THE MUSCLE AS AN ENGINE

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Abstract: We speculate on principles governing energy conversion efficiency. It has appeared to many that muscles achieve higher efficiency than allowed by the Second Law of Thermodynamics (i.e., by Kelvin's formula for the efficiency of a reversible Carnot engine). However, when reinterpreted in terms of energy per degree of freedom rather than temperature, Kelvin's formula appears general enough to include heat engines, muscles, and pure mechanisms. As a result, it may be possible to achieve in man-made engines higher efficiency than would be supposed from conventional Carnot engine lore.

INTRODUCTION

We sometimes encounter statements of the genre: "Kelvin's formula for the efficiency of a reversible Carnot engine

$$e = 1 - T/T' \quad , \tag{1}$$

shows that the efficiency of every type of energy converter has a theoretical upper limit that cannot be exceeded." We wish to point out that Kelvin's result applies, not to every type of energy converter, but only to heat engines -- i.e., engines which operate by extracting heat from one reservoir which is at thermal equilibrium at some temperature T' and delivering heat to a similar reservoir at a lower temperature T.

But there is no reason why (1) should apply to engines that deliver work by a different mode of operation. Indeed, the world's most universally available source of work -- the animal muscle -- presents us with a seemingly flagrant violation of that formula.

Our muscles deliver useful work when there is no cold reservoir at hand (on a hot day the ambient temperature is at or above body temperature) and a naive application of (1) would lead us to predict zero, or even negative efficiency. But according to Lehninger (1965), under these conditions they still deliver an efficiency of about 20%.

According to Alberts, *et al.* (1983), under favorable conditions the efficiency of a muscle can be as high as 70%, although a Carnot engine would require an upper temperature T' of about 1000 K to achieve this.

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The answer, of course, is that a muscle is not a heat engine. It draws its energy, not from any heat reservoir, but from the activated molecules produced by a chemical reaction. That is why we should always stress the word "heat" when discussing Carnot engines.

Only when we first allow that primary energy to degrade itself into heat at temperature T' -- and then extract only that heat for our engine -- does the Kelvin efficiency formula (1) apply. If we can learn how to capture that primary energy before it has a chance to degrade, as our muscles have already learned how to do, then we should be able to achieve higher efficiency than one would suppose from (1) in a man-made engine. Of course, this would not be a violation of the second law; rather, to achieve it will require a very clear understanding of what the second law really is.

THE ANTI-CARNOT EFFICIENCY

What efficiency might one hope for in such an anti-Carnot engine? There is no reason to doubt that, with proper understanding, the performance of our muscles could be at least equalled ***in vitro***. Now, whatever the theoretical maximum efficiency, it can always be written in the form (1) if we wish to do so; the question then becomes: "What are the effective upper and lower temperatures?"

As a partial answer we imagine that our engine will, like our muscles, eventually discharge some heat to the outside world; then let us take T as the ambient temperature -- which is, for our muscles, body temperature. What is the effective upper temperature T'? It appears to us that this was answered in a penetrating remark made by J. Willard Gibbs in a letter to Sir Oliver Lodge, in 1887; it is the highest temperature to which the activated molecules could deliver heat.

If the molecules with activation energy Q can deliver a fraction fQ of that energy to a heat reservoir at temperature T'', then we could in turn use it to run a conventional Carnot engine with upper temperature T''. Thus the theoretical maximum efficiency must be at least as high as the maximum attainable value of

$$f(1 - T/T'') \quad . \tag{2}$$

This little hint from Gibbs is all we need to understand the efficiency of a large class of energy convertors.

If in the Kelvin formula (1) we replace temperature by what it amounts to -- energy per degree of freedom $W = (1/2)kT$, we see before us an explanation and generalization of (1):

$$e = 1 - W/W' \tag{3}$$

which does not look very different at first; but now we have removed the limitation of thermal equilibrium on our energy source and sink. For "temperature" is defined only for a system in thermal equilibrium, while "energy per degree of freedom" is meaningful not only in thermal equilibrium, but for any small part of a system -- such as those activated molecules -- which might be far from thermal equilibrium.

One might then question whether such a nonequilibrium generalization of (1) is valid. We may, however, reason as follows. Although conventional thermodynamics defines temperature and entropy only in equilibrium situations, it cannot matter to an engine whether all parts of its energy source are in equilibrium with each other. Only those degrees of freedom with which the engine interacts can be involved in its efficiency; the engine has no way of knowing whether the others are or are not excited to the same average energy. The same applies to the low temperature heat sink.

Therefore, since (3) is unquestionably valid when both reservoirs are in thermal equilibrium, it must be correct more generally, if we take W and W' to be the average energy in those degrees of freedom with which the engine actually interacts. But then (3) has a simple intuitive meaning.

To see this, note that at room temperature T the average thermal energy per degree of freedom $W = (1/2)kT$ is about 1/80 ev. A chemical reaction might leave a product molecule in an excited state with perhaps $E = 0.5$ ev of excitation energy. If this is concentrated in, say, $N = 2$ vibrational degrees of freedom, it thus represents a tiny "hot spot" with energy E/N per degree of freedom. The activated molecules would have, as a class, an effective temperature $T^* = 2W/Nk$, of the order of 20 times room temperature.

