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The Nervous System as a Pathway for Exercise to Improve Social Cognition

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LUDYGA, S., T. ISHIHARA, and K. KAMIJO. The nervous system as a pathway for exercise to improve social cognition. *Exerc. Sport Sci. Rev.*, Vol. 50, No. 4, pp. 203–212, 2022. *Specific nervous system functions and the regulating roles of oxytocin have evolved because of the necessity to negotiate increasingly complex social systems. We hypothesize that acute and long-term physical activity and exercise have the potential to benefit social cognitive abilities, such as emotion recognition and regulation, by operating on these functions.* **Key Words:** physical activity, aerobic fitness, social brain, theory of mind, oxytocin, polyvagal theory, evolution

Key Points

- Functions of the autonomous and central nervous system that evolved to cope with complex social systems determine a wide range of social cognitive abilities but also are sensitive to physical activity and exercise.
- Initial evidence suggests that acute endurance exercise and aerobic fitness influence emotion recognition and regulation aspects of social cognition.
- Changes in resources shared with other cognitive domains and increased expression of oxytocin may underlie acute benefits of endurance exercise (at moderate intensity).
- Higher aerobic fitness may translate into better social cognitive abilities because of its positive association with autonomic balance, as well as function and structure of social brain networks.

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INTRODUCTION

An evolutionary perspective suggests that the large size of the human brain (relative to other species) is mainly attributable to the necessity to cope with complex social systems (1). When faced with multiple threats and limited resources, the negotiation of social contracts was a key to survival. Such contracts can be understood as a set of rules that govern interactions within and between groups. Social cognitive abilities are required to understand and follow these rules. They further allow the identification of characters that may potentially be harmful for oneself or the group from a set of social cues (2). This applies to "fair-weather friends" (stay committed as long as we do not need real help, and who abandon us when we are most in need of support), "cheaters" (individuals breaking rules of social contracts), "free riders" (seek benefit without incurring personal costs), and "defectors" (individuals who benefit from the group's performance but leave the group as soon as they should increase their personal costs). As social contracts are a fundamental component of modern societies, social goals determine a large proportion of our everyday behavior. The domain of social cognition summarizes neuropsychological functions that support the planning and achievement of these goals, and distinct functions encompass the recognition of emotions (from visual or auditory features), the regulation of emotions, Theory of Mind (*i.e.*, predict actions based on other individuals′ beliefs and desires), and mirroring (*i.e.*, empathize with other individuals′ emotions by motor resonance) (3). These functions have a predictive value for many aspects of life including academic achievement (4), relationships with peers (5), and career success (6). Social cognition also is associated with mental health, given that general impairments in this domain and difficulties in socioemotional processing are transdiagnostic outcomes of mental (*e.g.*, major depressive disorder, bipolar disorder), developmental (*e.g.*, attention deficit hyperactivity disorder, autism disorder) and neurological disorders (*e.g.*, Alzheimer disease, Parkinson disease) (7,8).

Beyond physical health, physical activity and exercise have known benefits for mental health across different age groups. The promotion of cognitive resources is one of many ways by which the engagement in these behaviors may influence mental health. In this respect, meta-analytical findings suggest that acute and long-term exercise elicit improvements in cognitive domains spanning attention (*i.e.*, active processing of specific information), memory (*i.e.*, encoding, consolidation, and retrieval of information), and executive function (*i.e.*, top-down control of behavior) (9,10). In contrast, the potential of physical activity and exercise to benefit social cognition has been overlooked so far. Instead, their association traditionally has been investigated from a different perspective. Models that build on social cognition have been used to predict and understand the engagement in and adherence to physical activity across healthy and clinical populations (11). Further pursuing this line of research, the role of personality traits linked with social cognition (*e.g.*, extraversion, which is characterized by seeking social interactions) for understanding interindividual differences in physical activity and sport preferences (12) also has received much attention in the last decade. This may be because of the fact that from a clinical perspective, social cognition mainly was attributed to personality. However, the actual guidelines for classifying neurocognitive deficits (part of Diagnostic and Statistical Manual of Mental Disorders, 5th edition) recognizes social cognition as a separate cognitive domain alongside executive function, complex attention, perceptual-motor function, language, learning, and memory (3). This also indicates a higher sensitivity of social cognition for changes given that cognitive abilities are interpreted as being more dynamic and adaptive than personality. Consequently, it may no longer be accurate to only focus on the predictive role of social cognition and related aspects for physical activity and exercise.

Giving rise to a reversed perspective, our review investigates the novel hypothesis that engagement in physical activity and exercise elicits changes in social cognitive abilities, especially the recognition and regulation of emotions, as well as Theory of Mind. Based on neurobiological models that take evolutionary influences into account, we highlight features of the (autonomous and central) nervous system and modulating influences of neuropeptides that determine social cognition but at the same time share a sensitivity to acute and regular physical activity and exercise (Fig. 1). We further support our novel hypothesis by reviewing the recent literature that investigated the association of these behaviors or its correlates (*i.e.*, aspects of physical fitness) and specific aspects of social cognition.

AUTONOMIC FUNTION AND SOCIAL COGNITION

Evolution of a Social Engagement System

Social cognition is a complex and adaptive set of abilities that underlies the influence of a variety of factors. Rather than disentangling this complexity, we discuss the pathways by which physical activity and exercise may influence social cognition. The adaptive nature of the nervous system is a precondition for physical activity to induce changes in this cognitive domain immediately when becoming active or after a period of regular engagement. With regard to autonomic function, the flexible modulation in response to changing internal and external demands has evolved early when mammals, compared with their reptilian ancestors, engaged more in social behaviors (*e.g.*, cooperation and coordination) (13). The occurrence of such behaviors required the downregulation of dominant defensive reactions by an autonomic nervous system that responds more flexibly to the current demands. According to the Polyvagal Theory (14), the autonomic nervous system retained defensive systems (*i.e.*, fight-or-flight mode and death-feigning behavior) but developed a social engagement system to account for these demands. The brain stem regulation of the vagus nerve and muscles of the face and head in particular form an integrated system that supports social behavior. The theory further posits that the activity of the defensive and social engagement systems change dynamically based on environmental challenges and signals from internal organs — when the environment or condition is safe, a state of autonomic balance primes the autonomic nervous system to support health, growth, and restoration. In contrast, the dampening or withdrawal of vagus nerve activity leads to a recruitment of one of the primary defense strategies. Whereas an increase in sympathetic activity contributes to mobilization (fight or flight), its depression along with increased dorsal vagal influence leads to immobilization strategies (fainting, defecation) (14).

