REVIEW

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Melatonin effects on animal behavior: circadian rhythm, stress response, and modulation of behavioral patterns

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Abstract

Melatonin plays a crucial role in various behavioral and physiological aspects of animals, including regulating their circadian rhythms. This review provides a comprehensive evaluation of the multifaceted effects of melatonin on animal behavior, such as temperament, stress, and aggression regulation. The focus is on the complex interactions between melatonin and the hormonal and neurotransmitter systems, highlighting how melatonin interacts with cortisol, serotonin, and dopamine to influence behavior. Additionally, it investigates the effects of melatonin on the hypothalamic–pituitary–gonada (HPG) axis and stress responses, emphasizing its potential to improve stress management and social interactions, thereby enhancing animal welfare. The review also examines the seasonal variations of melatonin and its impact on aggression and reproductive activities related to photoperiods, as well as its effects on learning and memory to suggest improvements in animal training methods and practices. Furthermore, it discusses the influence of melatonin on appetite and physical activity regulation, implying its involvement in metabolic processes. In conclusion, further research is needed to elucidate the complex mechanisms underlying the extensive influence of melatonin on animal behavior. Through this review, the aim is to integrate the overall knowledge about melatonin and animal behavioral temperament and to propose new research areas for animal management based on behavioral and hormonal regulation.

Keywords: Circadian rhythms, Neuroendocrine, Neurobehavioral, Temperament

INTRODUCTION

Animal temperament refers to the behavioral and emotional responses exhibited by animals, which are influenced by various factors, including genetics and environment [1,2]. Conversely, hormones are chemical transporters produced by various glands in animals and play an important role in controlling physiological processes. Hormones, such as oxytocin and serotonin, can affect an individual's behavioral pattern and emotional response depending on the amount of secretion [3–5]. Understanding the

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Upon reasonable request, the datasets of this study can be available from the corresponding author.

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intricate interplay between hormones and animal temperament is crucial for enhancing animal management, welfare, and training effectiveness, while also improving care practices and recognizing the paramount importance of animal welfare. This has generated considerable scientific interest, supported by abundant research [6–8]. For example, the stress hormone cortisol is associated with increased fearfulness and reactivity in animals, while low serotonin levels are associated with increased aggression and impulsive behavior [9,10].

Melatonin is a hormone that is primarily involved in regulating sleep-wake cycles and has been found to potentially affect various aspects of animal and human behavior. Recent studies have emphasized the importance of a potential correlation between melatonin and animal temperaments, suggesting that melatonin may also affect animal temperament, including certain patterns of behaviors and emotional responses [11]. Furthermore, research highlights the significant role of melatonin in modulating behavioral responses to environmental stimuli, including the regulation of exploratory behavior, anxiety levels, and responses to stress [12]. Several studies examining the relationship between melatonin and temperament in some animals have shown that melatonin levels are positively related to specific temperaments such as depression and anxiety-like behavior, while no particular correlation was found in mice and rats [13,14]. However, research on the relationship between melatonin and temperament, especially in animals like horses, remained limited. Therefore, this review aims to elucidate aspects of animal behavior currently not fully understood, particularly focusing on the effects of melatonin in specific animal populations with scant research. This review seeks to contribute valuable insights into behavioral regulation and management skills, potentially informing future studies and improving animal welfare strategies.

SYNTHESIS OF MELATONIN

Melatonin is well-known as a hormone that plays an important role in controlling the circadian rhythm in animals. The circadian rhythm is a kind of biological clock that is responsible for various actions such as body temperature, sleep-wake cycle, and release of hormones, including controlling various physiological and behavioral processes of animals [15–17]. The synthesis of melatonin is largely influenced by environmental factors, especially regulated and influenced by exposure to light [18]. The secretion of melatonin is maintained through the interaction of various factors through melanopsin, the pineal gland, and the suprachiasmatic nucleus (SCN) [19]. When light enters through the retina, the melanopsin found in intrinsically photosensitive retinal ganglion cells (ipRGC) is activated and sends an electrical signal within the ipRGC to SCN [20]. Specifically, melanopsin has the highest sensitivity to the blue light spectrum, particularly within about 460 to 480nm, which inhibits the production of melatonin [21]. Exposure to blue light, either natural or artificial, during the daytime hours, suppresses the synthesis and release of melatonin. Conversely, in conditions of darkness, such as in the evening when not exposed to blue light, melanopsin activity is reduced, allowing for the secretion of melatonin [22].

