

Review

Physically activated modes of attentional control

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As we navigate through the day, our attentional control processes are constantly challenged by changing sensory information, goals, expectations, and motivations. At the same time, our bodies and brains are impacted by changes in global physiological state that can influence attentional processes. Based on converging lines of evidence from brain recordings in physically active humans and nonhumans, we propose a new framework incorporating at least two physically activated modes of attentional control in humans: altered gain control and differential neuromodulation of control networks. We discuss the implications of this framework for understanding a broader range of states and cognitive functions studied both in the laboratory and in the wild.

Understanding cognition requires understanding global physiological states

Whether one is a motorist on a busy street, an air traffic controller monitoring flight paths, or a high-school student in an algebra class, good performance requires efficient and selective processing of task-relevant information. Control over selective information processing involves multiple perceptual and cognitive mechanisms, particularly attention, working memory, and executive function [1]. Current theoretical frameworks of attentional control are largely focused on understanding the changes in performance that occur due to changes in task demands, motivation, expectations, experience, and physical properties of the environment [2–7]. As we navigate our day-to-day activities, these factors are in a continual state of flux, but so too are the global physiological states of our bodies. Global physiological changes occur largely due to the natural regulatory cycles of the body, but they can also occur as a response to repetitive movements, physical activity, and exposure to acute challenges in the environment [8–10]. Changes in global states not only impact the physiological functions of the body but also have dramatic impacts on cognition.

In this review we present a framework for understanding how changes in global state influence cognition, with a specific emphasis on physical activity-induced states and attentional control in humans. We begin by summarizing what global states are, how they are controlled, and why they are important for understanding cognition. Much of the evidence linking the neural bases of global states, sensory processing, and cognition comes from studies in nonhuman species that compare stationary and moving states. A key theme emerging from this work is that global states have a direct impact on mechanisms regulating arousal and attention. We then discuss current models of attentional control. This focus on attentional control is motivated by the link between global states and attention, the importance of attention in selective information processing, and because attention is integrated with many other cognitive processes. Emerging from this discussion is the key point that current state-of-the-art frameworks of attentional control do not provide comprehensive accounts of how global states affect the cognitive processes that control selective information processing. To address this gap, we propose that studies comparing rest and physically active states offer convergent evidence that global states impact cognition in the human brain. Based on this evidence, we suggest that there are at least two physically activated

Highlights

Human sensory, cognitive, and physiological systems are constantly challenged by changes in the environment, goals, and expectations, and natural regulatory mechanisms that are a part of the body's effort to anticipate and respond to physiological demands caused by a variety of factors, including physical activity.

Evidence from awake and behaving non-human species has clearly shown how physiological states can impact systems associated with arousal and attention, but there is no similar understanding of the interplay between states and attentional processes in humans.

We bridge this gap using convergent evidence from studies of humans engaged in physical activity and simultaneous noninvasive neural recordings, and we propose that there are two physically activated modes of attentional control: altered gain control and differential neuromodulation of cortical control networks.

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modes of attentional control: altered gain control and differential neuromodulation of cortical control networks. We end by discussing the implications of this framework for understanding a broader range of cognitive functions studied in the laboratory and in the wild.

What are global states?

As we go through the day, we transition through a variety of global physiological and behavioral states, from sleep to awake, from hunger to satiety, and from stationary to moving. Across these states, the brain's regulatory drive coordinates complementary mechanisms that anticipate the physiological resource demands of a given state (i.e., allostasis) and that provide corrective feedback (i.e., homeostasis) in the event the predictions are incorrect [11,12]. States are organized hierarchically, where the top level of the hierarchy consists of a distinction between sleep and wakefulness [13]. Here, we focus on wakeful states (Box 1). Based largely on evidence from nonhuman species, there are six key features of behavioral states and their neural/neuromodulatory bases [8–10,13]. First, global states are high-dimensional phenomena characterized by patterns of behavior, physiology, and neural activity that are repeatable. Externally observable indicators (i.e., patterns of behavior, pupil size, respiration, perspiration, etc.) can be used to infer that an organism is in a specific internal state, multiplexed set of states, or transition between states, but not all changes in internal state at the neural/physiological level can be observed externally. Second, states can occur in isolation, co-occur independently, or be multiplexed, and changes between them can be discrete or continuous. Third, state changes can be evoked by external stimuli, tasks, and goals, or other internal processes. Fourth, while some state triggers can be controlled voluntarily, many internal states are controlled by the body's regulatory drive. Fifth, the response to exogenous or endogenous triggers can scale with intensity and persist in the absence of the triggering stimulus, but the size and duration of the responses can habituate over repeated exposures. The presence and extent of habituation to repeated exposures likely depends on the specific state (e.g., externally triggered vs. internal state). Sixth, several states are highly correlated with arousal. As such, the brain systems involved in arousal and associated cognitive functions, such as attention, are affected by the regulation of global states.

