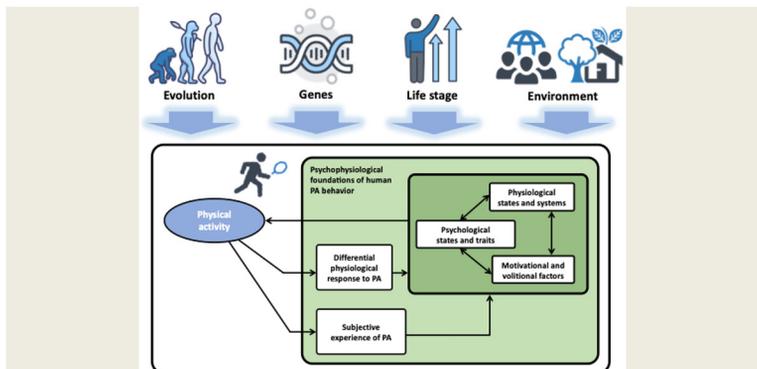# PSYCHOPHYSIOLOGICAL FOUNDATIONS OF HUMAN PHYSICAL ACTIVITY BEHAVIOR AND MOTIVATION: THEORIES, SYSTEMS, MECHANISMS, EVOLUTION, AND GENETICS

Integrative psychophysiological model of physical activity behavior

CONCLUSION

Multidisciplinary and holistic approaches are needed to better understand human physical activity behavior by linking traditional cognitive-behavioral theories, physiology, and evolutionary science

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KEY WORDS

evolution; exercise; motivation; neuroscience; physical activity

CLINICAL HIGHLIGHTS

Physical activity behavior is a meaningful part of human lives, starting before birth and lasting until death. It facilitates growth, learning, and exploring in early stages of life, offers an opportunity for leisure time and high-performance activities, and supports activities of daily living in adult life. Regular physical activity is an important aspect of overall health, which makes decreasing levels of physical activity a global topic of interest. Despite the ascribed level of importance, to this day we still do not know all there is to know about what drives human physical activity behavior and motivation. Theories, models, and frameworks provide us with potential explanations for the source of behavior, drawing from behavioral and cognitivist psychology, neuroscience, evolution, and genetics. From a psychophysiological point of view, characterized by mind and body reciprocity, we can add depth by taking neural networks, neurotransmitters, hormones, etc. as well as interactions with environmental cues in both conscious and automatic decision-making into account. This is facilitated by new technologies allowing increasingly accurate brain imaging. Although evolution predispositioned humans to be both physically active and inactive, it is time to broaden our perspectives and to consider knowledge from different disciplines to facilitate the promotion of physically active lifestyles.

PHYSIOLOGICAL REVIEWS®

REVIEW ARTICLE

PSYCHOPHYSIOLOGICAL FOUNDATIONS OF HUMAN PHYSICAL ACTIVITY BEHAVIOR AND MOTIVATION: THEORIES, SYSTEMS, MECHANISMS, EVOLUTION, AND GENETICS

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Abstract

Physical activity is a meaningful part of life that starts before birth and lasts until death. There are many health benefits to be derived from physical activity; hence, regular engagement is recommended on a weekly basis. However, these recommendations are often not met. This raises the question: when and why are people motivated to be physically active? Attempts to explain the motivation for physical activity (or lack thereof) have been a research interest for many years and in many disciplines. In this review, we provide evidence suggesting that physical activity behavior and the psychophysiological foundations thereof are influenced by evolution, genetics, life stage, and the environment. The psychophysiological foundations in turn comprise motivational and volitional factors as described in traditional psychological theories, psychological states and traits such as affective and stress reactions, as well as physiological states and systems (e.g., anatomical development and neural networks and transmitters). Importantly, physical activity elicits differential physiological responses and subjective experiences, which may impact future physical activity behavior and motivation. In summary, the interplay of psychophysiological mechanisms and the importance of examining the ultimate mechanism for physical activity behavior are emphasized. The synthesis of knowledge provided in this review provides impetus for theory development and can facilitate the promotion of physically active lifestyles.

evolution; exercise; motivation; neuroscience; physical activity

1. INTRODUCTION

When and why are people motivated to become and stay physically active? This essential question has concerned sport, exercise, and health scientists since the middle of the twentieth century and has become even more important since physical inactivity has become one of the leading causes of death worldwide (1–3). Today, public health experts agree that physical activity (PA) is a complex phenomenon that depends on a multitude of influencing factors. Obtaining a complete and accurate picture of the mechanisms underlying PA motivation has so far been complicated by the fact that most studies have focused on cognitive-behavioral and environmental factors, while remaining silent about the psychophysiological mechanisms and evolutionary foundations underpinning PA behavior and motivation. The time is ripe to take on a multidisciplinary and more holistic approach by establishing links between traditional cognitive-behavioral theories, physiology (in this article with a special focus on brain networks and neurotransmitters), and evolutionary biology/psychology. Such new impetus is warranted, as traditional approaches have proved to be only modestly effective in increasing levels of PA and in initiating behavior change (4–8).

1.1. Physical Activity Behavior

According to the World Health Organization (WHO), PA is defined as "any bodily movement produced by

1213

CLINICAL HIGHLIGHTS

Physical activity behavior is a meaningful part of human lives, starting before birth and lasting until death. It facilitates growth, learning, and exploring in early stages of life, offers an opportunity for leisure time and high-performance activities, and supports activities of daily living in adult life. Regular physical activity is an important aspect of overall health, which makes decreasing levels of physical activity a global topic of interest. Despite the ascribed level of importance, to this day we still do not know all there is to know about what drives human physical activity behavior and motivation. Theories, models, and frameworks provide us with potential explanations for the source of behavior, drawing from behavioral and cognitivist psychology, neuroscience, evolution, and genetics. From a psychophysiological point of view, characterized by mind and body reciprocity, we can add depth by taking neural networks, neurotransmitters, hormones, etc. as well as interactions with environmental cues in both conscious and automatic decision-making into account. This is facilitated by new technologies allowing increasingly accurate brain imaging. Although evolution predispositioned humans to be both physically active and inactive, it is time to broaden our perspectives and to consider knowledge from different disciplines to facilitate the promotion of physically active lifestyles.

skeletal muscles that requires energy expenditure" (9) and can be performed during leisure time (e.g., cycling to work, shopping, gardening) or in an occupational context (e.g., manual labor) (10). A distinction can be made between light [1.6–2.9 metabolic equivalents (METs)], moderate (3–5.9 METs), and vigorous (≥6 METs) PA (11).

It is also used as an umbrella term covering the related concepts of exercise, fitness, and sport (10) (**FIGURE 1**). Exercise (e.g., jogging, swimming, dancing, weight training) is typically planned or structured and requires repetitive bodily movements with the aim of maintaining or improving health through physical fitness, well-being, and social interaction (9). Physical fitness, in turn, is considered a measure of the capacity to perform PA or exercise (12). Sports (e.g., football, athletics, gymnastics) are typically practiced for performance and competition (10) or for the experience (e.g., trend sports, risk sports, nature sports) (13–15). A more recent definition of PA takes a broader approach in which PA "involves people moving, acting and performing within culturally specific spaces and contexts, and influenced by a unique array of interests, emotions, ideas, instructions and relationships" (16). Here, it becomes evident that PA is more than mere energy expenditure but involves complex and context-specific processes, which are addressed throughout this review. The most widely used PA recommendations are those from the WHO (17, 18), which offer specific guidelines for different populations, including children and adolescents, older adults, people with disabilities, and pregnant/postpartum women. For adults, WHO PA recommendations currently state the need for ≥150 min of moderate to intense PA per week (19) (**FIGURE 2**).
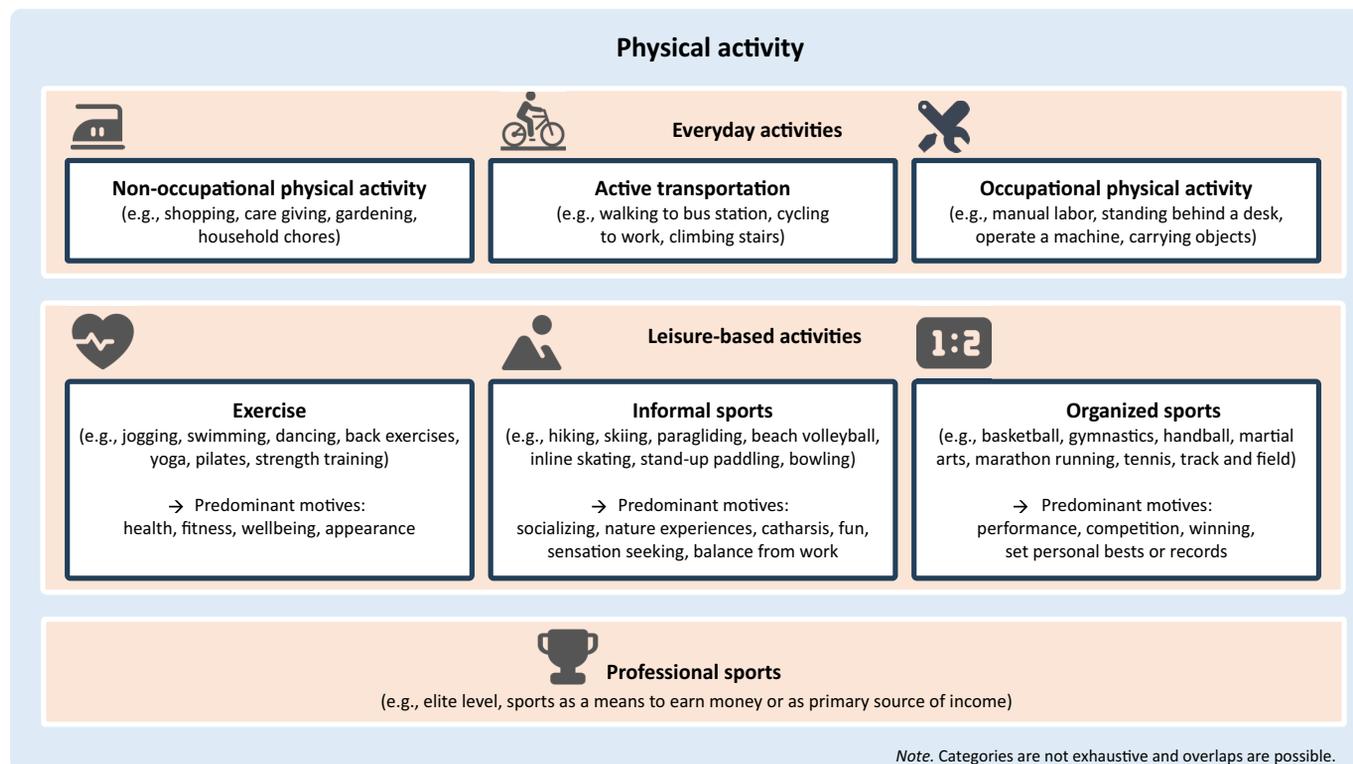

FIGURE 1. Physical activity is an umbrella term for both everyday and leisure-based activities. Everyday activities can be considered as nonoccupational, active transportation, or occupational, whereas leisure-based activities can be considered as exercise or informal or organized sports. Adapted from Fuchs et al. (10). Used with permission.

FIGURE 2. World Health Organization (WHO) recommendations for physical activity and sedentary behavior displaying that every move counts and varying recommendations according to categories (www.who.int/health-topics/physical-activity). Used with permission.

Even before birth, children can benefit from PA, as regular maternal PA during pregnancy has been associated with positive health and neurodevelopment in children (20–25). Newborns have a natural drive to learn about themselves and their environment through movement, which intensifies during infancy (26). Drive describes a motivational state, which is characterized by arousal and perceived tension and which energizes an organism to meet a basic need (27). Like food, water, and sleep, movement is a biological necessity, which has its greatest impact before adolescence (27). During childhood and adolescence, PA is important for motor, social, emotional, and cognitive development (28–35). During preschool years, when fundamental motor skills develop with maturation (36, 37), regular PA plays a central role in the development of fine and gross motor skills (38–45). Additionally, children who regularly engage in PA show fewer problematic social interactions with peers, parents, and teachers than their less active counterparts (46). A positive association with higher PA levels was also found for cognitive performance (including executive function) and academic achievement (47–50). In adulthood, PA is associated with numerous health benefits, including reduced risk of premature mortality and prevention of a wide range of chronic diseases (**FIGURE 3**) (51, 52). Participation in regular PA has also been associated with improved quality of life (53–56), increased capacity to cope with stress (57–64), improved sleep (65–69), and reduced risk of developing mental health issues such as depression (70–74) or anxiety disorders (73, 75–78). In older age, PA helps maintain independence (79–82), counteracts increasing frailty (83–87) and social isolation (88–91), and may counteract cognitive decline (92–96) and reduce age-related multimorbidity (97). Hence, PA is part of life from the very beginning, contributing to growth, development, and health.

Despite the well-documented benefits of a physically active lifestyle for both physical and mental health, the rates of PA remain low to modest at the population level (98–112). A recent WHO report showed that the (self-reported) global prevalence of insufficient PA was 27.5% among adults, with a particularly high prevalence in high-income countries, with more than one-third of adults (36.7%) not meeting recommended levels (107).

1.2. Physical Activity Motivation

Motivation can be defined as "the energizing of behavior in pursuit of a goal" (113), and thus in a classical sense
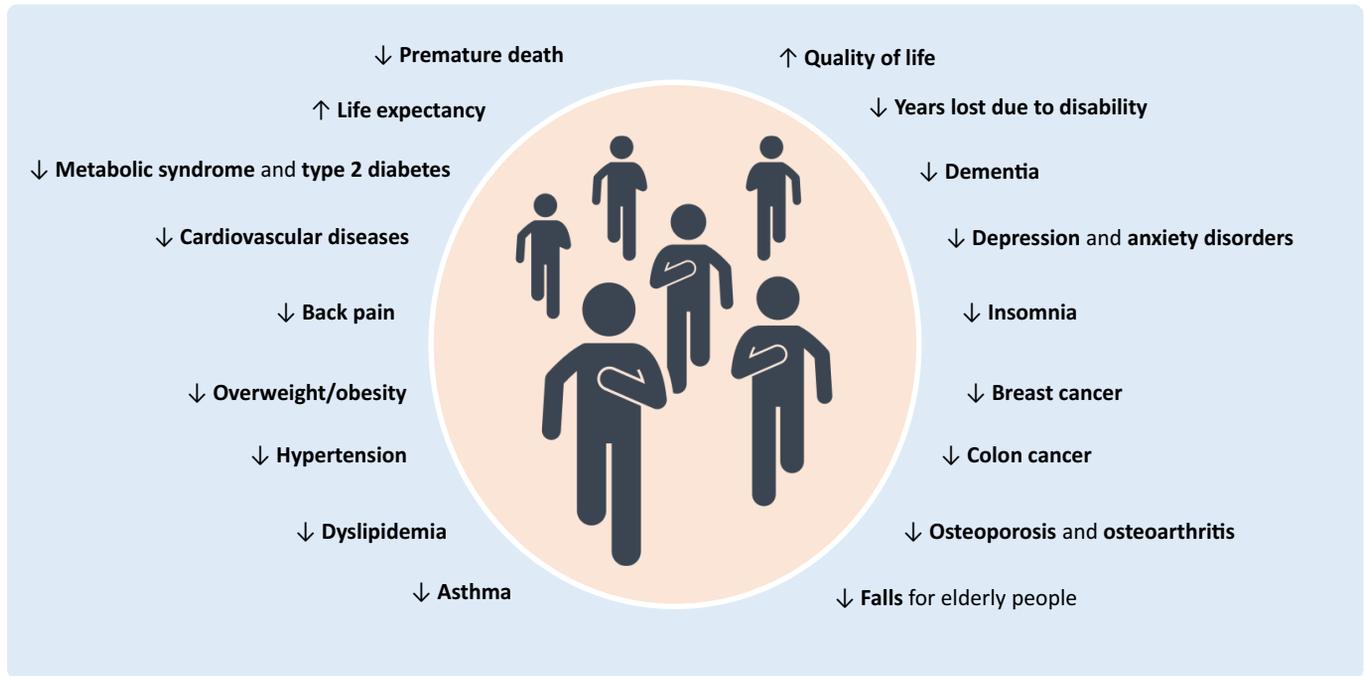
FIGURE 3. Adults engaging in regular physical activity may benefit from reduced risk of premature mortality, prevention of (chronic) diseases, increased life expectancy and quality of life, as well as decreased years lost because of disability and risk of falls.

motivation precedes the aforementioned behavioral outcomes and is necessary to obtain basic needs (113). Importantly, developments in research show that motivation is no longer considered one entity but a process (114). As such, it is crucial not only to understand psychological mechanisms but also to explore what occurs on a deeper level with the help of tools such as neuroimaging (113). As behavior varies, so do the level and orientation of motivation, e.g., the underlying reasons (the "why") of actions. For instance, an individual may feel more or less energized to perform an action out of interest or obligation or to avoid a less favorable outcome (115).

Overall, PA motivation has typically been thought of as relatively stable, with changes occurring over weeks (27, 116). However, a shift has occurred to focus on motivation states, such as momentary changes in motivation that occur over much smaller time periods (e.g., 1–5 min), which appear to influence intentions to be physically active and activity behavior (117, 118). These findings have resulted in studies investigating motivation to move and be sedentary "right now" or "in this very moment," which have advanced with developments in increasingly accurate instrumentation, such as the Cravings for Rest and Volitional Energy Expenditure (CRAVE) scale (116). The results of these studies have indicated that momentary changes may be due to a multitude of different influences, including various social, environmental, behavioral, and biological factors (116, 119–121). For example, an Ecological Momentary Assessment (EMA) study demonstrated that motivation states to move, be active, and be sedentary

followed a circadian pattern for the majority of participants, with peaks in motivation to be active around 3:00 in the afternoon (117). In healthy populations, motivation states may follow a paradigm similar to satiation, peaking when deprived and sharply falling when satisfied (27, 122). Indeed, the desire to move greatly decreases with vigorous activity and increases with long periods of sitting (116). Some data indicate, however, that not all types of PA produce the same effect. For instance, short bursts of PA, such as sprint intervals of 5–6 s, appear to energize and increase motivation (120, 123).

The loss of the desire to be physically active may be adaptive or maladaptive (26, 124–127). For example, when an individual becomes ill (e.g., food poisoning, flu), a sudden loss of drive to be physically active is likely adaptive, facilitating recuperation when energy is needed to fight infection. However, a sustained loss of motivation leading to dysfunction in daily life is maladaptive and may manifest in a variety of different ways (26, 27, 119). Amotivation refers to a state in which individuals cannot perceive a relationship between their behavior and that behavior's subsequent outcome, but it is often simply thought of as a lack of motivation or a motivational-null state (128, 129). Amotivation must be distinguished from low motivation, as it appears to have distinctive etiology, biophysical characteristics, and behavioral consequences (129–134). Disturbed motivation is frequently seen in a number of hyper- and hypokinetic psychiatric disorders and physical conditions (**TABLE 1**). For instance, individuals with depression were found to exhibit markedly

Table 1. *Nonexhaustive list of disturbed motivation and related disorders*

Disorder	Symptoms	Physical Activity Consequence	Possible Physiological Explanations
Depressive disorder	- Lack of motivation - Psychomotor retardation - Alterations of reward perception - Anhedonia - Apathy/disinterest	- Low desire to be physically active (135) - Agitated movement behaviors (136) - Less willingness to engage in effort to be physically active (137) - Undermining efforts to be physically active	- Elevated neuroinflammation (137) - Inhibited dopamine signaling (137) - Decreased relative left frontal EEG activity
Anxiety disorder	- Anxious apprehension - Anxious arousal	- Low levels of PA	- Relative left frontal EEG activity - Symmetrical frontal alpha activity (138)
Chronic fatigue syndrome (CFS)/ myalgic encephalomyelitis (ME)	- Delayed and prolonged stress response - Mental and physical fatigue - Debilitation (139–143)	- Postexertional malaise (PEM) (135)	- Dysfunctional endothelial perfusion function - Dysfunctional mitochondrial perfusion function - Dysfunctional neuroglial perfusion function - Dysfunctional cerebral perfusion function (140)
Parkinson's disease	- Motor apathy (144)	- Impaired motivation for PA	- Degeneration of the dopaminergic neurons in the substantia nigra - Changes in the ventral striatum - Changes in inferior prefrontal gyrus - Changes in anterior and posterior cingulate - Altered mesocorticolimbic circuit - Low gray matter density in the bilateral inferior frontal gyrus and the right prefrontal gyrus (144)
Attention deficit/hyperactivity disorder (ADHD)	- Motivational dysfunction - Inability to attend to delayed rewards vs. immediate gratification	- Lower levels of healthful PA/ exercise behavior (145)	- Hypoactivity of the mesolimbic dopaminergic pathway (146)
Restless legs syndrome	- Restless legs - Restless arms - Restless trunk	- Pathological urge to move	- Iron deficiency - Excessive dopamine in the substantia nigra and thalamus - Problems with endogenous opioids - Problems with melanocortin system - Genetic factors (147)

EEG, electroencephalogram; PA, physical activity.

higher risks of insufficient engagement in PA compared to their healthy counterparts (71, 112, 148, 149). This disparity has been attributed to motivational (e.g., reduced self-efficacy, weaker goal intentions), volitional (e.g., lower action and coping planning, perception of more behavioral barriers), affective (e.g., reduced experience of pleasure during exercise), and social (e.g., limited availability of social support) factors (150–158). Previous research also suggested that various physiological influences play a role in explaining why people with depression are less likely to engage in PA, including alterations in brain structure and function (159–167), neuroendocrine regulation (168–171), growth factors (172–176), inflammation (177–183), oxidative stress (184–186), and cardiorespiratory fitness (187–194). Interestingly, many of these physiological factors are also identified as potential

mechanisms underlying the antidepressant effects of exercise training (195–197). Additionally, psychoactive substances and medications such as caffeine and haloperidol are known to have significant effects on the drive to be physically active (198). Long-term use of antipsychotics frequently results in movement disorders, such as tardive dyskinesia, associated with jerky and uncoordinated movements (199, 200). Previous research has further shown that the use of some antidepressants and antipsychotics can lead to substantial weight gain (201–203) and increased fatigue (204, 205). These side effects may influence individuals' self-esteem, self-efficacy, and body image (206–212), potentially diminishing their motivation to engage in physical activity (212–219). Disturbed motivation may also result in an abnormally high desire to

be physically active (206–208). This may be the case for individuals with exercise addiction (also termed exercise dependence), who exhibit rigid adherence to exercise regimes, often without any competitive motivation (209). Affected individuals report symptoms akin to substance-related disorders, such as increasing exercise volume in response to diminishing feelings of reward, exercising despite severe illness or injury, lying to friends and family about their activities, and feeling unable to stop or reduce their exercise volume (210). These symptoms appear to remain stable over time and are frequently accompanied by other psychiatric comorbidities (211). Nevertheless, although excessive exercise can pose a problem for some people, the number of individuals affected by exercise addiction is relatively low in comparison to the number of those who fail to achieve sufficient levels of PA (210, 212). This raises the question of why so many exercising individuals are able to resist exercise addiction (212–216) and, conversely, why exercise appears unrewarding for so many (217–219), particularly as participation in PA was shown to cause the release of certain mood-enhancing neurotransmitters (220–224) and endocannabinoids (225–227). Notably, there is a paradoxical nature of structured exercise training being both enjoyable and frequently also draining and, at higher intensities, even painful (228). A parallel may be drawn with eating disorders, behavior forms that are both rewarding to sufferers and carried out compulsively despite also involving severe physical discomfort (229–231).

1.3. Aim and Structure of the Review

As we have learned so far, PA is a complex behavior, part of life from the onset, essential for development and health, and is guided by complex motivational processes. Additionally, we know that, globally, a large number of individuals are insufficiently physically active. For these reasons, it is essential to improve our understanding of multifaceted motivational processes required to promote PA behavior and improve population health. To address this, we aim to summarize current knowledge in the fields of psychology, neuroscience, and evolutionary science. In our opinion, it is time to broaden our perspective and to consider knowledge from different disciplines to advance theory development and to facilitate the promotion of physically active lifestyles. Our review will make an important contribution by highlighting blind spots in the current empirical landscape, and by suggesting new territories that could be explored in future research.