Melatonin is a neurohormone synthesized through complex enzyme reactions, starting with the conversion of amino acids called tryptophan. Tryptophan is absorbed into the bloodstream, transported to the pineal gland, and used for the synthesis of proteins involved in melatonin production [23]. Tryptophan is converted into 5-hydroxytryptophan by tryptophan hydroxylase enzyme, then into neurotransmitter serotonin through the action of aromatic amino acid decarboxylase [24]. Enzymes are biological catalysts that speed up chemical reactions [25]. Two enzymes are involved in the process of converting serotonin into melatonin: serotonin-N-acetyltransferase (SNAT) and hydroxyindole-O-methyltransferase [26,27]. Darkness, characterized by the absence or minimal presence of light, naturally occurs at night and is essential for initiating

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the synthesis of melatonin, a process facilitated by the increased activity of SNAT enzymes [28]. Brightness, or exposure to light, especially blue light during daytime, inhibits SNAT enzyme production, resulting in a reduced amount of melatonin [29]. Melatonin is synthesized in response to darkness and spreads through the bloodstream to reach the target cells. Melatonin receptors 1 (MT1) and 2 (MT2) are part of the G protein-coupled receptor family located in the cell membrane. When melatonin binds to its receptors, the structural changes within the receptor and G protein begins to activate [30]. Moreover, the binding of melatonin reduces the activity of cyclic adenosine monophosphate (cAMP) production, which is a second messenger in cellular signaling derived from adenosine triphosphate (ATP) [31]. This reduction in cAMP levels enhance to activity of potassium channel activity, leading to increased potassium flow out of the cell [32]. As a result, this activity decreases neuro-excitability, affecting nerve cell function and potentially calming neuronal activity [33].

Melatonin's interaction with its receptors initiates cellular signals, elucidating internal pathways. Key players in cellular signals are protein kinases, notably protein kinase C (PKC) and protein kinase A (PKA) [34]. The signaling pathway of melatonin receptors is associated with intracellular signaling pathways other than cAMP, and PKC's activity begins through the release of G proteins or Ca2+ ions, inhibiting cAMP-mediated melatonin receptors [35]. In addition, the activity of melatonin receptors has been shown to control various physiological effects. The part where melatonin is widely known to regulate physiological functions is that it regulates the sleep-wake cycle. However, the sleep-wake cycle affects adolescent control and reproductive process control and affects the activity and proliferation of immune cells through the production control of inflammatory cytokines [36].

