Reply to J. E. Morel's letter to the editor

Dear Sir:

We have read with interest the alternative explanation offered by Morel for the force velocity curve during lengthening. While not wishing to enter into a debate about Morel's theory of contraction in general, we prefer our original explanation of the behavior of muscle during stretch in terms of intersarcomere dynamics for the following reasons:

(*a*) Morel's explanation requires the assumption that the Fenn effect or some analogue of it applies during stretching. Indeed his original model is based very heavily on energetic measurements. While it is true that the energetics of stretching muscle are not well known, such measurements as there are do indicate that the dependence of heat generation on velocity for lengthening is different than for shortening. (For a discussion see Woledge, R. C., N. A. Curtin, and E. Homsher. 1985. *In* Energetic Aspects of Muscle Contraction, Monographs of the Physiological Society No. 41. Academic Press, London. 209–217.)

(*b*) The force velocity curve that Morel postulates for lengthening is of the same form as for shortening with a change in the sign of velocity and a new arbitrary choice of constants. It has a step in tension between slow shortening and slow lengthening. While the experimental relationship is certainly steep at this point, and is probably steeper for a sarcomere than for a fiber, it is definitely not infinitely steep. The shape of the Morel curve, though a plausible fit to the data, has quite a different shape from a curve of best fit to the data, being rather flat for lengthening velocities between zero and $-V_{max}$, and then falling off toward zero for greater stretch velocities.

(*c*) While agreeing that the rates of binding and releasing may well be different for lengthening than for shortening, we find the number of apparently arbitrarily chosen constants rather unsatisfying, particularly when such fundamental constants as the actin spacing are required to change substantially. As pointed out above, the formalism alone gives a shape which is not particularly appropriate, and virtually all the fit that is obtained comes from the choice of constants, without any constraints from the shortening region. While this does not disprove the model, it does make it less attractive.

(*d*) Morel's theory is not able to explain all the other phenomena that can be explained by intersarcomere dynamics, in particular the continued rise during stretch with a fall in stiffness, the permanent extra tension after stretch, muscle damage from eccentric exercise, and the variability of mechanical measurements on stretching muscle.

Furthermore, sarcomeres with the force-velocity curve postulated by Morel would certainly be instantaneously unstable during stretch, simply because the tension falls with increasing velocity. This means that extreme nonuniformity of lengthening would still occur in Morel's model. If it is going to occur anyway, why not use it to explain the observations? Our explanation involved no postulates other than the existence of some degree of nonuniformity in sarcomere lengths and/or strengths. We simply deduced that the observed behavior of muscle inevitably implies instability of sarcomere lengths during stretch, and then showed that such instability can explain many observed phenomena, without taking such a severe step as abandoning the idea that cross-bridges are responsible for the tension.

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