To this end, the present review is structured as follows: First, we highlight early and more contemporary psychological theories, models, and frameworks explaining PA behavior and motivation and developments in various fields of research (sect. 2). We then turn our attention to the neuroscience of motivated behavior, including the emergence of "health neuroscience" with approach versus avoidance, need versus incentive, as well as conscious and nonconscious aspects of behavior (sect. 3). In a next step, we link the aforementioned early psychological theories and frameworks with neuroscientific findings shedding light on the role of different brain networks and transmitter systems in motivated behavior (sect. 4). Furthermore, we explore the potential of evolutionary science in explaining PA as well as inactivity (sect. 5). We then briefly address two further issues important for an enhanced understanding of PA motivation: the role of sleep (deprivation) and the potential of modern technologies and digitalization for the promotion of PA on a population level (sect. 6). In the final part (sect. 7), we attempt to provide an integrative model and present a reflection on possible practical implications.

2. THEORIES, MODELS, AND FRAMEWORKS TO UNDERSTAND PHYSICAL ACTIVITY BEHAVIOR AND MOTIVATION

In this section, theories, models, and frameworks explaining PA behavior and motivation are introduced. A theory must fulfill four criteria to be considered as such, including conceptual definitions, domain limitations, relationship-building, and predictions (232). Theories are typically based on empirical data and supported by rigorous testing (233). Models are simplified representations of complex systems, serving to better understand the system and make predictions (234). Frameworks are typically an organization or classification of information, often used for decision-making or problem-solving (235). In the following, a nonexhaustive selection of the most popular theories, models, and frameworks used to better understand and influence health behavior in general, and PA in particular, is presented.

2.1. Early Psychological Research on PA Behavior

Early research in PA psychology was primarily based on secondary data analyses, using data from clinical trials or epidemiological cohort studies to predict PA and adherence (236, 237). Findings highlighted a wide range of psychological measures (so-called determinants) linked to PA behavior (238–242). The nature of this early research was largely atheoretical, and insights about the causal interplay of different psychological variables remained on a superficial level (243, 244). Consequentially, this early research provided neither reliable explanations nor useful intervention theories on which future PA interventions could be based. Progress took place in the late 1980s

when researchers created and applied more complex theoretical frameworks specifying the causal structure between variables, which led to the development of testable hypotheses and refinement of theories (245–247).

Since then, research efforts have been clearly directed either toward understanding psychological aspects, particularly within the domains of sport, exercise, and health psychology (236, 246, 248–250), or toward examining environmental factors (251–256), specifically within the broader context of public health (99, 257–262). This dual focus suggests a dichotomy in research priorities between individual psychological factors and broader environmental influences. The question revolves around identifying the factors that contribute to shaping an individual's behavior in relation to PA (236). To address this question and to learn more about human PA motivation, researchers have applied diverse theories, models, and frameworks, hereby particularly focusing on humanistic, social cognitive, and socioecological paradigms.

2.2. Self-Determination Theory

Early humanistic (or organismic) theorists departed from behaviorism by emphasizing intrinsic needs and challenging the idea that behavior is a sole reaction to reinforcement or punishment (263–265). A central concept that emerged was self-actualization, suggesting that human actions stem from an innate drive to grow, develop, and fulfill one's potential. Along these lines, Ryan and Deci (266) developed the self-determination theory (SDT) in 1985. SDT posits that individuals strive to satisfy three basic psychological needs: autonomy, competence, and relatedness (267, 268). Autonomy denotes an internal locus of control and the perception of being in control of one's own actions. Competence describes a sense of mastery and the perception of being effective in one's own actions. Relatedness is characterized by a feeling of being connected to and cared for by others. Striving to fulfill these needs leads to the participation in activities. In turn, the extent to which these needs are met (or thwarted) describes an individual's motivational regulation, which is said to occur on a continuum ranging from amotivation to intrinsic motivation (269). Intrinsic motivation is regulated intrinsically and is characterized by high autonomy and internalization. Actions are performed for enjoyment, pleasure, and fun. Further along the continuum lies extrinsic motivation, consisting of four different regulation modi: integrated regulation, where behaviors are fully incorporated in the process of satisfying psychological needs; identified regulation, where actions are performed to uphold personal values; introjected regulation, where actions are performed to avoid disapproval; and external regulation, where actions are performed to gain external

reinforcement or avoid punishment. The four regulation modi are characterized by decreasing internalization and autonomy. Along these lines, integrated and identified regulation modi are considered autonomous, whereas introjected and external regulation modi are considered controlled. Amotivation is characterized by acting without a clear reason or rationale (**FIGURE 4**) (270, 271). A connection between psychological need satisfaction and PA has consistently manifested across diverse populations (272–277). Studies indicate that more intrinsic forms of motivation correlate with PA behavior and maintenance, whereas extrinsic forms exhibit a weaker association. Furthermore, the fulfillment of basic psychological needs, particularly competence, emerged as a positive predictor of engagement in PA (272).

2.3. Social Cognitive Frameworks

The social cognitive frameworks originated from a shift in psychological research toward cognitive paradigms, incorporating social learning and mental representations of motivation. Initially applied to health behaviors (278), these frameworks posit that people form and act upon expectancies of behavioral events and outcomes, with valued outcomes and expectancies crucial to subsequent actions (279). Additionally, self-efficacy, i.e., an individual's belief regarding their capabilities to perform an activity (280), is emphasized. Hence for a desired behavior to take place, individuals must not only expect favorable outcomes but also believe in their own capabilities to perform the behavior. In the following, we present three of the best-known theories/models as examples so that we can build on them in later sections to establish links to neuroscience.

2.3.1. Health belief model.

The health belief model (HBM) was developed by Hochbaum, Rosenstock, and colleagues (281–284) in the mid-1960s (**FIGURE 5**). It includes the following key constructs: perceived severity, perceived susceptibility, perceived benefits, perceived barriers, and self-efficacy, which in turn may be subject to modifying factors such as demographics (age, sex, or ethnicity) and psychological characteristics (personality, skills, attitudes). Additionally, cues to action (e.g., media messages, advice from health professionals) are said to influence behavior (282). The model suggests that individuals' beliefs about their health significantly influence their health behaviors (285–288). Perceived susceptibility refers to an individual's belief about the likelihood of experiencing a health issue, whereas perceived severity refers to the belief about the seriousness of the consequences of a health issue. Perceived benefits involve weighing the positive outcomes of adopting a
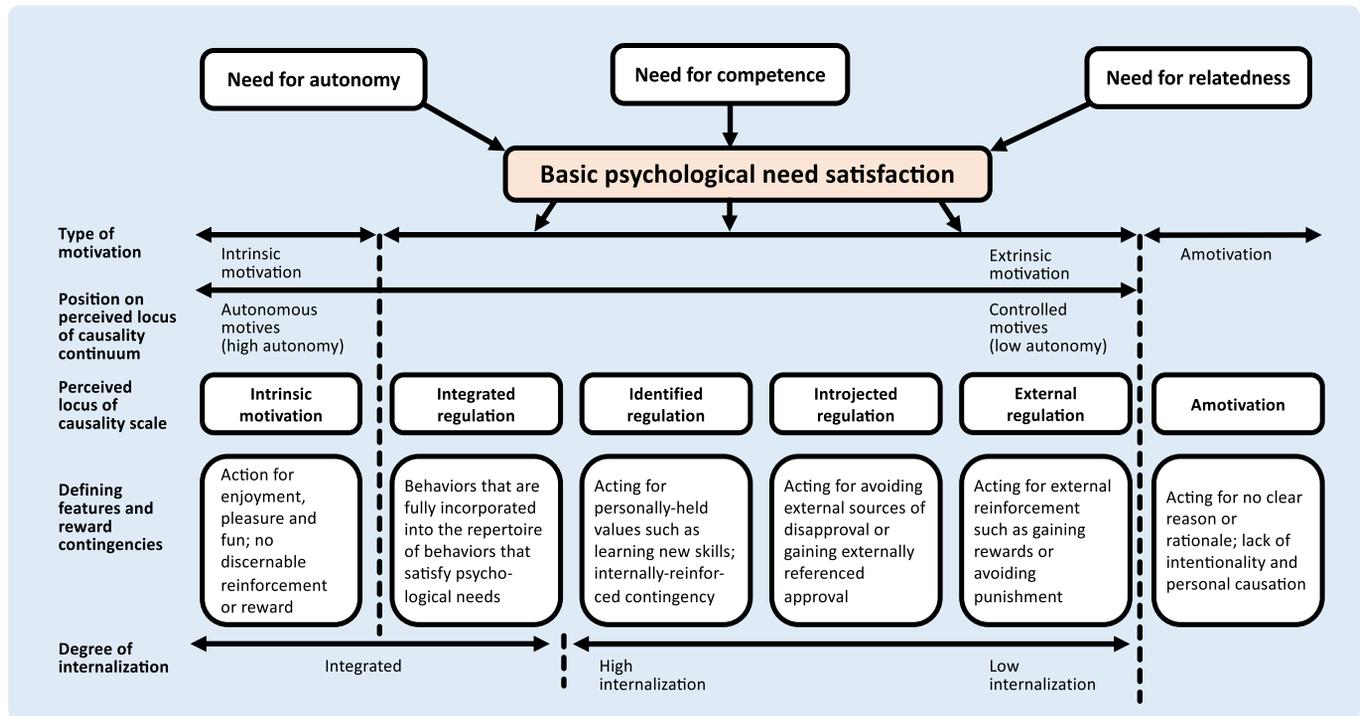
FIGURE 4. Summary of the self-determination theory, in which type of motivation, ranging from intrinsic and autonomous motivation to extrinsic and controlled motivation to amotivation, is determined by the fulfillment of the 3 basic psychological needs: autonomy, competence, and relatedness. Adapted from Hagger et al. (270, 271). Used with permission.

health behavior, whereas perceived barriers refer to potential obstacles or costs that may be associated with the behavior (281). The HBM has been used in PA promotion, especially as a basis of educational interventions to increase PA levels (289, 290).

2.3.2. Social cognitive theory.

Social cognitive theory (SCT), a competence-based theory, was developed in the late 1970s by Bandura (291–293) (**FIGURE 6**). It originates from social learning theory and posits that learning occurs through a dynamic and reciprocal interaction between the individual (self), environment, and behavior (294). Several psychological concepts are relevant, including perceived self-efficacy, outcome expectations, sociostructural factors, and intentions. Outcome expectations refer to the anticipation of the consequences of one's actions, which in turn significantly influence decision-making. Thereby, the evaluation of potential actions involves the consideration of possible outcomes that can be expected to result from the behavior and additionally involves the likelihood, the time frame, and the perceived value of these outcomes. As documented in previous reviews and meta-analyses, social cognitive theory has frequently been used to predict PA and was able to explain substantial amounts of interindividual variance in this behavior, although not all variables had similar predictive power (295–298).

2.3.3. Theory of planned behavior.

The theory of planned behavior (TPB), a belief-attitude theory, was developed by Ajzen (299, 300) in the mid-1980s (**FIGURE 7**). The TPB assumes that an intention is the central predictor of behavior. The formation of intentions is influenced by behavioral, normative, and control beliefs (299). Behavioral beliefs, referred to as attitudes, represent the degree to which an individual has a favorable or unfavorable evaluation of a specific behavior and directly influence the formation of intentions (299). Normative beliefs, referred to as subjective or social norms, are the perceptions of social expectations to adopt a behavior and can shape and reinforce attitudes, which in turn influence intentions (301). Finally, control beliefs, referred to as perceived behavioral control, represent the perceived ease or difficulty of performing a certain behavior and are assumed to reflect past experiences as well as anticipated impediments and obstacles associated with intended action (302). TPB belongs to the group of most frequently used theories to explain and promote PA (303–307).

2.4. Socioecological Frameworks

Socioecological frameworks take a holistic approach and posit that behavior is influenced by factors at various levels, spanning from the individual (as those
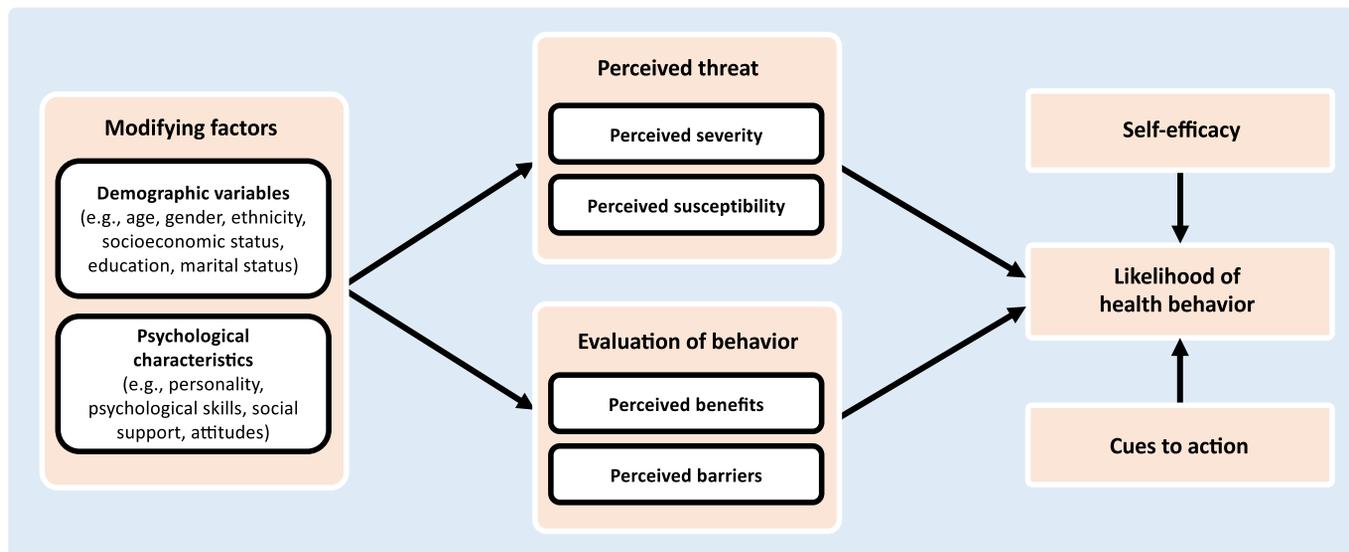
FIGURE 5. Summary of the health belief model, including perceived threat and evaluation of behavior, which are influenced by moderating factors and lead to the likelihood of a health behavior, which is also influenced by self-efficacy and cues to action. Adapted from Orbell et al. ([281](#)). Used with permission.

presented in the models above) to the environment and social policy ([308–310](#)). Bronfenbrenner ([311](#)) developed the ecological systems model in the late 1970s, which became the basis for various contemporary socioecological frameworks (**FIGURE 8**). Typically, these models comprise several concentric layers, such as individual, interpersonal, organizational, community, and policy levels. In the context of PA, the socioecological models

emphasize the environmental settings level, complementing individual-level approaches ([312](#)). Numerous literature reviews have explored the relationship between PA and environmental features, such as land use ([313–315](#)), street connectivity ([316–318](#)), crime and neighborhood safety ([319–322](#)), neighborhood infrastructure quality and aesthetics ([254](#), [323–327](#)), and PA policies ([328–331](#)). However, the effect sizes for these
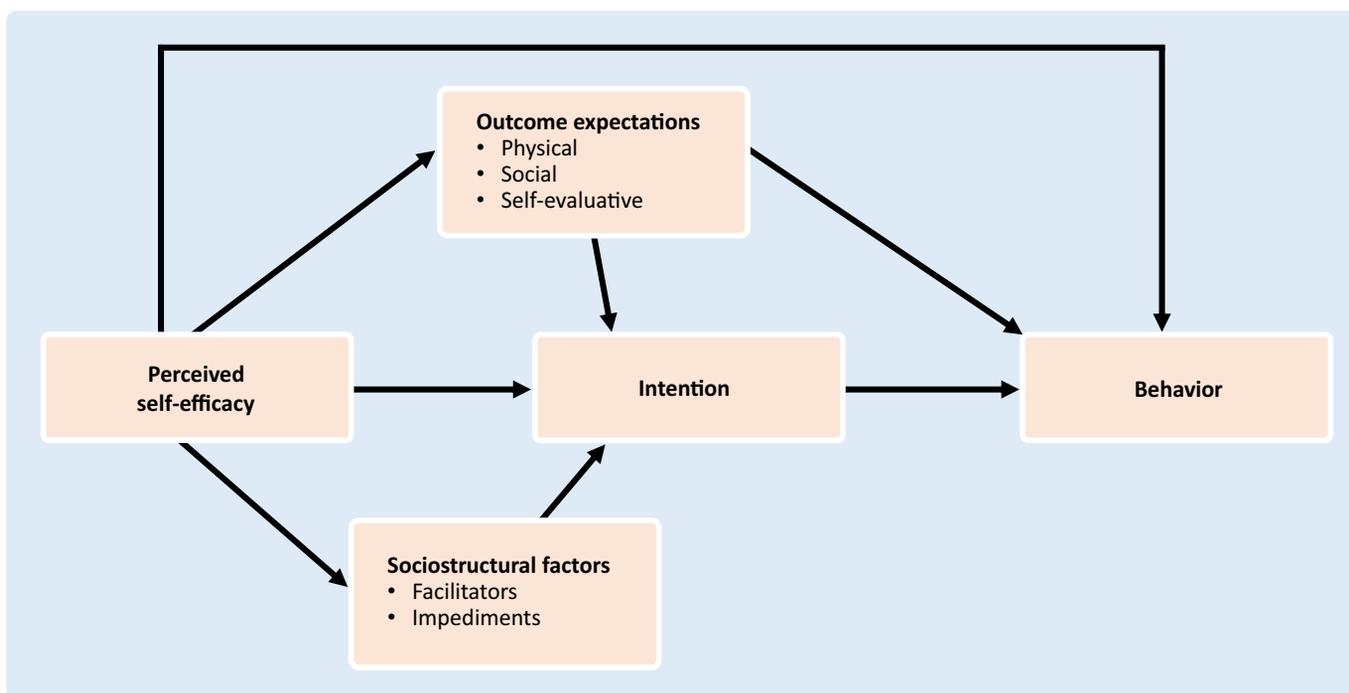

FIGURE 6. Summary of the social cognitive theory, including perceived self-efficacy influencing outcome expectations, sociostructural factors, as well as the behavior directly; intention, which is influenced by perceived self-efficacy, outcome expectations, and sociostructural factors; as well as behavior, which is influenced by outcome expectations, intention, and self-efficacy.
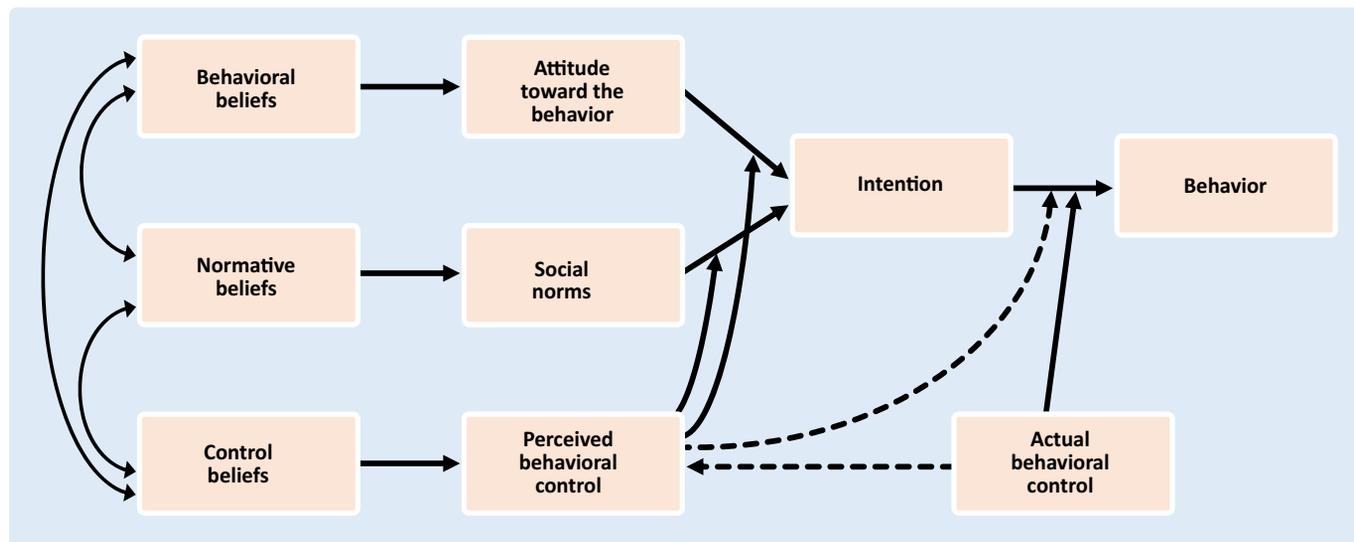
FIGURE 7. Summary of the theory of planned behavior, including behavioral beliefs leading to an attitude toward the behavior; normative beliefs leading to social norms; control beliefs leading to perceived behavioral control; intention, which is influenced by both attitudes and social norms directly and perceived behavioral control indirectly; and behavior, which is influenced by intention, which in turn is impacted by actual behavioral control. Adapted from Ajzen and Schmidt (299). Used with permission.

relationships are generally small and sometimes inconsistent (332–334).

2.5. Stage Models of Behavior Change

Alongside social and ecological factors, the element of time has been integrated in some models. So-called stage models of behavior change do not rely on solely one theory but allow for multiple theories applied to stages representing motivational readiness to initiate a new behavior or change an existing one. A marked difference from the above-described (structural) theories, models, and frameworks is that in stage models processes are not considered on a continuum but moves can be made dynamically between stages (335). One of the most frequently used models is the transtheoretical model (TTM) of behavior change developed by Prochaska and DiClemente (336, 337) in the early 1980s. The model includes six stages, in this example adapted to exercise behavior (**FIGURE 9**): precontemplation (no intention to exercise), contemplation (intention to exercise within 6 mo), preparation (some irregular exercise), action (exercising regularly for <6 mo), maintenance (exercising regularly for 6 mo or more), and termination (maintained behavior without risk of relapse). It is posited that individuals go through the stages cyclically. Hence, individuals may go through each stage several times before long-term behavior change (termination) is reached. So-called processes of change including experiential processes (e.g., consciousness raising, environmental reevaluation, self-reevaluation) and behavioral processes (e.g., counterconditioning, reinforcement management, stimulus control) lead to transitions between stages. Furthermore, decisional balance (weighing the pros and cons of the behavior) and self-efficacy facilitate progression through the stages, whereas temptations represent negative urges that impede regular engagement in PA (338–343). In a recent systematic review, results show that there is inconsistent evidence to support TTM-based interventions to increase PA levels [with 5 randomized controlled trials (RCTs) showing significant and 6 no effects] (344).

2.6. Health Action Process Approach

Aspects from different paradigms have also been taken and mixed (hybrid models). As an example, the health action process approach (HAPA) combines elements from SCT, TPB, and TTM. HAPA was developed by Schwarzer (345–348) in the 1990s (**FIGURE 10**). It is a further stage model and is designed as a comprehensive theoretical framework to explain and predict health behavior change over time and to address the gap between intention and action (349, 350). This model integrates both preintentional and postintentional phases of behavior change, offering insights into the processes that individuals undergo from the formation of intentions to the maintenance of health-related actions. The model consists of two main phases: the motivation phase and the volition phase. In the motivation phase, individuals form intentions to engage in a specific health behavior, influenced by factors such as action self-efficacy, outcome expectancies, and risk perceptions. The volition phase focuses on the translation of
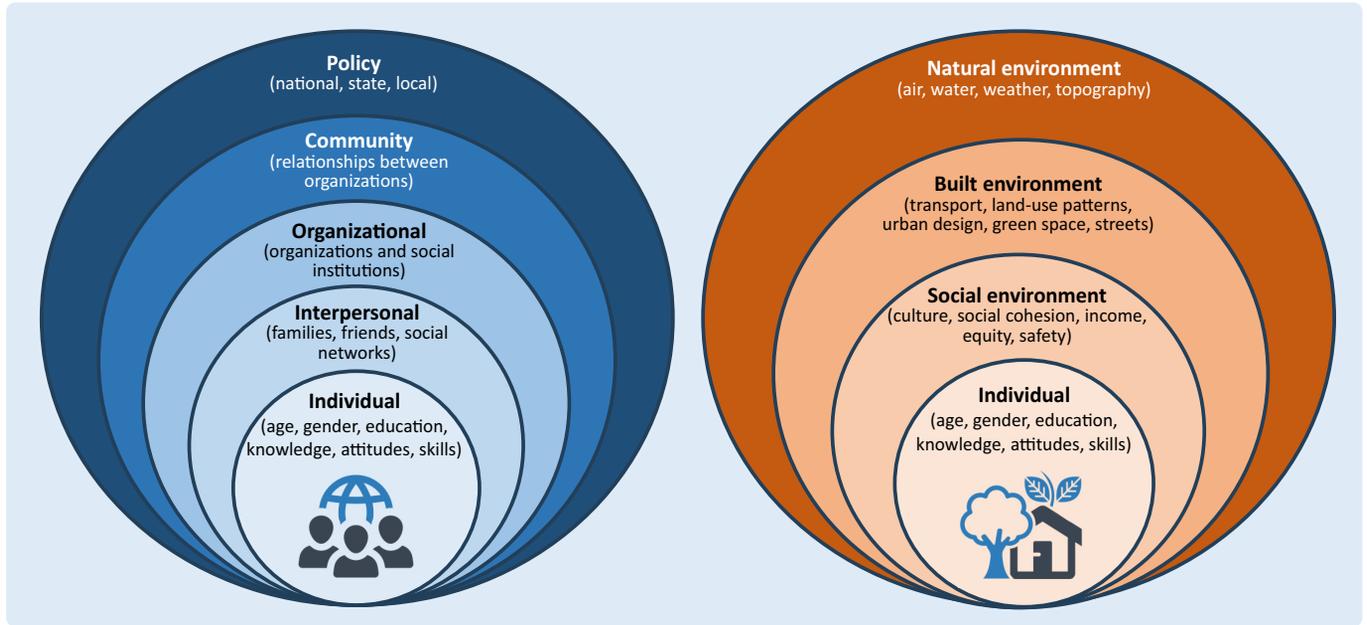
FIGURE 8. Different types of socioecological frameworks, including individual, interpersonal, organizational, community, and policy levels, as well as social environment, built environment, and the natural environment.

intentions into action and the maintenance of behavior change, incorporating factors such as action and coping planning, coping and recovery self-efficacy, as well as self-monitoring to readjust goals (347). In recent years, the HAPA has been widely used to predict PA behavior (351) or to guide PA interventions (352–354).