THE LOCALIZATION OF MELATONIN RECEPTORS IN VARIOUS ORGANIZATIONS

Melatonin receptors are pivotal in the signaling pathway, mediating the transmission of melatonin's signals upon binding, which in turn initiates physiological responses [24]. Melatonin has two types of receptors called MT1 and MT2 showing specific distribution patterns in various tissues. Melatonin receptors are distributed in the retina, gastrointestinal tract (GI), and skin, especially in various parts of the brain, such as the hypothalamus, cerebral cortex, and hippocampus [25–27]. Melatonin receptors mediate various physiological effects such as antioxidant and radical elimination. Antioxidant action is activated through the activity of melatonin receptors, which protect cells from oxidative stress and reduce damage caused by free radicals, playing an important role in the preservation and maintenance of cells [28]. MT1 and MT2 are mainly located in the brain, especially in the parasympathetic nucleus and SCN which regulates the sleep-wake cycle [37,38]. However, MT2 receptors are also found extensively in the brain and peripheral tissues that activate arousal regulation [39,40]. Melatonin receptors distributed in areas of the brain are related to behavioral regulation, such as the cortex of the frontal lobes [41]. Ultimately, intracellular signaling pathways that affect behavior are activated by melatonin through melatonin receptors [42]. One of the main functions of the secretion of melatonin is to regulate circadian rhythms. The receptors located in the SCN, melatonin perform the overall function of controlling health and sleep-wake-up cycle. Through this knowledge, melatonin-signaling disorders are associated with various sleep disorders [43]. Furthermore, melatonin has the function of mood control. Melatonin receptors located in the hippocampus and amygdala affect mood conditions, reducing stress, and regulating anxiety-like behavior, and depression-related behaviors [44,45]. Another function of melatonin receptors is the regulation of cognitive and memory processes. Activation of melatonin receptors improves multiple cognitive abilities, including learning and memory enhancement [46]. Moreover, melatonin affects the seasonal behavior of animals through changes in receptor signaling [47]. Several studies have confirmed that MT1 and MT2 are also expressed in ipRGC of the retina and contribute to regulating photoreceptor sensitivity and daily rhythm [48]. Binding melatonin and its receptors are involved in protecting against damage caused by excessive exposure to light or UV light to retina by reducing the oxidative stress and provide protection [49]. In addition, the expression of MT1 and MT2 can control dopamine released from the retina [50]. Dopamine is a neurotransmitter responsible for various functions, including visual signal processing in the retina, and melatonin receptors are affecting the regulation of dopamine release [51]. As a result, melatonin and receptors are distributed in various tissues and act as intermediates.

VARIATIONS IN PHENOTYPES ACCORDING TO RECEPTORS SNPS

Phenotypic variations can indeed be caused by single nucleotide polymorphisms (SNPs) in various receptor genes, leading to differences in receptor function, structure, and expression levels [52]. These variations can affect signaling through ligand interactions and have implications for drug responses, hormonal regulation, and neurological disorders. Melatonin receptor SNPs specifically refer to SNPs occurring in genes encoding melatonin receptors, such as MT1 (encoded by MTNR1A) and MT2 (encoded by MTNR1B). These SNPs can influence the function, structure, and expression levels of the receptors, potentially impacting the melatonin signaling pathway [53]. These SNPs are associated with changes in melatonin receptor function and have been linked to various physiological conditions. Variations in phenotypes associated with melatonin receptor SNPs include sleep patterns, circadian rhythms, reproductive health, and mood disorders [54–56].

In mammals, multiple clock genes are expressed in the pars tuberalis, which is driven by SCN. It has been found that the expression of multiple clock genes regulates both circadian and photoperiodic rhythms [57,58]. Also, in mice, the association between specific SNPs of melatonin genes and anxiety-like behaviors and stress responses was identified [59,60]. Different variants of this SNP can result in variations in sleep quality and quantity among individuals. Changes in melatonin receptor genes can affect the timing and synchronization of circadian rhythms, potentially leading to disruptions in sleep patterns and other physiological processes governed by the circadian system [55]. Furthermore, melatonin receptor SNPs have been implicated in reproductive health. According to research on sheep, melatonin is involved in regulating fertility and menstrual cycles, and SNPs in melatonin receptor genes can influence the timing and intensity of melatonin signaling, potentially affecting reproductive functions in both males and females[61,62]. In addition, melatonin receptor gene SNPs have beeRn associated with mood disorders [63]. Melatonin is involved in regulating mood and emotional processes, and variations in melatonin receptor function can impact neurotransmitter systems involved in mood regulation. Certain melatonin receptor SNPs have been linked to an increased risk of mood disorders such as depression and bipolar disorder.

THE EFFECT OF MELATONIN ON THE TEMPERAMENTS OF ANIMALS

Melatonin's role in modulating animal behavior has been known across multiple studies, indicating its association with various animal temperaments, including stress reduction, reduced anxiety and fear, and hormonal equilibrium [64–66]. However, the effect of melatonin on animal temperaments

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may vary depending on species and individual differences. The hypothalamic-pituitary-adrenal (HPA) axis is a central component of the stress response system in various animal species [67]. Its activation in response to stress plays a key role in mediating physiological stress reactions, leading to the release of cortisol in humans, cattle, and fish [67–69]. In contrast, amphibians, reptiles, and some other species release corticosterone [70]. The release of these different hormones highlights the adaptive evolution of stress response mechanisms, which can affect behavioral and physiological outcomes on a species-by-species basis [71–73].