Going beyond a theoretical level, studies have used different proxies to gain further insights into the association between

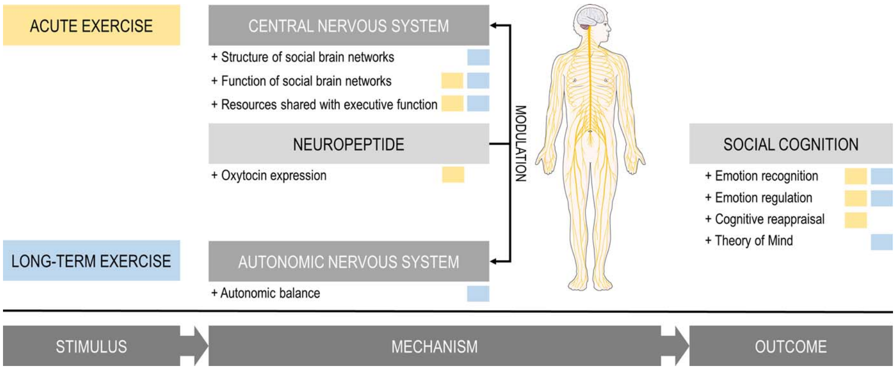

Figure 1. Proposed pathways by which physical activity and exercise promote social cognition. Acute and regular engagement in these interventions may promote social cognition by a facilitation of both shared and distinct pathways to social cognition. Whereas both paradigms seem to promote central nervous system functions, different effects are suggested for the neuropeptide oxytocin and the autonomous nervous system function. Notes: Based on the current evidence, the squares indicate which physical activity and exercise paradigm has been associated with the mechanism and outcome.

autonomic function and social cognition. In this respect, heart rate variability (HRV) is the most prominent marker and describes the beat-to-beat variation of a time series in the electrocardiogram. Whereas high HRV indicates an inhibition of the sinoatrial node (responsible for pace of heartbeats) by increased vagal tone, low HRV signals a reduced regulation of autonomic functions (15). The autonomic state is adaptive, meaning that a calm visceral state is maintained when the environment is considered safe, but metabolic output is changed rapidly in a situation that threatens safety (16). In support of the hypothesis that the social engagement system is dominant during autonomic balance, high-frequency HRV, indexing dominance of parasympathetic activity, has been linked with the recognition of emotions (17). In turn, emotion regulation difficulties, especially the inability to accept negative emotions, have been related to a withdrawal of parasympathetic activity (18). This association emerged not only from resting-state recordings but also ambulatory assessments that measured HRV continuously through 24 h. Experimental findings further support causality because transcutaneous stimulation of the vagus nerve enhanced the recognition of emotions from facial cues (19). Interestingly, there is a strong evidence base that suggests physical activity and (endurance) exercise directly influence autonomic function (20,21). Consequently, related processes that are indexed by HRV may serve as a mechanism by which these behaviors can impact on social cognition.

Exercise and Autonomic Function

When describing the HRV response to exercise, there is a need to differentiate between acute and long-term effects. A recent review of the existing experimental evidence showed that endurance exercise, coordinative exercise, and multicomponent training improved autonomic control as indexed by an increase in HRV at rest (21). In many included studies, a change toward increased HRV was accompanied by improvements in aerobic fitness and other factors associated with physical health. This relation between fitness and HRV is supported further by meta-analytical findings showing that athletes are characterized by a higher parasympathetic activity than nonathletes (22). Consequently, improvements in physical fitness after physical activity and exercise are expected to promote a state of autonomic balance that may translate into an optimal condition for the social engagement system according to the Polyvagal Theory (14).

Long-term effects of exercise and physical activity on HRV differ from the changes that can be observed in response to a single exercise bout. A recent review highlighted a pronounced dose-response relation for the acute effects of a single endurance exercise session (20). Indicating a parasympathetic withdrawal, HRV decreases in a curvilinear trend with no further or only minimal decreases beyond moderate-to-high intensity. Moreover, prolonged duration also seems to decrease HRV because of increasing internal load, especially when the intensity does not exceed moderate-to-high intensity. The qualitative synthesis further revealed that intensity determines the postexercise recovery in a way that higher intensity prolongs the time needed to return HRV to baseline. Most experimental studies investigating acute effects of exercise on cognitive performance have performed cognitive testing in this time window (*i.e.*, 10 or more min after exercise) (10). The particular focus on the recovery period is probably because of the assumption that acute cognitive benefits are of practical relevance, if they remain as long as possible after the cessation of exercise. Applying the Polyvagal Theory (14), a more pronounced withdrawal of parasympathetic activity after higher exercise intensity is expected to downregulate the social engagement system. This may eventually lead to detrimental effects on social cognition unless cognitive testing is postponed until HRV has recovered. Even if acute exercise does not induce autonomic balance, a temporary enhancement for social cognition also can be promoted by other mechanisms.

CENTRAL NERVOUS SYSTEM AND SOCIAL COGNITION

Evolution of Social Brain Networks

Similarly to the autonomous nervous system, the need to cope with increasingly complex social systems also influenced the central nervous system. The observation of disproportionally large brains for body size in primates compared with all other vertebrates led to the Social Brain Hypothesis (1). This theory posits that brain regions underpinning social cohesion and cognition evolved to deal with predation and allow for a transmission of foraging skills. Indeed, a meta-analysis of neuroimaging findings verified that large parts of the brain are involved in social cognition, with four networks contributing to its associated subdomains (23). This encompasses the amygdala network including amygdala and orbitofrontal regions, the mentalizing network including medial prefrontal and superior temporal regions, the empathy network with insula and amygdala regions, and the mirror network including prefrontal and parietal regions (Fig. 2). The structure-function relation is supported by the observation that damage to these structures leads to specific social deficits so that, for example, lesions of the amygdala are associated with impaired recognition of emotions and fear in particular (23). The composition of the four networks further supports that unimodal (*i.e.*, regions involved in sensory processing) and transmodal cortices (*i.e.*, regions sharing high interconnectivity and top-down modulation) interact when social cognitive functions are demanded. Unimodal cortices, including contributions of the insula, are associated with autonomic system-mediated changes during abstract and social cognition tasks (26). This underlines contributions of both the autonomous and central nervous system, as well as their interaction to functions summarized under the domain of social cognition.