2.7. Dual-Process Models

Dual-process models and the HAPA model share common ground in the sense that both provide an explanation for the intention-behavior gap (355–357). One of the earliest formulations of a dual-process model
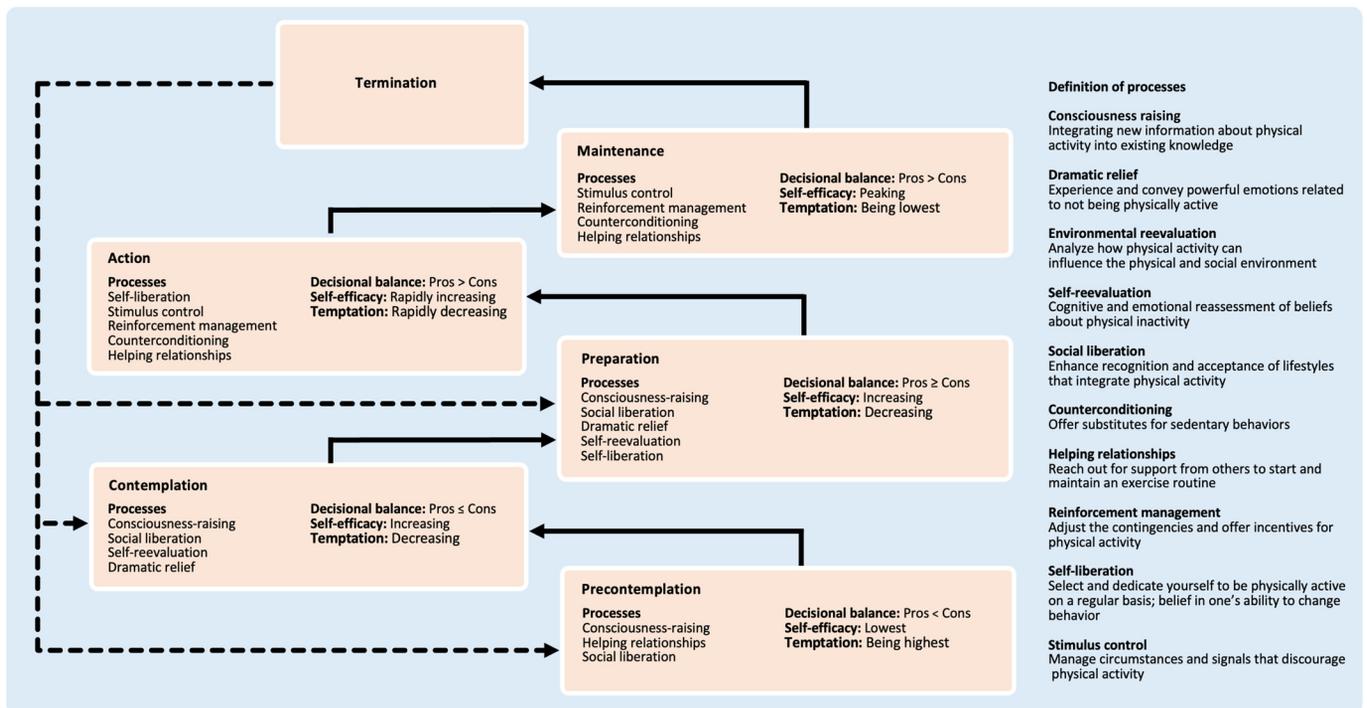

FIGURE 9. Summary of the transtheoretical model of behavior change with the cyclically occurring stages: precontemplation, contemplation, preparation, action, maintenance, and termination, eventually leading to sustained behavior change without risk of relapse. Based on Di Clemente and Graydon (337) and Nigg and Geller (338).
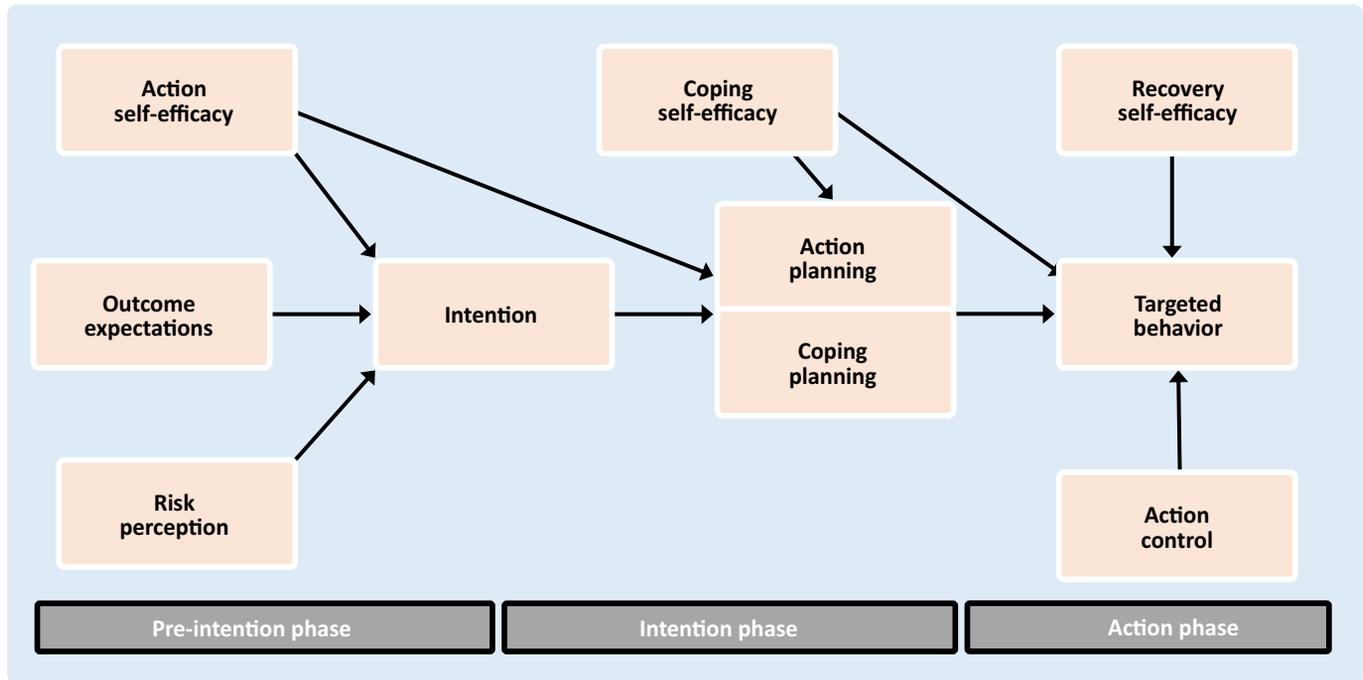
FIGURE 10. Summary of the health action process approach, with a motivational stage consisting of intention formation that in turn is influenced by action self-efficacy, outcome expectation, and risk perception and a volition stage consisting of action and coping planning, in turn influenced by coping and recovery self-efficacy leading to a target behavior, which is also influenced by action control. Adapted from Schwarzer and Hamilton (345). Used with permission.

was coined by James (358) in the late nineteenth century, in which he distinguished two mental processes, one described as "associative" thinking, which is automatic, and the other as "true thought," which requires conscious effort. Later, dual-process models gained increased attention through Kahneman and Tversky in the 1970s and 1980s through their research on decision-making, whereby they distinguished between "System 1" entailing automatic, intuitive processing and "System 2" entailing controlled and deliberative processing (359). With this, there has been a paradigm shift from the assumption that behavior, including PA behavior, is a result of solely conscious, controlled, and deliberative processing to the inclusion of associative, automatic, and intuitive processing (360). As is already evident, terms are used to describe the dual processes depending on discipline and school of thought of these models, including and not limited to "conscious versus nonconscious," "explicit versus implicit," "rational versus affective," "controlled versus automatic," and "reflective versus nonreflective" (361).

Importantly, the construct of "affect," which is more prominently addressed in dual-process models, can be processed both consciously and nonconsciously (4, 362–365). Hence, conscious affective evaluation can be understood as a cognitive appraisal of emotions that occurs in a reflective or controlled manner and can

(often) be communicated explicitly (362). Besides the cognitive appraisal of emotions, other appraisals take place, such as the appraisal of the above-described social cognitive and behavioral constructs (e.g., outcome expectancies, self-efficacy, perceived control). Thus, these individual-level determinants are typically categorized as reflective processes (366). Nonconscious affective valuations can be understood as assigning affective valence (positive or negative) to experiences, which occurs in an associative and automatic manner and can typically not be communicated explicitly (4).

2.7.1. Affective-reflective theory of physical inactivity and exercise.

Similarly to Kahneman's 1/2-System (359), the affective-reflective theory (ART) of physical inactivity and exercise, presented by Brand and Ekkekakis in 2018 (367), posits two types of processing (**FIGURE 11**). Both processes are initiated upon the exposure to a PA-related stimulus. The Type 1 process is characterized by an activation of automatic associations and is linked to encoded affect and cognition. Associations elicit an automatic affective valuation leading to an impulse to either engage or not engage in exercise. Simultaneously, Type 2 processes, i.e., reflective evaluations, take place, which may be influenced by the automatic affective valuations and

lead to an action plan to either engage or not engage in PA. Similar to Lewin's force field theory (368), which posits that behavior is the result of an interaction between driving and restraining forces whereby the behavior occurs when the driving forces are stronger than the restraining ones, the individual may or may not engage in PA depending on both the action plan and impulse. Hence, PA will occur if the plan and the impulse are congruently in favor of exercise or if there are sufficient self-control resources in place to implement the plan to engage in PA in case of a discrepancy between the plan (engage in PA) and the impulse (not engage in PA) (367). Additionally, ART emphasizes that based on repeated engagement in PA, this concept is paired with positive or negative responses of pleasure or displeasure, respectively. As with conditioning, learned associations are suggested to lead to contextual cues that are paired with automatic affective valuations. In turn, these valuations influence controlled/reflective processes, which are needed, for example, to integrate a prescribed PA program in a daily routine (369).

2.7.2. Wants and aversion for neuromuscular tasks model.

Another recent model that has attempted to integrate motivation states for physically active and inactive behaviors is the wants and aversions for neuromuscular tasks (WANT) model developed by Stults-Kolehmainen and colleagues in 2020 (26). This model describes the influence of weaker (e.g., desire/wants) and stronger (e.g., urges/cravings) motivational forces from an approach and avoidance perspective (370). The model may be seen in four quadrants with a horizontal axis ranging from dread, aversion, desire, to craving to move and with a vertical axis ranging from dread, aversion, desire, to craving to rest (**FIGURE 12**) (26). The manners in which these desires interact are flexible and so provide a wider behavioral spectrum in the face of stress. The purpose of the stress response is to energize and motivate action. The most basic stress responses were described by Cannon (371, 372) and include fight or flight (373), which have been expanded to also include fright, freeze, faint, and fawn (374). When stressed, an individual may be activated to move (e.g., fight or run), inhibited from moving (e.g., freeze), or a flexible combination of the two in some series of actions as the threat changes in nature (375). In terms of acute and momentary stress, consider the example of watching a horror film, where one might be "frozen," with an active desire to keep still and not move. When watching a close matchup between two competing teams, one might be ecstatic and highly energized to move, with no desire to be still or rest at all. Chronic stress may have different patterns, as energy systems are dysfunctional and drained under such conditions (376). Generally, chronic stress can lead to more or less desire to move and to be still, depending on a variety of factors such as whether movement and exercise are used as coping mechanisms (375, 377). How motivation states (e.g., desires, urges) propel PA has been explained by a variety of different theories, including drive reduction theory, satiation models, hedonic theories of behavior, and the incentive sensitization model (26, 27, 370).
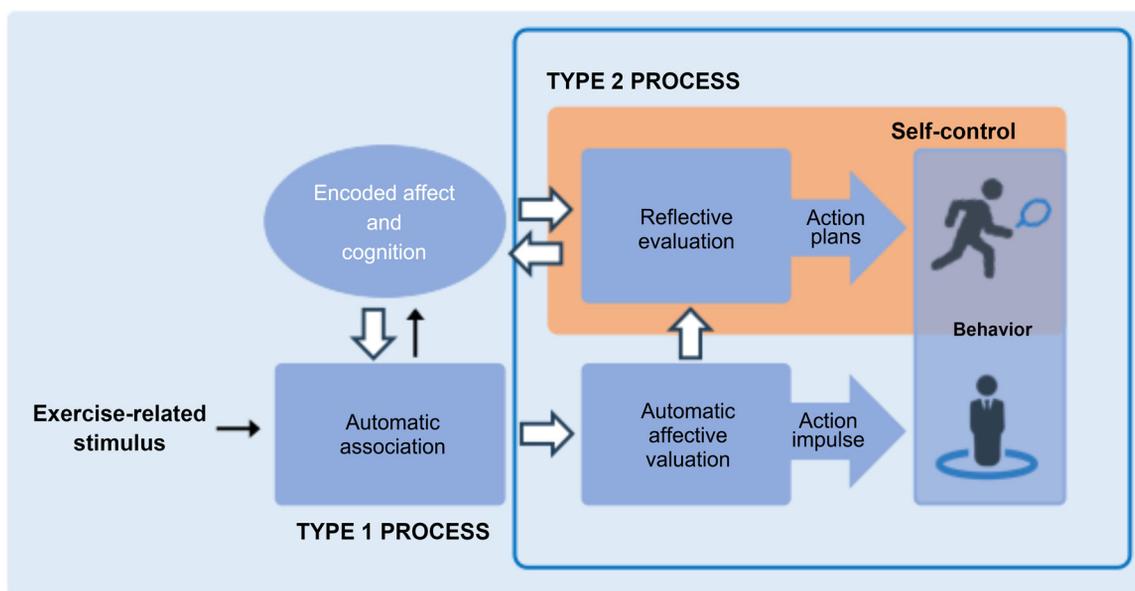
FIGURE 11. Summary of the affective-reflective theory of physical inactivity and exercise, composed of Type 1 and 2 processes to explain behavior. The Type 1 process starts with the stimulus evoking automatic associations, which leads to an automatic, affective valuation leading to an action impulse. The Type 2 process is also triggered by the stimulus as well as the automatic association, which feeds into a reflective evaluation leading to an action plan. Self-control resources are needed in case the action plan and impulse are incongruent and the plan for activity needs to override the impulse for inactivity. Adapted from Brand and Ekkekakis (367). Republished under CC 4.0.

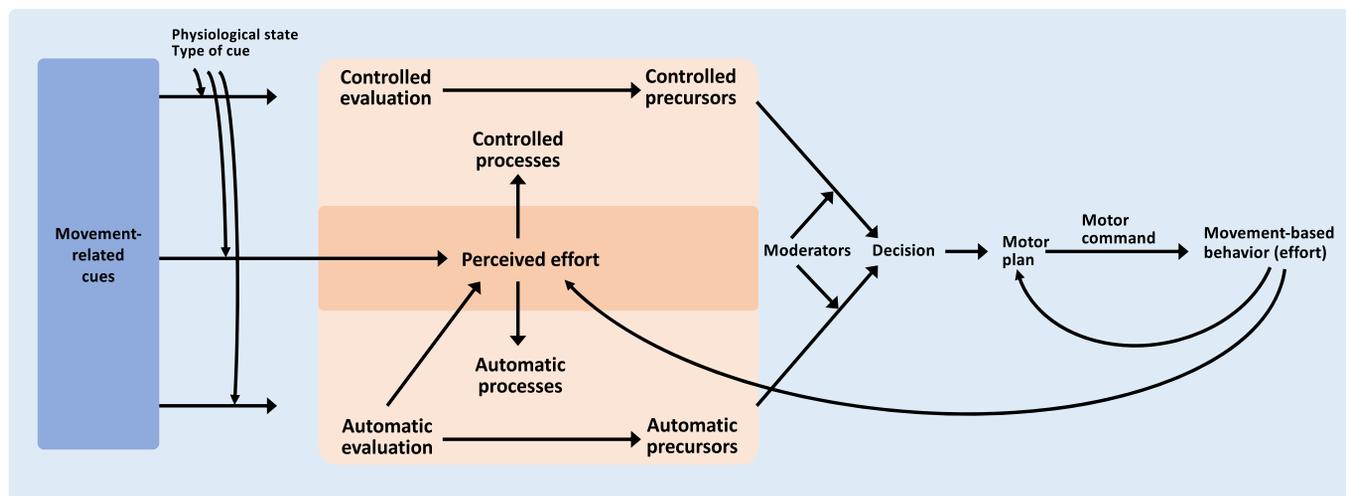**FIGURE 12.** Summary of the wants and aversion for neuromuscular tasks model, with 4 quadrants in which a range of feelings (dead tired, confused, terrified, energized) are presented, triggered by various situations (illness, stress, perceived danger), leading to a spectrum of behavioral outcomes. Adapted from Stults-Kolehmainen et al. (26). Republished under CC BY 4.0.

2.7.3. Theory of effort minimization in physical activity.

The theory of effort minimization in physical activity (TEMPA), introduced by Cheval and Boisgontier in 2021 (378), represents a further relevant theory highlighting that PA behavior is partly regulated by automated processes. According to TEMPA (**FIGURE 13**) (378), movement-related cues lead to a perception of effort as well as controlled and automatic evaluations leading to controlled and automatic precursors, respectively. The perceived effort in turn also prompts controlled and automatic processes. Importantly, the automatic evaluation may also impact the perceived effort. Along with moderating factors, a decision is made, leading to a motor plan, a motor command, and movement-based behavior (effort). The automatic tendency to minimize physical effort has been widely demonstrated in diverse fields such as biomechanics (379, 380), neuroscience (381–385), and evolutionary biology/psychology (386–389). Despite this pervasive tendency, the role of effort minimization in regulating PA behavior has been largely overlooked. This oversight is critical, as this automatic drive to minimize effort can act as a restraining force, impeding the translation of conscious intentions into

actual behavior (390–393). For example, Cheval et al. (393) recently showed that intentions predicted moderate-to-vigorous PA (MVPA) as measured by accelerometer, but only among participants with low or moderate automatic approach tendencies toward sedentary behavior. In other words, a strong automatic attraction toward sedentary behaviors appeared to negate any positive effect of intentions on subsequent PA. TEMPA also emphasizes the fundamental role of affective mechanisms (e.g., pleasure derived from PA, intrinsic motivation) in promoting the initiation and maintenance of PA across the lifespan. Specifically, according to TEMPA positive affective experiences, by reducing the perceived effort associated with PA, may influence decision-making processes to favor PA over sedentary alternatives (394).

2.8. Psychophysiological Frameworks

To get a deeper and more hard-wired perspective on PA motivation and to move research on PA motivation forward in the twenty-first century, it has been claimed that adopting a inter-/multidisciplinary approach that integrates physiological and psychological concepts is crucial (395–397). Integrative approaches considering

FIGURE 13. Summary of the theory of effort minimization in physical activity, showing how movement cues lead to the perception of effort as well as both a controlled and an automatic evaluation of the cue. Following this, a decision is made and motor plan and commands may lead to the execution of movement-based behavior (i.e., effort). Adapted from Cheval and Boisgontier (378). Republished under CC BY 4.0.

ecological, genetic, and physiological factors, along with evolutionary history, have been proposed (398) but have rarely been implemented in empirical research, despite the fact that it has been claimed by sport and exercise psychologists since the 1980s that psychobiology is a promising field of research that could help to better understand the relationship between psychological and physiological variables underlying behavioral outcomes (399, 400). Although efforts to explore the psychophysiological foundations of motivated behavior have been made in the ART, WANT model, and TEMPA, the overall lack of psychophysiological approaches to the study of motivation is a major drawback as explanations of motivation remain largely circular when only psychological and behavioral measures are applied to deduce causal effects of motivation (263). For instance, in traditional social cognitive theories, participation in structured exercise activities (explanandum) is explained by an individual's intention (explanans). However, in these frameworks the explanandum is inferred from what is observed or what a person is saying (e.g., Why is she exercising? Because she has a strong intention. And how do you know that? Because I see her exercising regularly and because she is telling me that she is determined.). In contrast to such purely behavioral accounts of motivation, psychophysiologists would go one step further and try to separate the explanandum from the explanans by focusing on certain brain regions or the release of certain hormones, in interactions with environmental cues, that precede or cause an individual's conscious or automatic decision to engage in exercise training. Psychophysiologists would also argue that such an approach is particularly applicable to PA, a behavior that is influenced by multiple physiological systems (e.g., endocrinology, cardio-circulatory and nervous

systems, metabolism) in addition to automatic and conscious cognitive processes and environmental factors (258).

Hence, psychophysiological frameworks, rooted in the reciprocal relations between the mind and body, are introduced. The origins of psychophysiology can be traced back to the late nineteenth and early twentieth century, when researchers such as Darwin (401), James (358), and Cannon (373) made first attempts to investigate the relationships between specific emotions and changes in physiological states. Today, psychophysiology is considered a broad field of research (396), encompassing various subdisciplines such as cognitive and social neuroscience, neuropsychology, and cardiovascular psychophysiology, with a core mission to explore the relationships between psychological states, physiological responses, and human behavior. In the context of motivation, these approaches strive to elucidate motivational phenomena through an understanding of the specific functions of the brain and the rest of the nervous system (263). This research often employs mammalian animal models (using lesions, direct recordings from neuron assemblies, brain dialysis, or pharmacological techniques), assuming that the brain's execution of motivational processes are largely analogous across related species. Consequently, findings from these animal models are extrapolated to apply to humans as well (263). Recent evidence, for example, suggests that a connection between the gut and the brain in mice impacts exercise performance by increasing dopamine signaling during PA. Findings suggests that gut-derived signals influence the rewarding aspects of exercise, offering a microbiome-dependent explanation for variations in individual exercise performance and the motivation for exercise (402).

Nevertheless, the understanding of the link between the brain and subjective states related to specific aspects of motivation is limited by the use of animal models, because animals are unable to describe their subjective states (263). To address this limitation, researchers are increasingly integrating human-focused investigations alongside animal studies. Human studies provide an opportunity to correlate measures of brain activity or physiological changes to both behavior and subjective states. For instance, research has shown that interindividual differences in PA behavior are partly attributable to differences in individual interest in this behavior (403–406). Individual interest is described as a psychological state and motivational variable that leads to reengagement in content-related activity (407). While individual interests generally develop through different phases, including an initial triggering phase, self-relatedness, novelty, intensity, etc. (408–411), the brain seems to play an important role in making interest rewarding through reward circuitry (410, 412). Importantly, the introduction of advanced brain imaging methods such as functional magnetic resonance imaging (fMRI) and electroencephalography (EEG), offering high spatial and temporal resolution, has played a crucial role in expanding and transforming psychophysiological research on motivational and emotional processes (263). This transformation has given rise to the emerging field of affective (413, 414) and health (415–417) neuroscience, and the application of brain imaging methods in the study of motivational and emotional processes has greatly enhanced our comprehension of these intricate phenomena (418).

