Torpor in insects

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Sleep is a biologically cyclical episode of brain and body which may be referred to as a behavioural and corporeal condition characterized by change in alertness, decrease in sensitivity to extrinsic stimuli and regulation of homeostasis. Basically sleep is considered to be a key requisite for all organisms including insects. The term 'Torpor' is used to denote sleep in insects which is not exactly similar to that of sleep as in case of human beings but is a sleep-like state where the insects remain in a state of decreased physiological activities, reduced body temperature and metabolic rate. The circadian clock and sleep homeostasis are the vital mechanisms known to regulate torpor. However, more precise and minute observations are required for studying the sleep pattern of the insect brain to draw a logistic conclusion on this aspect, which needs further research.

Keywords: Circadian clock, *Drosophila melanogaster*, homeostasis, insects, torpor.

SLEEP is a naturally recurring state of mind and body which is characterized by alteration in consciousness, inhibition of sensory activity and almost all voluntary muscles, and declined interactions with the surroundings[1]. Sleep can be differentiated from wakefulness by reduction in the potentiality to respond to stimuli; however, this phase can be easily reversed when compared to the phase of being comatose. In non-human animals, sleep has been referred to as a behavioural and physiological state characterized by altered consciousness, reduced responsiveness to external stimuli and homeostatic regulation. Sleep is observed in mammals[2], birds[3], reptiles[4], amphibians[4], some fishes[5], and in some form, even in simpler organisms such as nematodes[6]. In diurnal organisms like humans, daily sleep during night-time is promoted by the internal circadian clock, whereas in nocturnal organisms like rodents it promotes sleep in the day[7]. However, pattern of sleep differs extensively between different species. Like human, sleep seems to be an essential requisite for almost all non-human organisms as well.

Sleep can follow both behavioural and physiological definitions which hold true for both human and non-human organisms, viz. animals, birds, rodents, etc. In the physiological sense, sleep is referred to as a phase indicated by unconsciousness that can be reversed, special brain-wave patterns, sporadic movements of the eye, decrease in muscle tone and a compensatory increase which is followed by deprivation of the phase[8]. Sleep in the behavioural sense is indicated by limited or no movement, static response/unresponsiveness to external stimuli (i.e. increased sensory threshold), adoption of a peculiar pose and possession of a particular location which is usually repeated at 24 h basis[9]. The earlier definition applies well to mammals and birds, but in case of animals having less complex brains, the behavioural definition is used more frequently[2,3].

In insects, sleep is somewhat different from other organisms in the sense that they cannot close their eyes because they do not have eyelids. Ommatidia present in the compound eyes are always found to be naked, which become less sensitive in the dark. The term which is used to denote sleep in insects is 'Torpor' which is not exactly similar to that of sleep as in case of human beings but is a sleep-like state where the insects remain in a state of decreased physiological activities, reduced body temperature and metabolic rate. The word 'torpor' was derived from the Latin word 'torpere' meaning 'to be numb or sluggish' and is known to be regulated by two major factors namely circadian clock and homeostasis[10,11]. The circadian clock plays a pivotal role in timing and consolidation of sleeplessness and slumber, whereas homeostasis reflects the requirement of sleep that cumulates during the course of sleeplessness or wakefulness and disappears during sleep[11]. Studies on sleep in insects date back to the publication of Rau and Rau[12] in 1916 and 1938. They observed that at around 10:00 am, the blue wasps did not show any significant movements because of the prevailing dark weather condition due to an approaching cyclone.

Fruit fly, *Drosophila melanogaster* Meigen, 1830 (Diptera: Drosophillidae) had been considered as one of the finest invertebrates on which various biological experiments have been conducted since time immemorial. The mechanism of sleep in sleep biology had been studied

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by linking molecular and neuronal processes of sleep behaviour with the neurophysiological, behavioural and genetic analyses, giving an insight on the utility of invertebrate models[13]. Presence of adenosine in the fruit-fly brain (also present in the human body), which increases during activities and decreases during sleep plays a major role in sleep and wakefulness. Light can cause *D. melanogaster* to take longer midday sleep, which is supported by the fact that they possess four cell Hofbauer–Buchner eyelets (Figure 1)[14]. When light falls on these eyelets, it activates the synthesis of histamine and acetylcholine (neurotransmitters). The neurons responsible for carrying out the activities during morning hours are activated by acetylcholine, whereas indirect inhibition of the circadian clock for evening peak phase is triggered by histamine that extends the inactivity phase[13].