Exercise and Brain Health

Physical activity and exercise have received growing attention in both exercise science and neuroscience because of its potential to promote brain health. Changes in brain regions that are part of social cognition networks provide a pathway by which long-term engagement in these behaviors influences associated functions. Evidence on the effects of physical activity and exercise on brain structure and function mainly has been obtained from children and adolescents, as well as older adults. This may be because of the assumption of a higher relevance and sensitivity of brain structure and function among developing individuals or those affected by cognitive aging. A synthesis of the experimental evidence in youth indicates that regular engagement in physical activity and exercise increased the activation of several regions including the frontal lobe, parietal lobe,

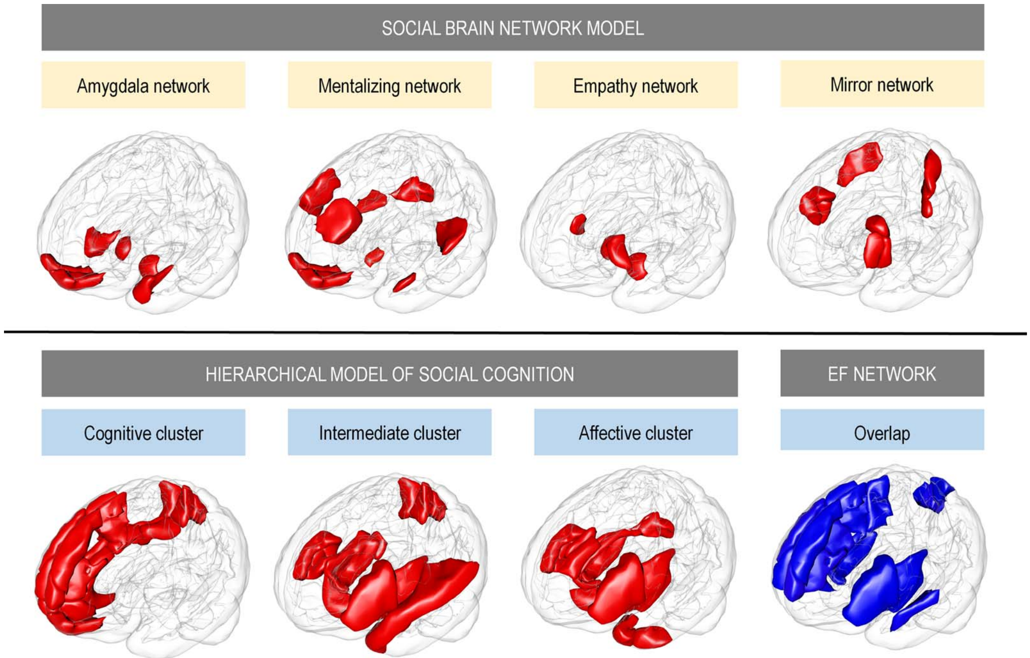

Figure 2. Main regions and networks that contribute to social cognition based on the Social Brain Network Model and the Hierarchical Model of Social Cognition, as well as overlapping regions with the Executive Function (EF) Network. Notes: The regions highlighted in both models are main contributors to the networks and clusters based on the original description of the models (23,24), meaning that not necessarily all contributing regions (or parts of regions) are shown. The regions highlighted in EF Network are those that overlap between the Hierarchical Model of Social Cognition and the EF Network (25). Brain images were created with the Scalable Brain Atlas (available from https://scalablebrainatlas.incf.org).

and anterior cingulate cortex (27). These intervention types influenced a similar set of regions among older adults. Based on a review of both cross-sectional and longitudinal studies, physical activity and exercise were related to increased gray matter volume and activity in frontal, temporal, and parietal lobes (28,29). These regions show a significant overlap with the mentalizing and mirroring networks (23) suggesting that physical activity and exercise may alter abilities that encompass the inference of actions from emotions and motor resonance.

Although a facilitation of brain structure may require regular engagement in physical activity and exercise, temporary changes in brain function may be stimulated by a single exercise session. It should be noted, however, that the studies in this field of research have mainly focused on changes within the frontal lobe (induced by aerobic activities). The Reticular-Activating Hypofrontality Model of Acute Exercise provides a framework that predicts the neurocognitive consequences of different exercise intensities (30). According to this model, the functions of the frontal lobe and the prefrontal cortex in particular need to change at higher motor demands because of limited resources of the brain. Whereas moderately intense exercise engages arousal processes that facilitate information processing, higher intensities require a downregulation of brain regions and function that are not crucial for maintaining the movement. The theory further suggests that the downregulation follows a hierarchical order, with higher order cognitive functions related to the prefrontal cortex being affected first by the metabolic demands of high exercise intensity. The changes that occur during an exercise bout are expected to influence brain function after its cessation. Comparing different exercise intensities, moderately intense endurance exercise elicited a greater recruitment of the prefrontal cortex during a subsequent cognitive task relative to an exercise bout performed at high intensity (31). The facilitation of brain function after moderate endurance exercise further seems to extend to other regions involved in the mirror neuron network. Independent from the individual fitness level, an increased activation of inferior frontal gyrus and premotor areas during an observe-and-execute paradigm was reported after moderate endurance exercise (32). This indicates a potential pathway by which acute exercise may influence social cognitive abilities related to mirroring and motor resonance in particular.

Shared Cognitive Processes

Although the initial differentiation of four social cognition networks holds information on brain regions involved in specific processes, a more recent framework proposes a three-cluster structure that reflects the contribution of different neurocognitive processes (24). According to this framework, cognitive processes are used when mentalizing demands self-generated cognition decoupled from the physical world, whereas affective processes are engaged when emotions of other individuals are recognized based on shared emotional, motor, and somatosensory representations. In addition, combined processes summarize situations requiring both cognitive and affective functions simultaneously. Comparing the clustered structures that were derived from the three types of processes (Fig. 2), the cognitive component is based mainly on regions engaged during conscious processing and top-down guidance of behavior (*i.e.*, executive function). This applies to prefrontal cortex regions, the anterior cingulate cortex, and precuneus in particular because these regions are recruited (along with the parietal lobe) during tasks tapping into executive function (25). Consequently, social cognition and executive function may be defined as different cognitive domains, but some functions rely on shared, more abstract cognitive processes. This partly explains why executive function is associated with both basic (*e.g.*, emotion recognition) and complex (*e.g.*, Theory of Mind) social cognitive functions (33,34). Based on the link between both cognitive domains (Supplemental Digital Content 1, Table S1, http://links.lww.com/ESSR/A59), it might be assumed that improvements in executive function may to some extent translate into social cognition benefits.

