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A mathematically scientific study of cyanobacteria's circadian rhythm based on induced memory by hysteresis structure of covalent modification as self-feedforward auto-control system

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Abstract
Life organisms is a continuum of control systems, which is deeply interested mechanically as well as biologically. For instance, the circadian rhythm is a very useful trait that is naturally and instinctively possessed by life organisms that continue to live on Earth, from single-celled microorganisms such as cyanobacteria to animals and plants in general, and mammals and primates. It is known that cyanobacteria and plants use this circadian cycle to naturally begin preparing for photosynthesis with auto-feedforward control. It is also known that circadian rhythms are realized with transcription-translation by use of clock genes and clock proteins at a cellular level in various life organisms. By Kondo's LAB's evolution experiment in Nagoya University, a mixture of the clock gene knocked-out strain and wild-type strain was in a test tube. They observed which one gets survived, as remaining competitively for several days, and it was reported that, according to the laws of evolution, the wild-type strain grew exponentially and overcame the knockout strain. In this way, the self-feedforward control mechanism is also very important because of the optimization of the benefit and cost ratio. In this paper, we overview our mathematically scientific points represented by our mathematical model of a system of ODEs.

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I. Introduction

This paper overviews our studies of mathematically scientific model investigations of mechanism of self-feedforward control system. Hysteresis bifurcation occurs in this basic model equations as a fundamental mathematical structure of auto feedforward control and we put a control term to realize self-feedforward control. We are here to summarize its characteristics and advantages. Feedforward control is widely known as very important mechanism, generally speaking. Feedback control is, surely, a popular control mechanism, but since it inevitably has a certain degree of overshooting, it is sometimes not enough. From this point of view, feedforward control is becoming increasingly important in engineering applications. Feedforward control uses some kind of signal, information communication, or transmission to predict the very near future (a few seconds or a few minutes future? It depends upon the system under consideration.) and prepare for it in advance. It is largely important not only in biology but also in engineering and is suitable for internal control such as in facilities where temperature, humidity, pressure, etc. must be controlled very precisely. Its characteristics include the fact that it is suitable for accurate control of facilities where the type and characteristics of disturbances and perturbations can be predicted to some extent in advance, but the time when they occur may be random. Such a certain kind of "memory", "future prediction based on that memory", and "quick response as a countermeasure" are important very much, and are used to instantly receive signal processing and information transmission and control to prepare for it. In life phenomena, it is well-known that circadian rhythm is exactly

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an example.

Circadian rhythm is an important property that forms the basis of self-feedforward auto-control, and based on this, they predict the situation surrounding them in the near future, make adaptive preparations, and actually behave according to that control. This function was acquired through evolution, and its superiority has been experimentally proven. Therefore, this also shows that feedforward control behaves adaptively and contributes greatly to optimizing the benefit/cost ratio. That is what is meant by evolutionarily advantageous. In fact, it is also known that circadian rhythm is realized by the transcription-translation cycle at the cellular level in various life organisms. By Takao Kondo's LAB's evolution experiment in Nagoya University, a mixture of the clock gene knocked-out strain and wild-type strain was in a test tube. They observed which one gets survived, as remaining competitively for several days, and it was reported that, according to the laws of evolution, the wild-type strain grew exponentially and overcame the knockout strain.([6])

This paper surveys and reports important points of our mathematical study of the basic structure of this "memory" and self-feedforward control system based on the memory, according as our studies ([7]), and ([8]). This is a system composed of several ordinary differential equations (ODEs) that cause hysteresis bifurcations. We have already reported in ([7]) from an applied mathematical and biological point of view. This paper will revisit this from the viewpoint of feedforward control systems and engineering.

II. Cyanobacteria and its circadian rhythm

Cyanobacteria is an important and interesting micro-organism which has improved environment of the earth, as having existed clearly for about 2.7 billion years at least. These inhabit with a lot of traits in various surroundings, especially, in hot springs of 70 degrees Centigrade (158 degree Fahrenheit) or within Arctic Circle ([3] Whitton and Potts 2000). Generically speaking, cyanobactera, basically composed of a single cell, has the following characteristics:

1. It is thought as a kind of prokaryotic eubacteria without possessing a nucleus in a cell.
2. It belongs to the group of Gram negative bacteria.
3. It can photosynthesize with oxygen outbreak type.
4. It has allosteric circadian rhythm of clock proteins KaiA, KaiB, and Kai C in Synechococcus elongatus PCC 794.
5. As having an enzyme named the nitrogenase, some species obtain the ability to perform biological nitrogen fixation (called BNF in what follows) in Nostochineae.

We investigate that cyanobacteria's circadian rhythm in ([8]). In detail, people refer to the papers ([8] and references therein). Here we review several points of properties, and give readers' convenience.

