic acid (2×10^{-3} μmole/ml), the doubling time during the exponential phase of growth was only 22 to 23 hours, confluent monolayers were formed, and these growth characteristics were maintained during the two additional transfers studied. Furthermore, the ability of the subcultures to support poliovirus multiplication was not detectably diminished (Table 1). Similar results were obtained with cells subcultured in a lactalbumin hydrolyzate—5 percent beef-serum medium enriched with a high level of the vitamin.

Table 1. Poliovirus production in subcultures of monkey-kidney cells. Plating efficiency was estimated as plaque-forming units per milliliter of a single pool of Parker type 1 virus, by a procedure similar to that of Dulbecco and Vogt (*4*). Virus yield per cell was measured by inoculating cultures containing 5 million to 6 million cells with the Parker virus at a multiplicity of about 1. After 48 hours, the supernatant fluids were obtained by centrifugation, and the yields of plaque-forming units were determined (*5*).

Monkey-kidney culture	Plating efficiency	Virus yield per cell
Primary	4.2×10^7	450
First transfer	9.4×10^7	470
Second transfer	2.2×10^7	240

As had been anticipated from studies with rabbit cells (*2*), it was found that in a medium containing glycine, the folic acid requirement of the monkey-kidney cells is completely replaceable by a mixture of thymidine and a purine (*6*).

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