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Changes in olfactory inputs modify the energy balance response to short days in male gray mouse lemurs

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Abstract

The role of olfaction/olfactory cues on photoperiodic responses was assessed in Malagasy primate, the gray mouse lemur. When exposed to short photoperiod (SP), this primate demonstrates rapid changes in energy balance as adaptive anticipatory response for winter survival. To follow early changes induced by SP exposure, body mass, food intake, resting metabolism (RMR) and free thyroxin levels in plasma (T4) were measured in males abruptly transferred to SP: six intact males (controls), eight males that underwent bilateral olfactory removal (BOX) and eight males exposed to male urinary cues (U-exposed). To assess the effect of SP exposure, two other groups were maintained for 6 weeks under LP: six controls and six BOX males. Whereas all studied parameters remained constant in controls and BOX males maintained under LP, exposure to SP led to different responses according to groups. In controls, SP exposure led to a regular increase in body mass and after 4 weeks under SP, plasma T4 levels, food consumption and RMR significantly decreased. Even if BOX males demonstrated hyperphagic patterns regardless of the photoperiod, an increase in body mass was also induced by SP exposure but without changes in RMR or food intake that were body mass-dependent. In U-exposed males, body mass gain was significantly reduced while food intake and RMR remained high. In both BOX and U-exposed males, SP exposure led to a transient but high increase in T4 levels compared to controls. These results suggest that olfaction/olfactory cues may delay the SP-mediated changes in energy balance.
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1. Introduction

Chemical cues are commonly used by mammals to communicate with each other in many social contexts. Most social behaviors involved in reproduction, in spatial repartition, in individual recognition or in parental care rely on olfactory cues [5,12,22,49]. Reproduction has been the main studied function for demonstrating the effects of chemical signals on behavior and physiology through direct effects between the olfactory bulbs and central structures regulating gonadotrophin secretion [13,15,19].

Basically, removal of the olfactory bulbs results in a remarkably broad set of behavioral, metabolic and endocrine changes [6,24–26,60]. Bilateral olfactory removal interacts also on daily rhythmicity such as alteration in the rest-activity rhythm, disturbances in endocrine or metabolic daily rhythms or delayed responses to light entrainment [17,42,46,47]. In addition, responses to photoperiod are modified in rodents deprived from olfactory bulbs as exemplified for reproduction or hibernation [43,45,50]. Likewise, in rats and mice considered as non-photoperiodic species, removal of the olfactory bulbs sensitizes animals to light stimuli, unmasking reproductive responsiveness [31,32]. By contrast, stimulation by olfactory cues has direct positive effect on daily rhythms and on responses to light entrainment [18,20] and increases *c-Fos* reactivity in the suprachiasmatic nuclei, a brain structure known to regulate daily and seasonal rhythms in mammals [1]. It has been suggested that observed effects of olfactory bulbs removal are not linked to anosmia per se but would proceed from interactions between the olfactory

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bulbs and brain structures controlling endocrine mechanisms and/or biological rhythms.

Although the role of olfactory communication on socio-sexual behaviors and reproductive function has been well documented in primates including humans [2,9,58], its interaction on non-sexual biological rhythms remains poorly investigated. The gray mouse lemur (*Microcebus murinus*), a nocturnal Malagasy primate, is a very convenient species to test such interaction. This primate mainly uses olfactory cues in social relationships and possesses highly developed olfactory and vomeronasal systems (2.6% of the total brain) that are specifically activated with urine from conspecifics [51]. Moreover, mouse lemurs exhibit daily and seasonal rhythms that are dependent on the photoperiod and can be reproduced in captivity by cyclic variations of the daylength [36,40]. Exposure to long days (>12 h light/day) entrains seasonal activation of reproductive function associated with increased behavioral and physiological activities. By contrast, exposure to short days (<12 h light/day) leads to pronounced fattening, reduced behavioral activities, torpor and complete sexual rest in both sexes. Typically, exposing mouse lemurs to short days induces in 6 weeks, a rapid increase in body mass, transient modifications in food intake, reduction in oxygen consumption and decrease in thyroxine levels [16,40], all these changes representing adaptive preparatory responses for winter survival.