Melatonin plays a crucial role in the body's stress response system by inhibiting the secretion of corticotropin-releasing hormone from the hypothalamus [74]. This leads to a decrease in the level of adrenocorticotropic hormone (ACTH) from the pituitary gland, which subsequently reduces levels of cortisol or corticosterone, the hormones known for their role in stress [75–77]. This mechanism suggests a potential for melatonin to modulate stress responses. However, the relationship between melatonin, cortisol secretion, and stress regulation is intricate. Depending on the body's mechanism, cortisol levels typically increase in response to stress. Decrease in cortisol levels through the action of melatonin does not necessarily interfere with stress response, potentially contributing to the maintenance of homeostasis in the body by preventing excessive secretion of cortisol, which can be detrimental over long periods [78, 79]. Chronic stress, characterized by prolonged psychological and physiological stress responses, leads to persistently high levels of cortisol [80]. This can adversely affect the nervous system and promote the production of reactive oxygen species (ROS) [81]. The regulation of cortisol secretion of melatonin is part of a wide range of adaptation strategies, and its stress regulation needs to be understood in the context of the body's overall homeostasis and stress resilience [82]. Increased cortisol levels resulting from chronic stress can lead to the production of ROS, causing oxidative stress and potential cell damage. Melatonin acts as an antioxidant, helping to neutralize ROS and reduce oxidative stress, thereby protecting nerve cells from damage [83]. Moreover, several studies have identified that tryptophan, a precursor of melatonin, decreases the secretion of ACTH, resulting in a reduction of cortisol levels [84]. The administration of tryptophan in pigs to demonstrate this correlation showed a decrease in cortisol levels [85]. These findings suggest that the production of enhanced melatonin promoted by tryptophan is likely to reduce the stress response in pigs. Melatonin also plays a role in interacting with mood-regulating neurotransmitters such as gamma-aminobutyric acid (GABA), serotonin, and dopamine. These neurotransmitters are involved in controlling stress and mood. By modulating the activity of these neurotransmitters, melatonin can contribute to stress regulation and emotional well-being [86]. In terms of social interactions, studies have shown that melatonin administration in rodents has increased social behaviors like grooming and play, as well as enhanced social identity [87]. Melatonin interacts with neurotransmitters such as serotonin and dopamine, which are involved in mood regulation, intimacy, and social reinforcement [88]. Additionally, melatonin affects the secretion of neuropeptides, particularly oxytocin and vasopressin, which play roles in social bonding, trust, and aggression control [89]. These mechanisms contribute to the influence of melatonin on social behavior, perception, and cohesion in various species. Moreover, melatonin has been linked to increased affinity or docility in certain animal species. Administration of melatonin to rodents and dogs has shown results such as reduced stress behaviors, increased tranquility, and improved adaptability. The regulation of neurotransmitters and the reduction of stress hormones through the modulation of the HPA axis activity are thought to contribute to these effects. However, it's important to recognize that the outcomes may vary significantly across different animal species and individuals, and further research is needed to fully understand the precise mechanisms involved.