Exercise and Executive Function

Compared with the limited evidence of physical activity and exercise on brain structure and function, there is much evidence on the effects of both interventions on behavioral performance in cognitive tasks (Supplemental Digital Content 1, Table S2, http://links.lww.com/ESSR/A59). Our quantitative synthesis of experimental studies showed that exercise programs lasting at least 4 wk elicited small benefits for executive function, attention, and memory across all age groups (9). Metaregressive analyses further revealed that exercise type was a primary moderator of these benefits. In this respect, coordinative exercise seemed to be more effective than endurance, resistance, or mixed exercise. Consequently, coordinative exercise may be expected to promote social cognition by improving a related cognitive domain (executive function). In contrast, much research suggests that endurance exercise benefits autonomic functions relevant to social cognition (20). Thus, different exercise types may have the potential to influence this cognitive domain by distinct pathways.

Moreover, possible mechanisms may differ between the paradigms used (acute vs long-term interventions). In contrast to the small long-term effects of endurance exercise on executive function and other cognitive domains, our meta-analysis indicates moderate effect sizes after a single endurance exercise session (at least in children and older adults) (10). These results suggest that exercise-induced benefits for executive function may partly translate into improved social cognition, but the exercise type that promises such benefits varies based on the paradigm used.

NEUROMODULATION BY OXYTOCIN

Oxytocin and Social Attachment

The autonomous and central nervous system may be primary pathways by which physical activity and exercise may influence social cognition. However, engagement in these behaviors also has the potential to induce changes in this cognitive domain by acting on secondary factors that modulate the nervous system. This applies to specific agents of the family of neuropeptides, which have been integral to reproduction and survival throughout evolution. Among them, a review suggests that oxytocin and its related peptide vasopressin in particular have contributed to social attachment and the expression of human sociality (35). This was explained by the promotion of an emotional sense of safety and the unique role of oxytocin in the facilitation of birth, lactation, maternal behavior, regulation of the growth of the neocortex, and the blood supply to the cortex. From an evolutionary perspective, these functions probably allowed for extended periods of nurture critical for the emergence of human intellectual development. Given the modulating role of oxytocin for the nervous system, a review suggested it as pathway to social cognition through the formation and maintenance of affiliative, cooperative relationships in different situations (36). This supportive effect of oxytocin was further related to an increased sensitivity to social rewards and social threats along with a reduction of thresholds for mentalistic cognitive and affective social information processing. Initial research into the association of oxytocin levels and social cognition was conducted in individuals with psychiatric disorders, meaning that an altered concentration of this neuropeptide could be seen as a trait. However, experimental studies extended this line of research by focusing on the effects of manipulating the oxytocin levels. A review of such experimental evidence showed that intranasal administration of oxytocin elicits benefits for social cognition including the recognition, processing, and interpretation of emotions from social cues (*e.g.*, faces, words) (37). Consequently, changes in oxytocin levels can directly translate into altered behavior and performance on tasks tapping into aspects of social cognition.

Exercise and Oxytocin Expression

In contrast to the effects of physical activity and exercise on the functions of the autonomous and central nervous system, less is known on how behaviors may influence neuropeptides. This applies to the long-term effects in particular, meaning that the influence of regular engagement in physical activity or exercise on oxytocin has not been examined in humans so far. However, animal studies provide a first indication that the concentration of this neuropeptide can be facilitated. In this respect, aerobic exercise has been found to upregulate brain or serum oxytocin levels in both female and male mice (38). Similarly, an aerobic exercise program (at moderate intensity) increased oxytocin expression in rats, but it should be noted that this effect was restricted to a subgroup showing sedentary behavior before the intervention (39). Consequently, it cannot be ruled out that oxytocin responds to a change toward an active lifestyle, but its concentration may not show a linear increase with total physical activity or exercise volume.

With regard to acute effects of physical activity and exercise, there is accumulating evidence from human populations suggesting immediate changes in oxytocin levels. Only 10 min of moderate endurance exercise led to an increased concentration of oxytocin in both male and female adults, and this elevation was maintained at least 30 min after completion of the exercise bout (40). Similarly, an upregulation of oxytocin was also found after prolonged endurance exercise (41). The expression of this neuropeptide does not seem to be sensitive to endurance exercise only because martial arts training at high intensity also led to an elevated concentration of oxytocin in saliva (42). A subsequent analysis of training forms further highlighted that ground grappling, which required close-contact tactile interaction, had a more pronounced effect on oxytocin than sparring while standing. These findings underline that a single exercise stimulates the expression of oxytocin, but the limited number of studies allow no conclusions on the exercise characteristics that serve as primary moderators of the response of this neuropeptide.

BEHAVIORAL EFFECTS OF EXERCISE ON SOCIAL COGNITION

Long-Term Effects

Evolution has shaped several pathways to promote social cognition, and some of them are sensitive to physical activity

TABLE 1. Overview of studies investigating the association of physical activity, exercise and fitness, and social cognition (emotion recognition and regulation)