Box 1. Why focus on global states?

The primary focus of this review article is on how global physiological states influence attentional control. However, it is important to acknowledge that humans transition through a wide range of other non-global states, such as affective or stress states, that can also significantly impact brain function and behavior. For instance, it is well documented that emotionally charged stimuli (e.g., fearful faces, snakes, spiders) can capture attention more readily than neutral stimuli [95]. These transient emotional states can interact with individual personality traits, such as anxiety, further influencing attentional biases [96]. Additionally, these emotional states can interact with global physiological states to impact cognition [97]. We distinguish between global behavioral states and other states, such as emotional, affective, and stress states, for three reasons.

First, our interest lies in the nexus between peripheral physiological processes that are more typically considered to have nonspecific effects on central nervous system function and cognition. This is not to say that affective states do not interact with peripheral physiology or cognition, they clearly do. Instead, we are more concerned with the peripheral physiological control of the body and its movement through the environment as a key factor in the efficiency of cognitive functioning. The importance of this link is underscored by evolutionary models of cognitive function suggesting that the development of hunting and foraging behaviors required the co-adaptations of increased cognitive and locomotive capacities [98].

Second, there is a significant gap between laboratory studies of attention and cognition, which are typically done with participants in a sedentary state, and the real-world functioning of attention.

Third, the emphasis on the engagement of the body and the interaction with cognition is further motivated by the importance of reconciling what are obvious and well-demonstrated effects of some behavioral states on cognition, and with a large body of literature that tends to show small positive effects of immediate changes of physical activity on cognition [53–55]. To the extent that the effects of a non-global state, such as emotion or stress, can influence one or more of the modes of control proposed here, then this framework can also be used to inform predictions about the effects of these states on performance, brain activity, and cognition.

How are global states controlled?

Advances in neural recording, stimulation, and inactivation techniques in awake and behaving mammals and invertebrates have led to corresponding advances in the mechanistic understanding of states and their physiological, neural, and behavioral consequences [10]. Collectively, this work has implicated two primary mechanisms for the control of states. The first is via neuromodulation induced by the selective action of neurotransmitter pathways [9], especially the cholinergic and noradrenergic pathways [14]. The cholinergic projections originating in the basal forebrain are particularly relevant in this context because they are stimulated by locomotor activity and play a role in regulating arousal [15,16]. This pathway can have both fast and slow effects driven by ionotropic and metabotropic changes that induce sustained shifts in membrane potential, depolarizing pyramidal cells in their respective cortical targets [9]. Optogenetic studies have implicated the basal forebrain's link with the locomotor system and the fast-acting neural circuit governing the state [15], as well as the indirect, slower, more diffuse neuromodulatory effects due to changes in arousal [16,17]. The noradrenergic pathway is mediated by the locus coeruleus (LC), which has long been implicated in arousal [18] and has broad projections to the entire neocortex [19]. The time-scale of this neuromodulatory pathway is slower than the fast-acting projections of the cholinergic pathway [9]. The second mechanism of control is at the level of neural circuits via cortico-cortical connections and thalamocortical connections [20,21]. These circuits promote changes in network activity via feedback connections within the network or feedforward connections from the thalamus, both of which rapidly alter neural activity in target regions, presumably to alter sensory coding of environmental stimuli [9,10]. Consistent with this hypothesis, reductions in low-frequency oscillations in cortical V1 neurons in mice have been associated with improved visual detection [22,23]. These pathways interact to alter the control of information processing on multiple timescales.

Why are global states important for understanding cognition?

Even though global states are controlled by a number of noncognitive factors, such as the organism's physiological regulatory drive and locomotor activity, they are important for understanding cognition because their control pathways are inextricably linked with arousal, sensory coding, attention, and other stages of information processing. Consequently, global states can be thought of as physiological, behavioral, and neural motifs that influence ongoing sensory and cognitive processes [9,10,17]. Compelling evidence supporting this notion comes from studies that have used locomotive behaviors to manipulate behavioral states. Invasive recordings of neural activity in invertebrates and non-primate mammals observed that the act of engaging in locomotive activity (e.g., walking, flying) modulates sensory evoked neural activity and can increase the gain in feature selective responses in some neural populations [24–27]. Optogenetic stimulation of circuits that code patterns of locomotive behaviors at levels that do not evoke movements can nevertheless induce changes in visual cortex activity responses to stimuli [15]. Similarly, locomotive behaviors are also associated with changes in pupil diameter [27–29], a classic indicator of arousal, the noradrenergic system, and attentional function [18].

