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Nonphotic entrainment in fish

Jose F. López-Olmeda *

Department of Animal Physiology, Faculty of Biology, Regional Campus of International Excellence "Campus Mare Nostrum", University of Murcia, 30100 Murcia, Spain

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A B S T R A C T

Organisms that live on the Earth are subjected to environmental variables that display cyclic variations, such as light, temperature and tides. Since these cyclic changes in the environment are constant and predictable, they have affected biological evolution through selecting the occurrence of biological rhythms in the physiology of all living organisms, from prokaryotes to mammals. Biological clocks confer organisms an adaptive advantage as they can synchronize their behavioral and physiological processes to occur at a given moment of time when effectiveness and success would be greater and/or the cost and risk for organisms would be lower. Among environmental synchronizers, light has been mostly widely studied to date. However, other environmental signals play an important role in biological rhythms, especially in aquatic animals like fish. This review focuses on current knowledge about the role of nonphotic synchronizers (temperature, food and tidal cycles) on biological rhythms in fish, and on the entrainment of the fish circadian system to these synchronizers.

Contents

1. Introduction

Organisms that live on the Earth are subjected to many geophysical variables that display cyclic variations, such as light, temperature and tides. Most of these cyclic changes in the environmental variables are generated by movements of the Earth, the Moon and the Sun. in relation to each other. As these cyclic changes in the environment are constant and predictable, they have affected the biological evolution through selecting the occurrence of biological rhythms in the physiology of all living organisms, from prokaryotes to mammals. These biological rhythms confer organisms an adaptive advantage as they can time their physiological processes to occur at a given moment of time when effectiveness is greater and the risk for organisms is lower (DeCoursey, 2004). Biological rhythms are present in a wide variety of processes and display a whole range of endogenous periods, from less than seconds (i.e. firing rate of some neurons and pacemaker cells) to a year (i.e. seasonal reproduction in many species) (Lewandowski et al., 2000; Goldman et al., 2004).

The circadian system is usually divided into three different components: input signals, the pacemaker and output pathways (Fig. 1) (Pando and Sassone-Corsi, 2002). The animal receives an input from a synchronizer, or *zeitgeber*, of either an external or internal origin, which acts on a pacemaker or oscillator by entraining the phase of its rhythm. A pacemaker constitutes a functional anatomical region

* Department of Physiology, Faculty of Biology, University of Murcia, 30100 Murcia, Spain.
E-mail address: jflopez@um.es.

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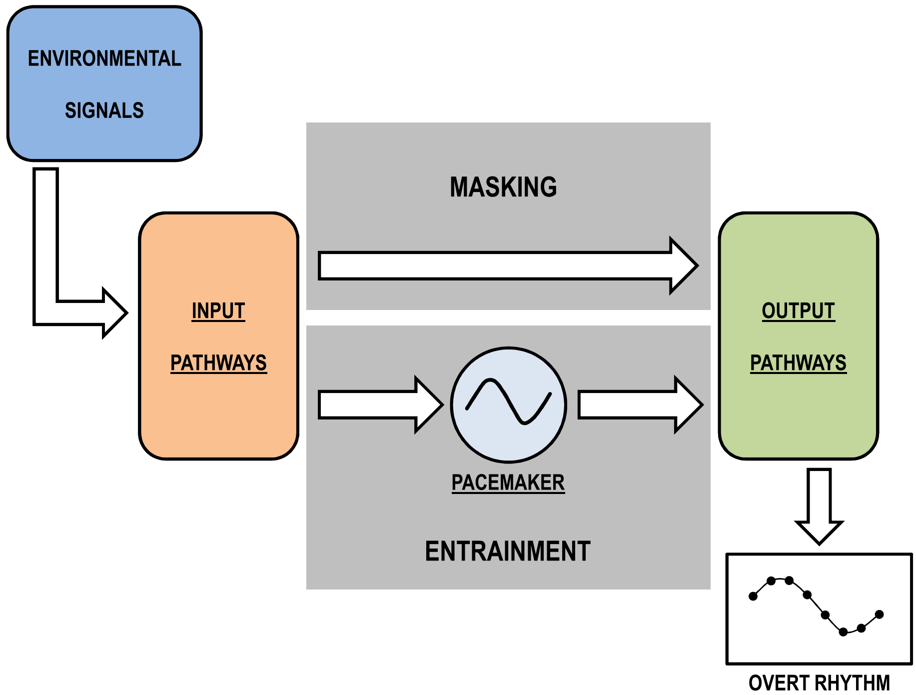