Author, Year	Sample	Design	Exposure or Focus	Cognitive Task	Outcome
Alarcon-Jimenez *et al.*, 2020 (43)	*N* = 60 f Age = 71.5 ± 4.8 yr $PA_{Baseline}$ = mixed	Cross-sectional	Accelerometer-based physical activity through 7 d	Reading the Mind Through the Eyes Test (36 trials)	Association: (+) VPA & accuracy (0) MVPA & accuracy
Cliff *et al.*, 2017 (44)	*N* = 107 f / 141 m Age = 4.2 ± 0.6 yr $PA_{Baseline}$ = mixed	Cross-sectional	Accelerometer-based physical activity through 24 h	Children-appropriate Theory of Mind task (5 trials); Test of Emotion Comprehension (23 trials)	Difference: (0) Theory of Mind and emotion understanding in children meeting vs not meeting PA guidelines
Ishihara *et al.*, 2022 (45)	*N* = 550 f / 477 m Age = 28.8 ± 3.7 yr $PA_{Baseline}$ = mixed	Cross-sectional	Physical fitness (submaximal endurance, gait speed, dexterity, muscular strength)	Animacy perception (10 trials) & emotion recognition from faces (40 trials)	Association: (+) Physical fitness & animacy perception, emotion recognition
Lott & Jensen, 2017 (46)	*N* = 146 f / 132 m Age = 9.7 ± 0.9 yr $PA_{Baseline}$ = mixed	Cross-sectional	Maximal exercise test (shuttle run)	Parent reporting on Emotion Regulation Checklist	Association: (+) $_e\dot{V}O_{2max}$ & ERC (lability/negativity) (0) $_e\dot{V}O_{2max}$ & ERC (emotion regulation)
Ludyga *et al.*, 2020 (47)	*N* = 71 f / 127 m Age = 38.6 ± 0.7 yr $PA_{Baseline}$ = mixed	Cross-sectional	Submaximal exercise test (ergometer cycling)	Emotion recognition (labeling/ matching) from faces/ eyes (practice +160 trials)	Association: (+) $_e\dot{V}O_{2max}$ & accuracy (controlling for reaction time)
Ludyga *et al.*, 2022 (48)	*N* = 67 f / 46 m Age = 13.0 ± 1.3 yr $PA_{Baseline}$ = mixed	Cross-sectional	7-d physical activity recall	Emotion recognition (labeling/ matching) from faces/ eyes (practice +80 trials)	Association: (0) MVPA & accuracy, reaction time
Zhang *et al.*, 2019 (49)	*N* = 60 f Age = 23.2 ± 1.5 yr $PA_{Baseline}$ = low	Experimental (2 groups)	I: 40-min jogging at moderate intensity and 60-min yoga (alternating) 3 times per wk through 8 wk C: Passive	Emotion regulation in response to affective pictures (40 trials)	Pre vs post: (+) Emotion regulation in I vs C

For outcomes, the direction of effects or associations are indicated by (−), decrease or inverse association; (0), no change or association; and (+), increase or positive association.

C, control group or condition; $_e\dot{V}O_{2max}$, estimated maximal oxygen consumption; I , intervention group or condition; MVPA, moderate-to-vigorous physical activity; $PA_{Baseline}$, baseline physical activity levels; VPA, vigorous physical activity; ERC, Emotion Regulation Checklist.

and exercise. Even though this highlights the potential for these behaviors to facilitate social cognition, studies applying a mechanism-based approach are lacking. Instead, the few studies that are available investigated the relation of physical activity, exercise, and their correlates with aspects of social cognition mainly on a behavioral level. This lack of a mechanism-based approach may limit causal inferences, but provides first indications on whether our novel hypothesis can be supported. With one exception, the sensitivity of social cognition to long-term exercise and physical activity was investigated using a cross-sectional design (Table 1). In contrast to our hypothesis, moderate-to-vigorous physical activity and the compliance with the recommended amount was not associated with emotion recognition and Theory of Mind in children and preadolescents (44,48). However, further differentiating the intensity of physical activity led to a different pattern of results in older adults. Although engagement in moderate physical activity still showed no association with aspects of social cognition, improved Theory of Mind abilities were found in individuals who spent more time in vigorous physical activity (43). Because higher intensities are considered to produce larger gains in physical fitness, these gains may be necessary to influence social cognition. This is supported by cross-sectional findings showing that higher aerobic fitness in children and adults is linked with better emotion recognition and regulation (46,47). However, other aspects of physical fitness, such as muscle strength and hand dexterity, have also been related to this subdomain of social cognition (45). The role of aerobic fitness in particular is further underlined in an experimental study that focused on emotion regulation. After 8 wk of an exercise program that included aerobic exercise and yoga, gains in aerobic fitness mediated the social cognition benefits of the intervention (49).

Our qualitative synthesis suggests that (aerobic) fitness rather than physical activity levels are associated with social cognition. This provides a first indication that long-term effects for this cognitive domain may be expected after exercise programs that target and effectively improve aerobic fitness. Conversely, this also implies that an increase in physical activity may not provoke improvements in social cognition unless it reaches an intensity that promotes aerobic fitness. The sensitivity of emotion recognition and regulation to aerobic fitness across different age groups provides an indication on the mechanisms triggering changes in behavioral performance. Both aerobic exercise and increased aerobic fitness have been associated with increased HRV (21), which in turn serves as a predictor of social cognitive abilities. In addition, most studies that informed long-term effects of physical activity and exercise on brain regions that are involved in the social brain networks have included interventions with a primary focus on aerobic fitness (27,29). Consequently, both the brain structure and function association of the social brain and assumptions made under the Polyvagal Theory might be applied to predict long-term benefits of exercise for social cognition.

Acute Effects

Compared with the long-term effects, the strength of the evidence for the acute effects of exercise on social cognition is higher because of the implementation of experimental designs and a more consistent pattern of results (Table 2). In adults, studies comparing an endurance exercise session at submaximal intensity with an active or passive control condition found improvements in both emotion recognition and regulation (50,51). Contrasting individuals with low and high physical activity, exercise-induced benefits for emotion regulation were

TABLE 2. Overview of studies investigating the effects of acute physical activity and exercise on social cognition (emotion recognition and regulation)

Author, Year	Sample	Design	Exposure	Cognitive Task	Outcome
Aguirre-Loaiza *et al.*, 2019 (50) Experiment 1	*N* = 54 Age = 20.7 ± 2.5 yr $PA_{Baseline}$ = high	Between-participants design (2 groups)	I: 45-min ergometer cycling at 75%–85% $_{e}HR_{max}$ C: 45-min passive	Emotion recognition from body and face (80 trials)	Pre vs post: (−) Error rate in I (0) Error rate in C
Aguirre-Loaiza *et al.*, 2019 (50) Experiment 2	*N* = 36 Age = 21.6 ± 1.8 yr $PA_{Baseline}$ = low	Between-participants design (2 groups)	I: 30-min ergometer cycling at 75%–85% $_{e}HR_{max}$ C: 30-min passive	Emotion recognition from body and face (80 trials)	Pre vs post: (0) Error rate in I and C
Bernstein *et al.*, 2017 (51)	*N* = 40 f / 40 m Age = 22.3 ± 15.4 yr $PA_{Baseline}$ > low	Between-participants design (2 groups)	I: 30-min jogging at moderate intensity C: 30-min stretching at light intensity	Difficulties in Emotion Regulation Scale after negative mood induction (video)	Pre vs post: (−) Difficulties in emotion regulation in I vs C
Brand *et al.*, 2019 (52)	*N* = 65 f / 41 m Age = 13.0 ± 1.2 yr $PA_{Baseline}$ = mixed	Between-participants design (3 groups)	I1: 35-min aerobic exercise (relay games) at moderate intensity I2: 35-min aerobic exercise with coordinative demands (relay games) at moderate intensity C: 35-min stretching at light intensity	Emotion recognition (labeling/ matching) from faces/ eyes (practice +80 trials)	Pre vs post: (−) Reaction time in I1, I2 vs C (0) Accuracy in I1, I2 vs C
Edwards *et al.*, 2017 (53)	*N* = 27 Age = ? $PA_{Baseline}$ = mixed	Between-participants design (3 groups)	I1: 15-min walking at light intensity I2: 15-min jogging at moderate intensity C: 15-min stretching at light intensity	Affective Circumplex Scale after negative mood induction (video)	Pre vs post: (−) Negative affect in C vs I1, I2
Giles *et al.*, 2018 (54)	*N* = 21 f / 15 m Age = 23.4 ± 3.6 yr $PA_{Baseline}$ = high	Within-participants design (2 conditions)	I1: 90-min walking at light intensity I2: 90-min running at moderate intensity	Cognitive reappraisal in response to affective pictures (72 trials)	Post: (+) Reappraisal success in I2 vs I1 (in participants who adhered to cognitive reappraisal only)

