



## Research report

# Differential activation and tyrosine hydroxylase distribution in the hippocampal, pallial and midbrain brain regions in response to cognitive performance in Indian house crows exposed to abrupt light environment



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## HIGHLIGHTS

- Hippocampus and pallium are involved in spatial and visual learning, respectively.
- Both cognition and neuronal activity were declined under constant light (LL).
- ZENK activation pattern differs with the light environment and learning task type.
- ZENK and tyrosine hydroxylase coexpression show role of dopamine in light-effects.
- Dopamine decrease in VTA and SN parallels cognitive deficits under LL in corvids.

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## ABSTRACT

Disruption of the cyclic feature of the day-night environment can cause negative effects on daily activity and advanced brain functions such as learning, memory and decision-making behaviour. These functions in songbirds, including corvids, involve the hippocampus, pallium and midbrain, as revealed by ZENK (a neuronal activation marker) and tyrosine hydroxylase (TH) expressions. TH is rate-limiting marker enzyme of the biosynthesis of dopamine, widely implicated in learning and memory. Here, we measured ZENK and TH immunoreactivity in the hippocampal, pallial and midbrain regions in response to cognitive performance (learning-memory retrieval) tests in Indian house crows (*Corvus splendens*) exposed to constant light environment (LL) with controls on 12 h light:12 h darkness. Along with the decay of circadian rhythm in activity behaviour, LL caused a significant decline in the cognitive performance. There was also a decrease under LL in the activity of neurons in the hippocampus, medial and central caudal nidopallium, and hyperpallium apicale, which are widely distributed with TH-immunoreactive fibres. Further, under LL, TH-immunoreactive neurons were reduced in number in midbrain dopamine synthesis sites, the ventral tegmental area (VTA) and substantia nigra (SN), with a negative correlation of co-localized ZENK/TH-immunoreactive cells on errors during the association tasks. These results show decreased activity of learning and memory neural systems, and underscore the role of dopamine in reduced cognitive performance of diurnal corvids with disrupted circadian rhythms under an abrupt light environment.

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**Abbreviations:** APH, area parahippocampus; DA, dopamine; HA, hyperpallium apicale; HP, hippocampus; LL, constant illumination; LMR, learning and memory retrieval; LD, light-dark; NCC, central caudal nidopallium; NCL, lateral caudal nidopallium; NCM, medial caudal nidopallium; RI, retention interval; SN, substantia nigra; TH-ir, tyrosine hydroxylase immunoreactive; VTA, ventral tegmental area.

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## 1. Introduction

Temporal partitioning of day-night periods is vital to the organization of behavioural and physiological adaptations including the advanced brain functions [1]. An abrupt light environment or exposure to light at night can disturb the cyclic feature of the day-night environment, and cause widespread negative effects on daily cycles of sleep, activity, energy homeostasis and brain functions. This mainly occurs due to disruptions of the temporal organization,

causing mismatch of an individual's internal circadian rhythms with its external light environment [1,2].

Increasing evidence suggests that cognitive abilities are intimately tied with the circadian rhythms, synchronized by light-dark (LD) cycle [1,2]. Hence, desynchronization of circadian rhythms conditions can severely impact the cognitive processes and performance. Experiments have shown that light at night attenuates learning and memory, increases anxiety and depression [3,4] and decreases neuronal plasticity such as the spine density [5] and neurogenesis [6] in nocturnal rodents. Mice under constant illumination show circadian rhythm disruption as well as associated sleep deficits, altered mood and depression-like behaviours [7]. Also, alterations in the natural LD environment significantly impacts sleep and singing behaviours in diurnal great tits, *Parus major* [8,9].

Hippocampus plays a major role in the acquisition of spatial learning and memory in both birds and mammals [10–12]. Avian hippocampus has been shown to be involved in homing behaviour (pigeon [13]), spatial orientation (zebra finch, *Taeniopygia guttata* [11,14]) and food cache memory (corvids [15]). Similarly, the nidopallium is important for visual learning [16] and working memory in birds [17]. The expression of ZENK, a neuronal activation marker, in response to the learning test paradigms has been used to show the role of the hippocampus and nidopallium regions in the learning and memory in birds [11,14].

