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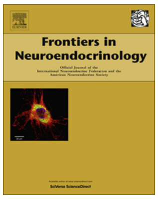

Review

Avian circadian organization: A chorus of clocks

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ABSTRACT

In birds, biological clock function pervades all aspects of biology, controlling daily changes in sleep: wake, visual function, song, migratory patterns and orientation, as well as seasonal patterns of reproduction, song and migration. The molecular bases for circadian clocks are highly conserved, and it is likely the avian molecular mechanisms are similar to those expressed in mammals, including humans. The central pacemakers in the avian pineal gland, retinae and SCN dynamically interact to maintain stable phase relationships and then influence downstream rhythms through entrainment of peripheral oscillators in the brain controlling behavior and peripheral tissues. Birds represent an excellent model for the role played by biological clocks in human neurobiology; unlike most rodent models, they are diurnal, they exhibit cognitively complex social interactions, and their circadian clocks are more sensitive to the hormone melatonin than are those of nocturnal rodents.

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1. Introduction

Each morning, and especially in the spring, we are greeted by a cacophony of small birds singing a dawn chorus. In eastern North America, spring mornings are sometimes defined by the merry roundelay of the American robin, *Turdus migratorius*, the varied staccato whistles of the Northern cardinal, *Cardinalis cardinalis*, the *hey-hey* of the white-breasted nuthatch, *Sitta carolinensis*, or even the cheery chirping of the introduced house sparrow, *Passer domesticus.* In the backdrop, we may hear the doleful *ooh-wah-hoo-hoo* of the aptly named mourning dove, *Zenaida macroura*, as the bass section above croons with the honking of migrating Canada geese, *Branta canadensis.* There is no particular order of who sings or who calls first, and the orchestration is peripatetic at best, seemingly random, although many of these garden songsters are reacting to each other's songs. And yet, there is a coordination of the rhythm and timbre of this dawn chorus. These birds all possess an internal biological clock that is coincidentally entrained to the identical environmental signal, the rising of the morning sun, and, in turn, these internal clocks are tuned to the expression of clocks by their intraspecific and extra-specific neighbors.

While these appear to be the melodious embrace of the warming sun, they are, in fact, a cold war, defining territory for breeding and foraging in anticipation of reproductive success (Marler, 2004; Williams, 2004). In no other group of animals are the seasonal changes in reproductive function so obvious to the casual observer. We hear them stake their claims. We see them build their nests, incubate the eggs, and raise and fledge their young.

At certain times of year, small songbirds fatten for their annual migrations and, at certain times of day, dusk usually, become increasingly agitated as they gather for their vernal and autumnal treks to breeding and wintering grounds (Gwinner, 1989, 2003). These birds typically eschew their nightly drifts into slumber during this time, sleeping little or not at all, a phenomenon called *Zugunruhe,* as they migrate during the night, avoiding the gauntlet of diurnal predators as they cross vast areas of our continent.

Each of these processes and more are strictly timed to a time of day and to a time of year (Cassone and Westneat, 2012). They are not restricted to eastern North America, either, as these processes are repeated time and time again throughout the world, albeit at different times of year, depending on the latitude and local environment (Kumar et al., 1996, 2002, 2010). The question that arises is, "Why do birds so strictly time so many of their behavioral and physiological functions, and how do they accomplish it?" In essence, the child-like question, "Why does the sparrow sing on spring mornings?", is also a scientific question that is beginning to be answered, and these likely entail an understanding of the biological clock or clocks that underlie all rhythmic processes. Specifically, understanding of the molecular, physiological and behavioral mechanisms underlying the temporal coordination of these complex processes and behaviors in birds will tell us more about human chronobiology as well, because like humans and unlike the standard laboratory rodent models for biological clocks, birds exhibit a complex orchestration of circadian behavior that controls daily patterns of sleep: wake, visual sensitivity, cognition and social behavior. Further, study of the mechanisms underlying annual cycles of reproduction, migration and metabolism in birds will provide clues to anticipated ecological changes due to climatic disruption. In essence, birds are images in our own mirrors, and we

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should pay attention to them more than current biomedical science might prefer.

2. Biological rhythms and the clocks that control them

Biological rhythms and the endogenous clocks that control them are fundamental properties of nearly all living organisms, ranging from cyanobacteria to humans (Bell-Pedersen et al., 2005). As diverse as the organisms that express biological rhythms, the formal properties of these rhythms are remarkably conserved (Pittendrigh, 1993). These biological rhythms are functionally tied to environmental cycles they estimate; of these, we will concentrate in this review on two-*circadian rhythms* and *circannual cycles*.

The daily 24-h cycle of day and night imposes a rhythmic cascade of positive and negative selective pressures on nearly all organisms on Earth (Pittendrigh, 1993). Daily light cycles provide the energy for photosynthesis, to warm water to a consistently liquid state and to maintain ambient temperatures for life. It also provides daily cycles in deleterious teratogenic, carcinogenic and desiccating wavelengths. It is therefore no surprise that most free-living organisms, if not all, have adapted to these cycles through the expression of endogenously generated circadian (*circa = approximately; dian = a day)* oscillations that entrain to local time through the process of *entrainment.* Rhythmic processes cannot be identified as *circadian* unless they are experimentally observed to persist for at least 1 or 2 cycles, preferably more, when the organism in question is experimentally placed in constant environmental conditions of either constant darkness (DD) or constant dim light (dimLL) (Constant high light, LL, may have other effects, frequently abolishing circadian rhythms altogether and/or damaging photoreceptive elements in the system (Aschoff, 1979). In fact, many circadian rhythms persist for weeks, months or years in constant environmental conditions.

