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JENSEN'S INEQUALITY AS A TOOL FOR EXPLAINING THE EFFECT OF OSCILLATIONS ON THE AVERAGE VALUES OF VARIABLES

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Nonlinear oscillatory systems, playing a major role in biology, do not exhibit harmonic oscillations. Therefore, one might assume that the average value of any of their oscillating variables is unequal to the steady-state value. However, it is known that for Lotka-Volterra systems, these values do equal each other. Also for a number of mathematical models of calcium oscillations, the average cytosolic calcium concentration (not, however, the average concentration in the intracellular store) has this property. We show that this also holds for the Higgins-Selkov model of glycolytic oscillations and the smallest chemical system with Hopf bifurcation, while it does not hold for the Goodwin oscillator often used to describe circadian oscillations.

Moreover, we apply Jensens inequality to analyse under which conditions the average value during oscillations is lower or higher than the steady-state value. Jensens inequality states that for a (strictly) convex function, the function value of the average of a set of argument values is lower than the average of the function values of the arguments from that set. By analytical calculations, we derive that, if the Ca2+ efflux is a strictly convex (concave) function of the cytosolic Ca2+ concentration, then oscillations lower (increase) the average Ca2+ concentration in comparison to the unstable steady state.

We discuss our results in view of the question which advantages oscillations may have in biology. For example, the implications of the findings for the decoding of calcium oscillations are outlined.

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