THE ROLE OF MELATONIN IN MODULATING AGGRESSIVE BEHAVIORS IN ANIMALS

Aggressive behavior in animals is influenced by various factors, including the living environment, heredity, and hormonal regulation [90]. While the role of hormones like testosterone in aggression is well-established, the specific effects of melatonin on aggression are still being studied and not yet fully understood. However, previous research provides some insights into the potential effects of melatonin on aggression. During the breeding season, aggression and territorial behavior are often observed in animals, and melatonin is closely associated with the breeding season [91]. Melatonin's association with the breeding season stems from its role as a regulator of seasonal reproductive behaviors, mediated through its ability to track changes in day length or photoperiod [92–94]. This regulatory function is crucial for animals that breed seasonally, as it ensures that reproductive activities are synchronized with the most favorable environmental conditions [95]. Studies have found that melatonin levels increase in certain bird species during the breeding season, particularly in birds displaying higher levels of territorial aggression [96]. This suggests that melatonin may be seasonally regulated and involved in territorial aggression. Another line of evidence suggesting a potential link between melatonin and aggression comes from studies on the interaction between melatonin and testosterone. Research on male mice has shown that melatonin administration can increase aggressive behavior. It is hypothesized that melatonin may influence aggression by altering the sensitivity of brain circuits that regulate aggression in response to testosterone [97,98]. Melatonin is known to interact with neurotransmitters such as serotonin and dopamine, which are involved in regulating aggression [99]. It has been proposed that melatonin may modulate aggressive behavior by influencing these neurotransmitters [100]. In addition, melatonin is widely known to control adrenal androgen to regulate aggression [98,101]. However, a majority of experimental research regarding melatonin and its connection to aggression has been conducted with rodents, leaving research on livestock notably lacking. Moreover, studies investigating the relationship between the level of melatonin in blood and aggression in pigs have yielded conflicting outcomes compared to those observed in rodents [102]. Moreover, the research on tryptophan intake in pigs was found to have no correlation with plasma cortisol levels, implying that melatonin may not be associated with aggression, even indirectly [103]. Studies on melatonin's effects on aggression in fish have yielded varied results, with some showing an increase in aggression, others showing a decrease, and some finding no significant effect [104]. These discrepancies may be due to differences in species, individual characteristics, and other factors such as diurnal or seasonal variations. Further research is needed to clarify the role of melatonin in aggression across different animal species. Moreover, melatonin is primarily known for its role in controlling the sleep-wake cycle and circadian rhythm. Disruptions in the sleep-wake cycle and circadian rhythm can affect various physiological processes, including mood and behavior. Imbalances in sleep patterns and circadian rhythms caused by melatonin may indirectly influence aggressive behavior by affecting an animal's arousal state, stress response, and emotional control. Studies in humans suggest that disturbances in sleep quality can impact aggressive behavior, implying that melatonin, as a regulator of the sleep-wake cycle, may have the potential to reduce aggression [105].

In conclusion, existing studies suggest that melatonin may influence aggression, but the results are conflicting and highly dependent on species, individual characteristics, and environmental factors. It is likely that melatonin's effect on aggression is multifaceted and may involve direct and indirect mechanisms. Further research is needed to elucidate the interactions and underlying mechanisms of melatonin and aggression across various animal species.

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CORRELATION BETWEEN MELATONIN AND TRAINABILITY

The relationship between melatonin and trainability in animals is an area that has received relatively less attention compared to other aspects of temperament and behavior. The ability to learn and accept training quickly can vary widely among individuals and is influenced by various factors. While the correlation between melatonin and training possibility is not well-established in livestock, some studies about rodents and humans suggest potential associations between melatonin and learning.