3. NEUROSCIENCE AND MOTIVATED BEHAVIOR

As highlighted above, research on the promotion of healthy behaviors such as PA has mainly used behavioral, social, and epidemiological approaches. Findings from neuroimaging were rarely considered, leading to a conceptual absence of the brain from health research. This changed with the introduction of health neuroscience, which attempts to understand how features of the brain can predict health behavior and underlie the relation of social and affective experiences of health (415).

The role of the brain in behavior was already investigated in animal studies decades ago. The aim was to understand the neural underpinnings of the motivation to satisfy basic needs in relation to both internal states and environmental conditions (113). Nevertheless, because of a reliance on animal studies, consciousness was difficult to measure and absent from initial

theoretical concepts but received increasing attention with findings from humans. Social cognitive theories that attempt to explain behavior change or maintenance assume that setting a goal requires a conscious reflection process and that the pursuit of this goal is linked with conscious intent (419, 420). In this respect, consciousness refers to the awareness of processes or relevant contents during motivation or behavior. Consciousness is a key concept for setting goals and initiating action. The latter refers to a behavioral activity, which is directed toward a particular goal and ends with the achievement of the goal (421). Cognitive control and the networks underlying associated functions are thought to guide action. During cognitive control, the frontoparietal network (FPN), including the dorsolateral prefrontal cortex (dlPFC), the anterior cingulate cortex (ACC), inferior and superior parietal lobe, and precuneus, is recruited (**FIGURE 14**) (422). Among these regions, the prefrontal cortex (PFC) is thought to guide the allocation of attentional resources and use information for action selection, generation, and perception (423). Based on this information, goal states can be maintained and updated according to actions and action plans. These processes rely on working memory and on a neural level dopamine signaling to prefrontal regions (424). These regions are connected with parietal junctions, and as a network they control the selection of a variety of information types (425). Based on this process, action emulation (e.g., replication of actions and behaviors) has been suggested as the core function connecting cognitive computations across different tasks: emulation leads to a dynamic representation of abstract movement kinematics, maintains its internal manipulation, and sustains the representation over a limited time period (426). However, translating intentions into action does not rely on the FPN alone (427). As shown below, other structures are involved.

Action can be considered the "smallest unit" of behavior change, given that initiating change starts with a sequence of goal-oriented actions (300). The involvement of the FPN has also been verified for the example of PA, given that findings indicate a predictive value for adherence to structured exercise programs (428). For behavior change, the role of the brain extends beyond processes associated with action. It further influences how external inputs, such as persuasion and social influences, affect this change. In this respect, the activation of the medial prefrontal cortex (mPFC) associated with the representation of message content has been linked with message-consistent behavior change (429). This may be due to a more general contribution of the ventromedial prefrontal cortex (vmPFC) and its connection to the anterior cingulate cortex (ACC) to the control of information seeking and the determination of actions
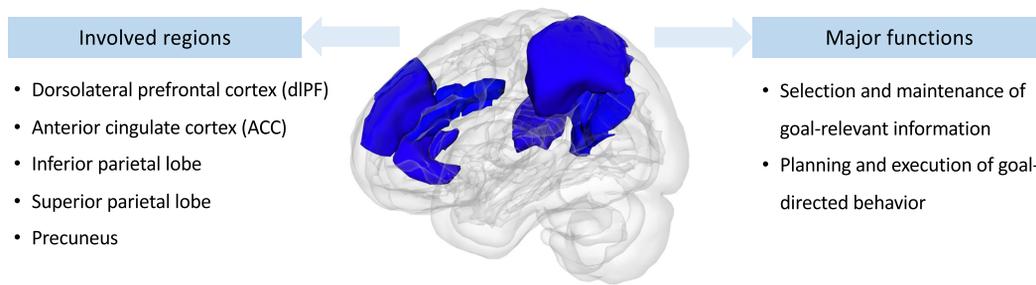
Involved regions

- Dorsolateral prefrontal cortex (dlPF)
- Anterior cingulate cortex (ACC)
- Inferior parietal lobe
- Superior parietal lobe
- Precuneus

Major functions

- Selection and maintenance of goal-relevant information
- Planning and execution of goal-directed behavior

FIGURE 14. Brain regions involved in and major functions of cognitive control, which is said to guide action. Figure produced with Scalable Brain Atlas Composer (www.incf.org).

or events that caused an outcome (430). Both processes underlie the generation and subsequent testing of a hypothesis, which assumes that a particular action will yield a particular outcome. Although actions are selected to allow the pursuit of an overall goal, such as becoming physically active to promote health, this process is not independent from associated costs, such as mental effort, discomfort, danger, and loss of opportunities (113).

3.1. Approach vs. Avoidance Motivation

Determinants of motivated behavior include the sensitivity to and experience of reward and punishment. These processes serve to stimulate approach or avoidance, meaning that behavior followed by a reward will become more frequent, whereas punishment decreases the likelihood of engaging in the antecedent behavior again (431). Different regions of the frontal cortex are involved in approach and avoidance behavior (**FIGURE 15**). The orbitofrontal cortex (OFC) is thought to estimate motivational value of a given stimulus by integrating contingency and value information (432). Its medial area is activated if a motivated behavior results in a reward, whereas the lateral part is recruited in the case that the anticipated reward is not received (433). Another structure involved in motivation is the ACC, which encodes the predicted motivational value associated with actions (434). The ACC influences how information on the current value impacts future actions (435). In addition to the recruitment of different structures, motivated behavior also causes laterality effects in the frontal cortex. That is, left hemispheric dominance is linked with both positively and negatively valenced approach motivation, whereas a greater activation of the right frontal cortex can be observed during avoidance motivation (436). Measures of frontal asymmetry have been applied in sport and exercise science, with left-sided dominance predicting both affective responses following exercise (437) and greater engagement in PA in the long term (438). Regions of the frontal cortex were also shown to interact with other structures of the brain, such as the nucleus

accumbens, to guide approach and avoidance, especially when the most beneficial or efficient course of action to pursue a goal remains unclear. In this type of situation, the core of the nucleus accumbens has the function to align approach behavior toward motivational stimuli while the shell inhibits behavior that is not relevant or rewarded to allow a more efficient pursuit of goals (439). The amygdala also shares a functional connectivity with the frontal cortex that seeks to engage attentional, executive, and motor circuits that are required for motivated behavior (440). In this network, the amygdala contributes to the storage of memories that link initially neutral stimuli with motivationally relevant outcomes via forms of conditioning (441).

The patterns of activation may vary based on the reward that motivates approach behavior. In this respect, wanting and liking are dissociable components of reward (431). As shown in sect. 2.7.2, the latter reflects a conscious experience of pleasure that will be pursued again. Liking is influenced by the OFC and nucleus accumbens (442). Stimulation of these hot spots may enhance the pleasure of liking and, therefore, facilitate approach behavior. In contrast, wanting resembles an incentive motivation that does not necessarily lead to a feeling of pleasure (443). It is linked to reward cues that trigger urges to direct behavior toward obtaining or consuming a reward without the feeling of pleasure (431). Neural systems that include dopaminergic projections to the PFC, nucleus accumbens, and amygdala mediate rewards that are wanted (444, 445). Because of the dependence of the wanting sensation on dopamine reactivity, states that increase this reactivity, such as stress and emotional arousal, also trigger a higher sensitivity to reward cues (446). There is accumulating evidence that dopamine expression following PA can promote long-term engagement, whereas lowered reactivity may have the opposite effect (447). In this respect, impaired dopamine signaling associated with obesity has been suggested to partly explain lower levels of (motivation for) PA (448).

The role of dopamine (as in wanting) in approach behavior has already been recognized by Gray (449),
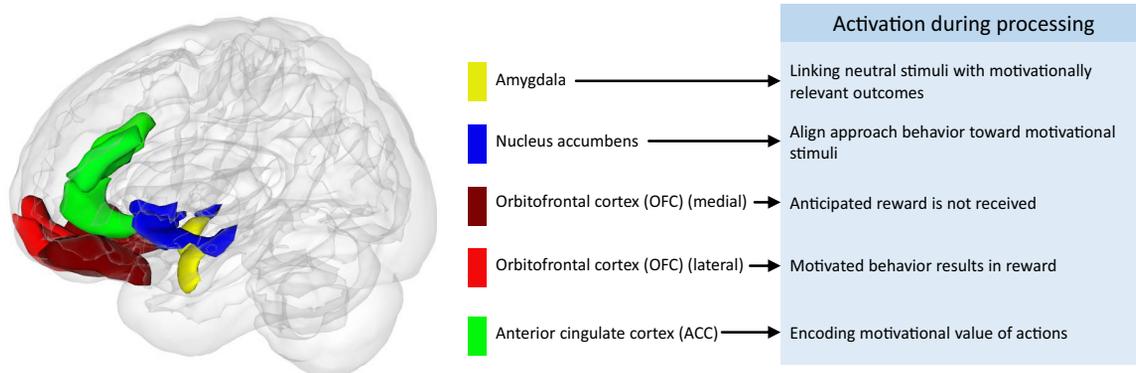
FIGURE 15. Brain regions involved in approach and avoidance motivation with corresponding types of activation during processing. Figure produced with Scalable Brain Atlas Composer (www.incf.org).

who proposed two neural systems for regulating the intensity of approach and avoidance behavior. More specifically, Gray suggested a behavioral activation system that responds to reward cues by facilitating approach behavior via dopaminergic signaling in the mesolimbic system. This component is opposed by a behavioral inhibition system that forms an inhibitory response to cues of threat and punishment due to the upregulation of noradrenergic and serotonergic activity in the septo-hippocampal system and the amygdala (450). In contrast to the behavioral inhibition system, the neural system underlying approach behavior has received more attention because of its relevance for the maintenance of a physically active lifestyle. However, in some cases, PA is perceived as a threat that needs to be overcome before this behavior can be experienced as rewarding (451–462).

3.2. Need vs. Incentive-Driven Motivation

In addition to the incentive value of a cue (e.g., wanting) or the outcome (e.g., liking), behavior may also be motivated by needs, such as physiological needs, safety, belonging, and esteem (463, 464). Needs from the physiological domain are expected to induce the strongest motivational drive to satisfy them, and examples are food, water, sleep, and rest (465). A high incentive value of a reward or its predictive cue can motivate behavior even when a need is satisfied (466). The capacity to perceive an incentive or potentially rewarding activity as pleasurable is described as motive, and two types are distinguished based on their processing scheme (467). Implicit ("nonconscious") motives are preferences for incentives that are based on affective experiences in early life and are therefore largely inaccessible to introspection, whereas the self-image and identification with values as well as goals reflect explicit ("conscious") motives (466, 468–470). Typically, individuals rely on explicit motives and goals when they are asked why

they engage in exercise and sport (e.g., body, appearance, contact, competition, performance, aesthetics, distraction, catharsis, fitness, health) (468, 470). These motives allow individuals to adapt the conscious regulation of motivational processes to changes in the environment by overriding the implicit motives that are formed early in life. As previous research has shown, exercise and sport activities are more likely to be maintained when individual motives and goals are met (247, 471).

The valuation of incentives is key to understanding behavior. Value indicates the quantification of a resource based on a cost-benefit analysis, the subjective desire or preference of one resource over another (113). In decision-making, processing information based on value complements information about the current world and past experiences stored in memory. It is proposed that deliberation between options, procedural action chains, and conditioned action-selection systems form the core systems of information processing in decision-making (472). Deliberation encompasses episodic future thinking as it describes the imagination and comparisons of future outcomes (473). The individual prefers and therefore values one choice over other options based on different representations of the future. With regard to health promotion, individuals contrast the value of PA with other behavioral interventions, and they consider whether the long-term gains of engaging in this type of behavior are higher than the losses associated with avoiding it (474). Along these lines, research has shown that when being physically active solely relates to good health, it is unlikely that individuals will chose PA over sedentary behavior (394). This evaluation process recruits the OFC (475) and further regions of the PFC that are suggested to play a role in approach behaviors (476). As deliberation requires both the maintenance and prediction of representations of the future, it requires intense processing (472). When a decision needs to be made within a short time, relying on this type of information processing may not be

optimal. For this scenario, the procedural system is more appropriate to identify the most appropriate or efficacious action by employing a combination of recognition processes and learned action chains (477). The recognition process includes the detection of parameters of a task to assess the most likely situation, and the associated reaction is referred to as willingness to pay (478). Applied to PA, the procedural system therefore asks if this behavior is the right choice at this moment, by considering the available resources or expected expenses. Meta-analytic findings indicate that such subjective values of choice recruit the ACC, different regions of the PFC, nucleus accumbens, and insula (479). Most of these regions also play a role in approach and avoidance, which is guided by conditioned action-selection systems (see sect. 3.1; **FIGURE 15**). The underlying valuation process of this system is influenced by the available reward as well as the need state of the individual and follows a hierarchy in conflicts (478).

3.3. Conscious and Nonconscious Aspects of Motivation

As highlighted in sect. 1, PA is important for learning and development in childhood. The necessity of PA dates back to the very beginning of our ancestry, as PA was necessary to search for food or shelter and avoid predators (392). As PA is no longer required for these purposes and has become an "optional" behavior, research on PA motivation has predominantly focused on the conscious rather than nonconscious aspects (249). Thus, as shown in sect. 2, commonly used psychological theories share that motivation is explained by rational processing and evaluation of information.

3.3.1. Conscious motivation.

3.3.1.1. CONSCIOUS MOTIVATION THROUGH SELF-REGULATORY SYSTEMS. Conscious behavior is controlled by orbitofrontal areas (**FIGURE 15**), such as the anterior ventromedial prefrontal cortex (avPFC), anterior cingulate, and lateral orbitofrontal and dorsolateral regions (480). These orbitofrontal areas operate through a deliberate "top-down" control process on decision-making, motor control, and perceptual control, which aligns behavior with reasoned attitudes and standards, necessitating significant self-control to inhibit automatic behavioral impulses (480, 481).

Self-regulatory systems operate through a network of cognitive control processes (e.g., FPN) supported by specific neural networks (482). Self-regulation includes the process of goal setting and striving to achieve these goals (483). Furthermore, self-monitoring and evaluative self-reflection, providing awareness and measurability of one's own behavior and its alignment with one's goals, are critical for effective self-regulation of health-related behaviors (482). As part of executive function, self-regulation is underpinned by various cognitive processes, such as attentional and inhibitory control, which are integral to managing and adapting one's behavior toward PA and reducing sedentary behavior (482).

Another domain of cognitive function that has emerged as a crucial dispositional construct for self-regulation is working memory capacity (481, 484). Individuals with higher working memory capacity are better equipped for goal-oriented processing and guarding their objectives from interference of automatic valuation processes (481). Consequently, reflective factors influencing health-related behavior are more predictive in those with greater working memory capacity, whereas automatic factors have a stronger predictive value in individuals with lower working memory capacity (481).

Apart from cognitive control mechanisms, self-regulatory processes include emotion regulation and self-associated control processes (485). Emotion regulation involves managing and responding to emotional experiences through acceptance, avoidance, cognitive reappraisal, and mindfulness. Self-associated control processes, involving strategies like self-affirmation and promoting self-efficacy, have a tremendous impact on goal selection and striving toward completion of selected goals (483, 485). These cognitive, emotional, and self-associated components of self-regulation are intricately connected, and their interaction plays a crucial role in effective goal pursuit and behavior change (486). Therefore, self-regulation has been identified as an effective target for interventions promoting health-related behavior changes (485, 486).

When deciding on initiating PA behavior, individuals engage in introspection and self-reflection on their PA-associated aspirations, goals, and action planning, activating the default mode network (DMN). The DMN includes many interconnected brain regions, such as the mPFC, the posterior cingulate cortex, the retrosplenial cortex, the medial and lateral temporal lobes, and the posterior interior parietal lobes (**FIGURE 16**) (482, 487). This network facilitates the internal recollection of personal preferences, beliefs, and feelings and enables introspective and adaptive mentation of goal-directed behavior (487). The activation of the DMN triggers internal mental processes aimed at overcoming self-regulatory barriers impeding PA behavior (482, 487). These processes are instrumental to the executive control of PA behavior and have been linked with increased functional connectivity within the DMN as well as between the DMN and the prefrontal networks (482, 488). Functional connectivity of
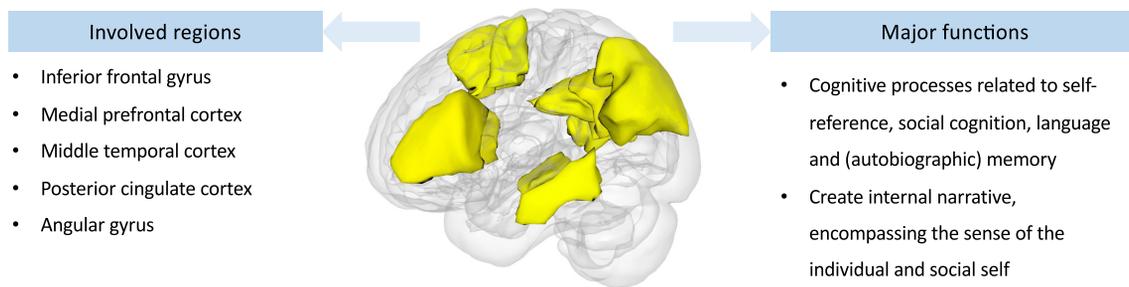
Involved regions	Major functions
• Inferior frontal gyrus • Medial prefrontal cortex • Middle temporal cortex • Posterior cingulate cortex • Angular gyrus	• Cognitive processes related to self-reference, social cognition, language and (autobiographic) memory • Create internal narrative, encompassing the sense of the individual and social self

FIGURE 16. Brain regions involved in and major function of the default mode network, which is said to guide self-reflection. Figure produced with Scalable Brain Atlas Composer (www.incf.org).

the DMN has demonstrated associations with aerobic fitness and memory capacity, related to exercise routine learning, indicating its relevance for PA regulation and adherence (482, 488, 489).

Converting PA goals into action necessitates the maintenance of focus on these goals, diverting attention from distractions, curbing competing impulses, and making strategic decisions on action planning. The self-regulatory processing involved in the executive control of PA behavior is implemented by prefrontal brain regions (482). The lateral prefrontal cortex (lPFC) is essential for response inhibition, flexible executive control, and behavior modulation, adapting to changing circumstances and managing the external and internal demands of physical activities. It formulates and implements complex, verbally represented goals and action plans while regulating the brain's reward-driven networks to shield these goals from reward-driven motivational impulses (467).

The goal-driven regulation of PA behavior requires distinct forms of cognitive control, which are facilitated by two key neural networks: the FPN (**FIGURE 14**) and the cingulo-opercular network (CON) (**FIGURE 17**). Whereas the FPN provides immediate adaptive control, prolonged goal-directed control is mediated through the CON (482, 490, 491). The FPN, comprising regions such as the dlPFC, inferior parietal cortex, dorsal precuneus, and middle cingulate cortex (MCC), enables rapid adjustment of cognitive control to align with fluctuating objectives or contexts. The dlPFC mediates

this rapid frontoparietal control mechanism, which operates through the integration, maintenance, and manipulation of goal-relevant information and attentional selection, shifting, and sustention. This control mechanism is crucial for adapting exercise strategies and maintaining focus on exercise goals amid distractions or fluctuating environments (467, 482). Empirical evidence has reported significant associations between dlPFC activation and successful adaptive self-regulatory control regarding health-related behaviors (492).

Complementary to this, the CON is pivotal for prolonged goal-oriented control and managing goal conflicts, providing the necessary cognitive support for long-term adherence and consistent regulation of PA behaviors (467, 482, 490). This network includes the anterior prefrontal cortex, vital for integrating self-regulatory processing into working memory and guiding attentional resources toward higher-order behavioral goals, to maintain focus on primary goals while managing subgoals (482, 493).

The ventrolateral prefrontal cortex (vlPFC) contributes to self-regulatory control through response selection and inhibition mediated by memory. This part of the CON operates through different regions specialized in retrieving knowledge from memory (left vlPFC) and exerting self-control, by suppressing routine or previously reinforced responses, facilitating the choice of delayed responses aligned with specific goals in conflict scenarios (right vlPFC) (482, 494). The occurrence of conflicting
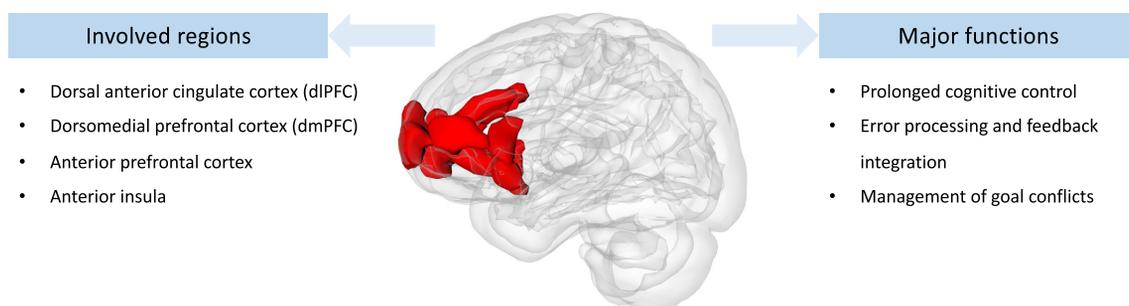

Involved regions	Major functions
• Dorsal anterior cingulate cortex (dlPFC) • Dorsomedial prefrontal cortex (dmPFC) • Anterior prefrontal cortex • Anterior insula	• Prolonged cognitive control • Error processing and feedback integration • Management of goal conflicts

FIGURE 17. Brain regions involved in and major functions of the cingulo-opercular network, which is one of the main networks facilitating cognitive control through goal-directed behavior. Figure produced with Scalable Brain Atlas Composer (www.incf.org).

goal-oriented representations and the initiated behavioral response activates additional regions, such as the dorsal ACC (dACC) and the OFC. The dACC plays a central role in managing conflicts among response options and behaviors requiring adjustment of self-regulatory control. By tightly operating with both cortical and subcortical regions, including the recruitment of the dlPFC, it engages in cognitive and emotional processing and error monitoring to address and resolve these goal-associated behavioral conflicts (482). The OFC serves as a connection hub between affective information and symbolic processing, linking prefrontal and subcortical regions. It plays a crucial role in assessing the motivational and emotional importance of information, guiding long-term decision-making and the evaluation of behavioral consequences (482, 493).

The degree of functional connectivity within the dlPFC, inferior frontal gyrus (IFG), and vmPFC network likely correlates with PA levels, where reduced activity in prefrontal cognitive control regions can tilt the balance toward subcortical reward systems, favoring immediate gratification and impulsive actions, potentially resulting in self-regulation failures and increased sedentary behavior driven by a heightened sensitivity to the rewards of inactivity (482, 495, 496).

3.3.1.2. THE RECIPROCAL RELATIONSHIP BETWEEN PA AND COGNITIVE CONTROL.
Research has consistently demonstrated the positive impact of PA on cognitive function (93, 94, 497–506) as well the positive effect of cognitive function on PA (507–519). Importantly, these associations are supported by underlying mechanistic explanations. First, several neurobiological mechanisms [e.g., brain-derived neurotrophic factor (BDNF), vascular endothelial growth factor (VEGF), or insulin-like growth factor-1 (IGF-1)] have been identified for the effect of PA on cognitive function. Additionally, structural changes such as modifications in white and gray matter volume and integrity, increased connectivity, synaptogenesis, neurogenesis, and angiogenesis and functional changes like improvements in neurovascular activity have been identified (520–525). Second, cognitive function is considered necessary to overcome the innate human tendency to minimize effort (see sect. 2.7.3) and promote engagement in PA (378). Furthermore, the effect of cognitive function on PA suggests a central role for higher executive function, as described above, in bridging the so-called intention-behavior gap (526–529). Examining specific self-control mechanisms, one study found that individuals with a lower ability to resist sedentary opportunities did not significantly translate conscious intentions into subsequent PA behaviors. Conversely, individuals with a higher ability to resist sedentary opportunities were more likely to act in accordance

with their intentions (393). Additionally, other neuropsychological studies have shown that resisting sedentary opportunities requires additional neural resources (390, 391, 507, 530). These findings are consistent with the temporal self-regulation theory (531), which emphasizes the role of executive functions in counteracting the behavioral prepotency (which may represent the automatic drive toward sedentary behaviors). As a result, individuals with stronger executive functions tend to have better PA adherence (500, 512, 516, 519, 526).

3.3.2. Nonconscious motivation.

Although positive affective experiences, e.g., the feeling of pleasure and happiness, can be an expected outcome, nonconscious affective qualities and judgments are underrepresented in expectancy-outcome theories (532). This is particularly unfortunate because meta-analytical findings indicate an association between exercise-induced positive affect and increased PA levels (533, 534). Today, PA studies often employ dual-process frameworks and so simultaneously test both conscious and nonconscious processes in predicting behavior (474, 535, 536). In the following, we address affective reactions and automatic valuations as key parts of nonconscious motivation.