Fig. 1. Schematic view of a circadian system formed by three main components: i) the pacemaker, a functional anatomical region capable of sustaining its own oscillations and of entraining other oscillations; ii) input pathways that carry information from external variables; iii) and output pathways that transmit rhythmic signals by generating an overt rhythm in a specific physiological variable. Environmental signals can act on the overt rhythm through their action on the pacemaker (entrainment) or directly on the output pathways (masking).

capable of sustaining its own oscillations and of entraining other oscillations. Besides different input signals that acting on the same pacemaker or oscillator, the idea of multiple circadian oscillators existing within the same organism should also be considered. In this situation, different oscillators could respond and be entrained by distinct environmental cues, like light, temperature or food alone (Fig. 2) (Mistlberger, 2009; Storch and Weitz, 2009; López-Olmeda and Sánchez-Vázquez, 2011). In addition, interactions could also occur between these different oscillators or they could act on the same overt rhythm, which would explain why some rhythms are affected by more than one synchronizer (Fig. 2) (López-Olmeda and Sánchez-Vázquez, 2011). Apart from circadian oscillators, organisms could also present oscillators with shorter (circatidal) or longer (circalunar, circannual) periods (Tessmar-Raible et al., 2011; Dardente, 2012). Pacemaker outputs are also called overt rhythms, and are defined as rhythms in an observable characteristic that is directly or indirectly controlled by a pacemaker (Johnson et al., 2004).

Although synchronization and entrainment are often used indistinctly, these terms in Chronobiology refer to different situations. Synchronization occurs when the period of the biological rhythm observed is the same as that of the external stimulus (or another rhythmic biological variable), and there is a stable phase relationship between both. In entrainment, the cyclic external variable (the entraining signal or *zeitgeber*) acts on the biological oscillator and makes it change its endogenous period to match the *zeitgeber's* period (Fig. 1). If the *zeitgeber* is removed, the rhythm continues with a phase determined by the entraining variable and a period determined by the oscillator's endogenous period (Johnson et al., 2004). On the other hand, organisms answer to external stimuli in a reactive manner; if the external stimulus is cyclic, it can directly affect or influence the manifestation of the biological rhythm in a phenomenon called masking (Fig. 1). Nevertheless, masking is considered to form part of the circadian system, and plays an important role, together with the entrainment of the circadian pacemaker, in animals' adaptation to changing environments (Mrosovsky, 1999).

In mammals, the master pacemaker of the circadian system is the suprachiasmatic nucleus (SCN) of the hypothalamus (Reppert and Weaver, 2002; Dibner et al., 2010; Welsh et al., 2010). In fish, the existence of a central pacemaker remains to be demonstrated to date. The pineal organ has been suggested to act as a central pacemaker, although posterior research has shown that many rhythms are maintained in pineal-ablated fish (Sánchez-Vázquez et al., 2000; Shedpure, 2002). Whitmore et al. (1998, 2000) demonstrated that all zebrafish cells are light-responsive and present an oscillator that can be directly entrained by light. Therefore, the circadian system of fish could lack a central pacemaker and would be formed by multiple oscillators with no hierarchical structure, some of which are more sensitive to a specific synchronizer: e.g. temperature or food (Fig. 2). So unlike mammals, the circadian system of fish would be a network of oscillators, which could be independently entrained and could interact to coordinate overt rhythms (Fig. 2) (Cahill, 2002; Pando and Sassone-Corsi, 2002; Vatine et al., 2011).

The generation of all circadian rhythms relies on the molecular machinery of the cell. At the molecular level, circadian rhythms are controlled by self-sustainable molecular clocks formed by both positive and negative loops (Shearman et al., 2000; Pando and Sassone-Corsi, 2002; Vatine et al., 2011). In vertebrates, the positive loop is formed by two transcription factors (CLOCK and BMAL) that activate the transcription of other genes by binding to a promoter region enhancer known as *E*-box (Gekakis et al., 1998; Reppert and Weaver, 2002). Among the genes activated by CLOCK:BMAL, there are several genes from the *Per* and *Cry* families, whose PER and CRY products translocate to the nucleus and repress CLOCK and BMAL, closing the negative feedback loop (Shearman et al., 2000; Reppert and Weaver, 2002).

Light is considered the most important environmental factor that synchronizes the SCN, hence this pacemaker has also been named light entrainable oscillator (LEO) (Reppert and Weaver, 2002; Johnson et al., 2004). Besides the light/dark (LD) cycle, many rhythms in most animals, from invertebrates to vertebrates, can be entrained by other external synchronizers such as temperature, food and tides (Rensing