Torpor in *D. melanogaster*

Hendricks *et al.*[15] conducted a study on torpor or sleep-like state in *D. melanogaster*. Whether torpor actually exists in *D. melanogaster* or not was understood by conducting a standard locomotor assay, where the flies were studied and observed individually using videotape recordings obtained through a CCTV camera (Cohu High Performance 4915–2000/0000) for a period of 48 h on a time-lapse videocassette recorder (Panasonic AG-6124) at 24 h speed[16]. The observations made during the period of investigation provided evidences on preference of location and immobility of *Drosophila* flies for periods of up to 157 min at a particular time in the circadian day. They also became relatively unresponsive to sensory stimuli. The total sleeping period for female flies was 400 to 800 min/day, whereas in case of males it was almost 1100 min/day[17]. Some flies having the *shaker* mutant gene usually sleep for only 3–4 h each day rather than 8–10 h (ref. 18).

Sleep-like state has been observed in insects like monarch butterflies, bugs, cockroaches, and social insects like honey bees and ants[19,20].

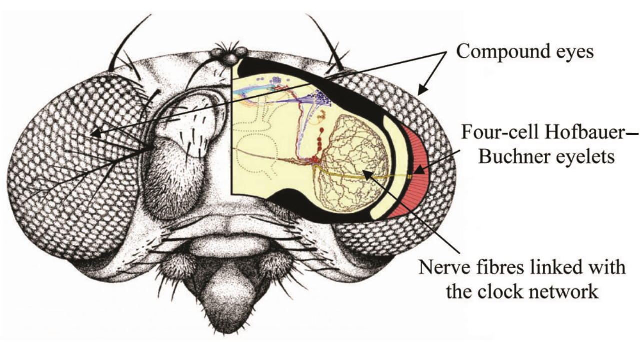

Figure 1. Regulation of sleep in *Drosophila melanogaster* in presence of light.

How do monarch butterflies sleep?

Monarch butterflies usually make a cluster of groups (congregate) and keep their wings folded during night-time while migrating to the south. They give an appearance of lifelessness prior to the next day's flight[19]. An additional advantage of sleeping in a clumped pattern is that their sleeping aggregation keeps the individuals safe from predators.

How do bugs sleep?

Signs of sleep in bugs include 'not moving, drooping in the direction of gravity and more relaxed muscles'. An additional indication is 'increased arousal threshold,' or time required to wrench the bug to alertness[19].

Torpor in cockroaches

Cockroaches also exhibit a sleep-like state. They are known to have rhythms related to activity indicating the stipulated time during the day when cockroaches do not show any signs of activity and remain quiet as well as hidden. On the contrary, they also have a wakeful phase when they show signs of activity by actively searching for mates, food and water. The session of rest in cockroaches can be observed when they fold their antennae. During rest they also exhibit reduction in the level of sensitivity against external stimuli. In general, cockroaches are active (i.e. awake) during the four hours after lights-out. They cue on that time when one normally shuts off all the lights during night ensuing four hours of activity which is enough for them to accomplish all their principal activities without human intervention.

Tobler and Neuner-Jehle[20], studied topor in *Blaberus giganteus* Linnaeus, 1758 (Blattodea: Blaberidae), a cockroach species. The test organisms ($n = 10$) were kept in isolation, where their behavioural study was carried out by preparing time-lapse video for a period of three consecutive 24 h. The study revealed the occurrence of nine behavioural states which were scored for 1 min real-time epochs, whereas on the basis of body posture and antennal position, the rest was subdivided into four sub-states. A nocturnal behaviour demonstrating locomotion was shown by the cockroaches during the onset of darkness that continued for several hours, followed by inclination for rest during the period of light. The predominating state during light period was the static behaviour or immobility, and both body and antennae were touching the substrate (state 1). Arousal threshold was measured to comprehend whether the sub-states of rest signified contrasting levels of vigilance by determining the latency of a behavioural response to a vibration stimulus. During light period, the arousal levels significantly differed, but these differences diminished in the dark period. The test organisms showed the lowest arousal in state 1, whereas arousal was highest in the activity states. Occurrence of the state with the highest arousal threshold was observed at the beginning of the light period. Thereafter, progressive enhancement in the arousal was observed that was relatively high during the dark period. The effect of 6 h deprivation of rest by gentle shaking of the cages whenever the organisms were immobile, resulted in a reduced latency to state 1, a small increase of state 1 and a more prominent initial increase of activity during recovery. Thus, it can be concluded that the study provided evidence for the existence of a 24 h variation of vigilance in the cockroach, further indicating that a 'rest deficit' leads to a compensatory response.