3.3.2.1. AFFECTIVE REACTIONS TO EXERCISE.
For decades, exercise was thought to generate arousal, ignoring the possibility of eliciting valenced affect, but this changed when subjective measures tapping into mood, feelings, and emotions accompanied arousal assessments (537). The distinction between acute affective responses and experiences, which form affective valuations from repeated engagement in exercise, is important given that outcomes may vary based on the time point of assessment. The acute response refers to transient changes elicited during exercise and post exercise.

In early studies investigating affect-paired measures of arousal with subjective ratings of mood or feelings, intensity received much attention as it is regarded a primary moderator of exercise-induced arousal (538). Low-to-moderate exercise intensity is suggested to elicit positive affect, whereas severe intensity is thought to result in negative affect across individuals. This homogeneous response at low to moderate intensity has been explained by a negligible influence of cognitive and interoceptive factors on affect. Limited interindividual differences are also assumed to be observable at severe intensity because of a major impact of interoceptive factors, such as sensations linked with muscular and respiratory exhaustion, on affect. In contrast, exercise at the lactate/ventilatory threshold can induce

positive or negative affect based on cognitions that rely on the frontal cortex, such as individual motivation, goals, or self-efficacy (**FIGURE 18**) (539). Because of this link, the limited number of studies that investigated mechanisms underlying exercise-induced affect focused on the frontal cortex and the relative activations of both hemispheres specifically. Experimental findings found that a frontal asymmetry at rest, which indicates a left-lateralized dominance, might be indicative of approach behavior during exercise due to its association with lower arousal (437) and greater positive affect (540). This relation has also been observed post exercise, suggesting that a dominance of the left frontal cortex over the right predicts a higher affect responsivity (541). During exercise, cerebral oxygenation (a proxy of brain activity) in both the left and right frontal cortex seems to increase with intensity, and once the respiratory compensation point has been surpassed, the increase is inversely correlated with affective responses (542). This might reflect the contribution of cognition to affective judgments and the inability to override sensations of effort at severe intensity. On a behavioral level, meta-analytical findings support that exercise at moderate intensity induces greater positive affective responses than high-intensity interval exercise, whereas no such difference was detected for continuous high-intensity exercise (543, 544). The affective response during moderately intense exercise has been found to be predictive of future PA and the affective judgment of such activities (534, 545–547). In contrast to the effects of a single exercise session on affect, intensity seems to have less influence on the effects produced by long-term exercise. For aerobic exercise interventions in particular, participation in low-intensity exercise three to five times per week over a period of several weeks produced greater positive affect

than every other constellation, but exercise intensity, frequency, and dose parameters showed only weak moderating effects (548).

The interplay of cognitions and perceived effort that shape affective responses to exercise at moderate intensity underlines the role of interindividual differences. For example, individuals with obesity tend to report lower positive affect during exercise than normal-weight counterparts, which has been attributed to greater social physique anxiety (549). Similarly, lower PA levels in combination with high perceived exertion have been linked with a more negative affective response to exercise, probably due to a lower capability to cope with interoceptive cues arising with symptoms of fatigue (550). The satisfaction of psychological needs seems to have a more general moderating role, because it determines how affective responses predict motivation (547).

3.3.2.2. AUTOMATIC VALUATIONS. Automatic influences operate according to associative, affective representations, which mediate between stimulus input and motor schemas of approach or avoidance by engaging areas involved in reward processing and emotional responses such as the amygdala and ventral striatum (480, 481). Memory functions as a network of associated concepts, activating behavioral influences through the elicitation of urges to approach or avoid circumstances depending on whether the stimulus leads to a positive or negative change in core affect (369).

Associative learning occurs when individuals repeatedly encounter certain health-related behaviors in contexts that elicit specific affective responses (369). Results indicate that stronger positive automatic affective valuations toward health-related behaviors result in higher tendencies to engage in these particular
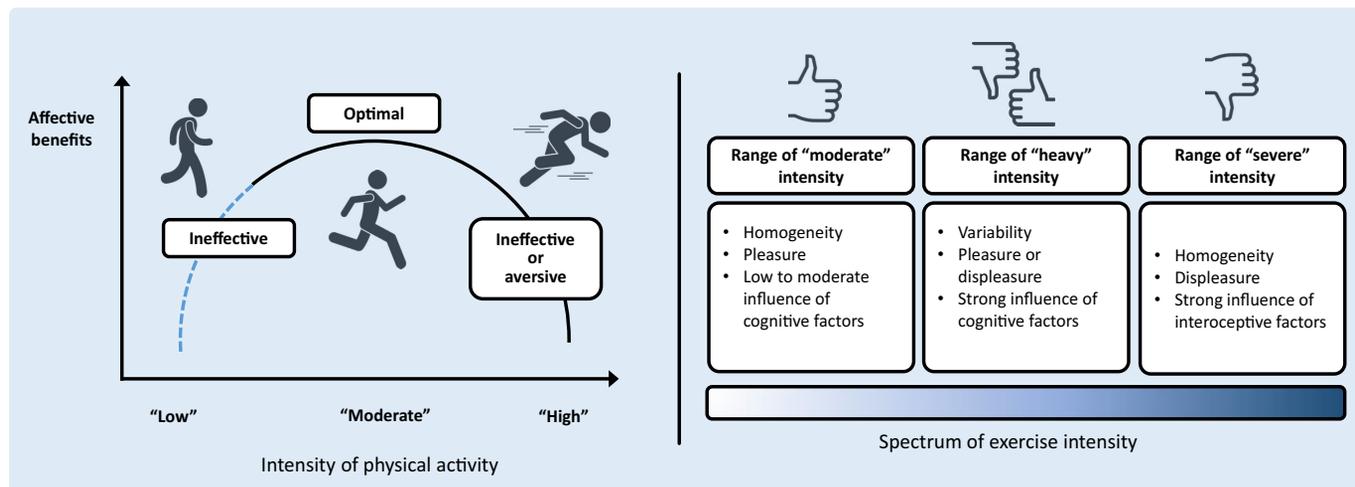

FIGURE 18. The affective benefits of physical activity based on the intensity of physical activity. Low-intensity physical activity tends to have no affective effect, whereas moderate-intensity physical activity tends to have an optimal, pleasurable effect and high-intensity physical activity tends to lead to aversive, unpleasant effects. Adapted from Ekkekakis (539). Used with permission.

behaviors (481). With regard to PA, empirical evidence shows higher tendencies to engage in physically active behavior for individuals with positive automatic valuations toward PA compared to individuals with negative automatic valuations (369, 551, 552). Positive automatic valuations have been demonstrated to be a good discriminating factor predicting adherence to PA programs and are a promising target for enhancement and maintenance of PA behavior (553). In experimental studies, automatic valuations of exercise were altered with evaluative conditioning, leading to higher positive automatic valuations toward PA, which subsequently were associated with increases in PA behavior (554, 555). In addition, previous studies have explored the malleability of automatic valuations as a consequence of PA behavior, as well as potential moderators of automatic valuations toward PA (556). Within a short time period of 1 wk, individuals who initially demonstrated unfavorable automatic valuations showed greater increases in self-reported PA if automatic valuations had become more favorable, compared with individuals whose unfavorable automatic valuations remained unchanged (556).

A study examining the moderating role of trait impulsivity has reported that the interaction between reflective PA intentions and automatic valuations toward sedentary behaviors predicted MVPA, especially in individuals with higher trait impulsivity (557). Furthermore, a prospective study examining potential moderating roles of trait impulsivity and core cognitive functions on implicit attitudes toward sedentary behavior and PA among participants with obesity found significant interaction effects of executive functions (558). In participants with low and moderate executive function performance, more favorable implicit attitudes toward sedentary behavior resulted in significantly lower PA engagement after 4 mo compared to peers with higher executive function (558). These results suggest involvement of attentional and cognitive processing within automatic valuation of PA behavior (558).

In line with this, empirical evidence has reported differences in automatic attentional processing regarding stimuli related to PA (551, 559, 560). Whereas individuals who engage in PA regularly showed an attention bias toward exercise-related stimuli (551, 560), physically inactive individuals showed an attentional bias toward sedentary lifestyle-related stimuli (559). The relationship between attentional bias and PA is dependent on the strength of affective valuation; thus, attentional bias toward exercise is more strongly associated with PA behavior among those with positive affective attitudes toward exercise (560). Moreover, the association between attentional bias and preceding PA was moderated by reflective attitudes (560). These results confirm that automatic affective valuations and associated attentional biases

toward PA stimuli account for variation in PA behavior beyond what is explained by reflective cognitive processes, and therefore automatic valuations might be a promising target for researchers and clinicians aiming at the promotion of PA behavior (369, 553).

4. LINK BETWEEN NEUROSCIENCE AND PSYCHOLOGICAL THEORIES OF BEHAVIOR CHANGE

Empirical evidence on the integration of classical psychological motivation theories (sect. 2) with findings of underlying neuroscientific mechanisms (sect. 3) is still in an early developmental phase. A key reason for this lies in the divergent evolution and the historical separation of the two fields of psychology and neuroscience. Whereas the empirical discipline of psychology dates back to the late nineteenth century, neuroscience constitutes a relatively young field of research (358, 416). Because of technological and methodological advances in recent years, neuroscientific research has gained significant momentum and increasingly differentiated itself thematically as a discipline aligned with natural sciences, further distancing itself from the humanities-oriented field of psychology (415, 416). This separation has resulted in a lack of integration of newly discovered neuroscientific knowledge into the established and evolving psychological theories of motivation of health-related behaviors. This circumstance seems somewhat surprising, as psychological and neurophysiological processes within health-related behaviors are highly interconnected and often exhibit a reciprocal relationship, as seen for the associations between cognitive control and PA. This challenge has been tackled by increased interdisciplinary efforts of the emerging field of health neuroscience in recent years (415). In this explorative section, we display possible links between psychological models of behavior change and neuroscientific findings by showing how shared cognitive processes might be intertwined with and influenced by underlying neural networks (**TABLE 2**).

4.1. Cognitive Evaluation and Decision-Making

Classical psychological theories of motivation collectively involve cognitive evaluation and decision-making processes while focusing on different aspects of these evaluations and their influence on decision-making. Evaluations are formed by the reflective consideration of existing attitudes in the context of new information regarding the stimulus, the situational context, and current outcome objectives (565). For instance, whereas TPB emphasizes the role of attitudes in the formation of intentions, SCT

Table 2. *Links between psychological theories and cognitive processes*

Theory	Psychological Concept	Cognitive Processes
Self-determination theory (267, 561)	Psychological needs - Autonomy - Competence	- Need fulfillment
	- Relatedness	- Social cognition - Emotional processing - Reward processing
	Extrinsic motivation - External regulation - Introjected regulation - Identified regulation - Integrated regulation	- Reward processing - Action inhibition
	Intrinsic motivation - Intrinsic regulation	- Reward processing - Action inhibition
Health belief model (283, 284)	Perceived susceptibility	- Risk assessment - Personalization risk
	Perceived severity	- Cognitive evaluation of potential outcomes
	Perceived benefits	- Reward processing
	Perceived barriers	- Reward processing - Risk assessment
	Self-efficacy	- Inhibit immediate impulses - Delay gratification - Focus on long-term objectives
	Cues to action	- Responsiveness to external triggers
Social cognitive theory (562, 563)	Outcome expectations	- Weighing the pros and cons - Assessing emotional and reward-related aspects of anticipated outcomes
	Goal setting (proximal, distal)	- Self-regulation - Executive control
	Self-efficacy	- Self-regulation - Executive control - Motor control
	Environment including sociostructural factors	- Observational learning - Cognitive flexibility - Imitation - Modeling - Attention - Memory
Theory of planned behavior (300)	Intentions	- Outcome anticipation - Emotion processing
	Attitudes	- Perception of social and subjective pressure to perform or avoid a behavior
	Subjective/social norms	- Social and conformity processes
	Perceived behavioral control	- Inhibitory control
Transtheoretical model of behavior change (336, 564)	1. Precontemplation	- Processes before risk and benefit evaluation
	2. Contemplation	- Risk and benefit evaluation - Weighing emotional and rational aspects of behavior change
	3. Preparation	- Goal setting and planning reliant on executive functions - Affective valuation - Outcome anticipation - Risk assessment - Motivational analysis
	4. Action	- Self-regulation - Executive control - Motor control

Continued

Table 2.—Continued

Theory	Psychological Concept	Cognitive Processes
	5. Maintenance	- Self-regulation - Executive control - Observational learning - Social cognition - Emotional processing
	6. Termination	- Final evaluation and processing
Health action process approach (346)	Motivational processes - Action self-efficacy - Risk perception - Outcome expectancies - Intentions (goal setting)	- Inhibit immediate impulses - Delay gratification - Focus on long-term objectives - Risk and benefit evaluation
	Volitional processes - Action planning - Coping planning - Coping self-efficacy - Recovery self-efficacy	- Self-regulation - Executive control - Overcoming barriers

focuses on self-efficacy and outcome expectations, and SDT involves the elements of intrinsic motivation and psychosocial need satisfaction. The HBM places these aspects in the context of health-related behaviors by focusing on perceived susceptibility, severity, as well as anticipated barriers and benefits of action. Finally, the TTM and HAPA introduce a temporal dimension.

Neuroscientifically, the valenced valuation in the TPB is linked to emotion processing and outcome anticipation primarily controlled within the limbic system and PFC (482, 493, 565). These neural mechanisms play a crucial role in evaluating action outcomes and deciding on behavioral engagement.

In SCT, the evaluation of outcome expectancies, deeply embedded in the process of decision-making, is likely to involve the same brain regions, including the PFC, which is responsible for weighing the pros and cons of different behavioral options according to their expected outcomes, and the limbic system, which is involved in assessing emotional and reward-related aspects of anticipated outcomes (482, 493, 565). Functional neuroimaging studies have shown that the anticipation of positive outcomes (such as achieving a goal) can activate the same neural circuits as those activated by the rewards themselves, thereby reinforcing behavior that is expected to result in a desirable outcome (566).

The SDT differentiates two different types of sources of reward: intrinsic and extrinsic motivation (270). This is particularly interesting, as neuroscientific studies have reported different neural networks associated in reward processing resulting from intrinsically and extrinsically motivated behavior (567). Intrinsic motivation is suggested to be closely tied to the dopaminergic reward systems in the midbrain and medial frontal cortex (MFC), involving both the anterior insular cortex (AIC) and the striatum (567, 568). Different experimental studies have

underlined the role of dopamine neurons' tonic and phasic activities in intrinsic exploratory behavior, associated with positive affect, cognitive flexibility, creativity, and behavioral persistence (567, 569). Additionally, neuroimaging studies have indicated a direct relationship between intrinsic motivation and dopamine D2 receptor availability in the putamen region of the striatum in individuals more inclined toward intrinsically motivated behavior (567, 570). Interestingly, studies have shown that initially intrinsically motivated behavior decreases as an external reward is introduced, indicating a change in cognitive evaluation through the integration of the external reward into the intrinsic value of the behavior (567). Additionally, these changes in behavior were accompanied by changes in activation of the corticobasal ganglia valuation system, with decreased activity in the anterior striatum and the prefrontal areas (567, 571).

The commonality of TPB, SCT, and SDT can be attributed to processes of cognitive evaluation and subsequent decision-making, which has been associated with specific functional neural networks: In the initial phase of a stimulus encounter, the thalamus processes the stimulus by dissection of perceptual information, which is then forwarded to limbic structures, activating the dopaminergic reward system, including midbrain areas, MFC regions, and the amygdala, for affective valuation (565, 567). Next, the extensive network emanating from the limbic system guides subsequent processing of valenced stimulus information in higher-order prefrontal regions associated with sensory perception and attention, such as the OFC and the ACC. The ACC is integral in resolving conflicts among response options and behaviors that necessitate adjustments in self-regulation. It collaborates closely with both cortical and subcortical areas, including the dlPFC, to

engage in cognitive and emotional processing as well as error monitoring, thereby addressing goal-related behavioral conflicts (482). Meanwhile, the OFC acts as a pivotal link between affective information and symbolic processing, connecting prefrontal and subcortical regions, and plays a role in affective processing, including the representation of rewards and forecasting the emotional consequences of actions (482, 493, 565). It is vital in determining the motivational and emotional significance of information, thereby influencing long-term decision-making and the future evaluation of behavioral outcomes (482, 493).

In the HBM, the components perceived susceptibility, perceived severity, and benefits to take action share the cognitive process of cognitive evaluation, decision-making, as well as risk perception and can be tied to different elements of other theories discussed above. Perceived susceptibility involves cognitive processes related to risk assessment and personalization of risk. Neuroscientifically, this component is likely to be linked to the function of the PFC, which is involved in assessing risk and future planning, and the insula, which is related to introspective awareness and emotional response to risk (572). The perceived severity involves the cognitive evaluation of potential outcomes and their impact on an individual. This component can be tied to the element of outcome expectations discussed for SCT, involving the PFC, weighing the pros and cons of different behavioral options, and the limbic system, involved in the assessment of emotional and reward-related aspects of anticipated outcomes (482, 493, 565). Finally, the component of benefits to take action requires the integration of information about potential benefits and the likelihood of those benefits being realized. This element can be tied to the processing of reward discussed above for SDT, including the dopaminergic reward systems in the midbrain and MFC, particularly the AIC and the striatum for intrinsic motivation, whereas extrinsic motivation relates to changes in the corticobasal ganglia valuation system, affecting the anterior striatum and prefrontal areas (567).

A study examining the neurocognitive correlates of health risk perception with fMRI reported higher brain activation in the medical frontal cortex, including the ACC and dorsomedial prefrontal cortex (dmPFC), as well as the parietal cortex and the insula and thalamus, during processing of health risks (572). In line with this, prior studies indicated the dlPFC, ACC, dmPFC, and the parietal cortex to be key areas activated during risk processing activities (573, 574). In a study investigating the prediction of health behavior change, specifically smoking reduction, different subregions of the mPFC were linked to various cognitive processes associated with risk processing (575). One mPFC subregion, known for predicting behavior change, was involved in self-related processing, while another was associated with valuation. These mPFC areas were predictive of behavior change in smoking habits within this study. Additionally, increased activity in the parahippocampal gyrus, related to memory and future behavior imagination, was also linked to behavior change. The study highlights the role of mPFC in integrating self-referential thinking, valuation, memory, and prospection, key elements of the DMN, in the context of health behavior change (575). It is to be noted that to date fMRI studies are predominantly correlational, as such causal implications regarding involved brain regions identified in the different mechanisms cannot be determined.

Interestingly, the constructs of the HBM are treated as distinct independent variables that collectively contribute to behavior prediction because of the absence of a formal proposal for their operationalization or combination rules. Moreover, the severity of a condition is conceptualized based on various expected outcomes, with perceived benefits linked to the prevention of these outcomes, whereas barriers are specific to each behavior (281). However, a study investigating how the brain processes risk decisions involving physical harm identified distinct brain regions that are sensitive to different aspects of risk assessment, indicating component interaction (576). The qualitative characteristics of risk, such as harm severity, activated regions including the bed nucleus of the stria terminalis, frontal cortices, and language-processing areas. Quantitative aspects like risk likelihood engaged a broad network of frontal regions and the ventral striatum (576).

4.2. Self-Regulation and Executive Control

Apart from cognitive evaluation processes, psychological theories of motivation collectively involve entities for self-regulatory processes on planned behavior employing executive control. Self-regulatory processing is highly associated with neurocognitive executive functioning predominantly located in the PFC (577). Recent research underscores the central role of the right inferior frontal cortex in self-regulation, detailing its diverse subregions, connectivity to key areas like the presupplementary motor area and subthalamic nucleus for response inhibition, and its involvement in reward-based decision-making and cognitive control (578–580). Further studies have shown how reward influences brain activity, particularly in the dlPFC and frontopolar regions, enhancing cognitive task performance and suggesting alterations in cognitive control strategies motivated by reward (578).

When considering self-regulation of goal-oriented behavior, it is important to distinguish between goal intentions and implementation intentions (581–587). Goal intentions refer to desired end states that an individual aspires to achieve by transforming these desires into binding objectives (588). Implementation intentions facilitate the attainment of these goals by detailing the specific circumstances and methods for initiating goal-oriented actions. Implementation intentions establish a mental association between a particular cue or situation and the corresponding goal-driven response, committing the individual to executing this response upon encountering the specified situation (589). Previous evidence indicated that defining specific cues and situations for initiation of goal-oriented actions resulted in higher rates of goal achievement than merely establishing goal intentions (349, 584, 590–594). Additionally, implementation intentions not only facilitate goal pursuit but also offer a protective defense against adverse internal states, such as disruptive thoughts or negative emotions (589, 595). The formation of an implementation intention protects goal achievement through key psychological processes: First, it increases the mental prominence of the chosen cue, making it more accessible and easier to recognize in relevant situations, even during other tasks, thus facilitating its recall. Second, the effectiveness of implementation intentions lies in the automatic initiation of the preplanned response; upon encountering the critical cue, the corresponding action is executed immediately and efficiently, without the need for further conscious deliberation (589, 596).

Whereas in the TPB an intention is the necessary precursor for behavior, its implementation into action is also dependent on behavioral control. Neuroscientific research has demonstrated that intention formation and resulting goal-directed behavior are associated with mPFC areas, as elaborated in sect. 3. The formation of intentions and the execution of intentional behavior include different decision-making processes based on when, what, and whether components (597, 598). These components of intentional action are associated with the activation of specific fronto-medial cortex areas, which have been identified in numerous neuroscientific experiments examining inhibition (597–600). Hereby, the "whether" component, which can be referred to as the response control component that determines whether an individual should execute an action, has been identified as the inhibitory control mechanism and has been shown to correlate with increased dorsal MFC activation (600). As highlighted in sect. 3, the specific activation of the dorsal MFC suggests that the intentional control of action involves a mechanism capable of inhibiting planned behavior, which might play a crucial role in self-control (597,

598). Similarly, in the TEMPA, the role of self-control is to inhibit the impulses toward sedentary behavior. As such, studies showed that avoiding or refraining from approaching sedentary behaviors was associated with increased response inhibition, as reflected by amplified evoked event-related potentials in the frontocentral cortex (391, 530). These findings not only suggest that low-effort behaviors have an intrinsically attractive value but also underscore the central role of cognitive functions in counteracting the innate tendency to minimizing effort and, consequently, in promoting engagement in PA (507, 509–511, 514).

For behaviors to persist over time, they necessitate reinforcement both from the environment as well as from the individual's own self-regulatory efforts (601). SCT posits that modification of behavior stems from alterations in self-regulation (519). Levels of self-efficacy have been associated with the ability to implement self-regulatory strategies associated with executive functions (602). Although neural underpinning of executive functions has been established in previous studies (603), the evidence on underlying neural regions and networks for self-efficacy still remains limited. A fMRI study investigating neural correlates of general self-efficacy in young adults reported reduced mean diffusivity (MD) values in the lenticular nucleus, encompassing both the putamen and globus pallidum, suggesting higher integrity and connectivity in neural structures employed in motor control and executive functioning for highly self-efficient individuals (604). The concept of self-efficacy is recognized as one of the most reliable predictors of a variety of health behaviors (291), notably including the engagement in PA (519). A study examining the mediating role of self-efficacy in executive functions and sustained PA behavior reported that executive functions correlated with increased exercise self-efficacy, which in turn predicted improved adherence to a long-term exercise regime. Essentially, individuals adept at self-regulatory processing and executive control demonstrated higher self-efficacy leading to increased behavioral adherence (519). An event-related potential (ERP) study focusing on how self-efficacy influences inhibitory control found larger N2 amplitudes in individuals with higher self-efficacy, indicating an enhanced ability to detect conflicts. However, self-efficacy did not significantly affect P3 amplitudes, suggesting that it does not influence the actual inhibition of responses once a conflict is detected. These results underline the role of self-efficacy in improving conflict detection and cognitive performance, particularly in tasks requiring attention and executive control, but not necessarily in the inhibition of the actions (602).

The HBM and HAPA also tie in with the concept of self-efficacy, emphasizing the pivotal role of self-

regulation and executive control in overcoming perceived barriers to health behaviors (281). These barriers encompassing both practical and psychological obstacles necessitate the ability to inhibit immediate impulses, delay gratification, and focus on long-term objectives. Key brain regions like the ACC and dlPFC play crucial roles in this process (605). The activity in these areas is indicative of the cognitive efforts involved in assessing and surmounting these perceived barriers. Ultimately, individuals' self-efficacy is central to their capability to self-regulate and maintain executive control, particularly when faced with challenging situations or barriers to overcome (281, 605).

