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Mechanisms and functions of coupling between sleep and temperature rhythms

Eus J.W. Van Someren [1 2]

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Abstract

Energy metabolism is strongly linked to the circadian rhythms in sleep and body temperature. Both heat production and heat loss show a circadian modulation. Sleep preferably occurs during the circadian phase of decreased heat production and increased heat loss, the latter due to a profound increase in skin blood flow and, consequently, skin warming. The coupling of these rhythms may differ depending on whether they are assessed in experimental laboratory studies or in habitual sleeping conditions. In habitual sleeping conditions, skin blood flow is for a prolonged time increased to a level hardly ever seen during wakefulness. Possible mechanisms linking the rhythms in sleep and core body and skin temperature are discussed, with a focus on causal effects of changes in core and skin temperature on sleep regulation. It is shown that changes in skin temperature rather than in core temperature causally affect sleep propensity. Contrary to earlier suggestions of a functional role of sleep in heat loss, it is argued that sleep facilitates a condition of increased skin blood flow during a prolonged circadian phase, yet *limits* heat loss and the risk of hypothermia. Sleep-related behavior including the creation of an isolated microclimate of high temperature by means of warm clothing and bedding in humans and the curling up, huddling and cuddling in animals all help limit heat loss The increase in skin blood flow that characterizes the sleeping period may thus not primarily reflect a thermoregulatory drive. There is indirect support for an alternative role of the prolonged period of increased skin blood flow: it may support maintenance of the skin as a primary barrier in host defense.

Introduction

Energy metabolism is strongly linked to the circadian rhythms in sleep and body temperature. To fulfill our energy requirements we obtain and consume food during wakefulness. This requires physical and mental activity and usually an upright body position, which consequently also increases energy expenditure, which is in turn associated with heat production. Even at complete rest the human metabolic rate is so high that it provides a continuous internal source of heating, accounting for about 60-75% of the total daily energy expenditure (Poehlman and Horton, 1990). During physical activity, there is an important additional source of heat generation in the muscles. When asleep, energy expenditure is reduced due to the supine position and lack of physical activity, and consequently, less heat is produced.

Although appealing in its simplicity, the picture sketched above is far from complete. The circadian modulation of body temperature is not restricted to differences between sleeping and waking in heat production, due to the behavior of keeping an upright body position and being physically active. Referring to the latter as *concomitant* physiology and behavior, there are also *intrinsic* differences in heat production during sleep and wakefulness. The basal metabolic rate during sleep is slightly lower than during wakefulness at complete rest (Guyton, 1991; Meijer et al., 1991). To complicate matters even more, a 24-h rhythm in resting metabolic heat production remains even in the absence of sleep (Kräuchi and Wirz-Justice, 1994). This has been demonstrated convincingly in the so called *constant routine* studies in which subjects are kept awake, inactive, in a supine position and fed in small portions at fixed time intervals, or using continuous infusion.

Complex as the regulation of heat production in relation to the sleep–wake cycle may already be with a circadian component in addition to intrinsic and concomitant changes related to sleeping behavior, this still does not give a complete picture of the coupling of sleep and temperature rhythms. This is because not only *heat production* but also *heat loss* shows circadian modulation and intrinsic and concomitant changes with sleep (Kräuchi and Wirz-Justice, 1994). At any time of the circadian cycle, core body temperature reflects the balance between the two processes of heat production and heat loss.

In the present review, a phenomenological description of the coupling between sleep and temperature rhythms will be given first, after which the theoretically possible underlying interaction mechanisms between the various levels of circadian regulation of sleep and body temperature will be addressed. Subsequently, the focus will be on one of these interaction possibilities: the proposed modulatory role of changes in *skin* temperature on sleep-regulating systems (Van Someren, 2000). Finally, considerations on the functional meaning of the relation between sleep and skin temperature will be given. It is proposed that one function of sleep may be to support a prolonged circadian phase of elevated skin blood flow. This phase of increased skin blood flow may support the maintenance of the role of the skin as the primary barrier in host defense.

Section snippets

Description of the coupling between sleep and temperature rhythms

The circadian cycles of sleep and core body temperature are intimately related. In daytime-active mammals, including humans, the major sleep period is initiated in the evening, during the decline in core body temperature. The next morning, when core body temperature has reached its minimum

and is rising again, the major sleep period ends. Thus, core body temperature is lower during our habitual sleep period than during our habitual waking period. This relationship is more than coincidence. …

Possible sites of interaction in the circadian regulation of sleep and body temperature

The present paragraph briefly mentions several theoretically possible interaction levels in the circadian regulation of sleep and wakefulness, before addressing one of them in more detail in the next paragraph. The paragraph numbers below match the numbers shown in Fig. 3.

1. Although hard evidence is not available and would be difficult to obtain at the present state of technological possibilities, it is very plausible that within the hypothalamic suprachiasmatic nucleus (SCN), the clock of the …

…

A modulatory role of body temperature on sleep-regulating systems

Indirect support for the possibility that changes in body temperature could modulate sleep-regulating systems is abundantly available in the scientific literature, and has been reviewed extensively before (Van Someren, 2000, Van Someren, 2003, Van Someren, 2004). Briefly summarized: subtle changes in skin temperature, within the thermoneutral range, modulate the firing properties of thermosensitive neurons in brain areas involved in sleep regulation. Such changes in skin temperature occur …

The functional direction of coupling between sleep and increased skin temperature revisited

As mentioned above, the focus has long been on the relation between core body temperature rhythm and sleep, whereas neurobiological findings and modeling studies (Van Someren, 2000) as well as recent human experimental findings (Raymann et al., 2005) suggest that changes in skin temperature may be more relevant in relation to sleep. It has long been recognized that the drop in core temperature that occurs during sleep is mainly the result of an increase in heat dissipation, and to a lesser …

An alternative function for the increase in skin blood flow

If, as we presumed in the mind experiment of the previous paragraph, the daily occurrence of a prolonged phase of skin blood flow does not primarily serve a thermoregulatory function, what other function might it serve? We recently argued that the increased skin blood flow is an important part of the previously proposed function of sleep in immunological *host defense* (Krueger and Majde, 1990). More specifically, we proposed that the increased nocturnal skin blood flow may crucially support the …

Sleep deprivation

For the hypothesized functional importance of a circadian phase of enhanced skin blood flow, sleep would not be strictly necessary. Thus, the hypothesis does *not* imply increased skin blood flow to be *the primary* function of sleep. Like wakefulness, sleep most likely supports many different functions rather than one single function, one of which may be to support a prolonged period of increased skin blood flow. The hypothesis put forward here is just that it is especially profitable and …

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