For outcomes, the direction of effects are indicated by (−), decrease; (0), no change; and (+), increase.

C, control group or condition; $_{e}HR_{max}$, estimated maximal heart rate; I, intervention group or condition; $PA_{Baseline}$, baseline physical activity levels.

only observed in physically active adults (50). In addition to such interindividual differences, a few studies have also examined the potential moderating roles of exercise intensity and coordinative demands. In comparison with an active control condition, both light and moderate endurance exercise of more than 15 min led to improvements in emotion regulation after negative mood induction (53). In contrast, a moderating effect of exercise intensity was indicated when the exercise bout was prolonged. After 90 min of moderately intense endurance exercise, adults showed a higher reappraisal success than after light endurance exercise of the same duration (54). Given that these findings are based on studies with adults, it remains unclear if exercise intensity also moderates exercise-induced benefits for social cognition in children. However, the limited evidence available in developing individuals has focused on the role of coordinative demands. In a previous study, we investigated the effects of moderate endurance exercise with and without additional coordinative demands on emotion recognition in preadolescent children. Relative to a an active control condition, both exercise interventions elicited benefits for this aspect of social cognition with no differences in effectiveness between them (52).

In summary, these findings suggest that improvements in emotion recognition and regulation can be expected after a single endurance exercise performed at moderate or higher intensity. The parasympathetic withdrawal induced by these exercise intensities has been linked with a decreased influence of the social engagement system according to Polyvagal Theory, meaning that such an immediate and temporary change in autonomic balance cannot explain the acute benefits for social cognition. We rather suggest that a modulation of the central nervous system provides a pathway by which a single exercise session benefits cognitive abilities such as emotion recognition and regulation. Compelling evidence suggests that executive function, which shares cognitive processes with social cognition, improves after a single exercise session at moderate intensity (10). Thus, similar effects for social cognition may be cause partly by an improvement in shared resources that translates into cognitive enhancements across both domains. This is further supported by evidence highlighting an acute exercise-induced facilitation of brain regions, which are overlapping between social brain and executive function networks. In addition, a single bout of endurance exercise may indirectly influence functions of the central nervous system by increasing oxytocin levels (36). Increased expressions of this neuropeptide have been detected even after short exercise periods (40), suggesting a potential contribution to the benefits for emotion recognition and regulation benefits observed after 15 to 90 min of endurance exercise.

Perspectives for Future Research

The few studies that investigated the acute effects of exercise on social cognition provide initial evidence for beneficial effects on emotion recognition and regulation. Similarly, cross-sectional findings (and a single experimental study) linking vigorous physical activity and aerobic fitness with these functions provide first indications that long-term effects on social cognition can be expected. However, these findings cannot inform on whether the relation between exercise and social cognition can be characterized as direct or indirect, given that associations have been examined on behavioral level only. The functions of the autonomic and nervous system that determine social cognitive abilities, but at the same time are sensitive to physical activity and exercise, may serve as moderators or mediators of this association. To gain a better understanding of the effects of both intervention types on social cognition and allow for casual inferences, we encourage future studies to use randomized controlled trials or crossover designs along with a mechanism-based approach. In this respect, interventions should be designed to elicit and control changes (via a manipulation check) in autonomous and central nervous system functions or modulating factors such as neuropeptides. Using mediation and moderation models (especially on studies with interim assessments), these changes need to be associated with potential benefits of the intervention for behavioral performance on tests of social cognition.

To delineate different pathways to social cognitive benefits, we further recommend systematic manipulation of exercise characteristics, including dose parameters (frequency, duration, intervention length, intensity) and intervention types. This is necessary because the current evidence already highlights that the autonomous and central nervous functions that contribute to social cognition are sensitive to some of these characteristics. Their systematic manipulation is expected to reveal whether there is a primary mechanism by which physical activity and exercise operate social cognition or whether different dose constellations trigger distinct pathways. With regard to the intervention type, our review of the available evidence indicates a strong focus on endurance exercise and its correlate aerobic fitness in previous research. This might be explained by a high number of studies supporting that aerobic exercise leads to benefits for other cognitive domains (executive function, attention, and memory). Moreover, the ability to control and adjust dose parameters more easily in aerobic exercise compared with mixed or other exercise types is a clear advantage that encourages its use in experimental studies especially those investigating dose-response relations. However, it should be noted that some pathways to social cognition are more pronounced by other exercise types. For example, our metaregression indicated that long-term coordinative exercise promises greater benefits for executive function and other cognitive domains (9). Based on the idea of shared neural processes, it is likely that such benefits may also translate into improvements in social cognition. In addition to coordinative demands, exercise types requiring close contact, such as martial arts and dancing, may have the potential to promote functions summarized under this cognitive domain. This is because of the observation that close contact induced an increased oxytocin expression (42), which in turn is likely to influence social cognition. Moreover, exercise that promotes social engagement and interaction, such as team-based and group-based training programs, may contribute to improvements in social cognition. This is because of the reliance of social interaction on the complex interplay of processes summarized under social cognition (55). Taken together, these findings suggest that future works should not focus soley on endurance exercise but also extend the focus to other exercise types that are expected to influence factors linked with social cognition.