According to SDT, the strive to satisfy basic psychological needs plays a critical role in cognitive processing and decision-making (267, 561, 606). Specifically, the satisfaction of autonomy and competence needs may be representative of self-regulation and executive control, as individuals acting autonomously are self-regulating their behavior in alignment with their personal values and interests and adjusting behavior to be aligned with their competences. The basic need of competence reflects the drive to effectively engage and interact with one's surroundings. It encompasses the aspiration to enhance and apply abilities. The satisfaction of this need involves actively seeking and facing challenges, exerting effort and strategic thought, and ultimately achieving development through learning experiences (569). Again, the effective use of strategies as well as adjusting learning and behavior requires self-regulatory processing and executive control, which may be at the core of need fulfillment (567, 607). Empirical studies examining the neural correlates of need satisfaction have reported higher levels of activation in the striatum and bilateral AIC and the interaction of these two areas during cognitive tasks that were competence satisfying (568). Reeve and Lee (607) suggested that these results represent the integration of perceived competence with reward-related information associated with the satisfaction of the basic need of competence. Studies investigating underlying neural areas associated with satisfaction of autonomy have reported the recruitment of reward-related areas, such as the midbrain and striatum, as well as areas associated with self-regulatory processing, such as the anterior insula (607). Additionally, studies have reported increased activation in the ACC as well as the amygdala and decreased activation in the vmPFC in tasks providing satisfaction of autonomy (608, 609). Decreases of vmPFC activation during satisfaction of autonomy are moreover suggested to be associated with enhancement of performance (609). In a study where participants engaged in a learning task, higher levels of perceived autonomy were linked to significant AIC activations. Furthermore, increased autonomy satisfaction was associated with greater striatum activations, and better recall performance correlated with enhanced dlPFC activations. These findings suggest that the AIC-striatum network is crucial for intrinsic motivation, whereas the AIC and dlPFC connection is vital for cognitive engagement and learning (607, 609).

A study investigating need satisfaction as a trait and self-regulatory processing during decision-making tasks reported higher activation of the ACC and mPFC, especially during resolution of self-related conflicts. These results indicate that individuals with higher overall need satisfaction exhibited increased neural activity in these areas, suggesting a correlation with task performance (610). Additionally, a study examining the basic need of autonomy as a motivational trait reported greater activation of the ACC in error detection during task performance. It is suggested that individuals who perceive situations with a greater sense of autonomy are likely to perform tasks more effectively because of enhanced self-regulation, particularly through improved monitoring processes (607, 611).

In line with results regarding cognitive evaluation of intrinsically and extrinsically motivated behavior, a recent study investigating the difference of internally versus externally controlled action inhibition as a function of executive control in the left dorsal MFC and the right inferior frontal cortex found differentiating results for inhibiting actions triggered externally (exogenous) and internally (endogenous). Functional MRI findings indicated that the dorsal MFC, linked yet distinct from the presupplementary motor area, was more active in scenarios where subjects chose to inhibit actions themselves, leading to its designation as the executive control entity. In contrast, the right inferior frontal cortex was found to be more involved in externally prompted action inhibition. The results, particularly from repetitive transcranial magnetic stimulation (rTMS) over the left dorsal MFC, reinforced the idea of distinct neural circuits for exogenous and endogenous action inhibition, demonstrating the crucial role of the left dorsal MFC in internally driven executive control (600). These results consolidate the assumption that there are crucial differences in neural correlates of intrinsic and extrinsic behavior and that there are social and environmental factors involved.

4.3. Social and Environmental Factors

SCT affirms two key premises from social learning theory (292). First, individuals acquire knowledge through observing the behaviors of others, and second, these behaviors are typically learned within social environments. The SCT asserts the profound impact of observational learning, imitation, and modeling on shaping behavior. It contends that the development of new behaviors and skills arises not

just from personal experiences but also from observing the behavior of others and their consequences (601). Observational learning fundamentally consists of the deduction of the intentions of others by observing their actions and the evaluation of the results of these actions. By synthesizing this information, individuals learn the associations between stimulus, response, and outcome (S-R-O), which are later employed to achieve favorable outcomes (612).

Neuroscientifically, the ability of observational learning is supported by the discovery of mirror neurons, which are suggested to enable an intuition for others' emotions and intentions through an automatic simulation of their motor state in the individual's own mirror neurons, as proposed in the theory of embodied simulation (613, 614). The neural mirroring facilitates the understanding and imitation of behaviors, providing a neurobiological basis for social cognitive processing (614). Studies examining the neural correlates of observational learning have identified the lPFC, particularly the dlPFC and vlPFC, as crucial for cognitive flexibility in order for individuals to rapidly learn rules by observing the actions of others and their outcomes. This form of learning, distinct from instruction-based learning, requires cognitive flexibility to adapt actions based on observed outcomes. It is hypothesized that observational learning might activate posterior parts of the lPFC, with a shift in activation patterns anticipated during practice (612). Additionally, observational learning shares neural networks with trial-and-error learning during rule acquisition and application but also engages additional networks: the dorsal frontoparietal, the fronto-striatal, and the cerebellar networks (615). These systems are instrumental in forming a task model that connects rule and response. The dorsal frontoparietal network (**FIGURE 14**) plays a key role in sensorimotor transformation and goal-directed attention, the fronto-striatal networks are vital for goal-directed operations and enhancing cognitive flexibility, and the cerebellar network contributes to the processing of early-stage outcomes and the acquisition of new motor patterns (612, 615).

During the retrieval of rules acquired via observation, activation occurs in several brain areas, notably the right pars triangularis, the right inferior parietal lobule, and areas in the posterior visual cortex (612, 616). Activations in the pars triangularis and posterior visual regions are associated with inhibiting action execution during observation and motor imagery as well as with top-down control of visual cortex functions. Furthermore, during observational learning, particularly when processing incorrect outcomes, notable activation is seen in the middle cingulate cortex, posterior medial frontal cortex, anterior insula, and posterior superior temporal sulcus, which are key regions for error monitoring and processing social information (612, 615, 616). In addition to observational learning, the

SCT emphasizes the concept of reciprocal determinism, which posits a bidirectional influence between individual characteristics (such as self-efficacy and behavioral executive control) and environmental aspects (like enabling conditions). This highlights a mutual interaction between personal and environmental factors (601, 617).

Beyond observational learning, the concept of cues to action highlighted in the HBM acknowledges the impact of broader external social and environmental factors on an individual's health behavior decisions and behavioral control. It encompasses the influence of social networks, cultural norms, and physical environments on health-related beliefs and resulting behavioral actions (281). In line with this notion, evidence has been reported of the link between health beliefs and sociodemographic factors like socioeconomic status, sex, ethnicity, and age. It is suggested that modifying health beliefs can lessen the impact of these sociodemographic factors on health behaviors, potentially reducing health inequalities, as health beliefs mediate the connection between sociodemographic variables and health actions (281, 618). Additionally, empirical studies revealed a direct association between individuals' likelihood of being influenced by social peers and their perceived risk of extrinsic morbidity (environmentally induced diseases), a finding consistent across online and laboratory environments (619). This link is neurologically grounded, as EEG activities demonstrated a significant association with the degree of perceived risk and an increased responsiveness to public information, indicating that environmental risks may adjust neural processes that govern susceptibility to social influence (619).

Normative attitudes, featured in the TPB, result from perceived social and subjective pressure to perform or avoid a specific behavior (299). Social norms are the unwritten rules that govern acceptable behavior within a society or group, shaping individuals' actions and interactions based on shared beliefs and expectations (620). Social norms influence behavior through social and conformity processes, which can be understood through the neural mechanisms underlying social cognition and observational learning (621). An extensive meta-analysis of fMRI studies by Zinchenko and Arsalidou (621) identified specific brain regions associated with representation of and compliance with social norms. The most significant brain activity was observed in the right insula and the left medial frontal gyrus, extending to the cingulate gyrus, with additional activity in the right superior and middle frontal gyri, left insula, and claustrum. Behavioral deviations from shared social norms (norm violations), however, have been associated with activation in regions such as the right insula, cingulate gyrus, left insula and claustrum, and right middle and superior frontal gyri (621, 622).

4.4. Temporal Evolvement

Behavior change is said to proceed in stages suggesting a temporal evolvement as posited in the TTM (299). To date, there are no specific studies examining the neural correlates of the specific stages of behavior change. We therefore aim to align the previously established cognitive processes and their neuronal correlates with the respective stages and thus hypothesize underlying mechanistic processes.

In the contemplation stage, individuals evaluate the risks and benefit of their current behavior versus the proposed change. As highlighted above, this evaluation process involves cognitive evaluation and decision-making circuits in the brain, including the PFC and the limbic system, which weigh the emotional and rational aspects of behavior change (337). During the preparation stage, the decision to change is solidified and specific plans are formulated. This stage involves cognitive processes such as goal setting and planning, heavily reliant on executive functions and the prefrontal areas of the brain (482). The contemplation and preparation stages involve cognitive evaluation and decision-making, engaging networks in the limbic system, PFC, and dopaminergic reward systems, as elaborated in detail in previous sections (482, 493, 565). The action and maintenance stages entail self-regulation and executive control, with neural correlates elaborated in previous sections (567, 607). The maintenance phase might bear a higher focus on the reward-associated pathways, as they are crucial for long-term behavior sustainment.

Although the TTM advocates for independent and separate stages, we argue that, upon closer examination, certain stages might share overlapping cognitive processes. Social and environmental factors play a role across all stages of the TTM, but their influence might be particularly pronounced in the initial stages of precontemplation and contemplation as well as during the maintenance stage. In the early stages, social and environmental cues can trigger the realization for the need to change. The social environment, including direct social interaction partners and social norms, may either facilitate or hinder the recognition of problematic behaviors (612). During the maintenance stage, external support systems and environmental factors are crucial in providing ongoing encouragement and mitigating the risk of relapse (612). Neurologically, this relates to the abovementioned neural areas associated with observational learning, social cognition, and emotional processing, which facilitate the understanding of social cues, norms, and interactions within interpersonal relationships (612, 623, 624).

Whereas the TTM explicitly defines stages of intentional behavior change, HAPA and habit theory (HT) also imply a progression of behavior into habit formation, from initial deliberate decision-making toward more automatic forms of behavioral regulation (625). These theories therefore emphasize the gradual shift from conscious to automatic cognitive processing and behavior (626–628). A consistent context in which behavior is repeatedly executed and rewarded leads to the formation of a habit. With numerous repetitions, mental representations of this habitual action develop, becoming automatically activated by environmental context cues, prompts, or events (625). From a cognitive standpoint, habits are initially formed through deliberate and conscious decision-making processes, typically grounded in goal-directed behavior. This phase is dominated by the PFC, which is associated with executive functions like planning and decision-making. Over time, as actions are repeated in a consistent context and rewarded, they transition from being goal directed to habitual. This shift involves a gradual decrease in cognitive control and reliance on conscious decision-making, with a corresponding increase in automaticity (625). The balance between cognitive and habitual control underpins active reward seeking. The shift from cognitive, goal-oriented strategies to habitual behaviors is intricately linked to neural changes in the brain. Initially, goal-oriented actions rely on the dorsomedial striatum, which processes outcome evaluations and adapts behavior to changing circumstances. Over time, with repeated successful actions, control shifts to the dorsolateral striatum, underpinning habitual behaviors that operate automatically without forward thinking. This transition from cognitive effort in the dorsomedial striatum to automated execution in the dorsolateral striatum marks the development of habitual processes (629, 630).

5. EVOLUTIONARY FOUNDATIONS OF HUMAN PHYSICAL ACTIVITY BEHAVIOR AND MOTIVATION

Whereas neuroscience has great potential to enhance our understanding of mechanistic (or proximate) causes of motivated behavior (e.g., how PA behavior occurs), it does not inform us about the ultimate, phylogenetic, and developmental causes of motivation (631, 632). Ultimate (or functional) causes explain why behaviors occur. In terms of human PA, this would explore why certain fitness-related behaviors evolved, focusing on their adaptive value or contribution to survival and reproduction. Phylogenetic causes assess behavior from the perspective of the evolutionary history of a species, e.g., how human PA behaviors parallel or contrast with such behaviors in closely related species. Developmental causes evaluate the development of behavior over an individual's

lifespan. This involves understanding how and why PA changes throughout different stages of human life influenced by both genetics and environment. Thus, motivated behaviors involve biological and psychological processes that have undergone evolution at numerous levels. Along these lines, human bodies have evolved over millions of years to thrive in specific conditions, diets, and lifestyles that are different from those prevalent in contemporary society. Evolution involves trade-offs. Certain traits or genetic predispositions that have been advantageous in one context could lead to vulnerabilities or diseases in another. Our susceptibility to diseases and our motivation to be physically active can be understood in the context of our evolutionary history. As shown in sect. 1, a large number of individuals avoid PA (633, 634), although it is well established that it is beneficial for health (635). Understanding the evolutionary basis for PA motivation can help inform efforts to promote healthier lifestyles and mitigate the impact of modern environments on our health and well-being (632, 636–639).

5.1. Potential of Evolutionary Science to Explain Behaviors

The fields of evolutionary biology and evolutionary psychology offer valuable perspectives for understanding behavior through the lens of human evolutionary history, which has largely been neglected in medical, behavioral, and PA research to date (640).

The key concepts in evolutionary biology (natural selection, reproductive success, selection pressure, adaptation) are explained in **TABLE 3** (641–643). For example, muscularity, a trait that is enhanced by PA, is frequently perceived as sexually attractive, potentially because it signals health and fitness (644, 645). In turn, muscular individuals may be perceived as more desirable mates, increasing their reproductive opportunities (646). Handgrip strength in males correlates with sexual behavior, body morphology, and aggression, traits that also may enhance mating opportunities and success (647). Similarly, both face and body, including fat-free muscle mass, are indicators of physical fitness and physical attractiveness in men (648–650). PA also impacts traits like vigor or vitality (651). Finally, regular PA, particularly at moderate intensity, can have beneficial effects on fertility, though this relationship is complex and depends on factors such as the type, frequency, duration, and intensity of the activity as well as on sex (652, 653). Although physical fitness may offer reproductive advantages, it comes with trade-offs, including higher caloric needs and potential risk of injury.

5.2. Evolutionary Adaptation to Physical Activity

Humans have evolved to be proficient in a range of physical activities (654). This includes long-distance walking and endurance running, which were crucial for persistence hunting and foraging (638, 655). Humans also adapted to perform complex motor skills, such as those required for tool use and construction, which need both fine and gross motor coordination (638, 654). Individuals with genetic traits that made them better adapted to PA and the environmental challenges had a higher likelihood of survival and successful reproduction. Being physically fit and adept directly impacted their ability to procure food, evade predators, and adapt to different environmental challenges. The inability to efficiently hunt and forage or failing to escape predators could lead to starvation or death. Consequently, the genes of less physically fit individuals were less likely to be propagated into subsequent generations (638).

Table 3. *Key concepts of evolutionary biology according to Darwin*

Concept	Description
Natural selection	The process by which certain traits become more common in a population over successive generations. Individuals with certain traits are more likely to survive and reproduce under specific environmental conditions. This increases the frequency of beneficial traits in the population, leading to a greater fit between the species and its environment. For a trait or behavior to be shaped by natural selection, it must fulfill 3 criteria: variation, heritability, and reproductive impact. Different individuals within the population must have different forms or levels of the trait. The trait must be at least partly heritable, meaning that it can be passed from parents to offspring. The trait must influence an individual's ability to survive and reproduce in order to be more likely to be passed on to the next generation.
Reproductive success	The passing on of beneficial genes to the next generations. Individuals with traits that are advantageous for survival and reproduction tend to leave more offspring. Such traits become more common in the population over time.
Selection pressure	Environmental factors that influence the survival and reproductive success of individuals within a population. These pressures can be biotic, like predators and competition, or abiotic, like climate or terrain.
Adaptation	The phenomenon of species becoming better suited to their environment.

Human athletic paleobiology, the study of athleticism to investigate evolutionary adaptations, is a promising framework to build knowledge on the origins and development of our species (654). Athletes are a unique population, characterized by high intrinsic motivation to be physically active, exposed to high psychophysiological stress and exercise loads (656–658). Humans are equipped with impressive aerobic capabilities, particularly in endurance running (659). An important evolutionary step in this direction was the transition to upright positioning (660). Accompanying changes in brain size, metabolism, thermoregulation, the human skeleton, and muscle structure might have influenced physical endurance and adaptability (660–662). The physique of elite athletes suggests that ancient humans had strong, well-developed bodies adapted to intense physical exertion. An interesting parallel between athletes and our hunter-gathering ancestors is the periodization of their PA behavior. Strenuous days were usually followed by a relatively easy day, but each day demanded a range of physical activities just to secure the basic needs for existence or success (663). Human bipedalism evolved gradually. The transition from quadrupedal ancestors to fully bipedal hominins took millions of years and involved multiple species in the human evolutionary lineage (664). Changes in vegetation and climate may have played a significant role. Forested areas gave way to more open environments like grasslands, favoring an upright posture to see over tall grass, spot predators, and forage more effectively (665, 666). As environments became drier, water sources and food became more dispersed, necessitating more efficient long-distance travel, for which bipedalism was advantageous as it is more energy-efficient than quadrupedalism (667–670). Anatomical adaptations and cognitive developments were associated with bipedalism. Upright walking freed the hands, which could have led to the use of tools and development of complex motor skills (671–673). Early hominins adapted bipedal postures while moving on flexible branches in trees, which later translated into bipedal walking on the ground (674, 675). The shift to bipedalism likely influenced the development of complex sensory and motor systems in the human brain (664, 676).

Homo erectus, an extinct species of early humans that lived around 1.9 million to 143,000 yr ago, is believed to have been one of the first hominins to engage in systematic hunting and gathering. The anatomical features of *Homo erectus*, such as long legs, short arms, and a nuchal ligament, suggest adaptations for long-distance bipedal locomotion. The typical daily behavior of the hunter-gatherer consisted of light to moderate PA, as it was necessary to walk long distances carrying objects or food. Typical daily distances ranged between 5 and 16 km (677). This light to moderate PA was regularly interspersed by interval-like exercise when hunting as well as escaping predators. The daily energy expenditure of *Homo erectus* was likely higher than that of modern humans living sedentary lifestyles (15, 33, 50), though this view has been challenged in a study where relatively small differences in energy expenditure were observed between Hadza hunter-gatherers in East Africa and United States Americans (678). Hunter-gatherers were lean and had a high proportion of muscle relative to fat mass, and obesity was virtually nonexistent (655, 679–681). Cooperative activities such as group hunting and gathering required significant physical effort and coordination as well as social cooperation. As part of cultural or societal celebrations and ceremonies, hunter-gatherers routinely participated in dancing, potentially promoting social bonding and stress relief (682).

5.3. Persistence Hunting

Persistence hunting is a strategy in which humans, equipped with their adapted endurance and thermoregulation, chased large prey animals over long distances in the hot midday sun. Although many animals are faster sprinters than humans, very few have the endurance to maintain high speeds for extended periods (683). The hunting of large animals led to a dietary shift toward higher fat content (684). Hunting contributed to the survival and dietary needs of early humans.

Persistence hunting was made possible by several key anatomical and physiological adaptations. The development of the musculus gluteus maximus, which is significantly larger in humans compared to other primates, played a crucial role. This allowed early humans to conserve energy while moving quickly and steadily over long distances (685, 686). Our ancestors developed short toes and long distal tendons, reducing the mechanical work during running and, thereby, improving running economy (687–689). Hunting also challenged the upper body. The human shoulder and arm adapted to the requirements of hunting, enabling humans to throw weapons effectively and store elastic energy in the shoulder (690, 691). The form and function of the human hand evolved not only for fine motor skills but also to aid in endurance running and hunting, through tools and weapons handling (692). The human pelvis adapted to accommodate bipedalism (693, 694). On the cardiovascular side, the pressure and volume handling in the heart became optimized for prolonged physical exertion (695). Some researchers have further suggested that hunting affected brain development, as it requires physical endurance combined with strategic thinking and planning (696, 697).

Persistence hunting led to a highly effective thermoregulation (683, 698, 699). This refers, for instance, to an increase in eccrine sweat glands, adaptations in skin and skin color, and the loss of body hair (700–702). Different ethnic groups have adapted differently to heat, highlighting the diversity in human thermoregulatory responses and the broader context of human evolution in different climates (703). From a lifespan perspective, it is important to understand how heat dissipation changes with age, indicating that this thermoregulatory advantage has limitations and deteriorates during a human life (704). In addition, researchers have argued that endurance running involves specific neurobiological rewards such as the increase of endocannabinoids, which helps to maintain high-intensity PA despite high energetic costs (227, 705–707).

Additionally, the regulation of fatigue and its role in human exercise tolerance is a complex phenomenon (708–712) but was a crucial aspect of persistence hunting (713). The ability to manage fatigue effectively is partly due to complex neural and physiological mechanisms that help distribute the energy load across the body and manage pain perception during prolonged exertion. This relates to adaptations in muscle fiber types, energy metabolism, and cardiovascular efficiency (711, 713). Others argue that the brain and the perception of effort, a psychological factor, play a critical role in humans' experience of fatigue and, thus, exercise tolerance (708, 709, 712, 714). In this regard, it is interesting that there is variability in affective responses to exercise, as individuals with higher tolerance of intensity often report more positive emotional states during strenuous activity. The Preference for and Tolerance of the Intensity of Exercise Questionnaire (PRETIE-Q) (715–718) has been used to explore how these psychological factors influence exercise adherence and motivation at various intensity levels (312, 719). In summary, the regulation of fatigue in humans is a complex and multifaceted phenomenon involving both physiological and psychological components (720).

As mentioned above, persistence hunting involved various complex cognitive processes. This includes spatial awareness, the ability to predict and anticipate prey behavior and make decisions about the best routes to follow, and the ability to coordinate group efforts to cut off escape paths. Complex cognitive processes, such as planning and problem-solving, were influenced by the demands of persistent hunting and long-distance travel, suggesting a link between exercise and the evolution of human brain function (721). Species with higher exercise capacities also tend to have larger brains, proposing that aerobic exercise might have played a role in the evolution of brain size and complexity in mammals (722).

Our evolutionary ancestors during the Paleolithic era (∼2.5 million to 10,000 yr ago) engaged in regular PA, like hunting, gathering, and traveling long distances on foot (638). Such high PA levels were normal and necessary for survival in the Stone Age (655, 663, 723). The active lifestyle of Stone Age people possibly contributed to lower rates of chronic noncommunicable metabolic and cardiovascular diseases compared to modern times (679, 681, 723). The PA levels in the Neolithic era, e.g., in mostly agricultural societies (∼10,000 to 120 yr ago), reflect a transition from the highly active hunter-gatherer lifestyle to one that included more sedentary and repetitive tasks associated with farming, although it was still physically more demanding than our current lifestyle in the modern industrial and technological age (∼120 yr ago to present) (638). The introduction of machinery in agricultural practices in modern times has reduced the overall PA levels among farmers. This shift marks a significant change from traditional farming, which was more labor intensive, and has potentially contributed to higher obesity rates (724, 725).

5.4. Lifetime History Framework

In evolutionary theory, life history frameworks emphasize that humans face trade-offs with regard to the optimal allocation of limited resources of time and energy among growth, reproduction, and maintenance (e.g., immune function, survival, longevity) (726, 727). Life history frameworks also highlight that traits, characteristics, or behaviors are only maintained over evolutionary time when cost of time, risk, and invested energy do not exceed the adaptive benefits (in terms of reproductive fitness). If the latter is the case, a behavior will be avoided to conserve energy (632). Importantly, being physically active and developing cardiorespiratory fitness is associated with relatively high energetic costs (632), which is reflected in the fact that muscles consume more energy than adipose tissue (636) and that cardiovascular and muscular fitness rapidly decrease after detraining (728–732). It has also been observed that after relatively short periods of reduced PA human metabolism seems to shift toward fat storage instead of allocation of calories to maintain muscles (733). This is attributed to the fact that efficient fat storage is a beneficial evolutionary trait as it helps to survive periods when access to food is limited (734).

PA also carries a risk of injury and brings along opportunity cost, as time spent being physically active cannot be used for other activities that are important for survival or reproductive success (632). Opportunity costs in particular can vary with sex and age, and the trade-offs described above between expending energy on PA versus reproduction are specially pronounced at some stages of life. This is particularly true for women of

childbearing age, where the pressure to spend more time and energy on reproduction increases. Research with rats, for instance, showed that the mother's undernourishment during pregnancy had negative effects on the development and PA behavior of its offspring, independent of postnatal feeding (735) or exercise level (736). This can be interpreted as an indication that individuals optimize their energy allocation depending on environmental influences. In other words, children who are exposed to malnutrition before birth as infants or young children (or later in life) may adopt a more conservative energy allocation that protects against further energetic stress (737). This may further result in less positive adaptations in response to PA (e.g., slower growth or muscle development) (738–740) or more psychosocial barriers (e.g., displeasure) that prevent these individuals from engaging in regular PA.

