ever, have found tetrodotoxin without effect on the Limulus RP (7, 8).

In addition, Duncan and Bonting quote our studies on the effects removing sodium from the extracellular fluid as evidence supporting their theory. They overlook our finding that the abolition of the RP is only transitory, even when the sodium substitute is a relative impermeant ion [for example tris(hydroxymethyl)amino methane and choline] (2) and they fail to show how this observation is consistent with ". . . the essential (sic.) role of the sodium permeability increase . . ." (1).

Because one can calculate from the Goldman equation any membrane potential desired by an arbitrary selection of the values for permeability coefficients and ionic concentrations, it is obvious that for such calculations to be relevant to any particular cell, one must employ values derived from the cell in question. Duncan and Bonting, however, have employed permeability and concentration values derived from squid photoreceptors and axons, which our preliminary results indicate are significantly different from Limulus photoreceptors. Furthermore, one must show that the light-induced permeability changes must reproduce the observed conductances. This Duncan and Bonting have failed to do. Moreover, it should be clear that the membrane conductance observed at any level of depolarization in the light should be greater than the conductance observed at that same level in the dark, if the permeability change caused the membrane potential changes which our results show clearly is not the case (2, figs. 1 and 2). This is to say that one must take into account the potential dependences or nonlinearities of the membrane characteristics in employing the Goldman equation. This also Duncan and Bonting have failed to do. We question, therefore, the relevance of their calculations.

Duncan and Bonting attempt to explain our results on the effects of inhibition of the sodium pump on the RP in terms of a depolarization of the membrane resulting from rapid changes in intracellular ionic concentration (1). First, our evidence is against a rapid change in ion concentration causing a depolarization. We observed that pump inhibition led to an intitial partial depolarization and abolition of the RP in a matter of minutes, which we ascribed to the inactivation of an electrogenic pump (3), followed over a period of hours by a steady and complete 6 JUNE 1969

depolarization which may be due to changes in ionic concentration of the kind proposed by Duncan and Bonting. Second, they propose that a depolarization with an increase in sodium conductance like that found during the production of an axonic action potential (9, p. 64) explains why pump inactivation reduces or abolishes the RP. In doing so, they imply that the RP is generated by the same membrane mechanisms as an all-or-none spike; however, it is well known and generally accepted that there are fundamental differences in the membrane mechanisms involved in graded, nonelectrically excitable, nonpropagated responses such as the RP or the end-plate potential and in all-or-none, electrically excitable, propagated responses like an action potential (10). Moreover, the data do not support Duncan and Bonting's explanation. Depolarization of the photoreceptor with current, by an amount equal to or even greater than that produced by pump inactivation, does not abolish the RP (7), as we also observed.

But even if the Limulus RP were similar to a spike, which it is not, our results contradict Duncan and Bonting's explanation. For example, increase in sodium conductance (sodium activation) associated with the onset of a spike is followed by a sodium inactivation which persists if the membrane potential remains depolarized, but this inactivation is removed if the membrane is hyperpolarized and the response is once again capable of being evoked (11). Therefore, in our experiments where the pump was inactivated with ouabain, the membrane partially depolarized, and the RP abolished, we should have been able to reestablish the RP by hyperpolarization. This was not possible (3). We actually performed the above experiment to rule out another possibility, namely, that pump inactivation had led a redistribution of ions such that the resting potential became equal to the equilibrium potential of the RP.

In conclusion, we see neither Duncan and Bonting's comment (1) nor our observations (2, 3) as supporting the CIM as the basis for the Limulus RP. As we noted in our papers, however, some complicated but as yet unformulated conductance change mechanism may underlie the RP (2, 3). Nonetheless, we still feel that the available data are accounted for more simply by alterations in an electrogenic sodium pump (3).

> T. G. SMITH, J. E. BROWN W. K. STELL, G. C. MURRAY J. A. FREEMAN

Laboratory of Neurophysiology, National Institute of Neurological Diseases and Stroke, National Institutes of Health, Bethesda, Maryland 20014

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## Selenodetic Implications of Mascons

The discovery by Muller and Sjogren (1) of mass concentrations at the circular maria on the moon has elicited a barrage of comment and interpretation in terms of lunar geologic evolution (2). Here I present the implications of the mascons for the selenodetic data analysis itself, as conducted at several space centers in the United States. For methods used in the past, the results are quite discouraging.

Plans for the Lunar Orbiter mission provided for two methods of data analysis. The first method was that used for

the earth satellites and consisted of estimating harmonic coefficients from the long-term variation in the orbital parameters (3). Unfortunately, the methods so suitable for sparse sightings, spread over a year or more for a rapidly spinning planet, were disappointing when applied to voluminous data packed into a few weeks or months about a relatively static body. Thus, most emphasis has been given to the second method-the "direct method" -in which the orbit parameters and coefficients of a truncated harmonic

Table 1. Proportional force error for truncation of harmonic series at n = 10; d, mascon depth; h, spacecraft height.