Models of attentional control typically do not account for global states

Although there is a variety of theoretical accounts of how attentional mechanisms control information processing priority [3–6,30–34], they have some common features (Figure 1). Sensory information is processed in spatial (retinotopic) and feature selective cortical representations (i.e., 'maps'). Selective information processing is achieved via the gain modulation of spatial and feature maps based on the physical salience of the stimuli or based on nonsensory factors, such as goals and expectations. These sources of information are integrated into a priority map of visual space which guides the selective processing of information [3–6,34]. Historically, the influences over priority control are typically divided into two main categories: top-down (goal-driven)

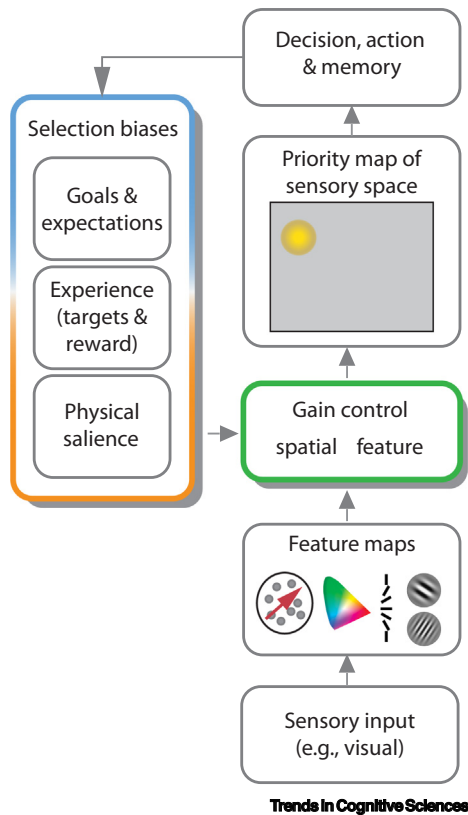


Figure 1. Current state-of-the-art in attentional control. A schematic depiction of the common features of current models of attentional priority control [3–6,30–34,49]. In these models, sensory information is processed in cortical representations of spatial locations in retinotopically organized visual cortex and specific nonspatial features (e.g., motion, color, orientation, and spatial frequency are shown here). The activity in these representations is modulated based on a number of selection biases (blue and orange box), ranging from the physical salience of the stimuli, to previous experience with the stimuli, to goals and expectations. The modulatory process is referred to as gain control (green box), and the outcome is a map of sensory space that prioritizes the processing of locations and features that are most impacted by the gain control process (e.g., the yellow dot). Information that is prioritized can serve as the basis for decisions and actions and be encoded into memory. These outcomes can also influence the future impact of the selection biases on subsequent information processing. In this schematic, the arrows are intended to indicate the general flow of information, not precise anatomical connections. Both feedforward and feedback connections exist.

and bottom-up (stimulus-driven) [31,35]. However, this dichotomy fails to capture experience-driven effects [1,3] like those associated with selection history [36], reward [37,38], spatial context [39,40], semantics [41], and social information [42]. We refer to these influences governing priority control as selection biases, emphasizing internal goals and expectations, physical salience, previous experience, and reward [3,6].

Priority control of visual attention is thought to reflect the interplay between two large-scale cortical networks which influence processing in cortical representations of features and locations [35,43–46]. One network is commonly referred to as the dorsal attention network. It includes bilateral posterior parietal cortex, the intraparietal sulcus, and superior frontal cortex, including the frontal eye fields, and is commonly thought to be responsible for goal-driven control over selective information processing [43,44,46,47]. The other network is more ventral, lateralized to the right hemisphere, and it includes regions of inferior frontal cortex and temporal parietal cortex. This network is referred to as the ventral attention network, and it is thought to be responsible for the control of stimulus-driven information processing [35,46].

A glaring omission in this discussion of the neural networks of priority control is the involvement of subcortical structures. The cortico-centric bias in the recent literature has been noted [30], but it has not always been the case. Classic accounts implicated subcortical structures as being responsible for regulating arousal to facilitate orienting [32,48]. More recently, the superior colliculus, pulvinar, and thalamus have been identified as key structures mediating the control over different stages of spatial attention [1,30,49]. The inclusion of subcortical structures in