Men can also experience a shift. Current research with subsistence-oriented populations shows that men have to transfer the highest levels of energy to their offspring when they are in their thirties. This is the time when their own children are still living at home and are old enough to have substantial caloric needs but do not yet contribute much to securing the household's energy resources. During this phase, the time invested in physical leisure activities decreases significantly in men, possibly also because the risk of injury increases for certain sports such as soccer or the recovery time becomes longer in the event of an injury (735). Understanding that PA is associated with individual opportunity costs can help in assessing when it is particularly difficult for people to start or maintain a certain level of PA, and under which circumstances conscious cognitive processes are likely to have a strong influence on our behavior (632).

From a life history framework, it is further important to consider childhood as a unique opportunity for PA free from energetic trade-offs, without direct investment in reproductive effort or pressing demands to produce food for oneself or family (632). Children generally remain dependent on adults to cover their energy needs for the first 10 yr of life. During this phase, most of their energy can be used for their physical, cognitive, and social development (e.g., development of muscles and bones, the immune system, the brain, social skills). The benefits of PA are great at this stage of life and serve, for example, to develop strength, endurance, and coordination skills that make it easier to survive in a particular environment. PA also helps children to get to know and understand the environment in which they live and the associated energetic demands. Playful activities with others promote strategic thinking and contribute to the development of social skills that are important for living together in a society (741). With this in mind, it is not surprising that most children like being physically active

and, as mentioned in sect. 1, that their activity levels increase up to the age of 12 yr, whereas adolescents often fail to meet recommended PA levels (742–744). Conversely, this also explains why the level of PA during childhood is lower in phases (e.g., between 3 and 5 yr) during which the brain is developing particularly strongly and has a particularly high energy requirement (745, 746). With the onset of puberty, the opportunity costs of PA gradually increase, as more energy is required for sexual maturation and accelerated body growth (747, 748). In line with this, research consistently shows that PA levels decrease earlier among girls, as they enter puberty at a younger age than boys (743, 744, 749), as well as in early- versus late-maturing girls (750, 751). This also accords with studies showing that sex-based differences in terms of decreasing PA become less substantial when the pubertal maturation of adolescents is taken into account (752–755). Against this background, changes in sleep behavior (increased need for sleep, later rising times) during puberty can be understood as a natural process that helps adolescents to restrict their PA behavior and therefore energy expenditure. In the same vein, the increasing level of stress perceived by adolescents (756–759) can, to a certain point, be adaptive, as an increase in associated depressive symptoms (760–763) leads to increased malaise, fatigue, and physical inactivity. Again, this can motivate adolescents to conserve energy for body growth and building up fat reserves. Although this can have an unfavorable effect on their fitness levels, reducing the amount of nonessential PA can be beneficial from the perspective of reproductive success (632). In line with this, a study showed that in older youth (>11 yr), even light PA was associated with reduced body fat, a finding that was not observed in younger children (764).

Whereas PA is key for growth and development in children, in adulthood energy is no longer required for body growth but more resources are needed to ensure reproduction, particularly among women (765–767). Therefore, the influence of energetics on reproductive function is essential for understanding the costs and benefits of PA in adults. Compared to women, reproductive physiology is energetically less costly among men and more stable in times of low energy availability (646, 647, 649, 650, 768, 769). In women, research shows that both dietary restriction and high exercise- or work-related energy expenditure can have a negative impact on ovarian steroid levels (766, 770–774). This may explain why many women are inclined to reduce their PA levels when they become pregnant or after childbirth (775, 776). However, this seems to apply more to moderate- and vigorous-intensity activities, whereas walking remained unchanged in women during and after pregnancy (777). This suggests that at this stage of life activities that do not

appear to have too high opportunity costs and are easy to combine with childcare or additional childcare support may be helpful in supporting young women to maintain a physically active lifestyle (632, 778).

From a life history perspective, selection for increased PA may also be linked to selection for extended lifespan (637). Thus, whereas wild-living chimpanzees typically get no older than 35–40 yr (10), hunter-gatherers live beyond the age of 70 yr once they have survived infancy and childhood (779, 780), and thus 20 yr longer than reproductive age. As shown in Hadza hunter-gatherers, postreproductive women forage on average 20% more than younger mothers, and they allocate more time to preparing food and other activities such as digging, walking, and carrying (781). In this way, hunter-gatherer grandparents are able to create energetic surpluses for their children and grandchildren. Thus, they contribute to reproductive success not only by imparting knowledge and skills but also via intergenerational energy transfer. Hence, natural selection seemed to favor reproductive longevity and continued engagement in moderate PA during older adulthood (637). This explains why only small age-related decreases are found for daily walking in the Hadza population (782, 783) and why declines in physical fitness [e.g., maximal oxygen consumption ($\dot{V}O_{2max}$), grip strength] are less pronounced in hunter-gatherer populations than in Westerners of similar age (784–788). In line with this, researchers have argued that health span and lifespan were more closely linked in former subsistence populations than is the case today in modern societies (789).

5.5. Evolutionary Adaptation for Physical Inactivity

From an evolutionary perspective, however, it must be acknowledged that the observation of humans being shaped to perform large amounts of PA, as described in the previous sections, is only half of the story. Rather, humans have also evolved to be physically inactive. In fact, the tendency to minimize effort likely arose during evolution to allocate maximum energy resources to reproduction and maintenance of homeostasis (790, 791).

Research suggests that reducing energy expenditure by avoiding the wasteful allocation of energy may enhance women's reproductive success during periods of energetic stress (767, 790, 792). This tendency has spread through living organisms through natural selection. The prevalence of physical inactivity in our societies could be attributed to this evolutionary residue, which urges us to avoid unnecessary physical exertion. Indeed, its influence is magnified in the modern environment, where opportunities to reduce physical effort abound (636). As highlighted in the TEMPA (sect. 2.7.3), this tendency to minimize physical effort has been extensively studied across multiple disciplines, encompassing biomechanics (379, 793), neuroscience (381–383), and evolutionary biology (386, 388, 636). Studies have shown that the energetic cost of movement influences motor adaptation during learning and drives optimization of human locomotion to reduce energy waste and increase efficiency (379, 793). In addition to these optimization processes during movement, other studies have argued that "not moving" also represents a fundamental, albeit largely neglected, motor function (794). In the field of neuroscience, several studies based on decision-making tasks have shown that the brain perceives physical effort as a cost (381–383). Furthermore, it has been shown that the subjective value assigned to a reward decreases as the physical effort required to obtain it increases (381). Finally, anthropological data show that the daily lives of our hunter-gatherer ancestors were characterized by long periods of nonambulation, suggesting that human evolution unfolded in a context of considerable physical inactivity (388). For example, Raichlen et al. (388) found that contemporary hunter-gatherers (e.g., the Hadza of Tanzania) exhibit high levels of nonambulatory time, ~10 h per day, akin to levels observed in industrialized populations.

5.6. Genetic Influences on Human Physical Activity Behavior and Motivation

Although PA levels differ between species, little is known about the genetic factors that underlie these differences. Among humans, some candidate pathways have been identified and proposed to explain our species-specific type and level of locomotion and movement (699, 705, 795). However, the recent reduction in PA levels (723, 796, 797) is unlikely to be explained by genetic factors, given the extremely short time frame in which changes in occupation, transportation, and other lifestyle factors have occurred. Among contemporary humans, our understanding of the genetic basis of interindividual differences in PA behaviors has grown remarkably in the last several decades.

An individual's phenotype is a result of genetic and environmental influences across the lifespan (798, 799). Twin, family, and molecular genetic studies have helped to reveal how interindividual phenotypic differences can be accounted for by both genetic and nongenetic (e.g., environmental) differences (800). By observing the traits of individuals along with those of their relatives, these types of studies can partly tease

apart genetic and nongenetic influences on a given trait. Studies based on twins across different countries show moderate to strong levels of genetic influence on PA, termed "heritability" ($\sim$30–70%), using both self-reported measures (801–806) and device-based measures (807, 808). Heritability estimates are generally higher for device-based measures than for self-reported measures (809) and tend to increase from early life to midlife, perhaps reflecting the fading influence of the childhood environment and active gene-environment correlation, whereby individuals select environments that fit their genetic profile (810).

Family and twin studies can also help to estimate the relative influence of the environment, while controlling for genetic differences, which is more difficult to achieve with population-based study designs. Part of this environmental influence is the shared environment, which consists of the household environment (food, geographical location, neighborhood, family activities, etc.). Estimates for the proportion of phenotypic variation that can be attributed to shared familial effects are moderate early in life and then fade substantially in adulthood, resulting in an increased heritability. The unique environment is partitioned together with the measurement error, and these estimates tend to be moderate to strong depending on the age group and type of PA (809, 811).

In the past 20 years, technological advancements in high-throughput molecular genotyping have increased our ability to read parts of an individual's DNA sequence. The genome-wide association study (GWAS) approach became a popular and efficient way to locate specific genetic variants associated with a given trait. We have learned that many, likely thousands, of genetic variants are associated with any given complex human trait, each with a tiny effect size (812). This combined with the heavy multiple-testing burden means that very large sample sizes were required to detect these genetic variants. The first two published GWASs of PA behaviors did not identify genome-wide significant loci (813, 814), likely because of a lack of power given the relatively small sample sizes used. Then, in a sample of nearly 14,000 Japanese adults, one locus was found to be associated with leisure-time PA behavior (815). In the past 6 years, the UK Biobank (816) prospective cohort study consisting of half a million participants provided a major boost to our ability to identify genetic variants associated with many traits, including PA measured via self-report and measured through wearable devices. GWASs conducted with data from this study, along with other studies, have led to the identification of many variants associated with self-report and device measures of PA (817–820). With some rare exceptions (see *CADM2* below) (820), how these variants may lead to PA behaviors is still unknown. The identified variants explain a small proportion of

the heritability that may be expected based on twin studies, suggesting that indeed thousands of variants spread across the genome underlie interindividual differences, each having tiny effects on average, and that a greater number and type of variants remain to be found. It should be noted that a small effect size does not mean that this approach could not point to important biological pathways (821–823).

The set of genetic variants associated with PA likely captures a variety of mechanisms ranging from physical capacities to personality traits (809). Examining the genetic basis of traits related to PA could reveal more precisely how a given genetic variant is implicated in PA behavior. Studies have examined the heritability of motivations, preferences, sensations, and responses related to PA (824–827), and, more recently, genetic variants have been identified for preferences for types, intensities, and other aspects of PA (828). Additional insight into how these identified genetic variants are related to PA can be gained by examining traits related to cardiovascular fitness, lean mass, metabolites, and disease outcomes. For example, phenomewide association studies of variants in a gene called *Cell Adhesion Molecule 2* (*CADM2*) have revealed associations with traits as diverse as neuroticism, impulsivity, allergies, and anxiety (829–832). More opportunities to identify mechanisms underlying specific genetic variants will emerge with other phenotypic measures such as body imaging, wearable devices, disease outcomes, and levels of proteins and other molecules in tissues.

Beyond insights into specific biological mechanisms underlying PA behavior, genetic measures can also provide insight into causal links between PA and disease and into potential precision medicine approaches (833, 834). Through the Mendelian randomization approach (835), it is possible to leverage our increased knowledge of the genetics of both PA behavior and disease traits to triangulate evidence for the putatively harmful or beneficial causal impacts of PA on disease. For example, this study design, which has its own set of advantages and drawbacks, has provided support for a causal relationship of PA with depression (836), cognitive function (503, 837), amyotrophic lateral sclerosis (838), and colorectal cancer (839), among others.

An increased understanding of the genetic basis of interindividual differences in PA behavior may help to identify the physiological pathways that underlie these behaviors, to tailor interventions more precisely and identify at-risk individuals. It will also help provide additional evidence for the causes and consequences of PA at the population level. Finally, there may be opportunities to leverage these genetic insights to trace evolutionary forces on PA behavior across different species and hominin lineages.

5.7. Evolutionary Mismatch vs. Exercise as Medicine

Modern sedentary lifestyles represent a significant departure from the conditions under which our ancestors lived, resulting in a mismatch between evolved physiology and modern sedentary lifestyles (640). Modern life is largely a product of technological advancements and changes in work and lifestyle patterns, characterized by numerous options for reduced activity and a disconnection of food intake from the need to be physically active (840). This shift has occurred much faster than evolutionary processes typically operate. The modern perspective of exercise as a preventative or medical tool is a relatively recent development, diverging from the primary (ultimate) evolutionary purposes of PA (636, 655, 663, 841).

As mentioned above, some level of physical inactivity was part of human evolutionary history, but within specific and limited contexts (632, 636, 842). Health risks associated with prolonged sitting (843–845) are somewhat paradoxical given that evolutionary pressure often favored energy-minimizing strategies. Whereas rest and some inactivity have always been part of human life, the persistent and extreme physical inactivity characteristic of many modern lifestyles is a recent phenomenon and not something against which there was strong evolutionary selection (636, 842).

In summary, we can state that the human genome was largely shaped during the Paleolithic era due to natural selection, a slow biological process. The postagricultural and industrial revolutions have dramatically altered our diet, PA, and other lifestyle factors in a relatively short time, which led to a sort of cultural selection. This rapid change has led to an evolutionary mismatch between our ancient genetic makeup and modern environment, contributing to the prevalence of most unhealthy conditions associated with modern lifestyles, targeting all major organic systems, namely the cardiorespiratory, musculoskeletal, nervous, endocrine, immune, digestive, and reproductive systems (640, 681, 846–850). From an evolutionary point of view, humans have evolved to be both physically active and inactive, with main drivers for PA being reproduction, survival and enjoyment (632, 663, 851). Importantly, there are links between the evolutionary aspects of motivation and psychological models. This has been highlighted in the ART, with enjoyment being understood as a key driver for PA, the predisposition for physical inactivity being a central foundation in the TEMPA, or the energizing and motivating function of the stress response in the WANT model. Although this line of interdisciplinary research is in an early stage, insights could be of great value to develop feasible interventions with more realistic goals by taking into account behavioral features that have emerged during human evolutionary history.

6. SLEEP AND MODERN TECHNOLOGIES: TWO FURTHER ISSUES LINKED TO PHYSICAL ACTIVITY MOTIVATION

6.1. Sleep

Research has suggested a bidirectional association between sleep and PA. As such, poor sleep has emerged as a predictor for reduced PA on the subsequent day (852). In fact, a majority of studies investigating the bidirectional relationship establish poor sleep as a more robust predictor of subsequent PA than vice versa (853), potentially contributing to a cyclic pattern of both poor sleep and physical inactivity (854). However, in a recent meta-analysis the bidirectional daily association was not supported. Sleep quality, efficiency, and wake after sleep onset were indeed associated with next-day PA, whereas daytime PA was associated with lower total sleep time the following night. These findings do, however, show high inter- and intraindividual variability and small effect sizes (69).

According to the American Academy of Sleep Medicine and the Sleep Research Society, adults over the age of 18 yr should sleep 7–9 h per night (855, 856). However, the amount of sleep required for optimal daytime performance is influenced by factors such as age, health, and individual sleep need. Only 5% of people are genetically disposed to be short sleepers, who require only 4–6 h of sleep per night to feel well rested (857, 858). Although there is a significant amount of literature regarding the effects of sleep deprivation on physical performance (859–862), there are relatively few studies that examine how sleep deprivation affects our motivation to perform (863–865).

Sleep deprivation in particular has been shown to have detrimental effects on endurance performance during prolonged treadmill walking, despite limited alterations in cardiorespiratory factors (e.g., oxygen uptake, respiratory exchange ratio, heart rate) (866, 867). Although cardiorespiratory or thermoregulatory functions may remain unchanged, the perception of effort (868), which plays a critical role in exercise tolerance as described in sect. 5.3., may increase significantly. Similarly, in a state of sleep deprivation, the brain struggles with the cost-benefit evaluation and is more likely to think the reward for doing something is not worth the effort (869). This phenomenon is called "effort discounting," a cognitive process where individuals subconsciously devalue or discount the perceived reward based on the effort required to accomplish it (863). Neuroimaging investigations show that sleep deprivation is linked to modified activity in the PFC (870–873); hence, individuals lacking sufficient sleep often struggle with maintaining discipline, making sound judgments,

and resisting immediate gratification, compromising their self-control capacity (874–876).

In the self-control strength or limited-resource model, a model rooted in the field of social psychology, self-control is conceptualized as a limited internal resource that becomes depleted through repeated acts of self-control, akin to muscle fatigue. This model also postulates that self-control energy resources sometimes deplete more rapidly than they are refilled (**FIGURE 19**) (877–883). The relationship between poor sleep habits and self-control involves complex mechanisms, including the processing and utilization of glucose, a key energy source (884). Circadian rhythms, governing sleep cycles and hormone secretion, are thought to influence this intricate system (874). Sleep disruptions negatively impact glucose metabolism (885, 886), and low blood glucose levels have shown to result in poorer self-control (871). Further research indicates that sleep deprivation is linked to higher psychological strain that quickly depletes the internal recourse of self-control (875, 876), which is in line with the foundations of the ART (sect. 2.7.1). Having good sleep habits contributes to maintaining a stable daily energy reserve (874), which allows us to carry out PA plans, which is particularly important for individuals who lack sufficient intrinsic motivation for PA (sect. 2.2).

Moreover, sleep deprivation has been consistently linked to an increase in negative affect, encompassing emotions such as irritability, mood swings, and heightened stress levels (887–890), as also described in sects. 2 and 3. The relationship between sleep and mood regulation is complex and involves various neurobiological processes (**TABLE 4**) (899, 900). One significant factor is the impact of sleep deprivation on the amygdala (901). Sleep loss tends to amplify amygdala reactivity, making individuals more sensitive to negative stimuli and less capable of regulating emotional responses, which contributes to an overall increase in negative affect. As highlighted in sect. 3.4., affective responses and automatic valuations play an important role in PA motivation. Along these lines, sleep deprivation increases negative affect (888) and perception of effort (868). Conversely, positive affective experiences can enhance the likelihood of exercise engagement (367). Bouwmans et al. (887) suggest that good sleep quality is predictive of positive affect, and positive affect compensates the depletion of self-control and facilitates self-control behaviors (902).

6.2. Modern Technologies and Digitalization

As described in sect. 5, an evolutionary shift has led to increased screen-based leisure activities (e.g., television watching) and screen-based work activities (e.g., computer use for work) resulting from digitalization that replace other activities associated with higher levels of PA (903). Additionally, there are concerns about the negative impact of technologies such as smartphones on mental health and the risk of addiction (904).
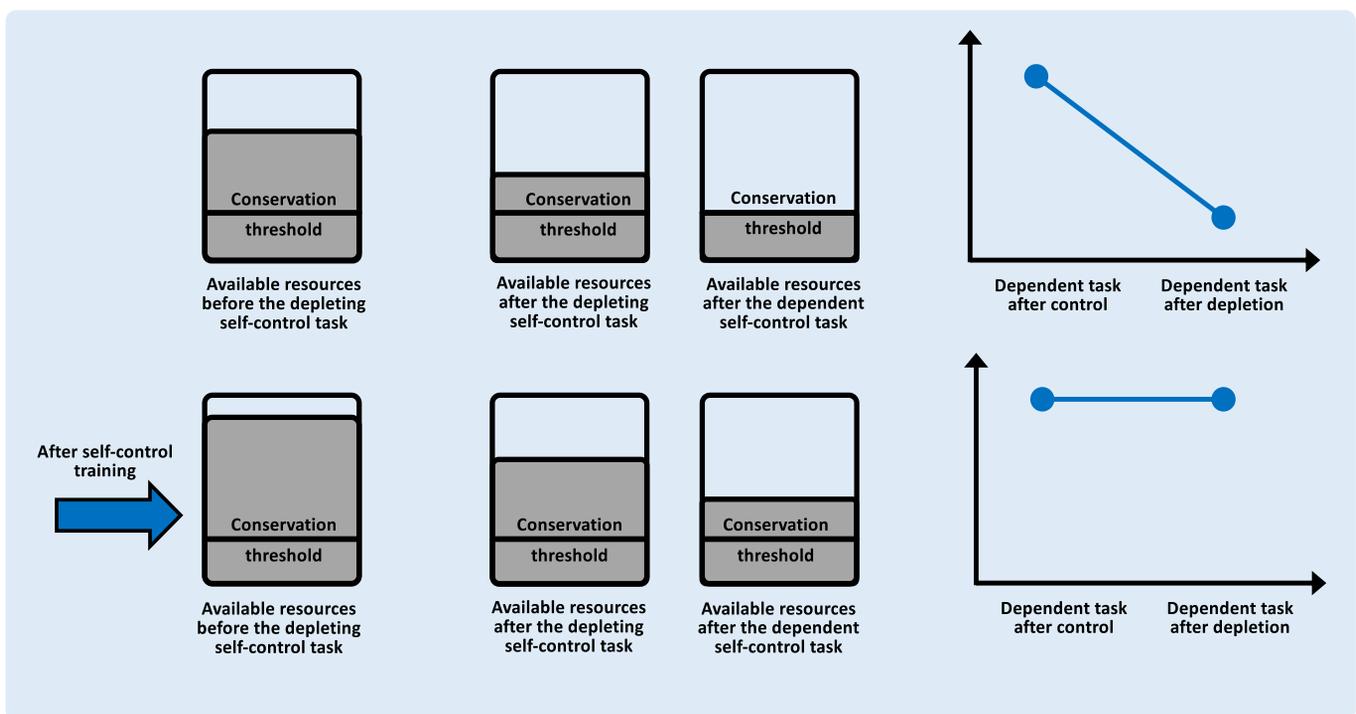
FIGURE 19. The self-control strength or limited-resource model posits that self-control is a limited internal resource that becomes depleted through repeated acts of self-control, akin to muscle fatigue. Adapted from Audiffren and André (877). Republished under CC 4.0.

However, technologies resulting from ongoing digitalization also hold the potential to promote PA. The interest in the technology's capability to enhance PA monitoring and promotion strategies is growing, supported by accumulating evidence from systematic reviews and meta-analyses (905, 906). Time- and location-independent digital interventions, such as smartphone applications or web-based interventions, have shown positive impacts on behavior change (907–909). Digital interventions offer broad accessibility, overcoming barriers such as waiting time and stigma while providing interventions at an individual's own pace (910–912). Despite their potential (913), it is important to note that apps and wearables, often seen as tools to promote PA, are not treatments themselves. Instead, they act as delivery mechanisms for the active elements of behavior change, similar to the casing of pharmacologically active agents in medication. Despite that, designing interventions poorly deployed through digital means can be likened to a digital placebo, lacking a defined target or active ingredient (914). A promising approach to unlock the potential of digital interventions for promoting PA could be combining them with personal contact with a therapist, coach, or specialist (915). Additionally, just-in-time adaptive interventions, employing decision algorithms to customize delivery based on individual moments of receptivity, opportunity, or vulnerability, represent an effective mode of delivering digital interventions (916).

Despite the potential of promoting PA via modern technologies, there is limited understanding of how the use of wearables and/or digital interventions impacts the motivation to be physically active. Future research should prioritize investigating the impact of digital interventions on motivation and potential neuropsychological mechanisms. Additionally, there is a need for specificity in targeting, identifying active ingredients, determining appropriate dosages, and establishing rules for adapting interventions based on individual and contextual differences when delving into the realm of digital interventions (914).