This, we conjecture, is the T' that we should use in Kelvin's formula (1) for the maximum theoretical efficiency of a muscle. It is not a real temperature, but only the effective temperature of those degrees of freedom that are supplying the energy. In effect, we are using the activated molecules themselves as the heat reservoir of (2), so $f = 1$ and $T' = T'' = T^*$, and we recover just Gibbs' statement.

If $T'/T = 20$ and we convert the little bubble of concentrated energy from a single molecule into useful work before it has a chance to thermalize by spreading out over 20 vibrational degrees of freedom, we should in principle be able to realize something like 95% conversion efficiency. Thus the values actually achieved by our muscles cease to be puzzling.

From this viewpoint, the basic reason for the "second law" limitation on efficiency is that we are trying to recapture energy that has spread in an uncontrolled way over many degrees of freedom, and concentrate it back into a single degree of freedom, the motion of a piston or tendon. But the engine must be able to do this reproducibly; i.e., whatever the details of excitation of all those molecular degrees of freedom.

It is then Liouville's theorem -- conservation of microscopic phase volume -- that places the limitation (3) on how much concentration of energy into a small phase volume is possible. As we have noted before (Jaynes, 1965), if we interpret entropy as $S = k \log V$, where V is the phase volume compatible with any macrostate, equilibrium or nonequilibrium, then the second law

$$S(\mathit{final}) \geq S(\mathit{initial})$$

follows immediately from Liouville's theorem, as a necessary condition for any process to be reproducible. But in a fast process, that happens in a time so short that thermal equilibrium of the whole system is never reached, only the phase volume of those degrees of freedom actually involved in the interactions needs to be considered.

Indeed, if the primary energy is concentrated in a single degree of freedom and we can extract it before it spreads at all, then our engine is in effect a "pure mechanism" like a lever and W' is the work delivered to it. The generalized efficiency (3) then reduces to $1 - kT/2W'$, or

$$(Work\ out) = (Work\ in) - (1/2)kT \quad . \tag{4}$$

The work we can expect to get out of a lever is not quite all that we had put in!

It may seem strange to see a pure mechanical formula thus amended by thermodynamics. But a little further thought makes it clear that (4) is indeed correct; the last term is just the mean thermal energy of the lever itself, which cannot be extracted reproducibly. At least, if anyone should succeed in doing this, then he would need only to wait a short time until the lever has absorbed another $(1/2)kT$ from its surroundings, extract that, and repeat -- and we would have the perpetual motion machine that the Second Law holds to be impossible.

The simple generalization (3) of Kelvin's formula thus appears to have a rather wide range of application.

TENTATIVE CONCLUSIONS

What do the known facts of biology tell us about these questions? The currently popular myosin bridge mechanism for striated muscle contraction (Alberts, *et al.*, 1983) fits in quite nicely with these speculations; the bending of that bridge is a degree of freedom that seems well adapted to transferring its energy, while resisting rapid thermalization.

Of course, we are not pretending to make any new contribution to biology by these remarks; rather we are speculating about the possibility of advancing the technology of energy convertors by taking hints from how Nature has managed it in biology.

Having seen this biological mechanism, it is easy to believe that many other kinds of macromolecules could be "designed" to do similar things, perhaps more easily. In time the design of useful anti-Carnot molecular engines (artificial muscles) might become about as systematic and well understood as the design of dyes, drugs, and antibiotics is now. However, a prerequisite to this is a clear understanding of the physical principles that must govern energy conversion in any system, biological or otherwise.

In the attempts of L. A. Blumenfeld (1983) to relate efficiency of biological energy conversion to physical principles, he states that (A) high efficiency requires the energy conversion process to be reversible; and (B) reversible behavior is fundamentally impossible in a system of molecular size, because of the uncertainty principle. In some similar remarks (C), Elsasser (1966) invokes the uncertainty principle to place fundamental limits on mechanistic analysis in biology. Our thinking has led us to just the opposite conclusions:

(A) The Carnot principle and low "second law" efficiency of present engines are only consequences of the thermalization process (the primary chemical energy is allowed to degrade into heat before being used). If we can avoid the thermalization, Carnot engine lore must be modified as noted above. It is satisfying that the same formula holds, only reinterpreted.

(B) For efficient conversion of chemical energy into mechanical energy the conversion must proceed directly and quickly. Far from being impossible in systems of molecular size, this almost requires that the moving parts receiving the primary energy be of molecular size, because the useful output energy must be delivered to a single degree of freedom. We speculate that this is just the reason why biological systems have accomplished it, and human engineers have not.

(C) Instead of present quantum theory placing limits on the possibilities of mechanistic analysis in biology, the continued success of mechanistic analysis in biology may some day show us the limits of validity of quantum theory.

Thus it appears to us that the second law and the uncertainty principle place virtually no limitations on what can be done in conversion of chemical energy to mechanical work; the field is wide open for clever inventors, who may at any time do what we have all been taught is impossible.

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