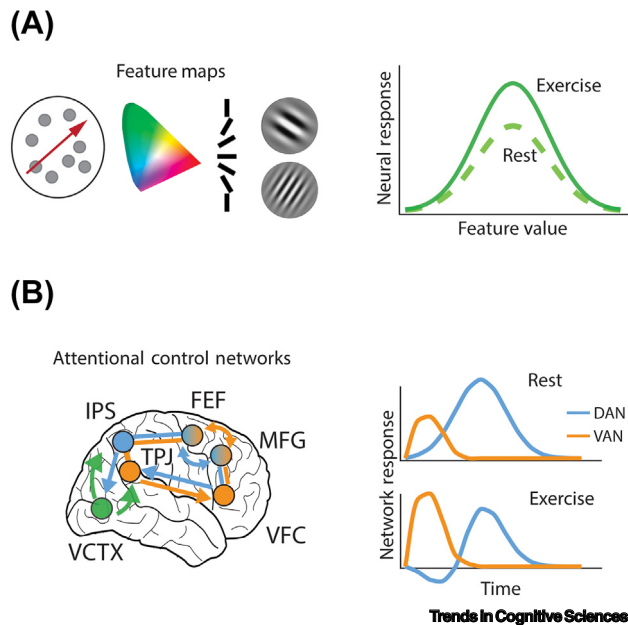


Figure 2. Physically activated modes of attentional control. We propose that physical activity triggers at least two modes of control over the attentional processes shown in [Figure 1](#): altered gain control and differential neuromodulation of cortical control networks governing selection biases. (A) Altered gain control. Left: visual cortex contains representations of location and features across the visual field (e.g., motion, color, orientation, spatial frequency, all shown here, and location, which is not shown but is also important in this process). Populations that represent these features respond more vigorously to (i.e., prefer) certain feature values. Right: feature selective responses at rest and during exercise. Global states (e.g., physical activity) can (but not always) act like a multiplicative gain on the feature selective response [24,26,61,63]. (B) Differential neuromodulation of attentional control networks. Left: nodes and connections within the dorsal attention network (DAN, blue: IPS, intraparietal sulcus; FEF; frontal eye fields; MFG, middle frontal gyrus), ventrolateral attention network (VAN, orange: TPJ, temporoparietal junction; VFC, ventrolateral frontal cortex; MFG, middle frontal gyrus) [2]. Both networks receive input from visual cortex (VCTX, green). The DAN mediates goal-oriented and experience-driven selection biases via signals to VCTX and MFG, the latter of which propagate to the VAN. The VAN can influence activity in the DAN via MFG, especially when triggered by VCTX activity evoked by a physically salient and/or unexpected stimulus is presented in the environment. Right: responses in the DAN and VAN over time at rest (top) and during exercise (bottom). We suggest that behavioral performance and neural responses are influenced by the relative differential activity of these networks at any given time point. While the activity of these networks during physical activity is not well known, these hypothetical time courses are based on what is known about the response of cortical networks evoked by acute stressors [73].

attentional control frameworks, particularly those that regulate arousal, is especially critical given the importance of these structures in regulating global states.

One implication of this cortico-centric bias is that models of attentional control typically do not account for the impact of global states on priority control. Even the models that do implicate subcortical structures involved in the regulation of arousal tend to rely on a classic inverted-U relating arousal to performance by generally upregulating or downregulating cognitive processes in a relatively global and nonspecific manner [50]. We agree that performance and brain activity can follow this prototypical pattern. Our central point, however, is that the factors that give rise to this inverted-U are intricate and not governed by a single mechanism. In addition, no model of attentional priority control, historical or contemporary, provides a detailed account of the impact of changes in global behavioral state, such as those caused by locomotion, despite their profound effects on neural activity.

Physical activity as an empirical tool to study states in humans

Much of the mechanistic understanding about the neuromodulatory and neural pathways controlling global states comes from studies of nonhuman mammals and invertebrates. Less is known about these pathways and the link between global states and cognition in humans. While there are some similarities between humans and some mammals (e.g., primates), there are well documented and obvious differences in neuroanatomy and neuromodulatory systems across species that can result in differential effects of global state on neural function [51,52]. Thus, one must be cautious when generalizing findings across species and integrating convergent evidence from human studies ([Box 2](#)).

Box 2. Challenges generalizing locomotion effects across species and tasks

Investigations across various species, including invertebrates, rodents, nonhuman primates, and humans, have shown that both locomotion and focused attention can similarly enhance how the brain processes sensory information [24–26,60,61,68,99,100]. Studies in rodents suggest that spatial attention and running engage overlapping neural pathways and share common mechanisms that modulate cortical activity [101–104]. However, there may be key constraints on the generalizability of these effects. For instance, one recent study demonstrated that spatial attention and running can independently modulate activity in mouse visual cortical neurons [105], while another observed task-dependent differential effects of running on visual cortical responses [106]. In primates, global states have a profound impact on cortex [107], but recent work examining movement-related signals in cortex has found them to be smaller than in rodents, albeit with some caveats in drawing direct comparisons between the two [51,52]. Specifically, running-correlated modulations of foveal V1 neurons in the marmoset brain are small and suppressive, seemingly contradicting findings in mouse V1 [51]. However, the same study also observed that peripheral V1 neurons were driven to a much greater extent than foveal V1 neurons during running, raising the possibility that peripheral visual processing in primates might be more functionally similar to mouse V1 in terms of its sensitivity to movement [108]. Another study observed that the influence of spontaneous body movements on cortical activity in the macaque brain is minimal when accounting for movement-related changes of the image on the retina [52]. This contrasts with observations in mice, where pronounced modulation of cortex by spontaneous movements is observed [109,110], raising the question of how much eye movements may also impact running and movement-correlated modulations in the mouse. While human studies have shown locomotion effects analogous to those reported in mice and invertebrates [60,61,63,75,84], these effects are not always consistent [76,111]. Furthermore, the coarse spatial resolution of noninvasive human imaging techniques means it is not possible to pinpoint the precise neural mechanisms involved. Together, these cross-species findings indicate a complex relationship between locomotion, sensory processing, and specific task demands, and underscore the need for caution when drawing broader conclusions about how locomotion impacts cortical processing both within and across species.

