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Effect of no-night light environment on behaviour, learning performance and personality in zebra finches

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A periodic day–night environment is critical for daily behavioural patterns and advanced brain functions such as learning and cognition in animals. We investigated whether a no-night light environment would impair these functions in parent and F1 and F2 zebra finches, *Taeniopygia guttata*. Particularly, we examined song acquisition as a measure of learning, tested cognitive performance with reference to spatial and colour association tasks, and assessed personality with respect to an exploratory trait, first in the parent (P) and subsequently in F1 and F2 birds born and raised under 12:12 h light:dark or constant light (hence no-night, LL) environments. Daily patterns in activity and singing were monitored as circadian response indicators. After initial decay, the rhythmic patterns in daily activity and singing were restored after several weeks in the majority of P and F1 birds under LL; F2 birds displayed robust circadian rhythms in both behavioural patterns under LL. Further, LL decreased participation and performance in cognitive tests and reduced exploratory behaviour in birds from all generations. Overall, we found negative effects of the LL environment on daily behavioural patterns, advanced brain functions (i.e. learning and cognition) and personality in zebra finches when adult and in subsequent generations. These results give insights into the possible impact on animals of night-time illumination such as in an overly lit urban habitat.

Birds, like other vertebrates, adapt to the cyclic light environment, and exhibit clear day–night differences in physiology and behaviour. Whereas diurnal birds are active during the day and sleep at night, nocturnal species are active at night and quiet during the day. At the regulatory level, circadian clocks govern changes in physiology and behaviour within each day; hence, behavioural and physiological functions exhibit daily and circadian rhythms under periodic daily light–dark (LD) cycles and constant dim light or darkness, respectively (Aschoff, 1981). Exposure to artificial light at night (ALAN) or constant light (LL) disrupts the daily or circadian rhythms and, in turn, affects biological functions (e.g. activity and feeding, temperature regulation and advanced brain functions; Benca, et al., 2009; Surbhi, Kumari, Rani, Tsutsui, & Kumar, 2015; Wang, Harpole, Trivedi, & Cassone, 2012). Nocturnal rodents under ALAN or LL experience a decay in activity rhythms, a decline in learning, the impairment of hippocampus-dependent spatial memory and cognitive abilities, an increase in anxiety and depression and a decrease in neuronal plasticity (e.g. spine density and neurogenesis; Bedrosian, Fonken, Walton, Haim, & Nelson, 2011; Ma et al., 2007). Also, LL disrupts the circadian rhythm leading to a sleep deficit, alteration in mood and depression-like behaviours in mice, *Mus musculus* (Fonken et al., 2009). Few studies have shown a significant negative impact of ALAN or LL on singing, sleep and cognitive performance in songbirds (Jha & Kumar, 2017; Kempenaers, Borgström, Loës, Schlicht, & Valcu, 2010; Raap, Pinxten, & Eens, 2015; Taufique & Kumar, 2016). Under ALAN, European songbirds sing earlier at dawn and also continue to sing after sunset (Da Silva, Samplonius, Schlicht, Valcu, & Kempenaers, 2014). Great tits, *Parus major*, wake up earlier, have less sleep and spend less time in the nestbox in an ALAN environment (Raap et al., 2015). In Indian house crows, *Corvus splendens*, LL decreases cognitive performance and neuronal activity of cognition-associated brain regions (hippocampus, medial and central caudal nidopallium and hyperpallium apicale; Taufique & Kumar, 2016).

Early life conditions influence behaviour, physiology and personality traits in adulthood, but subsequent generations may be affected too (Burton & Metcalfe, 2014). Exposure to unpredictable, chronic maternal separation during the postnatal period induces depression-like behaviours, and alters the behavioural response of mice to an aversive environment when adult (Franklin et al., 2010). Also, F1 and F2 generation mice are more sensitive to odour fear

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conditioning to which their parents were exposed before conceiving them (Dias & Ressler, 2014). Similarly, exposure to poor nutritional conditions or stress early in life affects learning in zebra finches, *Taeniopygia guttata*, when adult and in the next generation: individuals on a low-quality diet gain body mass faster and learn faster when trained to remove lids from food wells (Brust, Krüger, Naguib, & Krause, 2014). Further, zebra finches raised in a large brood or on a reduced food supply show reduced reproductive success with negative effects on offspring condition, and this is carried over to the next generation (Naguib & Gil, 2005; Naguib, Nemitz, & Gil, 2006). Also, juvenile zebra finches suffering induced stress via exogenous corticosterone learn from unrelated adults, but not from their male parent (Farine, Spencer, & Boogert, 2015). A lack of maternal care during early life also causes hyperresponsiveness to isolation in zebra finches (Banerjee, Arterbery, Fergus, & Adkins-Regan, 2012).

