A FEEDBACK MODEL FOR AN INSECT CIRCADIAN CLOCK

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ABSTRACT

Hemideina thoracica is a nocturnal orthopteran insect which exhibits clear circadian locomotor rhythmicity in constant conditions. Analysis of the free-running rhythms leads to the hypothesis that the underlying clock mechanism has two major interacting components; one responsible for the overt locomotor rhythm, and another whose output is not directly related to locomotor activity. A model comprising two linked populations of feedback oscillators accounts for much of the free-run lability seen in the real data.

INTRODUCTION

In natural conditions the Orthopteran insect Hemideina thoracica is nocturnal, remaining in the daytime in holes in trees, and emerging to forage at sunset, to return to its cover before dawn. As a test of the internal biological clock hypothesis, the locomotor activity rhythms of individual insects were recorded in the laboratory in constant temperature and total darkness. In these conditions all subjects exhibit clear endogenous circadian locomotor rhythms which often persist for many weeks. The period of the rhythms is temperature compensated with temperature coefficient (Q_{10}) close to 1.0, although the rhythms are entrainable by temperature cycles [1]. The rhythms are also sensitive to light, and entrain to light cycles, and in constant dim light show an increase in period [2]. Many locomotor rhythms provide evidence for two rhythmic components, typically one with a period of less than 24 hr, and another of longer period, resulting in a scolloped appearance to the locomotor rhythms [3]. In addition to the locomotor rhythm, the deposition of cuticle is also rhythmic in constant conditions, but with periodicity different from the locomotor rhythm. This suggests that there may be two major underlying clock systems in this insect [4]. Additional evidence for the nature of the circadian clock is provided by the after-effects following a variety of experimental light conditions and the desynchronisation of the rhythms after a critically-timed light pulse [5].

THE MODEL

Based on these findings, we have developed a model for the circadian system of this insect in which we link together two populations of coupled time-delayed feedback oscillators; one population (the Y population) times the locomotor activity rhythm, and the other (the X population) is responsible for the cuticle rhythm. Each unit oscillator (Figure 1) incorporates the synthesis of a chemical (having a concentration at any time of Ct.) Synthesis of the chemical is temperature dependent and is controlled through the difference between a reference value (Cref) and a time-delayed value of Ct (the error). There is continuous loss of chemical from the system at a rate dependent on its concentration; light perturbations reduce the chemical. The oscillators of each population are linked together by partial sharing of their time-delayed feedback information, and the X and Y populations interact by positive coupling through the exchange of small unequal fractions of their current mean values. Light only perturbs the locomotor (Y) population, although both populations are sensitive to temperature. Computer simulations with this model demonstrate that we can account for many of the basic properties of the Hemideina rhythms, including temperature compensation and entrainment, and explain the origins of the spontaneous changes in period and scolloping of the real data.

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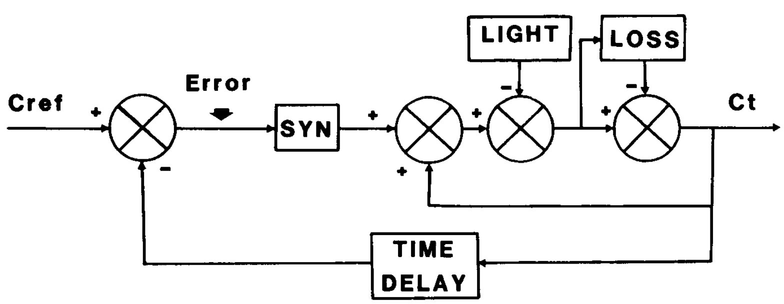

Figure 1. Control systems diagram of a unit oscillator.