Foundational work in other species has shown the impact of global states on neural function by comparing conditions in which the organism was stationary and moving [24–27]. In humans, the most similar methodological approach compares conditions in which the participant is stationary versus conditions in which the participant is engaged (or recently was engaged) in an acute bout of physical activity. There is a large literature investigating the impacts of physical activity on cognition [53–57], and it is clear from this literature that the body's response to single, acute bouts of physical activity is well-aligned with the six themes common to frameworks of global state. Physical activity induces a range of physiological, neural, and behavioral effects that are repeatable. Activity-induced changes can occur independently of or in concert with other states. Physical activity is a volitional act that can be triggered as a reaction to external events or an internal goal. The body's response to physical activity scales with the intensity and duration of the activity and can persist after cessation of the activity. Finally, physical activity is associated with changes in neuromodulatory function, especially in pathways associated with arousal. This tight alignment between physical activity and the features of global states supports our assertion that physical activity is a viable approach to studying global states in humans.

If physical activity induces changes in global state, then in order to be used as a tool for understanding the impact of states on cognitive and neural function in humans, we need methods for measuring performance and brain activity while people are engaged in physical activity. In the past decade there have been significant developments in hardware, empirical strategies, and computational approaches that have made it possible to acquire measurements of behavior and noninvasive recordings of neural activity while human participants are engaged in physical activity (Box 3). Numerous studies in the literature, including several from our laboratory, have used these strategies to investigate the impact of physical activity on visual neural activity in humans [58–64]. These studies have provided consistent evidence for enhancements of sensory evoked responses, feature selective responses, and changes in pupil diameter during brief bouts of exercise and locomotive activity [60,61,63].

Box 3. Measuring physical activity triggered changes in state and cognition in humans

Measuring brain activity during physically active states (or soon thereafter) is methodologically challenging. One of the most tractable methods for doing so is scalp-recorded EEG, which can be coupled with concurrent eye-tracking, pupillometry, and physiological monitoring during simultaneous exercise and cognitive task performance (Figure 1) to provide a rich understanding of the effects of physically active states on cognitive and neural function. In recent decades there have been dramatic changes in the form factor of the equipment and recording approaches that have made EEG more portable and robust to environmental electrical noise. However, the need for portability is only one of the issues introduced by physical activity. Physical activity introduces a number of physical and biophysical artifacts (e.g., muscle activity, sweat, disrupted electrode contact, cable sway); however, in the past number of years, four strategies have emerged to address movement-related artifacts: (i) take advantage of movement silent periods [112–114], (ii) experimental randomization of task-related signals and movement [60], (iii) experimental separation of movement noise and task-related signals [60–63, 115, 116], and (iv) computational separation of noise and task-signals [111, 117–120].

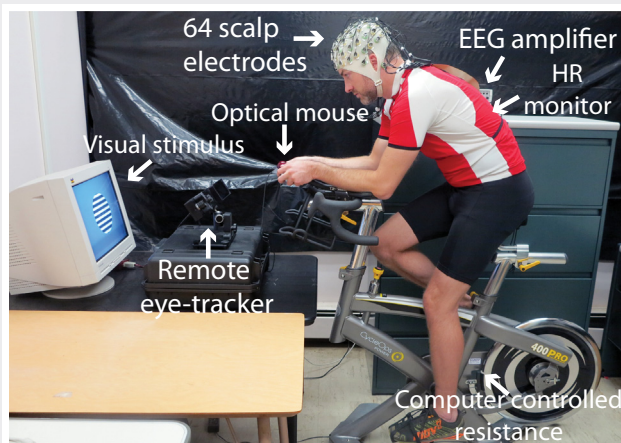
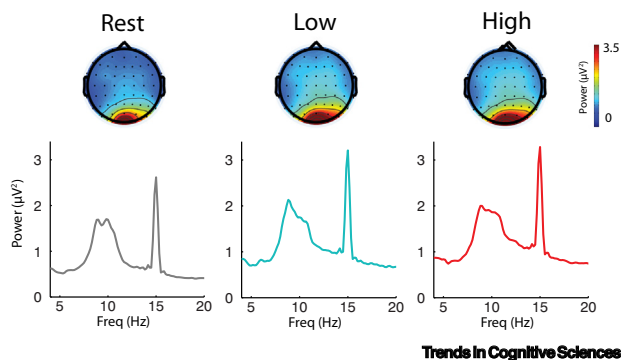