In this scenario, organisms will repeatedly express patterns of behavior, physiology or biochemical processes with a period, τ, of close to but rarely exactly 24 h (Fig. 1). These endogenously driven rhythms must then be *entrained* to the relevant environmental cycle, typically the light: dark cycle (LD) of day and night, such that the internal phase, ϕ_i, of the organism's clock corresponds appropriately to the external phase, ϕ_e, of the LD cycle. Thus, a diurnal bird's locomotor activity pattern entrains to the LD cycle so that activity onset ϕ_i corresponds approximately to dawn ϕ_e, maintaining a stable phase relationship, ψ_{ie}.

Similarly, annual environmental cycles correspond to *circannual rhythms* expressed by many organisms when placed experimentally in constant photoperiods of 12 h of light and 12 h of dark (LD12:12) or another constant photoperiod (Gwinner, 1989, 2003). Under these conditions many organisms, including birds, will express cycles of approximately 365 days. These in turn are believed to be entrained to the annual cycle by changes in photoperiod (Gwinner, 1989) and/or a physiological proxy, such as the duration of the hormone melatonin (see below). Circannual cycles are not as well understood as are circadian rhythms, but they are likely linked physiologically (Gwinner and Brandstätter, 2001; Gwinner et al., 1997).

The role of the circadian clock in annual cycles has been known for some time (Bünning, 1969; Follett et al., 1992; Konishi et al., 1987; Menaker and Eskin, 1967; Rowan, 1926). In many species of birds, exposure to photoperiods of longer than 11.5 h/day results in the rapid induction of the hypothalamo-hypophysial-gonad axis, causing development and growth of testes and ovarian follicles. Although there are differences among species of birds and between birds and other taxa, neither the absolute length of the photoperiod, length of the scotoperiod (the duration of the dark phase) or their ratio is the proximal causes of gonadal induction. Rather, it is the circadian ϕ at which light impinges on photoreceptive elements that causes reproductive changes. For example, male Japanese quail, *Coturnix japonica,* and white-crowned sparrows, *Zonotrichia leucophys,* which are maintained in LD 6:18 will exhibit regressed testes. However, if the last hr. of the 6 h. photoperiod is extended each long night to a specific "photoinducible phase", ϕ_{pi}, usually 11–12 h following the onset of the short photoperiod, reproductive activity is commenced. Thus, birds exposed to LD 6:18 or L5: D1: L1: D17 (a single 1 h light pulse interrupting the night) will retain regressed gonads, but if the 1 h pulse occurs 5 h later (L5:D6:L1:D12), gonads will recrudesce (Follett et al.,

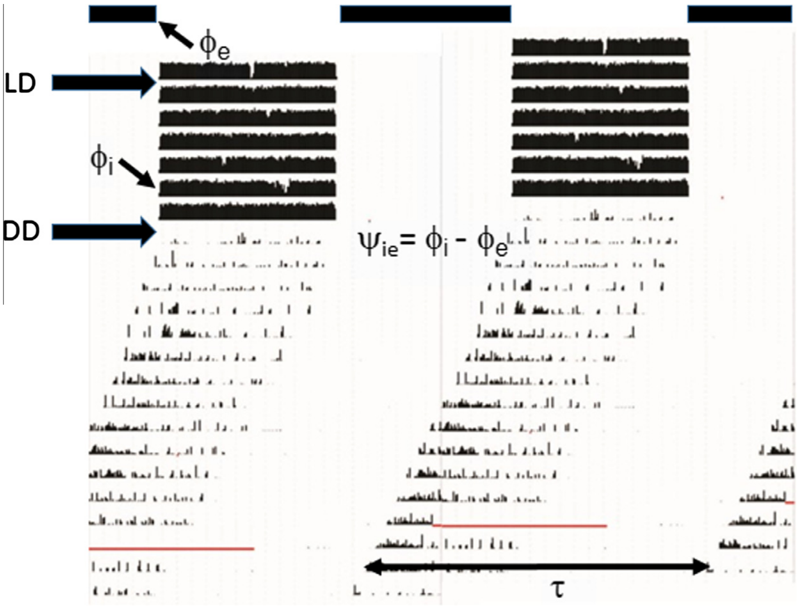

Fig. 1. Actogram of locomotor activity from a single zebra finch, *Taeniopygia guttata.* The top bars indicate the times during which lights are off (black) vs. on (white). These are plotted in a 48 h timespan in order to "double-plot" the data. The time off lights on, ϕ_e, indicated by the arrow, is a phase reference determined by the investigator. The internal phase, ϕ_i, is determined to be the activity onset. The relationship between ϕ_i and ϕ_e is called ψ_{ie}. This relationship may change depending on the time of year and physiological condition of the bird. The internal period, τ, is indicated here as the average interval between activity onsets.

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