A known moderator of cognitive enhancements after physical activity and exercise (at least for the acute exercise paradigm) is age, given the disproportionate effects in developing individuals and those affected by an age-related decline in cognition (10). The few studies that investigated the effects or associations of these behaviors with social cognition have included mainly young adults. Thus, it remains unclear if findings can be generalized to other age groups and if the developmental state and maturation processes influence possible exercise-induced benefits for social cognition. Although the evidence we reviewed was limited to healthy populations, we note that there are studies that have investigated effects of physical activity and exercise in clinical samples characterized by deficits in social cognition. By comparing potential benefits of these interventions between healthy and clinical populations, the question whether physical activity and exercise have normalizing or enhancing effects on social cognition can be addressed. We recommend experimental studies to include subgroup analyses for interindividual differences on age and baseline cognition to reveal who can actually expect (the most) benefits for social cognition.

Even though we hypothesized that physical activity and exercise benefit social cognition, the limited evidence does not allow predictions on associated functions that are more sensitive to these interventions. This is because of previous studies focusing mainly on emotion recognition and regulation in particular. Complex social cognitive abilities, such as Theory of Mind, mirroring, and developing insight, rarely have been investigated, and results are inconsistent. Although these abilities, in part, also may rely on emotion recognition and regulation, it remains unclear whether physical activity and exercise induce a more general or specific (*i.e.*, limited to one or more subdomains) effect on social cognition. Future research can address the nature of the effect by using tasks that assess different social cognitive abilities and comparing the relative effectiveness of interventions between these tasks. Moreover, the measured subdomains of social cognition must also be considered in studies using a mechanism-based approach because their sensitivities to autonomous and central nervous system functions may differ.

CONCLUSION

Physical activity and exercise behaviors are not only a consequence of personality traits linked with social cognition. Because there is much potential that physical activity and exercise interventions also influence this cognitive domain, their relation seems to be biderectional. This further extends the role of these interventions for the promotion of mental health by showing that benefits may not be limited to more abstract cognitive functions. The ability to enhance social cognition by engagement in physical activity and exercise has implications for many aspects of life, for example, peer relationships and acceptance, academic performance, as well as career success. Even improvements in social cognition after single exercise bouts have a practical relevance because they might be used to temporarily enhance abilities crucial for social interactions, which might help individuals of different societies and cultures to connect.

We suspect that physical activity and exercise may promote social cognition by pathways that primarily evolved because of the necessity to cope with increasingly complex social systems. These pathways include not only functions of both the autonomous and central nervous system, but also the neuromodulating effects of the neuropeptide oxytocin. Initial evidence suggests that acute endurance exercise elicits immediate benefits for emotion recognition and regulation. Increases in aerobic fitness because of regular endurance exercise type may further promise long-term effects for these aspects of social cognition. Applying a mechanistic approach to the interpretation of these findings, acute and long-term physical activity and exercise seem to influence social cognition by both overlapping, but also distinct, pathways. In interdisciplinary collaborations, we encourage exercise scientists to investigate these pathways along with the behavioral effects of physical activity and exercise on social cognition.