Figure 1. Measuring brain activity during exercise. Top: example experimental set-up that combines simultaneous measurements of electroencephalography (EEG), visual task performance, eye position and pupil size, and heart rate while engaged in physical activity on a stationary bike. Bottom: sample EEG data acquired at rest and during low- and high-intensity exercise. Adapted with permission from Bullock *et al.* [61].



Physically activated modes of attentional control in humans

Using the current attentional control frameworks as a starting point, we propose two physically activated modes of control: altered gain control and differential neuromodulation of cortical control networks (Figure 2).

Altered gain control

One of the primary consequences of manipulating attention is a change in the magnitude and form of neural responses. In humans, when visual stimuli are presented in a specific location or possess a specific feature, the sensory evoked response measured with electroencephalography

(EEG) or fMRI is larger when the stimulus location (or feature) is attended compared with when it is unattended [65–67]. This enhanced response reflects an increase in gain of the neurons that represent the attended location or feature [68], and is thought to reflect a key mechanism of attention that affords attended stimuli enhanced processing. Importantly, gain control is not merely an increase in neural activity but can instead take multiple forms [69,70]. Evidence from humans and other species is consistent with the notion that state-related changes evoked by physical activity can alter some forms of gain control. For instance, human studies comparing visual responses measured using EEG at rest with those during physically active states revealed increased sensory evoked responses and increased feature selective responses [60,61,63,71]. This finding converges with evidence from invertebrates and non-primate mammals discussed earlier showing that changes in global state induced by locomotive behaviors are associated with changes in the sensory evoked responses and multiplicative gain of feature representations. Although the precise mechanism in humans is unclear, based on evidence from other species, altered gain control triggered by physical activity could be the result of localized and fast-acting neuromodulator activity and rapid depolarization from cortico-cortical feedback and/or thalamic inputs, resulting in the desynchronization of low-frequency inhibitory oscillations [9]. If true, altered gain control should be tightly linked with the onset and of the triggering activity, present when walking, flying, or engaging in physical activity, but absent when stationary [24–26].

Differential neuromodulation of cortical control networks

The sources of the behavioral and neural consequences of attention are thought to be the dorsal and ventral attention networks, which interact based on the influence of the various selection biases present at any given point in time. These attentional networks are heavily influenced by multiple neuromodulators, but especially acetylcholine, noradrenaline, and dopamine [7,69]. These neuromodulatory pathways are influenced by physical activity [57]. Thus, we propose that physical activity can trigger fluctuations in these large-scale cortical networks due to differential neuromodulatory activity. Whereas altered gain control likely depends on fast activity, the differential neuromodulation of control networks likely depends on the diffuse and relatively slower-acting projections from the basal forebrain (cholinergic), LC (noradrenergic), the ventral tegmental area (dopamine), and the substantia nigra (dopamine).

The clearest causal influence of locomotive activity on these pathways comes from studies focusing on the cholinergic projections from the basal forebrain and the noradrenergic projections from the LC [14–16]. While dopamine levels are certainly influenced by regular physical activity [57], the impact of single, acute bouts of activity is less well understood. Moreover, while recent evidence suggests that portions of the dorsal attention network show increased responses during an attentional cueing task post-exercise [72], the dynamic neural and neuromodulatory changes that occur within the cortical control networks during physical activity are unknown. We do know, however, that acute stressors can evoke increases in both the release of catecholamines, such as noradrenaline and dopamine, as well as corticosteroids (e.g., cortisol) [73]. Critically, bouts of physical activity have long been considered acute stressors [74].

Based on these converging lines of evidence, it is reasonable to infer that the relative activity in these pathways likely depends on the intensity and duration of the physical activity and, as a result, the functioning (either improved or degraded) of different components of the attentional control system (i.e., dorsal attention network, ventral attention network). If these effects do indeed rely on slower, less spatially specific neuromodulatory pathways, then, relative to the effects on gain control, evidence for the differential neuromodulation of attentional control networks is likely to emerge more slowly from the onset, and persist beyond the cessation of the triggering physical activity.