<i>d</i> (km)			
15	50	100	200
.98	.93	.82	.56
.93	.86	.73	.48
.83	.74	.62	.39
.61	.53	.43	.26
	15 .98 .93 .83 .61	<i>d</i> ( 15 50 .98 .93 .93 .86 .83 .74 .61 .53	d (km)           15         50         100           .98         .93         .82           .93         .86         .73           .83         .74         .62           .61         .53         .43

series are estimated simultaneously by a least-squares fit of the tracking data (4). Estimates made prior to the mission were that truncation at about the 5th degree should adequately represent the lunar potential. (Since the number of gravity parameters to be estimated increases with the square of the degree of the model, about 30 significant coefficients were anticipated.) But as actual data became available and was processed, it became clear that large systematic patterns remained in the data after a 5th-degree fit, so the degree of truncation was pushed out toward 10 (about 100 gravity parameters); but the same problems persisted. A third class of methods attempted involved modeling the moon as a finite collection of mass points or rings, but in the absence at that time of any clues as to the structure to be assumed, no progress was recorded.

As a result of the mascon discovery, three principal approaches have been suggested:

1) Extend the direct method by using harmonics only and consider models up to the 15th degree or so. This would more than double the number of gravity parameters over a 10thdegree model.

2) Determine harmonic coefficients by fitting a 15th-degree model to the gravimetric contours obtained by Muller and Sjogren. This is the quickest method suggested.

3) Extend the direct method by adding a set of "mascon parameters" (perhaps center-of-gravity and mass for each of the Muller-Sjogren mascons) to a low-degree harmonic model (perhaps 4th to 6th degree). One hundred gravity parameters would allow a 5thdegree model and about 16 four-parameter point-masses.

The following calculations indicate that the first two methods proposed are inherently incapable of accurately representing the moon-with-mascons gravity field for Apollo-type orbits (15 to 200 km). We treat the potential and force due to a point-mass acting on a

spacecraft directly above it. This is admittedly a worst-case calculation, but the results are discouraging enough to suggest that a global analysis would provide scant comfort.

Since Muller and Sjogren have demonstrated that the effect of the mascons is considerable, we tabulate only the proportional errors. We concentrate on the force, or acceleration, since it is measured more directly and exhibits the biggest errors.

So consider a point-mass (mascon) and a spacecraft at distances s and r, respectively, from the center of the moon, with the spacecraft directly over the mascon. The potential due to the mascon at the spacecraft is

$$P(r,s) = \frac{A}{(r-s)} = \left(\frac{A}{r}\right)_n \sum_{n=0}^{\infty} \left(\frac{s}{r}\right)^n \quad (1)$$

and the force is

$$F(r,s) = \frac{B}{(r-s)^2} = \left(\frac{B}{r^2}\right)_n \sum_{n=0}^{\infty} (n+1) \left(\frac{s}{r}\right)^n$$
(2)

The spherical harmonic series has the form

$$\left(\frac{1}{r}\right)_n \sum_{n=0}^{\infty} \left(\frac{1}{r}\right)^n S_n(\varphi,\lambda)$$
 (3)

where  $\varphi$  and  $\lambda$  are latitude and longitude. Comparing Eq. 1 and Eq. 3 we see that, for the contribution of the mascon.

$$S_n(\varphi,\lambda) = As^n$$

So if series Eq. 3 for the moon is truncated beyond the nth degree, then the error in the contribution of the mascons is the same as truncating series Eq. 1 at n, and the force error will be that of similarly truncating series (2). Letting  $P_n(r,s)$  and  $F_n(r,s)$  denote the truncated series, we compute the proportional errors as

$$p_n(r,s) = \frac{P(r,s) - P_n(r,s)}{P(r,s)} = \left(\frac{s}{r}\right)^{n+1}$$
$$f_n(r,s) = \frac{F(r,s) - F_n(r,s)}{F(r,s)} =$$
$$1 + (n+1)\left(1 - \frac{s}{r}\right) \left\{ \left(\frac{s}{r}\right)^{n+1} > \left(\frac{s}{r}\right)^{n+1} \right\}$$

Taking the lunar radius R as 1738 km, we compute the proportional force error  $f_n(R + h, R - d)$  for various depths d of mascon and height h of spacecraft for n = 10 (Table 1) and n = 15(Table 2). Here 15 km represents the perilune of the Apollo lunar mod-

Table 2. Proportional force error for truncations of harmonic series at n = 15; d, mascon depth; h, spacecraft height.

<i>h</i> (km)	<i>d</i> (km)			
	15	50	100	200
15	.97	.87	.69	.37
50	.87	.75	.58	.29
100	.71	.59	.43	.21
200	.42	.34	.24	.11

ule orbit, and 100 km the command module parking-orbit altitude. The references indicate that the mascons could be anywhere from on the surface to several hundred kilometers below the surface. We see from the tables that in most cases of interest a 15th-degree model (from whatever source) must "lose" over half of the mascon's effect. Of course, the force is not really "lost" -instead, the higher-degree effects would be spread over the lower-degree coefficients by the fitting process, thus the mascon would disturb not only the estimates of nearby orbits but distant ones as well.

The conclusion is inescapable that pure-harmonic models of the proposed dimensions cannot represent lunar gravity close to the surface; thus some sort of mixed model will probably be necessary, as the third approach suggests.

It is hard to specify a suitably reliable and flexible mixed model. From Muller and Sjogren's comments, which pictured deep, roughly spherical masses, it appeared that a center-of-gravity-plusmass description would suffice. But the consensus of the subsequent interpretation (2) seems to favor a wide, shallow puddle of denser material on or close to the surface. Finding an adequate parametric representation for such a mascon which will not exclude other possible structures seems to be a formidable task.

WILLIAM M. BOYCE Bell Telephone Laboratories, Inc., Murray Hill, New Jersey 07974

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10 March 1969

SCIENCE, VOL. 164