Torpor in honey bees

Hussaini *et al.*[21] reported that formation of memory remains unaffected by sleep in honey bees, *Apis mellifera carnica* Pollman, 1879 (Hymenoptera: Apidae). They showed that retention of extinction learning is significantly reduced in the bees that were sleep-deprived. They concluded that some bees of family Apidae (mostly males) clamp onto a plant with their jaws in the evening and stay in that position till the next morning.

Torpor in fire ants

Cassill *et al.*[22] carried out an experiment to study the impact of light and dark periods on the activity of fire ant (*Solenopsis invicta* Buren, 1972) workers and queens in an artificial nest chamber. Observations were made on their sleep location, position and posture, including the sleep/wake cycles. During the experiment, they observed that the workers preferred to sleep in one out of three locations, viz. centre of the chamber floor, against the chamber wall or on the ceiling. Prolonged sleep episodes were observed in workers that slept against the chamber wall or on the ceiling compared to those that were at the centre where most of the activities related to feeding and grooming occurred. An average of ~253 episodes of sleep were observed in workers which lasted 1.1 min each making a total of ~4.8 h of sleep/day. The indicators of deep sleep in ants are as follows:

- Unresponsive towards the contact of other ants and antennae are folded followed by rapid antennal movement (RAM sleep).
- Queens have about 92 episodes of sleep/day, each 6 minutes long.
- Queens synchronize their wake/sleep cycles.
- Workers show an approximately 253 sleep episodes per day, each 1.1 min long.

Evidence of sleep-like state or torpor in fire ants, *S. invicta* can be understood by an experiment where queen activity/inactivity was taken into account[23]. During queen activity, three different stages were observed:

(i) Sensing environment – when they moved their heads or while walking, the queens stretched out their antennae keeping the scape in front of the eyes; funiculi and scape made an obtuse angle. Also mandibles were partly extended (Figure 2 *a*).

(ii) Ingesting food – queens kept their antennae in such a way that the scape and funiculi made an acute angle with scape extending in front of the eyes while ingesting fluids. The terminal antennal portion poked and probed the glossae of workers or the anal slit of larva (Figure 2 *b*).

(iii) Regurgitating food – queens while regurgitating food to another queen or a worker stretched out their antennae with the scape in front of the eyes, which formed a right angle with the funiculi. Mandibles were found to be open and the glossae were found to be fully extended (Figure 2 *c*).

During queen inactivity, two distinct stages were observed:

(i) Deep sleep – indicated by complete retraction of antennae (scape and funiculi), unresponsiveness of queens to contact by workers and RAM of the folded antennae of queens which was similar to the rapid movement of the eyes (REM) in vertebrates (Figure 3 *a*).

(ii) Dozing – partly extended antennae, with scape and funiculi at right angles, mandibles partly opened in such a way that the tips of the teeth were only touching, but not overlapping. Queens in dozing state were more likely to respond to the contact of workers or other queens via movements of the antennae (Figure 3 *b*).

The location of queen was distinguished based on its positions during sleep and wakefulness. When queens were inactive, they huddled together during sleep episodes (Figure 4) whereas during activity, queens were close but avoided touching each other (Figure 5).

Significance of sleep-like state[24]

(a) Retention of extinction learning and precise communication. (b) Essential for basic survival. (c) Protection against predators.

Status of sleep deprivation in different insects

Sleep deprivation is a common physiological behaviour in some insects. It occurs due to lack of proper sleep or resting period in insects under unfavourable condition(s) created artificially in their habitats[12,25]. It results in different behavioural changes and modification of daily activities in insect bodies. A few examples are given below.

Sleep deprivation in honey bees

Klein *et al.*[25] found that sleep-derived honey bees, *Apis mellifera ligustica Spinola*, 1806 showed reduced foraging activities, failed to communicate properly with other nest mates via waggle dance and there was a gradual loss of fitness of bee colonies. Another study revealed that forcibly inducing sleep deprivation in honey bees on the first night was accompanied by arousal in fixedness of antennae on the next night when the honey bees were kept undisturbed, due to prolonged interlude of fixedness (immobility) of antennae[26]. This sleeping mechanism of sleep deprivation is fully controlled by regulatory mechanisms like in other arthropods[27] and mammals[28]. Torpor is more likely to play a much greater role than restoration of energy in honey bees. Kaiser *et al*.[29] also comprehended the behaviour of resting in honey bees against a temperature gradient.