We suggest that while these two modes of control can occur independently, this is rare. More commonly, they likely operate simultaneously to varying degrees depending on the type, duration, and intensity of the physical activity. If this is true, then the impact of these physical activity-induced changes at the neural and behavioral levels, whether positive or negative, reflects the combined influence of these modes of control over the attentional system. Moreover, there may even be an interaction between the cognitive demands of the specific physical activity and the execution of a concurrent cognitive task (Box 4).

Implications for attentional control, working memory, and executive function

Based on the convergent evidence from studies of humans and nonhuman species reviewed herein, the neuromodulatory and neural mechanisms underlying the physically activated modes of control have different temporal and spatial properties. Altered gain control is mediated by fast-acting changes tightly linked with locomotive activity [15,24]. Differential neuromodulation

Box 4. The importance of coordinating the body and cognition

Inherent in many models of attention, working memory, and other cognitive functions is the notion that processing capacity and/or resources are limited. Behavioral states may also be resource-demanding, either because of the volitional control of the activity (e.g., coordinating large muscle movements) or the proactive self-monitoring of one's state [121]. The presence of these demands during physical activity makes the natural prediction that if these processes draw significantly on a common resource pool, they may degrade performance on other tasks. In effect, physical activity may induce dual-task interference. Consistent with this conjecture, performance can be degraded and neural responses to task-relevant information can be reduced during locomotive behaviors [62,115]. These reports of negative effects of concurrent physical activity and cognitive task performance could be driven by the need to access a common resource, by interference between the cortical networks supporting the motor activity and cognition, or by some combination of these causes [75]. However, there is also evidence indicating that the motor and attention systems, while dissociable, are also tightly coupled: when the goals for action and attention are aligned, performance and neural activity are enhanced relative to when they are not aligned [122–124]. Thus, the specific direction of the effect of resource competition, whether positive or negative, will likely depend on the match/mismatch between the goals/instructions, the relative timing of executing the motor action, and the ongoing cognitive activity (Figure 1). If they are largely independent, they may result in divided action/attention costs impairing performance. However, we propose that if the goals of the motor action and cognitive activity are more integrated, such that the engagement of the body is required in service of the task, then performance may actually not degrade and may even be enhanced [125].

This emphasis on the coordination of the body and cognition also offers insight into the apparent contradiction between evidence showing negative effects of concurrent locomotor activity [60,112] and the concept of altered gain control highlighted in this review. The negative effects of concurrent physical activity and cognitive task performance could be driven by the need to access a common resource, by interference between the cortical networks supporting motor activity and cognition, or by some combination of these causes [73]. We suggest that the mechanisms that mediate altered gain control and competition for cognitive resources are likely dissociable and occur at different stages of information processing. Thus, it is possible that under some conditions, altered gain control and the competition for cognitive resources imposed by a physical task could have opposing effects. As a result, the negative effects of physical activity should be considered in the context of the relative contributions of the effects of physical activity on the physically activated modes of control and the possible competition for limited cognitive resources imposed by the physical activity itself.

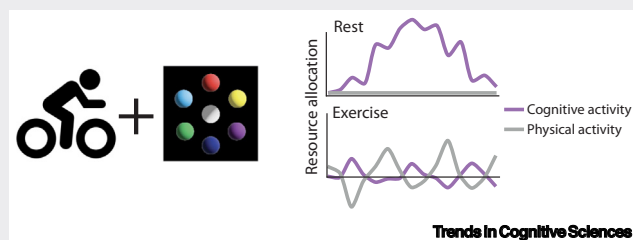


Figure 1. Cognitive tasks and physical activity may require access to common resources. Left: both behavioral tasks and physical activity draw on cognitive resources. Right: when these tasks are not integrated in the service of the same goal, the performance of the task and the physical activity may interfere with each other. For example, at rest (top), the resource

demand of physical activity (gray) is minimal and most resources are allocated to the cognitive task (purple). During simultaneous physical activity (bottom), both tasks require cognitive resources, resulting in competition over time.

of cortical control networks relies on slower-acting neurotransmitter projections. This difference suggests that evidence for altered gain control should start soon after physical activity begins and end soon after it stops. The effects of differential neuromodulation should take longer to emerge, persist after exercise, and the specific activity in the dorsal and ventral attentional control networks will show different time courses [73]. Consistent with this proposal, EEG investigations of sensory processing during exercise have generally shown enhanced early-stage visual processing [60,61,63,75], but not always [76]. By contrast, to our knowledge, the earliest consistent effects measured post-exercise occur later [72,77].