Life organisms can be considered to be a complex, but delicate, sensitive, and efficient system of organism obtaining high reproducibility and high evolvability in order to grow up, to undergo metabolic change, to react to stimulation, to control its feature in both feedback and feedforward manners, and so forth. For embodying these purposes, it is important to memorize and to communicate information on the past about themselves as precisely as possible. An organism can survive more stably, if the memorization is more correctly and more steadily, and if the communication is more rapidly. It is considered that these characters must be realized by a combination of some biochemical reactions. Especially, it is important how a strage element is constructed in a cell. In this paper, we propose a kind of standard structure of mathematical model constructing a binary digit of storage element in a cell by use of covalent modifications and analyses it to elucidate its characteristic and important properties. We have already studied them in [8]. Readers refer to [8] in detail. Here we pointed out the importance of circadian rhythm, which is a major basis of the feedforward control by which life organisms will make predictions and will make behavior adequately, as this allows them to know the time correctly and to prepare and react to changes in surroundings soon, in addition to feedback control.

On the other hand, terrestrial cyanobacteria of Nostochineae (for example, *Anabaena, Nostoc, Scytonema, Anabenopsis, Dichothrix* and so forth) has a filamentous form constituted of trichome, heterocyst, akinete (dormant spore) cells, and sheaths of the quality of agar surrounding them. We investigate mathematical mechanisms of the BNF in ([7]). So here, we explain it a little in order to help reader's comprehension, according to our paper [7].

In a heterocyst cell, they produce ammonium nitrogen with BNF, separating it spatially away from trichome cells in which it photosynthesizes to release oxygen since nitrogenase is beaten by oxygen. Generally, in ecological system of boreal forest (in, for instance, pacific northwest of North American continent or

Scandinavian Peninsula) ([2] DeLuca et.al. 2002; Lindo and Whiteley 2011), inorganic nitrogen seems to be insufficient very often, but the terrestrial cyanobacteria with mutualistic symbioses of feather moss (*Pleurozium schreberi* and *Hylocomium splendens* are dominant species) is an important source of supply of the ammonium nitrogen there.

When feather moss is placed in nitrogen-starved situation, it takes some attractive chemical substances (which are slightly different from each other and dependent upon species) out of itself to induce the filamentous cyanobacteria of Nostochineae to come to itself. Cyanobacteria of Nostochineae will make hormogonia differentiation to change their form to the hormogonia from the usual one and make gliding movement to go toward feather moss by its chemotaxis. In Bay et.al. 2013, they perform micro ecosystem experiments to study this interaction for *Pleurozium schreberi* and *Hylocomium splendens* in details. Their chemical is mighty enough to enchant it to the incurve of its leafy gametophyte completely. If the cyanobacteria (it is *Nostoc spp*. here) arrives at the "cozy" place, then it goes back to the original form of filament and create the heterocyst cells in which it produces the available ammonium nitrogen with BNF. Recently, this function is thought of as an important role of the mutual symbioses between the filamentous cyanobacteria of Nostochineae and feather moss in the boreal biome of boreal forest ([3] DeLuca TH et.al., (2002) , and [4] Lindo and Whiteley 2011).

In 2011 ([4] Lindo and Whiteley 2011), they took an attention to an remarkable role of old trees in the boreal forests of pacific northwest of North American continent (Actually, they made investigations in the Clayoquot sound UNESCO Biosphere Reserve, Vancouver Island, or British Columbia in Canada.) They have studied the ability of output of BNF of the filamentous cyanobacteria of Nostochineae (here, it is *Scytonema*) making mutual symbioses with epiphytic bryophytes in the high canopy of a coastal temperate rain forests there. As a marked result, they found that the stand-level ability of BNF at 30 m height in the canopy is almost three times higher than that in the forest floor. Here, the old trees act as the third sub-member of this mutual symbioses to reinforce the BNF ability of the main members configuring the mutual symbioses. The objective of this paper is structural characterization of this mutual symbioses by a certain mathematical skeleton model (it is a kind of "on"-"off" frequency model with scale effect) and explain the qualitative mechanism of this reinforcement theoretically in view of micro ecosystem analysis by use of it.

Nitrogenase is the enzyme of BNF by which the filamentous cyanobacteria of Nostochineae make the available ammonium nitrogen from atmospheric nitrogen molecules (N2). If cyanobacteria with BNF is put in nitrogen-starved situation, then Nitrogenase's activation is let higher, and if it is in nitrogen-rich state, then the switch turns off. It is regulated by other proteins which can detect deficiency of nitrogen or oxygen. BNF function of the cyanobacteria basically obtains the switching mechanism responding density of ammonium nitrogen around it. One of devices working well to realize it is to create good memory element. It is well-known that a robust device to memorize the "on"-"off" two-state makes its adapting potential ability higher to environment (for example, a molecular realization of circadian rhythm). We present a mathematical frequency model describing such two-state as a skelton structure of the function. This model also obtains a scale effect, which can depict scale merit of the phenomena. This is derived from the nonlinearity of the reaction after all, and is one of the important structural characters of the system. We will attempt to explain a piece of feature of BNF of the mutual symbioses between the filamentous cyanobacteria of Nostochineae and feather moss in the boreal biome with old trees by use of this structural character. From the viewpoint of evolutionary ecology, this system is composed of the main two species' mutual symbioses added by extra sub-species of old tree. Sub-species is almost neutral for itself, but it often gives good effect to the system. Our model will explain this effect theoretically without any ad-hoc hypothesis. In more details of background of cyanobacteria's properties, refer to [7] and [8].

