

global change in effective population size ( $N_e$ ) (which, like divergence time, is assumed to be similar for all proteins) or from changes over time in neutral mutation rates of individual proteins. Under the infinite-allele model of neutral alleles, the expected heterozygosity after  $t$  generations is given by:

$$H_t = H_\infty + (H_0 - H_\infty) e^{-t/(2N_e(1-H_\infty))} \quad (1)$$

where  $H_\infty$  is the steady-state heterozygosity and  $H_0$  the initial heterozygosity. It is easy to show by numerical analysis of this equation and equation (1) of Chakraborty and Hedrick that at steady state a change in  $N_e$  will affect the slope of the relationship between  $D$  and  $H$  but will not cause a positive intercept of the  $D$  axis. However, it is true that changes in  $\nu$  with time could result in intercepts of either the  $D$  or  $H$  axes. For example, a positive  $D$  intercept would be obtained if the low heterozygosity proteins originally had much higher global heterozygosity and, in moving to the present low values as a result of a reduction in neutral mutation rate, have accumulated more genetic distance than would have been predicted from the steady-state model on the basis of their present heterozygosity values. Yet such a *post-hoc* hypothesis is arbitrary and seems implausible. After all, one of the basic tenets of neutral theory is the assumption of constancy of neutral mutation rates for a given protein over long periods of time<sup>2</sup>.

Finally, we agree that the positive correlation between heterozygosity and genetic distance is precisely that expected under neutral theory assuming differences in neutral mutation rate among proteins. We have stated this elsewhere<sup>3</sup>. It was not, however, this aspect of the results which we wished to draw attention to as being difficult to reconcile with present neutral theory, rather the non-zero regression intercept and relatively high genetic distance of low heterozygosity proteins.

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## Measurements on a shock wave generated by a solar flare

MAXWELL AND DRYER<sup>1</sup> have criticized our radio-scattering observations<sup>2</sup> of the 18 August 1979 shock wave, on two accounts.

First, for the purpose of estimating the shock velocity using the Rankine-Hugoniot relations, Maxwell and Dryer argue that the value of post-shock velocity used should have been 1,250 km s<sup>-1</sup> instead of the 2,600 km s<sup>-1</sup> that we used. This leads to an inferred shock speed of 2,300 km s<sup>-1</sup> instead of 3,500 km s<sup>-1</sup>. While their arguments might be valid if the solar wind profile were obtained from point measurements, they do not apply to our path-integrated radio-scattering measurements. For the wind velocity deduced from radio-scattering measurements to represent the post-shock *in situ* velocity, a significant fraction of the radio line-of-sight path must be immersed in the post-shock gas. Thus, to estimate accurately the post-shock speed from the radio-scattering measurements, one must choose the maximum of the radio-scattering deduced velocity-time curve. Velocity points on the rising edge will systematically underestimate the true post-shock gas velocity, and, therefore, underestimate the inferred shock speed. Indeed, for a shock speed of 3,500 km s<sup>-1</sup>, a significant portion of the line-of-sight path is filled by post-shock material after 20 min, the observed rise time of the radio-scattering deduced wind profile (see Fig. 3c of ref. 2). Thus, 3,500 km s<sup>-1</sup> remains the best estimate of the shock speed at 13.1R<sub>0</sub>, within the limitations of the radio method (such as, not knowing the shock normal).

Second, Maxwell and Dryer also point out that the shock velocity based on the transit time from the flare region to 13.1R<sub>0</sub> should have been 2,350 km s<sup>-1</sup> instead of 3,509 km s<sup>-1</sup> (ref. 2). The shock velocity deduced<sup>2</sup> from the transit time was only a secondary estimate, and did not affect the conclusions of ref. 2. Moreover, a corrected estimate of 2,800 km s<sup>-1</sup> had already been published by Cane *et al.*<sup>3</sup>, who presented the first determination of the heliocentric dependence of the shock velocity in the heliocentric distance range 0.05–0.4 AU. These results were based on a combined analysis of the ISEE 3 interplanetary Type II burst drift rate and scintillation measurements of both the Pioneer 11 and Voyager 1 (ref. 2) radio signals.

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MAXWELL AND DRYER REPLY—We would like to point out that one cannot estimate an *in situ* shock velocity by using a plasma velocity other than the immediate post-shock value. Our concern is simply with the radio technique's ability to specify the post-shock velocity immediately behind the shock in the same sense that is presently done by *in situ* spacecraft.

Woo and Armstrong suggest above that "a significant fraction of the radio line-of-sight must be immersed in the post-shock gas". We believe, however, that their peak plasma velocity (Fig. 3c in ref. 1) represents some 'mean' value of the solar wind velocity in the disturbed plasma well behind the shock and not the immediate post-shock plasma velocity. Woo and Armstrong refer to the fact that "velocity points on the rising edge (of the plasma velocity-time curve) will systematically underestimate the true post-shock gas velocity". We point out that our estimate<sup>2</sup> of  $v_2 = 1,250$  km s<sup>-1</sup> makes adequate compensation in keeping with their point. Hence, if measurements by the radio technique involve uncertainties for such highly spatial- and time-dependent flow, then the uncertainty in the actual plasma velocity immediately behind the shock ought to include our value of 2,300 km s<sup>-1</sup> as well as their value of 3,500 km s<sup>-1</sup>. Thus, we suggest that the latter figure is not necessarily the 'best estimate'. Additional studies of this and other similar events by Woo, Armstrong, and other radio astronomers familiar with the radio method are needed.

Referring to their second point, we draw attention to Fig. 2 of ref. 3; from the points out to 75 R<sub>0</sub>, we deduce that the data are best fitted by a straight line that gives a constant shock velocity of ~2,300 km s<sup>-1</sup> rather than the 2,800 km s<sup>-1</sup> value that is now asserted by Woo and Armstrong. We are, of course, encouraged to notice that the 2,300 km s<sup>-1</sup> value for the velocity agreed so closely with the estimate given in our paper<sup>2</sup>.

Finally, a discussion such as this underlines the necessity for combining data sets and analyses of additional events before further progress can be made in this exciting topic of solar-generated travelling interplanetary phenomena.

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