Working memory is tightly coupled with attention and recruits many of the same underlying neural networks [78–80]. Accordingly, it would be reasonable to expect state induced changes in working memory processes. Consistent with this hypothesis, we, and others, have observed reduced latencies in the P3 event-related potential (ERP) component during and after exercise [57,60,81]. The P3, and its subcomponents, are thought to index multiple stages of information processing, including the selection of task-relevant information, detection of novel events, and the updating of working memory [82]. The fact that P3 latency and amplitude are impacted by exercise aligns with studies showing facilitated visual working memory during exercise [83]. When coupled with evidence suggesting that attentional selection and distractor suppression mechanisms are enhanced during exercise [84], these findings suggest that the gating of information into working memory may be modulated by active states. However, the precise interplay between exercise-induced states, attention, and working memory remains unclear due to discrepant results in the literature [62,85,86]. This variability may be the result of varied contributions of gain control processes and neuromodulation of the cortical control networks due to differences in exercise protocols and the type and timing of cognitive tasks.

Unlike the studies of physical activity and working memory, single acute bouts of exercise consistently enhance executive functioning processes [54]. Often, these enhancements are observed post-exercise as reduced response time and reduced interference in tasks that introduce response conflict [87], and performance on these tasks can correspond to changes in the amplitude and latency of the P3 component [54,59]. Executive function involves multiple cognitive subfunctions, and many of these functions depend on hubs in the cortical networks discussed here [88,89]. While it is beyond the scope of this article to provide a detailed account of exercise-induced effects on all executive processes, these effects are likely associated with the differential neuromodulatory processes. More broadly, we suggest that leveraging evidence from human and nonhuman studies can help map the effects of physical activity onto the neural and neuromodulatory circuits that control these executive processes.

Concluding remarks

Our bodies and cognitive systems are constantly challenged by the body's physiological regulatory drive and the controlled drive to maintain performance through managing goals, expectations, and responses to unexpected events. There have been significant recent advances in understanding the neural and neuromodulatory control of behavioral states in other species, but the interplay between global physiological states and attentional control in humans is not well understood. Herein, we have leveraged converging lines of evidence from studies of nonhumans and humans engaged in physical activity to inform the development of a framework for understanding how physiological states may impact human attentional control processes. We propose that there are at least two physically activated modes of attentional control: altered gain control and differential neuromodulation of control systems. This framework not only advances the understanding of attention, but the core approach leads to novel questions about attention, cognitive processes, and other states (see [Outstanding questions](#)).

Outstanding questions

Does physical activity influence all forms of gain control? The current evidence in the literature has revealed multiplicative gain effects of locomotive activity, but other forms of gain control may be altered by physically active states.

How do different physiological states impact attentional control when the physical demands are executed in the service of the cognitive task? In many real-world tasks, the engagement of the body is integrated within the goal structure of the cognitive task, a feature that is missing from studies in the literature, including many of those that use physical activity as a trigger for global states.

How does locomotion impact attentional priority control in freely roaming humans? The dynamic nature of our natural environment, combined with head and eye movements, results in a stream of visual input that is constantly in flux, yet most attention tasks require head- and gaze-fixed participants. Recent studies have started recording from the brains of freely moving mice while simultaneously recording head and eye position and the visual scene from the perspective of the mouse. With noninvasive mobile brain imaging techniques it is possible to implement analogous protocols with humans.

What are the effects of systematically varying different aspects of physiological state (e.g., duration, intensity, and type of physical exercise) on different components of attentional priority control?

How long do the effects of physiological arousal on attentional control endure after cessation of physical activity, and what are their temporal dynamics?

What is the tipping point at which physical activity starts to negatively impact attentional control? Most laboratory-based investigations of exercise on cognition employ brief bouts of moderate-intensity exercise, and relatively few have tested the impact of prolonged bouts, with less conclusive results.

Our proposed framework also has implications that translate to other fields. For example, in the exercise literature, acute exercise effects across different cognitive domains have been mixed [53,54]. However, when one considers the range of exercise types, durations, and intensities that are used in that literature in the light of the evidence reviewed here, the reasons for these inconsistent results become clear [57]. Variability in exercise protocols likely leads to a high degree of variance in the response of the physically activated modes of control, resulting in a range of effects on behavioral and neural outcome variables.

Our proposal also offers an approach to understanding performance outside the laboratory. The current understanding of attention and performance is based largely on tightly controlled laboratory experiments in which participants are seated in front of a computer doing tasks designed to manipulate and measure different stages of information processing. The evidence reviewed here demonstrates that even simple physical activities can alter attentional control processes and implies that traditional laboratory experiments may not fully account for real-world behaviors. Physical activity manipulations are an important tool for understanding the human brain and behavior in the laboratory. Human mobile brain imaging techniques [63,90–92] and augmented reality technologies that integrate visual information into the physical world [93,94] provide the opportunity to study the impact of movement on cognition outside the laboratory. Indeed, tasks that require the integrated action of the body and cognitive system in the service of the same goal may significantly advance our understanding of human cognition and performance in the wild.

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Declaration of interests

The authors declare no competing interests.

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