Sleep deprivation in D. melanogaster

D. melanogaster is known as one of the most promising agents for genetic dissection of sleep because of huge similarities between flies and mammals. After screening 9000 mutant lines, *mns* lines of *D. melanogaster* showed no significant changes in their behaviour due to reduced sleep but *shaker* lines showed reduced lifespan as they encode voltage-dependent potassium channel controlling membrane repolarization and transmitter release thus they can regulate sleep and its efficiency[18]. Some mutant flies tested could sleep for 24 h due to the presence of circadian genes like *cycle*, *period* or *clock* which destroy the natural circadian rhythms[27]. Even after 24 hours of sleep deprivation, ability to move from a place to another after getting some stimuli was also impaired significantly. Cirelli and Bushey[30] reported that sleep deprivation in *D. melanogaster* reduced vigilance and daily performance of the fruit flies. A decrease in sleep fragmentation, measured by episodes of brief awakening, was also observed after a long sleep deprivation[31]. Some experiments also showed that due to long sleep deprivation, learning and memory of flies are impaired gradually though a mechanism that is still unknown[32]. Some mutants of *D. melanogaster* like *cyc*^{01} and *HSP83* died after 10 h of sleep deprivation[33]. Presence of mutant dopamine transporter gene in *D. melanogaster* helps reduce the sleeping period and leads to sleep deprivation[34].

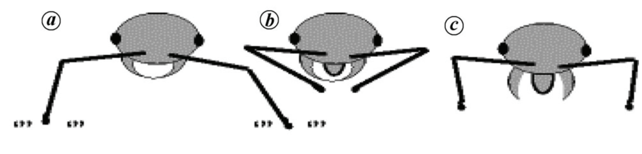

Figure 2. Activity of the queen: (***a***) sensing environment (***b***) ingesting food and (***c***) regurgitating food (adopted from ref. 22).

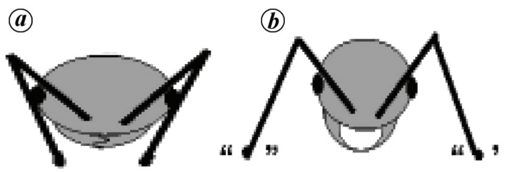

Figure 3. Queen sleep or inactivity: (***a***) deep sleep and (***b***) Dozing (adopted from ref. 22).

Evidence of inverse relationship between the activity of protein kinase A (PKA) and sleep has also been established in *D. melanogaster*, wherein it had been observed that increased PKA activation leads to reduction in the amount of daily sleep[35]. The amount of sleep may either decrease or increase depending on the expression of PKA in neurons present in the mushroom bodies by inducing the expression of a constitutively active PKA transgene via GAL4 drivers (major patterns of expression within the brain)[35,36]. PKA was found to be expressed mainly in the γ lobes and the core region of the α and β lobes, with the 201Y GAL4 driver showing increase in the amount of sleep whereas with c309 where expression of PKA occurred in the α, β and γ lobes, excluding the core region, the amount of sleep was found to be decreased[36]. Thus, the expression of PKA transgene (constitutive) in the mushroom bodies or pan-neuronally also leads to reduction in sleep. However, it is still not clear how the output from the mushroom bodies regulates the interval of sleep[36].

Sleep deprivation in cockroaches

Among arthropods, sleep deprivation or rest deprivation has been studied for the first time in cockroach species

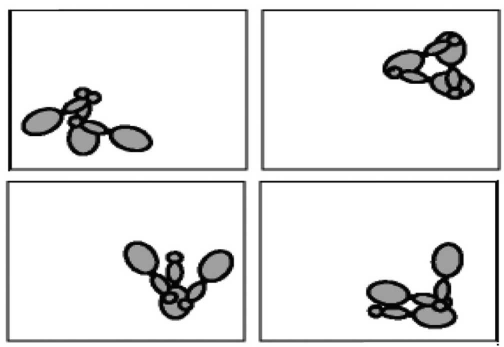

Figure 4. During inactivity – queens huddled together during sleep episodes.