Table 4. *Effects of sleep deprivation on brain functions relevant to physical activity participation*

Affected Brain Region	Change in Function	Relevance for PA Behavior
Midbrain ventral tegmental area (891)	Increased ventral striatum activity → impaired motivation and decision-making during anticipation and receipt of rewards	**Reward and incentive processing** - Alterations may diminish the perceived benefits of regular PA, affecting adherence to exercise routines. - Impaired reward discrimination accuracy can hinder the ability to recognize the long-term benefits of PA, affecting commitment to regular exercise. - Overgeneralized reward bias may diminish the perceived value of PA compared to other rewarding activities (e.g., sedentary behaviors, snacking). Thus, seeking immediate gratification from nonphysical activities downsizes the priority to invest in long-term health through exercise. - Slower learning of reward-based learning may hinder the formation of new PA habits.
Striatum (892, 893)	Impaired function → reduced motivation, altered reward perception, difficulties experiencing pleasure (reward processing), mainly due to change in dopamine (814) receptors relevant for reward-related learning	
Basal ganglia (892, 894)	Modified dopamine receptor sensitivity and availability → increased impulsivity, risk-taking, and sensation seeking	
Medial prefrontal cortex (891, 895–897)	Impaired function → increased risk-taking, impulsivity [dopamine receptor imbalance (D1 vs. D2/D3) and changes], poor reward discrimination impacting decision-making, poor emotion regulation due to reduced connectivity to amygdala	**Motivation and impulsivity** - Reduced motivation and increased impulsivity may decrease PA participation. - Increased sensitivity to emotionally pleasurable stimuli may lead to a preference for sedentary activities over exercise. - Reduced optimal decision-making may lead to decreased motivation for engaging in PA. - Impulsive decision-making regarding PA engagement may lead to inconsistent PA participation.
Anterior insula (891, 898)	Altered activity → impaired emotional processing, increased sensibility to stress and anxiety	
Anterior cingulate cortex (897)	Impaired function → increased emotional instability, difficulty making decisions	
Amygdala (895)	Increased reactivity → exaggerated emotional responses, particularly to negative stimuli. Altered dopamine receptors (D2/D3) relevant for sensory perception and reward-associated learning	**Aversive stimulus response** - Exacerbated negative emotional states such as anxiety and stress may lead to decreased motivation for PA. - Increased emotional sensitivity and impaired emotional discrimination may hinder exercise enjoyment and adherence. - Heightened emotional reactivity and decreased ability to regulate negative emotions may reduce motivation for PA.

PA, physical activity.

7. INTEGRATIVE MODEL, IMPLICATIONS, AND CONCLUSIONS

In this review, we have synthesized findings from neuroscience and evolutionary biology/psychology to complement traditional behavioral approaches and highlight psychophysiological factors in describing human motivation for PA behavior. In this final section, we introduce an expansion of an existing integrative model to bridge the historical and methodological divide between the fields of evolutionary sciences, psychology, and physiology, particularly in the context of human motivation theories. We recommend a quality assessment of psychological theories based on evolutionary and physiological underpinnings indicating an ultimate mechanism (answering "why"). This could play a key role in advancing and reshaping our theoretical models and practical interventions.

7.1. Toward an Integrative Model of PA Behavior and Motivation

An integrative evolutionary model of PA has been proposed by Caldwell (632), in which she includes ultimate, developmental, environmental, and proximate factors that impact PA behavior. The central assumption is that proximate predictors of a behavior are directly or indirectly linked to ultimate (or functional) predictors. For an ultimate explanation of behavior, it is important to understand how a given behavior, or the underlying psychological or physiological factors driving it, were shaped by natural selection, which operates through inherited natural variation and reproductive success.

According to the model shown in **FIGURE 20**, ancestral environments provided selection pressures (external forces that determined which traits/behaviors led to greatest reproductive success), which influenced the evolution of factors impacting PA on a population level. For a given individual, genes, epigenetic change, and environmental factors impact the developmental trajectory of energy allocation throughout the lifespan. Former (e.g., environment exposed to during pregnancy, childhood) and current environmental factors are multifold and have been addressed in socioecological models of PA (sect. 2.4). Current environmental factors include the availability of and access to resources, the natural environment, exposure to pathogens/infections, as well as availability of modern technologies and digitalization and the social and built environment. Development (e.g., early/late maturation), life stage (e.g., prenatal, childhood, puberty/adolescence, reproductive and postreproductive age), as well as socioeconomic (e.g., education, income), physical (e.g., basal metabolic rate, immune system, body composition) and mental (e.g., social integration, personal well-being, sleep, psychopathology) condition influence the

costs and benefits associated with PA for an individual during a specific moment in time. Proximate mechanisms underlying PA are influenced by the abovementioned individual level factors and consist of physiological [e.g., hypothalamic-pituitary-adrenal (HPA) axis, central nervous system, metabolism] and psychological (e.g., cognitive processes) mechanisms.

We have expanded on the proximate mechanisms from a psychophysiological point of view (632). As highlighted in **FIGURE 20**, psychophysiology plays a key role in elucidating the relationships between physiological states and systems, motivational and volitional factors, and psychological states and traits. Physiological states and systems may include, for example, specific brain networks and neurotransmitters (as illustrated in sect. 3). Motivational and volitional factors may include self-efficacy, outcome expectancies, intentions, beliefs, and planning and coping strategies (as described in sect. 2). Psychological states and traits may include affective and mood states as well as personality traits. Additionally, specific to PA behavior, differential physiological responses (e.g., lactate, cortisol, adrenaline, heart rate, body temperature) and subjective experiences (e.g., pleasure or displeasure, pain, flow) are elicited by PA that, in turn, impact the core proximate mechanisms. It is important to note that although we focused on brain networks and transmitter systems in the present review, further physiological systems should be considered from a broader psychophysiological perspective, as they are also important for the regulation of energy allocation. Such systems and processes include the HPA axis (375, 917–921), the hypothalamic-pituitary-gonadal (HPG) axis (921–930), the central nervous system (720, 931–936), the human metabolism (122, 937–940), the gut microbiome (402, 941–945), and the immune system (946–955).

Importantly, Caldwell (632) criticized health psychology and public health for not sufficiently questioning proximate factors for their ultimate function. From this perspective, focusing on behavioral intentions to explain behavior seems insufficient, as such intentions do not tell us anything about the ultimate function (the "why") of PA behavior. It is therefore no surprise that such proximate factors only explain limited variance in PA (307). The same is true for outcome expectancies, which in most studies (and instruments) narrowly focus on the health-related benefits of PA (956, 957). However, from an evolutionary perspective, the ultimate goal of PA has never been to increase health but to maximize reproductive success (636). The "exercise is medicine" movement (958–961) is a relatively new phenomenon and should be understood as a reaction to the increasing mismatch between our evolutionary history and rapid emergence of our modern environment. This explains
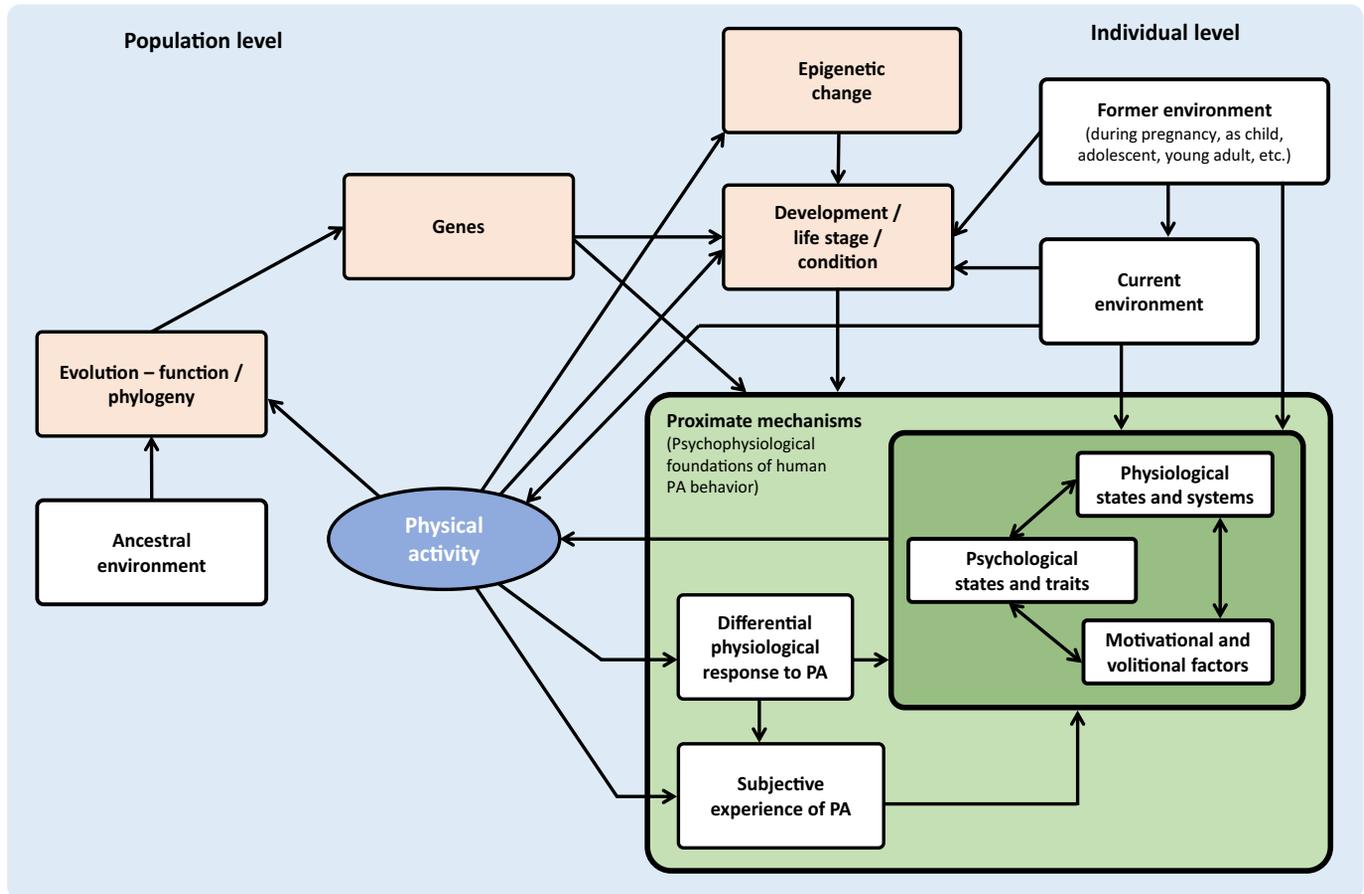
FIGURE 20. The extended integrative evolutionary model according to Caldwell (632). On a population level, the ancestral environment is said to influence evolution including our function and phylogeny, which in turn influences our genes. On an individual level then, genes, epigenetic change, and the former as well as current environment influence our development, stage of life, as well as socioeconomic, physical, and mental condition. These factors directly or indirectly impact the proximate mechanisms of physical activity (PA). The proximate mechanisms can be understood as the psychophysiological foundations, including physiological states and systems; psychological states and traits; motivational and volitional factors; as well as the physiological and subjective responses to and experiences of physical activity. Used with permission.

why the sole knowledge about the health benefits of a physically active lifestyle is not a strong motivator for many people (962), although some scholars today call PA a "miracle cure" (963, 964). In line with this, studies have highlighted that people who exercise mainly because of the expected physical health benefits engage in less exercise than their counterparts who want to improve quality of life (394, 965).

As highlighted by Caldwell (632), seeking the ultimate explanation for PA behavior is to understand how the behavior was shaped by natural selection. Additionally, thoroughly exploring proximate mechanisms may allow a better understanding of why and when some mechanisms are more or less likely to influence behavior. As such, evolutionary models may have an edge over more traditional approaches. Along these lines, we suggest that the theories, frameworks, and models used in PA promotion may be evaluated based on whether an ultimate explanation is presented. As such, the SDT provides an ultimate explanation in the form of satisfying

the three fundamental psychological needs, the ART in the form of enjoyment, the TEMPA in the form of effort minimization, and the WANT model from a coping with stress perspective (sect. 2).

If these concerns are taken seriously, motivational psychology will hardly be able to avoid integrating psychophysiological approaches in the future. Our review showed that neuroscience has already taken some efforts to advance our understanding of human PA behavior and motivation (sect. 3). We also pointed out to what extent classical behavioral theories provide starting points that would be suitable for neuroscientific studies (sect. 4; **TABLE 2**). And, fortunately, we also observed that some psychological theories and models have been developed in recent years (such as the ART, TEMPA, and WANT model) striving to integrate insights from evolutionary science and trying to get to the bottom of the underlying physiological mechanisms.

In the last two sections, we provide examples to demonstrate that important practical implications can be

drawn from both a neuroscience and an evolutionary perspective on human PA motivation.

7.2. Practical Implications from a Neuroscience Perspective on Motivation

In the words of Di Domenico and Ryan (567), it can be said that there are three key reasons why neuroscience is a crucial frontier in motivational research. First, both experience and behavior are brain mediated, necessitating an understanding of the neural systems underpinning (intrinsic and extrinsic) motivation. Second, neuroscience enables the examination of internal processes beyond the reach of self-reports or behavioral observations, promising new insights. Third, neuroscience offers a finer resolution in investigating motivational processes compared to experiential and behavioral methods, potentially refining conceptual understanding by elucidating detailed processes (567, 607). A concrete example of how neural data shed light on the processes can be found in a recent EEG study (391). Whereas on a behavioral level results suggest that people tend to automatically avoid sedentary behaviors, on the neural level avoiding sedentary behaviors was found to require higher inhibitory control. The clinical implications are that inhibitory control could be a relevant target for intervention. With only behavioral data, this suggestion cannot be drawn. Hence, the integration of diverse data streams fosters robust and adaptable theoretical explanations, not restricted to a single experimental methodology (567, 966).

Utilizing neurophysiological variables to predict adherence to interventions could be highly beneficial in tailoring approaches for individuals with varying levels of self-regulation. Recent findings suggest that differences in cognitive control on behavioral and neurophysiological levels significantly impact an individual's ability to guide goal-directed behavior, which in turn affects self-regulation capacity (482). This capacity is crucial for adhering to interventions aimed at reducing sedentary behavior and increasing PA (481). By identifying individuals with weaker cognitive control abilities, practitioners could anticipate potential challenges in adherence to interventions. This foresight could allow for the provision and implementation of alternative, individualized interventions, specifically designed to address these challenges. Training and enhancing cognitive control abilities may be a key component of these tailored interventions, especially for those with lower expected adherence due to neurophysiological markers indicating lower self-regulation capacity (482). As previous studies have provided evidence of enhanced cognitive control abilities through combined cognitive and physical training (967, 968), neurophysiological markers

could provide an indication of which individuals would benefit from a combined intervention, promoting sustained PA commitment by reinforcing self-regulation abilities (415, 482). Recently, exergaming has been proposed as an activity that aligns well with these requirements (969–972). More specifically, scholars have argued that by incorporating game elements and a variety of motivational features (e.g., instant visual and audio performance feedback), virtual reality-based exergames have the potential to make exercise training more interesting, interactive, adapted, meaningful, and enjoyable compared to traditional (often repetitive) exercise activities (973–976). Moreover, as most exergames demand relatively high levels of concentration because they typically present a cognitive challenge to the participant (977), they stimulate both the body and the mind and are thus a potentially powerful tool to simultaneously enhance cardiorespiratory fitness and cognitive performance (978, 979). As highlighted by Klasen et al. (980), active video games activate the mesolimbic dopaminergic pathways and the associated reward system of the brain. In line with this, research in cardiac rehabilitation showed that patients enjoyed participating in exergaming, which had a positive effect on adherence and energy expenditure (981–983). These findings suggest that exergames may be particularly effective for populations at risk of declining physical fitness, cognitive function, and motor performance, such as older adults or individuals with chronic conditions (984–987).

A more specific example of cognitive training is an inhibitory control training based on the go-no-go task, during which individuals are trained to consistently refrain from button presses when faced with tempting stimuli such as unhealthy foods, sedentary behaviors, or addictive substances. Other methods, such as episodic future thinking (988), increasing self-awareness (989), mindfulness meditation (990), or even using the nondominant hand for daily activities (991), have been proposed to improve self-control skills. Furthermore, based on the neurobiological insights from the self-control mechanisms, interventions involving transcranial direct stimulation of the dlPFC (992) or real-time fMRI neurofeedback to regulate dlPFC activity (993) have been used in drug and food contexts, respectively. Likewise, interventions aimed at promoting cognitive function may be particularly important for individuals with low cognitive reserve, who are more likely to experience clinical manifestations of the aging process more rapidly than individuals with higher cognitive reserve (994, 995). Such interventions, particularly computerized training, offer an efficient method to enhance cognitive control abilities, with studies indicating modest enhancements in cognitive performance (967, 968). These gains are more pronounced when training incorporates feedback, adaptive progression, and multitasking and is tailored

to specific cognitive domains (967). Furthermore, strategies that promote PA can be used to improve cognitive control, which in turn may favor increased engagement in PA through positive feedback loops. It is important to note, however, that not all forms of PA produce identical cognitive benefits (525). The effects of PA on cognitive function may depend on individual characteristics such as age, sex, or the presence or absence of clinical conditions (50, 530). In addition, variations in the type, intensity, frequency, duration, and modality of PA also play an important moderating role. In particular, research suggests that certain physical activities (e.g., complex tasks that warrant coordination and strategic thinking) promoting cognitive function may provide greater benefits than others (48, 525, 996, 997). Moreover, considering the interplay between automatic and deliberate cognitive processes in decision-making, interventions might benefit from creating environments where PA is a more automatic choice, reducing the reliance on conscious, effortful decision-making, which can be a barrier to exercise (998). From a decision-making point of view, framing exercise in a way that aligns with innate reward systems may increase motivation (999). Additionally, enjoyment of PA may be boosted with music, immersive virtual reality, and the use of protocols that allow the self-selection of intensities and optimal distribution of different loads across a single session (1000).

7.3. Practical Implications from an Evolutionary Perspective on Motivation

As shown in sect. 5, motivated behaviors involve both biological and psychological processes that have undergone evolution at numerous levels. It can therefore be helpful to adopt an evolutionary perspective on human PA behavior to explain why so many people are avoiding PA even though it is vital for their health (632, 636–639). Nevertheless, as Caldwell (632) prudently pointed out, it is unlikely that "there is some critical unknown factor that made our ancestors so active, which we have somehow lost in recent history." It is also unlikely that knowledge of such a factor would help us to develop "some ideal paleo exercise program that would prescribe the proper intensity and duration of exercise, appeal to humans everywhere and restore health and well-being around the world" (632, p. xvii). Nevertheless, the application of evolutionary theory can add many missing pieces of the puzzle needed for a better understanding of human PA behavior.

For instance, an evolutionary perspective can help tailor PA interventions by understanding and leveraging innate human behaviors and preferences (7, 636). These behaviors evolved to optimize survival, reproductive success,

and energy use (7, 636). Our ancestors were physically active either when it was necessary (hunting, foraging, escaping predators) or when it was fun or socially engaging. Consequently, it might be promising to restructure environments in a way that requires or supports being more physically active as well as making PA more meaningful or enjoyable (228, 636). For instance, making environments more energetically demanding can help to counteract the inborn tendency of humans to conserve energy (427). Additionally, interventions could be designed to mimic ancestral environments, such as incorporating more naturalistic and functional movements (1001, 1002). For instance, engaging in outdoor activities can resonate with our evolutionary connection to nature. Programs that include exercises in natural settings, like parks or trails, can enhance the appeal and provide health benefits beyond physical fitness (1003–1005).

Incorporating elements of play, which was crucial in human evolutionary history for skill development and social bonding, is a further option to make PA more enjoyable. Introducing novelty and variety in the workouts can keep participants engaged and interested, as it stimulates the brain in ways similar to how our ancestors would have experienced new and changing environments. Interventions could focus on the social aspects of PA, like community sports, team sports, or group challenges, leveraging our evolved predisposition for social engagement and cooperative activities (1001, 1002, 1006) to enhance the appeal and effectiveness of PA programs. Additionally, competition can tap into our evolutionary drive for status and success. Our ancestors were goal oriented, focusing on concrete, survival-related achievements. Modern exercise programs can mimic this by setting clear, attainable goals and providing regular feedback on progress.

It has also been suggested that the concept of evolutionary mismatch can be used as a tool in initiating positive behavior change. Basile et al. (1007) proposed using an evolutionary mismatch narrative to educate patients about the origins of modern lifestyle diseases, namely by explaining to patients that many common health issues arise because our bodies are adapted to conditions that differ significantly from today's environment, particularly concerning diet, PA, and social structures. These authors further suggest that a mismatch narrative may help patients understand that their health issues are not solely due to personal failings but are also a result of a broader mismatch between our evolutionary adaptations and the modern world. In this regard, patients may feel more empowered and motivated to adopt healthier behaviors. Thus, a mismatch narrative may be more persuasive than statistical evidence, particularly as it

contextualizes health behaviors within the larger story of human evolution and history, making the information more engaging and memorable (1008, 1009).

From a life history perspective, we further learn that PA is associated with opportunity costs. Opportunity costs can vary considerably with age, sex, and individual condition. With other words, there are some stages of life where reducing energy expenditure is functional, particularly when there is a high need to allocate resources to growth (e.g., middle childhood), sexual maturation (e.g., adolescence), reproduction (e.g., young adulthood), and maintenance (e.g., when own children are small) (726, 727). This knowledge may help health interventionists to design more realistic interventions that are more acceptable and meaningful to the target populations. For instance, activities that are compatible with childcare or more childcare opportunities can help reduce the costs of PA for women in the reproductive age (777, 778), an age when maintaining PA is a particular challenge (775, 776). Finally, an advanced understanding of genetic factors that contribute to PA can be helpful in the identification of people who are at especially high risk for physically inactive lifestyles. Such knowledge can also be used for individual tailoring of PA interventions in the sense that particular attention can be paid to individuals with unfavorable genetic dispositions (817, 820, 1010–1012).

7.4. Conclusions

PA is a well-defined construct with a plethora of invaluable health benefits. Nevertheless, the global adherence to PA recommendations is low to modest. Both adaptive and maladaptive reasons have been found for the lack of (or abnormally high) desire to be physically active, as well as common temporal and seasonal variations in PA patterns. The quest for a better understanding of human motivation for PA has been looked at through psychological research, resulting in theories, models, and frameworks including causal concepts, holistic approaches, and stage as well dual-process models. Additionally, through the lens of evolution, it can be said that humans are destined to be both physically active and inactive in a delicate interplay, with the cost of PA taking on a different meaning depending on the stage of life (childhood, adolescents, adulthood). The role of neuroscience in the understanding of PA motivation is a more recent addition and reveals brain networks and neurotransmitter systems underlying conscious and nonconscious processes that shape the motivation for PA behavior. Based on this knowledge, predictions can be made on how processing of social and affective experiences influences the engagement in PA. An integrative model from an evolutionary perspective including psychophysiological mechanisms and a clear ultimate mechanism may vastly improve our understanding and intervention possibilities going forward. In conclusion, it can be said that, despite the complex nature of PA behavior, insights from neuroscience and evolution deliver possible intervention strategies, such as strengthening cognitive function, reshaping environments, and boosting enjoyment, to promote PA for overall health.

GLOSSARY

ACC	Anterior cingulate cortex
AIC	Anterior insular cortex
ART	Affective-reflective theory of physical inactivity and exercise
avPFC	Anterior ventromedial prefrontal cortex
BDNF	Brain-derived neurotrophic factor
CADM2	Cell adhesion molecule 2
CON	Cingulo-opercular network
CRAVE	Cravings for rest and volitional energy expenditure
dACC	Dorsal anterior cingulate cortex
dlPFC	Dorsolateral prefrontal cortex
DMN	Default mode network
dmPFC	Dorsomedial prefrontal cortex
EEG	Electroencephalogram
EMA	Ecological momentary assessment
ERP	Event-related potential
fMRI	Functional magnetic resonance imaging
FPN	Frontoparietal network
GWAS	Genome-wide association study
HAPA	Health action process approach
HBM	Health belief model
HT	Habit theory
IGF-1	Insulin-like growth factor-1
lPFC	Lateral prefrontal cortex
MCC	Middle cingulate cortex
MD	Mean diffusivity
MET	Metabolic equivalent
MFC	Medial frontal cortex
mPFC	Medial prefrontal cortex
MVPA	Moderate-to-vigorous physical activity
OFC	Orbitofrontal cortex
PA	Physical activity
PFC	Prefrontal cortex
rTMS	Repetitive transcranial magnetic stimulation
SCT	Social cognitive theory
SDT	Self-determination theory
S-R-O	Stimulus, response, and outcome
TEMPA	Theory of effort minimization in physical activity
TPB	Theory of planned behavior
TTM	Transtheoretical model of behavior change
VEGF	Vascular endothelial growth factor
vlPFC	Ventrolateral prefrontal cortex
vmPFC	Ventromedial prefrontal cortex

WANT   Wants and aversion for neuromuscular tasks
WHO   World Health Organization

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DISCLAIMERS

The content is solely the authors' responsibility and does not necessarily represent the official views of their institutions.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

M.G. prepared figures; M.G., B.C., R.C., F.C., V.H., Y.C.K., C.L., V.N.L., S.L., M.S.-K., and O.F. drafted manuscript; M.G., B.C., R.C., F.C., V.H., Y.C.K., C.L., V.N.L., S.L., M.S.-K., and O.F. edited and revised manuscript; M.G., B.C., R.C., F.C., V.H., Y.C.K., C.L., V.N.L., S.L., M.S.-K., and O.F. approved final version of manuscript.

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