Two-state frequency model with scale effect

We state our model of system of ODEs briefly. In detail, could you please consult our papers [8]. We have already studied what follows mathematically scientific and applied mathematical point of view [8]. We state it again only for readers' convenience.

We basically consider a two-state (S and T) model. T stands for inactive state, and S for active state. They represent two states of the cyanobacteria concerned with BNF. The number n represents magnitude of scale of the system under consideration, which means scale of population of the cyanobacteria. As n is bigger, the whole number of nitrogenases is increasing, hence the scale of the system is larger. Currently, a variable of a frequency model means rate of "on"-state (or "off"-state) in the whole group, which cannot obtain the ability to give expression to size of scale. But, generally speaking, if the system has nonlinear interaction, then the behavior of the system may change qualitatively, or sometimes drastically, even if the scale varies moderately. The system has at least the Michaelis-Menten type nonlinear reaction, which is an enzyme reaction catalyzed by nitrogenase. Therefore our model needs scale variable "n". This is based on the model in the classical work of

Professors S. Asakura and H. Honda (Asakura and Honda 1984), where they have originally considered about the problem of temporary reaction and post-adaptation process in a cell. We utilize it as modifying it a little. This two-state frequency model is expected to memorize whether the state is "on" or "off". This switching mechanism is realized by regulation proteins, which is symbolized as *A* in the model. Hence *Atotal* is a given constant which stands for the N-starved degree, and *Atotal* is consist of free *A* and trapping *A* (the intermediate state *T'* (from *T* to *S*) possesses *A* temporarily in the catalysis). The total quantity of nitrogenase is denoted by *Ctotal*, and

$$A_{total} = A + \sum_{i=0}^{n} T_i' \tag{1}$$

$$C_{total} = \sum_{i=0}^{n} (S_i + T_i) \tag{2}$$

We illustrate our model in the following:

Fig. 1

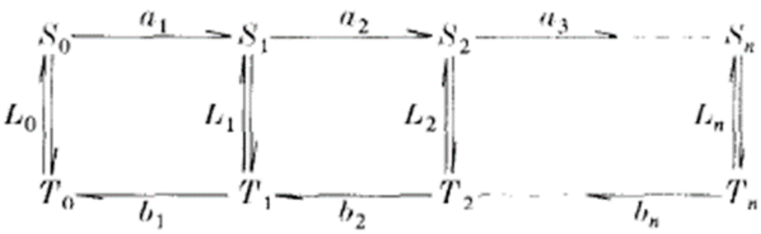

Fig. 1 Conceptual figure of two-state frequency model with scale effect

The intermediate state *T'i* is actually arising in reaction process *Li* in Fig. 1 and this reaction arrive at the equilibrium very rapidly. Therefore the usual argument leads the following Michaelis-Menten type nonlinearity:

$$A = \frac{A_{total}}{1 + \sum_{i=0}^{n}(k_i T_i / \lambda_i)} \tag{3}$$

Consequently, the model equation is the following:

$$\begin{cases} \frac{dS_0}{dt} = k_0 A T_0 - (\gamma_0 + \alpha_0) S_0 \\ \frac{dS_i}{dt} = k_i A T_i + \alpha_{i-1} S_{i-1} - (\gamma_i + \alpha_i) S_i \\ \frac{dS_n}{dt} = k_n A T_n + \alpha_{n-1} S_{n-1} - \gamma_n S_n \\ \frac{dT_0}{dt} = -k_0 A T_0 + \gamma_0 S_0 + \beta_0 T_1 \\ \frac{dT_i}{dt} = -(k_i A + \beta_{i-1}) T_i + \gamma_i S_i + \beta_i T_{i+1} \\ \frac{dT_n}{dt} = -(k_n A + \beta_{n-1}) T_n + \gamma_n S_n \end{cases} \tag{4}$$

Here, i = 1, 2, 3, ... , n - 1, and $\alpha_i, \beta_i, k_i, \lambda_i, \gamma_i$ are positive constants. It is easy to understand that the total quantity of *Ctotal* is preserved. In fact, clearly we understand that $\frac{d}{dt}(\sum_{i=0}^{n}(S_i + T_i))=0$ by summing up all the equations of the system of equations (4).

About theoretical and numerical results of this model, readers can refer to [7] and [8].

III. Conclusion

In this paper, we overview and review our results in mainly [8] (and also [7]), and have discussed significant meaning from the viewpoint of self-feedforward auto-control. Circadian rhythm is the so-called memory of time, by which life organisms behave more adequately to their. environment. In evolution of life context, this is valid too, because, at least, cyanobacteria have been survived for 2.7 billion years, and moreover, nowadays almost all life organisms have it and use it to live adaptively more, which means that it is not but optimization of benefit /cost ratio by use of the feedforward control. At this point, we can also construct more adaptive and more adequate system engineering field, for instance, by use of biomimetic techniques.

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