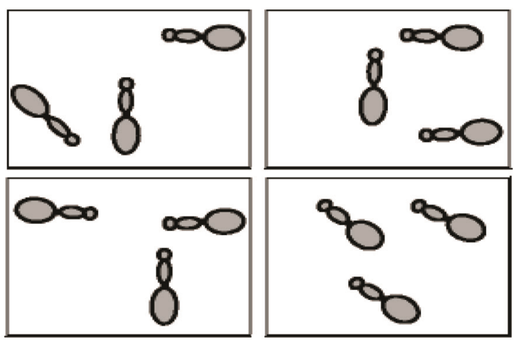

Figure 5. During activity – queens remained close, but did not touch each other (adopted from ref. 22).

Leucophea maderae and *Blaberus giganteus*, and also in three scorpion species[20,37,38]. Deprivation of rest for 3 h in *L. maderae* by inducing forced activity caused increase in the duration of immobility during the first hours of recovery[37]. Deprivation of rest for 6 h in *B. giganteus* by gentle handling led to an increase in the duration of rest substate, characterized by minimal arousal and reduction in the latency of the state[20].

Sleep rebound in insects

Sleep rebound is also an important part of insect lives especially after certain sleep deprivation; sleep rebound is a must to get back to their normal livelihood. There is not much evidence till now about sleep rebound, but some authors have provided information/observations on particular insect species. Sleep rebound is the immediate action after a long sleep deprivation. After sleep deprivation, insects need immediate resting mode or sleep-like state, which is basically called as sleep rebound and without this state, insects cannot get back to their daily activities after sleep deprivation. Hence sleep rebound is the main cause of sleep deprivation.

Sleep rebound in *D. melanogaster*

Cirelli and Bushey[30] found that *D. melanogaster* needs a long duration of sleep recovery/rebound succeeding a certain distress of sleep. The sleep rebound provides energy for daily activities and increases their arousal threshold (vibratory, visual and auditory stimuli) and brief awakenings. Shaw *et al.*[27] reported that after going to sleep deprivation for 24 h, some mutant flies can even show sleep rebound for a certain period. A total of four mutant lines have been recorded where no sleep rebound has found after 24 h of distress due to lack of homeostatic response[30]. *Drosophila shaker* mutant which is short-sleeping, shows sleep rebound after a short sleep deprivation[18].

Sleep rebound in honey bees

In case of honey bees *A. mellifera ligustica*, it is mandatory to go for a recovery sleep or sleep rebound after a long sleep deprivation[25]. Sleep recovery helps them to carry out better foraging activities field, and honey bees regain their lost communication ability (due to sleep deprivation) and communicate with their nest mates through waggle dance again[25].

Conclusion

Sleep can be considered as a key biological phenomenon but its function is still unclear despite repeated studies in insects. The difficulty in understanding the role of sleep can be partly attributed to the varied manifestations of sleep in different organisms. Cockroaches have been shown to sleep for around 14 h a day and in this state they are significantly less reactive to outside stimuli, whereas in case of fire ants, queens have about 92 and workers about 253 sleep episodes per day. However, further evidence is required to establish their fact.

Sleep may be defined as an easily and speedily alterable condition of motionlessness and substantially decreased sensory responsiveness[39]. It is recognizably different from plain rest and/or enduring conditions, viz. hibernation. In a generalized way, humans and mammals are known to form specified and distinct electrical patterns in their brains during sleep; however, whether these patterns are found in insects or not is a question which needs to be answered. Thus, a more advanced study on sleep in insects is required.

It may be concluded, this study on different insects provide a baseline for studying the function of sleep in a highly social organism with a caste system of short-lived and long-lived siblings and also in other groups of insects. Precaution should be taken while using herbicides, because it has been found that glyphosate adversely affects the sleeping behaviour of honey bees[40].

Future challenges and prospects

As sleep is an important phenomenon for all animals, the study of sleeping mechanism has become essential, specifically in insects. Some future challenges and prospects are listed below.

- Verification of two major mechanisms (circadian rhythm and homeostasis) in most of the insect species to develop a suitable mechanism or model.
- Exploring the possible linkage between molecular and physiological approaches during sleeping period of insects.
- Proper study of relationship between genetics and physiology during sleep deprivation and sleep rebound.
- Effect of mutation in insect genes on sleep of different insect species.
- Exploring proper biological function of sleep in various insect species.
- Exploring the role of any organs or specific nerves in the mechanism of sleep in insects.
- Exploring chemical changes during sleep in the insect body.
- Electrophysiological, electromyographical and behavioural studies during sleep in insects.

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