Memory is very closely related to the expression of the clock genes expression in the biological rhythm systems [106,107]. In particular, one of the important nuclei in the brain called SCN is known to play a crucial role in regulating biorhythms [108]. Moreover, light has the most important role in controlling circadian rhythm, and SCN acts as a kind of channel to control body rhythm by detecting light signals. Exposure to inappropriate light interferes with the normal function of SCN, leading to disturbances in the circadian rhythm. These can cause long-term memory impairment that affects daily life [109]. Previous research has shown that melatonin can improve symptoms of neurodegenerative disorders, indicating its potential to enhance memory and learning [110]. Melatonin has been found to reduce neurooxidative stress, promote short-term memory, and have a reverse promotional effect on the memory process [111]. In mouse models of sporadic Alzheimer's disease, melatonin has been observed to mitigate anxiety and memory deterioration [112]. However, other experimental results have not demonstrated a consistent correlation between melatonin and memory. For example, in zebrafish, learning and memory formation were more active during the day compared to night, and pineal gland resection affected nocturnal memory improvement [113]. Thus, conflicting findings emerge depending on the animal species, experimental settings, and methodologies employed. Further research is necessary to fully understand the relationship between melatonin and memory. Several mechanisms and hypotheses have been proposed to explain the potential effects of melatonin on memory and learning. One hypothesis is that melatonin is associated with neuroplasticity, which refers to the brain's ability to undergo structural and functional changes through experience and learning [114]. Melatonin has been found to enhance neurogenesis, synaptic plasticity, and neuron connectivity, all of which are crucial for learning and memory formation [115–117]. These effects suggest that melatonin may have a positive impact on acquiring and retaining new learning behaviors and skills during training. Melatonin also plays a role in regulating attention and alertness, which can contribute to improved cognitive function and long-term attention [118]. Enhanced cognitive and long-term attention can facilitate better information processing and response to new signals, potentially enhancing training outcomes [119]. Melatonin is well-known for its influence on emotions and moods, and in animal models, it has been observed to promote emotional stability by regulating emotional responses and reducing anxiety [120]. This suggests that animals with a calmer and more positive mindset may have increased access to training opportunities. Furthermore, melatonin's regulation of the HPA axis can lower the secretion of stress hormones, thereby reducing stress during training and creating a more comfortable environment for learning [65]. Melatonin's ability to regulate social relationships, behavior, and bonding may also impact training possibilities. Studies have indicated that melatonin influences social cognitive abilities and affiliative behaviors, potentially strengthening human-animal relationships and increasing active cooperation [121]. Strong social behavior is expected to enhance trainability by reinforcing motivation and relationships during training. While there are several mechanisms and hypotheses proposing the effects of melatonin on training possibilities, the exact reasons are still unknown, and clear differences between animal species exist. Further research is needed to elucidate the specific mechanisms and understand how melatonin may influence training outcomes in various animal species.

THE REGULATION OF MELATONIN ON APPETITE AND MOTOR ACTIVITY

Melatonin plays a significant role in various behaviors, with substantial evidence pointing to its effects on appetite control and exercise behavior in animals. Research has shown that melatonin administration can lead to a reduction in food consumption, thereby decreasing calorie intake [122]. This effect is believed to be mediated by melatonin's influence on neuropeptides such as leptin and ghrelin, which are involved in regulating appetite. Melatonin has also been found to affect eating patterns, with changes observed in mealtime and duration following supplementation. In rodents, melatonin administration has been linked to increased satiety during darkness. Additionally, preferences for specific nutrients or flavors have been shown to change after melatonin administration, with rodents exhibiting a decreased preference for high-fat and sweet foods [123]. These findings indicate that melatonin can modulate appetite-related behaviors in animals. Moreover, melatonin has been found to influence exercise behavior and motor activity in animals. Administration of melatonin has been shown to affect the level and behavior of motor activity, possibly through interactions with neurotransmitters associated with behavior, such as dopamine and GABA [124,125]. Studies in rodents have demonstrated changes in motor performance after melatonin administration, and the presence of melatonin receptors in the cerebellum, an important brain region for motor control, suggests that melatonin is involved in regulating exercise activity.

Taken together, these findings highlight the diverse roles of melatonin in regulating various behaviors, including appetite control and exercise behavior. The interaction of melatonin with different neurotransmitters and brain regions likely contributes to its effects on these behaviors. However, further research is needed to fully understand the mechanisms underlying melatonin's influence on appetite, eating patterns, and exercise in different animal species and contexts.

CONCLUSION

Melatonin significantly impacts animal behaviors, influencing not only the sleep-wake cycle but also aggression, trainability, appetite, and motor activities. It plays a crucial role in synchronizing biological functions with environmental cues through a complex interaction with the hormonal and neurotransmitter systems. There are still many aspects to be clarified regarding the mechanisms through which melatonin affects various animal behaviors and the reasons behind species-specific responses. The diversity of effects across different species and individuals underscores the complexity of melatonin's impact on physiology and behavior. Future research should focus on the molecular actions of melatonin, especially its interactions with neurotransmitters and hormonal pathways. Comparative studies across species could illuminate the evolutionary aspects of melatonin's effects, and uncovering melatonin's potential could offer innovative approaches to enhancing animal welfare and health. Although considerable research has been conducted on melatonin, further investigation into the specific mechanisms by which melatonin influences animal behavior is necessary. Continued research is essential for deepening our understanding of animal physiology and behavior, offering promising insights for both scientific and practical applications in animal management.

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