X chromosomes and dosage compensation

SIR—D.A. Smith (*Nature* **315**, 103; 1985) uses the term "dosage compensation" to mean that effect on the rate of transcription of X-linked genes in the male which enables it to survive the lack of one X chromosome; X inactivation in the female is, then, a further compensatory step to enable *it* to get over the problem of overactive X-linked genes. By suggesting that evolution could have somehow "resolved" the situation arising from aneuploidy for an entire X chromosome in the mammalian male, G.P. Maroni (*Nature* **317**, 22; 1985) asks whether the inferences drawn by Smith are valid. Purely in terms of the physiology of gene action, precisely what evolution had to "resolve" is not clear: in the course of their extensive analysis of the problem of dominance, Kacser and Burns[1] have shown that — special cases apart — metabolic fluxes are extremely insensititve to whether an enzyme is represented by one structural gene or two.

I wish to draw attention to a point that usually is not taken into account. Sex chromosomes are expected to include one or more sex-determining genes. If the mammalian X chromosome indeed contains genes determining primary sex, what such genes might require is not dosage compensation but full expression, or even exaggeration, of the difference in dosage between XX and XY genotypes. Thus it can be argued that dosage compensation (in the usual phenotypic sense) is unlikely to be the primary reason for X inactivation. Is it possible that X inactivation has a function more vital than dosage compensation? I have suggested that sex determination may be such a function[2]. The observed dosage compensation of *G6PD*, *HPRT*, *PGK* and such other X-linked housekeeping genes would then be, in the evolutionary sense used by Maynard Smith[3], an effect of X inactivation, not its function. This model requires that a distinction be made between dosage compensation at the level of the phenotype and that which might render the effective copy number of particular X-linked genes equal between XX and XY genotypes. Details are given in ref.2.

In *Drosophila melanogaster*, the Bridges ratio, X/A, is central to both sex determination and X-chromosome dosage compensation. Sex-specific lethal mutations such as *mle* and *Sxl*[fl] affect both sex determination and dosage compensation, demonstrating that some genetic elements are common to the two processes[4,5]. Thus it appears that sex determination and dosage compensation may be two facets of the same regulatory process. A plausible genetic regulatory model has been proposed for intracellular measurement of the X/A ratio and the remarkable phenotypic effects of certain of these mutations[6]. An attempt has been made to interpret mammalian X inactivation in terms of this model, on the assumption that X inactivation also is based on some type of ratio measurement or intracellular counting of chromosomes[7].

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The Grand Menhir re-examined

SIR—Commenting on P.G. Bahn's alerting us[1] to C. T. LeRoux's discovery that the capstones of three tombs in Brittany once formed a single decorated 14m long menhir, one of the decorations being a carving of a *hache-charrue* (axe-plough), I suggested in *Scientific Correspondence*[2] that Le Roux's discovery requires a re-examination of the date and function of the over 20m long now fallen and broken menhir called the Grand Menhir Brisé. My suggestion assumed the validity of the assertion first made by R.S. Minot[3] and then by E. Twohig[4] that there is also a *hache-charrue* carved on the latter menhir.

I recently examined the Grand Menhir Brisé and could not discern a *hache-charrue* carved on it even after I checked my observations against the sketch by Minot in his 1965 article and against the small scale drawing furnished to me by Twohig. There are unevennesses on the surface of the granite of the second fragment of the Grand Menhir Brisé (counting the largest fragment as the first fragment) which may be interpreted as possibly depicting an axe head, but there is no indication that these are man-made rather than natural, and the presence of the rest of the alleged *hache-charrue* seems to depend upon the imagination of the beholder[5] (See *Hamlet*, Act 3, Scene 2, "Shape of cloud").

Twohig, in the course of her careful and thorough research, did not always find carvings reported by Minot to be genuine, (personal communication) and Minot's sketch of the alleged *hache-charrue* differs from Twohig's drawing in substantial ways, including not showing a loop on the haft. Because of its size and weathered nature, Twohig did not make a rubbing, photograph or full-scale tracing of the alleged carving, and the small scale drawing on which she bases the drawing in her book reflects what she saw but does not necessarily record what others will see.

One further observation should be made. LeRoux interprets the three granite fragment now serving as capstones of La Table des Marchands, the tomb of Gavrinis, and the tumulus of "er-Vinglé", as having once formed a single carved *menhir*. R.J.C. Atkinson suggests that the three granite fragments determined by LeRoux to once have been a single standing stone was a very long *capstone* which was later broken, its fragments then used as capstones in three separate tombs (personal communication). A very long capstone would be consistent with the shape of the stone when unbroken, and we know that dolmens were constructed which could utilize very long capstones, such as Le Grand Dolmen at Bagneux (Maine-et-Loire).

Atkinson points out that menhirs, unlike upright stones and capstones used in tomb construction, do not have carvings on them, except, in rare instances, for some markings at the base, and certainly not halfway up the menhir. In such event the date of construction of the Gavrinis tomb of about 5200 to 5000 BP would be irrelevant to the determination of the date of erection of the Grand Menhir, and a possible date of about 3600 BP initially proposed by Alexander Thom[6] and A.S. Thom in connection with their lunar observatory hypothesis would not be affected by LeRoux's discovery.

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