A periodic light environment is known to affect a developing circadian clock, and LL has both acute and long-term disruptive effects (Ohta, Mitchell, & McMahon, 2006). However, the consequences of exposure to LL, which has been widely used as an experimental paradigm to disrupt biological functions governed by the circadian clock, has not been well investigated with reference to the advanced brain functions of F1 and F2 offspring in songbirds. Lindquivst et al. (2007), though, reported that an unpredictable light–dark (LD) cycle impaired learning in chickens, *Gallus gallus*, with effects passed on to the F1 generation. Therefore, the main aims of the present study were (1) to investigate, in a songbird species, the behavioural effects of disruption of endogenous daily (circadian) timing under LL, (2) to examine responses to chronic exposure to LL, and (3) to assess whether LL-induced effects persist in the next generation. We hypothesized that an LL, hence no-night, environment, would negatively affect behavioural patterns controlled by the circadian clock, learning-related performances and cognitive abilities, and personality in adults, and that LL-induced effects would be carried over to the next generation. We studied zebra finches, first the parents (P) and then the F1 and F2 generations born and raised under LL, with controls in 12:12 h LD. We used zebra finches as an experimental system for two reasons. (1) They breed in captivity, which allowed us to track their age and sexual maturity to understand LL-induced effects on singing, which is a complex behaviour learnt from the parent/tutor only within a critical window early in life. (2) They respond to both acute and chronic changes in the environment (see above), so we could assess the consequences of these effects in the next generation. Recent studies have also used zebra finches to investigate circadian rhythms in activity and singing behaviour (Deregnaucourt, Saar, & Gahr, 2012; Jha & Kumar, 2017; Wang et al., 2012). Using daily patterns of activity and singing behaviour as circadian response indicators in the P, F1 and F2 zebra finches, we evaluated song characteristics to assess song acquisition as a measure of learning, performance in spatial and colour association tasks as a measure of cognitive ability, and exploratory behaviour in response to a novel object and a novel environment as a measure of personality.

METHODS

General Methods

We performed experiments on adult zebra finches from our own colony-bred stock which was maintained under 12:12 h LD and 22 ± 2 °C. The birds were 120 days old, which is when they are considered sexually adult (Roper & Zann, 2006). Groups of male and female zebra finches were moved to separate rooms and housed in same-sex cages ($N = 5$ per cage, size = 42 × 30 cm and 54 cm high) equipped with two perches under 12:12 h LD, as before, without visual and acoustic contact with the opposite sex. This was done to acclimatize birds to a caged condition, and to break any existing pair (male–female) bonds. Those females that laid eggs during this period were excluded from the experiment, to avoid any carryover breeding effects. At the end of 2 weeks of acclimation, birds were weighed on a top pan balance to an accuracy of 0.1 g, and the gonads were measured to assess their maturation. The size of gonads reflects the summation of gametogenic activity over time (Lofts, 1975).

Birds used in the experiment had similar body mass (12.7 ± 0.8 g, $N = 64$) and were in a similar gonadal state (testis volume = 6.2 ± 0.4 mm^3; ovarian follicle diameter = 1.3 ± 0.2 mm, $N = 32$ each; testis volume was calculated using the formula $4/3\pi ab^2$, where '*a*' and '*b*' denote half of the length and width of the testis, respectively). First, male zebra finches were singly housed in cages each with two perches and a rectangular nestbox (9 × 6 cm and 11 cm high) with a front opening (5 × 5 cm, 2 cm above bottom). The zebra finches were exposed to LL (hence no-night; $N = 16$) or remained under 12:12 h LD (light on 0600 h, light off 1800 h; $N = 16$; L = 150 ± 5 lx) which served as a control. Although not objectively recorded, regular observations and photographs showed that birds were not in darkness, and at best might have shaded illumination at the extreme rear end when inside the nestboxes during the light period. Next day, into each male cage we introduced a female from the same-sex cage kept in the other room under 12:12 h LD. These pairs (parents, P generation) lived and bred together under the respective light condition for the next 24 weeks. The F1 progeny lived with their parents until 90–100 days old, when they were considered adult (Roper & Zann, 2006) and moved out. Adult F1 males and females from each light condition were again randomly paired and separately housed in breeding cages in the same light condition, and they lived together until we had F2 adults. Thus, we had three (P, F1 and F2) generations, which were used for different measurements, as described below.

Experiment 1: Activity and Singing Behaviours

Daily activity and singing patterns were recorded at the end of the breeding protocol of the male parents, and after about 150 and 120 (± 20) days posthatch of F1 and F2 adult males, respectively. We investigated song acquisition in 60 birds in LD (14 P, 35 F1 and 11 F2 birds) and 52 birds in LL (14 P, 33 F1 and five F2 birds). For this, birds were moved to separate activity/sound-recording cages (42 × 30 cm and 54 cm high). The activity was monitored continuously over a 10-day period at the end of the experiment. Daily activity was recorded as described in Singh, Rani, and Kumar (2010). Briefly, a passive infrared sensor (digital PIR motion detector, LC-100-PI) mounted on the cage continuously monitored the individual's general activity and transmitted it in 5 min bins to a designated channel of the computerized data-recording system. The collection, graphics and analysis of activity were done by 'The Chronobiology Kit' software program of Stanford Software Systems (Stanford, CA, U.S.A.). For better visual resolution, we obtained a double-plotted activity record (actogram), wherein successive days' activity was plotted sideways and underneath. A daily activity profile was further plotted in a graph format, for which the activity record over a 7-day segment was first averaged for each hour for every individual and then plotted over 24 h.

Similarly, the calls, song and daily singing pattern of each male were recorded at the end of the experiment by a Behringer C-2 Studio Condenser microphone fitted in each cage, using M-Audio Profire 2626 8-channel Sound Card and Nuendo application software (Steinberg Media Technologies GmbH, Hamburg, Germany) over about a 48 h period with reference to the onset of singing; hence the recording covered 2 circadian days (2 × period length of daily