In this primate, previous studies have demonstrated that urinary cues, acting pheromonally, interfere on photoperiod-mediated changes in reproductive function [34] and elicit different sexual responses according to the photoperiodic conditions to which the animals are exposed [39]. In addition, bilateral olfactory removal leads to changes in sexual responses to photoperiod, characterized by reduced testosterone levels during the breeding season and delayed sexual recrudescence under short days [38,52]. These effects of chemical cues or olfactory bulbectomy on reproductive function would depend on specific neural connections between olfactory bulbs and hypothalamic structures regulating gonadotrophins. However, the effect of olfactory inputs on seasonal sexual responses would possibly rely to changes in photoperiod responsiveness since, in mouse lemurs, photic and chemosensory systems project on suprachiasmatic nuclei which are implicated in the organism's rhythmicity [10,28]. The aim of this paper is to investigate the role of olfaction/olfactory cues on photoperiod responsiveness in mouse lemurs using a non-sexual response: the early changes in energy balance induced by exposure to short photoperiod.

2. Materials and methods

2.1. Animals

Thirty-six (2–5-year-old) male gray mouse lemurs (*M. murinus*) were used in this study. All animals were born in the laboratory breeding colony (Brunoy, MNHN, France, European Institutions Agreement no. 962773) from a stock originally caught in southern Madagascar 30 years ago. They were kept in controlled conditions with constant ambient temperature (24–26 °C), constant relative humidity (55%) and food available ad libitum. All experiments were carried out in accordance with the European Communities Council Directive (86/609/EEC).

To ensure highly synchronized changes in biological rhythms within individuals, captive animals were routinely exposed to an artificial photoperiod regimen consisting in a 20-week period of winter-like short days (SP: 10 h light/day) followed by a 22-week period of summer-like long days (LP: 14 h light/day). These daylengths have been chosen to approximate natural photoperiod amplitude between solstices found in southern Madagascar.

All studied animals had been raised under LP for 22 weeks before the start of the experiments. At that time, all males had regressed testes [36]. They were housed individually in cages (0.5×0.5×0.5 m), visually separated from each other by wooden partition, and provided with nest and branches. Olfactory isolation was ensured by continuous air flow ventilation. To follow early changes induced by exposure to SP, three groups of males were abruptly transferred to SP: six intact males (controls), eight males that had their olfactory bulbs removed (BOX) and eight males exposed to urinary chemosignals (U-exposed). Body mass and parameters involved in energy balance were measured 1 week before the photoperiod shift, every week during the 4 weeks following SP exposure and 2 months after. To assess effect of SP exposure, two other groups were maintained for 6 weeks under LP: six intact males and six bulbectomized males.

2.2. Bilateral olfactory bulbs removal

Removal of the olfactory bulbs was performed according to a method previously described [52]. Later premedication with atropin (0.05 mg/kg s.c.), surgery was performed under Valium (Valium, Roche, Neuilly sur Seine, France, 5 mg/kg i.p.) plus ketamine (Imalgen, Rhône Mérieux, Lyon, France, 8 mg/kg i.p.). Bilateral bulbectomy was created by aspiration of the olfactory bulbs through a hole drilled medially in the nasal bones behind the lamina cribosa. To avoid possible regeneration of olfactory glomerular structures in the forebrain, the empty olfactory bulb cavities were packed with gelfoam (HOUDE Laboratory, Paris, France). Surgery was done 2 months before the beginning of the experiment. In previous studies using the same procedure [38,52], histological examination showed that the cavity was empty of neural tissue 1 year after surgery.

2.3. Exposure to urinary chemosignals

To test the effect of urinary chemosignals, males were exposed to the volatile compounds of urine from sexually

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