In mammals, the executive functions including manipulation of the informations in working memory and decision making are mainly ascribed to the prefrontal cortex (PFC) and frontostriatal neural circuits, which heavily rely on neuromodulation, particularly on dopamine (DA) [18]. The contribution of DA and its receptors in PFC to learning and memory processes has been shown in several species [18,19]. The functional equivalent of mammalian PFC is the avian lateral caudal nidopallium, NCL [20,21]. Several recent studies have confirmed the role of NCL in the working memory and decision-making behaviour [22,23] including those required during the learning of associations [24], judgements of numerical ability [25] and executive control of behaviour in corvids [26]. Therefore, investigations of the role of dopaminergic (DA-ergic) system could be a vital step in understanding the learning, memory and decision-making processes in birds.

The DA-ergic system is very similar in anatomy between mammals and birds [27,28]. DA neurons originate in several closely lying midbrain nuclei, in particular the ventral tegmental area (VTA) and substantia nigra (SN), and project to many brain areas including hippocampus and pallium [27]. The identity of the DA neurons can easily be ascertained by immunohistochemical localization of the catecholamine-synthesizing enzymes, namely tyrosine hydroxylase (TH), aromatic amino acid decarboxylase, and dopamine- $\beta$ -hydroxylase [29,30]. As a rate-limiting enzyme of the pathway [27,29,30], TH has been commonly used as a reliable marker of the dopamine synthesis [27]. Further, DA synthesis and its functional roles as shown by DA receptor expressions in target brain areas have been reported to be under the circadian clock control [31,32].

The consequence of circadian rhythm disruption on neural processes underlying cognitive processes and performance under abrupt light environment has not been well understood. We hypothesized that disruption of the circadian rhythms, as evidenced by activity behaviour, would negatively affect the activity of learning and memory neural systems and dopamine synthesis, and in turn would result in decreased cognitive performance. We tested this in a diurnal corvid species, the Indian house crows (*Corvus splendens*) in which the timing of activity, ingestive and grooming behaviours has been shown to be under the circadian rhythm control [33]. In general, corvids are ideal avian model systems for studying the reward-based learning and memory processes, and they are at par with the mammalian system when it comes to

**Table 1**

A summary of the experimental protocol for cognitive performance tests.

Cognitive performance	Spatial learning	Pattern learning
Training	5 trials for each crow to learn the rewarded location (same location of the reward)	10 trials per day to learn two patterns (one rewarded and one un-rewarded) till the crows reach 80% success in 2 consecutive session location of the pattern was changed in each trial to avoid spatial association
Testing	1 h retention interval (RI) – 1 h after completion of training (10 trials) 24 h retention interval (RI) – 24 h after completion of 1 h RI testing (10 trials) location of the reward was same for both training and testing trials for each crow	testing included discrimination of the rewarded pattern (during training) from other five un-rewarded patterns. location of the pattern was changed in each trial to avoid spatial association.

the cognitive abilities [15]. Therefore, we examined ZENK and TH expressions in hippocampal, pallial and midbrain regions in order to assess alterations in the activity and DA synthesis in response to cognitive performance (learning-memory retrieval, LMR) tests in Indian house crows under constant illumination (LL), with controls on 12 h light:12 h darkness. We predicted disruption in circadian rhythms in activity behaviour as well as decline in the cognitive performance of crows under LL. We also expected an overall decrease in activity of the hippocampus and pallium regions, and reduction in number of TH-ir neurons in the VTA and SN of crows under the LL condition.

## 2. Materials and methods

### 2.1. Subjects and experiments

Adult Indian house crows (*Corvus splendens*) were caught from the wild, and thus were naive to the experimentation. These crows were brought to the facility and were housed individually in cages (100 × 80 × 80 cm), each fitted with two perches and mounted with a passive infrared motion sensor (DSC, LC100 PI Digital PIR detector, Canada) on the top of the cage. These cages were illuminated by compact florescent lamps (Phillips CFL lamp, 5 W, 220–240 V). Temperature of the room was always maintained at 24 ± 2 °C. Food (prepared meal consisting of bread crumbs, egg, fruits and cheese) and water were provided *ad libitum*. During the training and testing for behavioural assessment crows were deprived of basic food for 2–3 h prior to the onset of training and test trials. All the training and testing were done in the same cage, in which crows were initially housed to avoid any effect of novelty during the test. The meat pellet, which was found to be preferred diet, was chosen to serve as the reinforcement (reward) during the training and testing.

Two experiments were performed. Experiment 1 (n = 12) tested the spatial learning and experiment 2 (n = 6) tested the pattern associative learning under periodic and aperiodic light conditions, as per the protocol summarized in Table 1. Crows were exposed first to periodic (12 h light:12 h darkness, 12L:12D) for a week, and then half of them were maintained on 12L:12D and other half were subjected to constant illumination (LL; Fig. 1a). This change in light

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