References

1. Dunbar RIM. The social brain hypothesis and its implications for social evolution. *Ann. Hum. Biol.* 2009; 36(5):562–72.
2. Vlerick M. The evolution of social contracts. *Journal of Social Ontology*. 2020; 5(2):181–203.
3. Sachdev PS, Blacker D, Blazer DG, et al. Classifying neurocognitive disorders: the DSM-5 approach. *Nat. Rev. Neurol.* 2014; 10(11):634–42.
4. Derks J, Jolles J, van Rijn J, Krabbendam L. Individual differences in social cognition as predictors of secondary school performance. *Trends in Neuroscience and Education*. 2016; 5(4):166–72.
5. Caputi M, Lecce S, Pagnin A, Banerjee R. Longitudinal effects of theory of mind on later peer relations: the role of prosocial behavior. *Dev. Psychol.* 2012; 48(1):257–70.
6. Momm T, Blickle G, Liu Y, Wihler A, Kholin M, Menges JI. It pays to have an eye for emotions: emotion recognition ability indirectly predicts annual income. *J. Organiz. Behav.* 2015; 36(1):147–63.
7. Henry JD, Hippel Wvon, Molenberghs P, Lee T, Sachdev PS. Clinical assessment of social cognitive function in neurological disorders. Nat. Rev. Neurol. 2016;12(1):28–39.
8. Kret ME, Ploeger A. Emotion processing deficits: a liability spectrum providing insight into comorbidity of mental disorders. *Neurosci. Biobehav. Rev.* 2015; 52:153–71.
9. Ludyga S, Gerber M, Pühse U, Looser VN, Kamijo K. Systematic review and meta-analysis investigating moderators of long-term effects of exercise on cognition in healthy individuals. *Nat. Hum. Behav.* 2020; 4(6):603–12.
10. Ludyga S, Gerber M, Brand S, Holsboer-Trachsler E, Pühse U. Acute effects of moderate aerobic exercise on specific aspects of executive function in different age and fitness groups: a meta-analysis. *Psychophysiology*. 2016; 53(11):1611–26.
11. Young MD, Plotnikoff RC, Collins CE, Callister R, Morgan PJ. Social cognitive theory and physical activity: a systematic review and meta-analysis. *Obes. Rev.* 2014; 15(12):983–95.
12. Wilson KE, Dishman RK. Personality and physical activity: a systematic review and meta-analysis. *Personality and individual differences*. 2014; 72:230–42.
13. Porges SW. Social engagement and attachment: a phylogenetic perspective. *Ann. N. Y. Acad. Sci.* 2003; 1008:31–47.
14. Porges SW. The polyvagal theory: new insights into adaptive reactions of the autonomic nervous system. *Cleve. Clin. J. Med.* 2009; 76(Suppl 2):S86–90.
15. Shaffer F, Ginsberg JP. An overview of heart rate variability metrics and norms. *Front Public Health*. 2017; 5:258.
16. Smith TW, Deits-Lebehn C, Williams PG, Baucom BRW, Uchino BN. Toward a social psychophysiology of vagally mediated heart rate variability: concepts and methods in self-regulation, emotion, and interpersonal processes. *Soc. Personal Psychol. Compass*. 2020; 14(3):e12516.
17. Quintana DS, Guastella AJ, Outhred T, Hickie IB, Kemp AH. Heart rate variability is associated with emotion recognition: direct evidence for a relationship between the autonomic nervous system and social cognition. *Int. J. Psychophysiol.* 2012; 86(2):168–72.
18. Visted E, Sørensen L, Osnes B, Svendsen JL, Binder P-E, Schanche E. The association between self-reported difficulties in emotion regulation and heart rate variability: the salient role of not accepting negative emotions. *Front Psychol.* 2017; 8:328.
19. Sellaro R, de Gelder B, Finisguerra A, Colzato LS. Transcutaneous vagus nerve stimulation (tVNS) enhances recognition of emotions in faces but not bodies. *Cortex*. 2018; 99:213–23.
20. Michael S, Graham KS, Davis GM. Cardiac autonomic responses during exercise and post-exercise recovery using heart rate variability and systolic time intervals-a review. *Front Physiol.* 2017; 8:301.
21. Grässler B, Thielmann B, Böckelmann I, Hökelmann A. Effects of different exercise interventions on heart rate variability and cardiovascular health factors in older adults: a systematic review. *Eur. Rev. Aging Phys. Act.* 2021; 18(1):24.
22. Da Silva VP, de Oliveira NA, Silveira H, Mello RGT, Deslandes AC. Heart rate variability indexes as a marker of chronic adaptation in athletes: a systematic review. *Ann. Noninvasive. Electrocardiol.* 2015; 20(2):108–18.
23. Kennedy DP, Adolphs R. The social brain in psychiatric and neurological disorders. *Trends Cogn. Sci.* 2012; 16(11):559–72.
24. Schurz M, Radua J, Tholen MG, et al. Toward a hierarchical model of social cognition: a neuroimaging meta-analysis and integrative review of empathy and theory of mind. *Psychol. Bull.* 2021; 147(3):293–327.
25. Niendam TA, Laird AR, Ray KL, Dean YM, Glahn DC, Carter CS. Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions. *Cogn. Affect. Behav. Neurosci.* 2012; 12(2): 241–68.
26. Gasquoine PG. Contributions of the insula to cognition and emotion. *Neuropsychol. Rev.* 2014; 24(2):77–87.
27. Valkenborghs SR, Noetel M, Hillman CH, et al. The impact of physical activity on brain structure and function in youth: a systematic review. *Pediatrics*. 2019; 144(4):e20184032.
28. Domingos C, Pêgo JM, Santos NC. Effects of physical activity on brain function and structure in older adults: a systematic review. *Behav Brain Res*. 2021; 402:113061.
29. Chen F-T, Hopman RJ, Huang C-J, et al. The effect of exercise training on brain structure and function in older adults: a systematic review based on evidence from randomized control trials. *J. Clin. Med.* 2020; 9(4):914.
30. Dietrich A, Audiffren M. The reticular-activating hypofrontality (RAH) model of acute exercise. *Neurosci. Biobehav. Rev.* 2011; 35(6):1305–25.
31. Moriarty T, Bourbeau K, Bellovary B, Zuhl MN. Exercise intensity influences prefrontal cortex oxygenation during cognitive testing. *Behav Sci (Basel)*. 2019; 9(8):83.
32. Xu Z, Wang Z-R, Li J, Hu M, Xiang M-Q. Effect of acute moderate-intensity exercise on the mirror neuron system: role of cardiovascular fitness level. *Front Psychol.* 2020; 11:312.
33. David DP, Soeiro-de-Souza MG, Moreno RA, Bio DS. Facial emotion recognition and its correlation with executive functions in bipolar I patients and healthy controls. *J. Affect. Disord.* 2014; 152–154:288–94.
34. Wang Z, Devine RT, Wong KK, Hughes C. Theory of mind and executive function during middle childhood across cultures. *J. Exp. Child Psychol.* 2016; 149:6–22.
35. Carter CS. Oxytocin pathways and the evolution of human behavior. *Annu. Rev. Psychol.* 2014; 65:17–39.
36. Crespi BJ. Oxytocin, testosterone, and human social cognition. *Biol. Rev. Camb. Philos. Soc.* 2016; 91(2):390–408.
37. Guastella AJ, MacLeod C. A critical review of the influence of oxytocin nasal spray on social cognition in humans: evidence and future directions. *Horm. Behav.* 2012; 61(3):410–8.
38. Yüksel O, Ateş M, Kızıldağ S, et al. Regular aerobic voluntary exercise increased oxytocin in female mice: the cause of decreased anxiety and increased empathy-like behaviors. *Balkan Med. J.* 2019; 36(5):257–62.
39. Martins AS, Crescenzi A, Stern JE, Bordin S, Michelini LC. Hypertension and exercise training differentially affect oxytocin and oxytocin receptor expression in the brain. *Hypertension*. 2005; 46(4):1004–9.
40. de Jong TR, Menon R, Bludau A, et al. Salivary oxytocin concentrations in response to running, sexual self-stimulation, breastfeeding and the TSST: the Regensburg oxytocin challenge (ROC) study. *Psychoneuroendocrinology*. 2015; 62:381–8.
41. Hew-Butler T, Noakes TD, Soldin SJ, Verbalis JG. Acute changes in endocrine and fluid balance markers during high-intensity, steady-state, and prolonged endurance running: unexpected increases in oxytocin and brain natriuretic peptide during exercise. *Eur. J. Endocrinol.* 2008; 159(6): 729–37.
42. Rassovsky Y, Harwood A, Zagoory-Sharon O, Feldman R. Martial arts increase oxytocin production. *Sci. Rep.* 2019; 9(1):12980.
43. Alarcón-Jiménez JJ, Nielsen-Rodríguez A, Romance R, Gómez-Huelgas R, Bernal-López MR. Physical activity and social cognition in the elderly. *Sustainability*. 2020; 12(11):4687.
44. Cliff DP, McNeill J, Vella SA, et al. Adherence to 24-hour movement guidelines for the early years and associations with social-cognitive development among Australian preschool children. *BMC Public Health*. 2017; 17-(Suppl 5):857.
45. Ishihara T, Miyazaki A, Tanaka H, Matsuda T. Association of cardiovascular risk markers and fitness with task-related neural activity during animacy perception. *Med. Sci. Sports Exerc.* 2022;(Epub ahead of print).
46. Lott MA, Jensen CD. Executive control mediates the association between aerobic fitness and emotion regulation in preadolescent children. *J. Pediatr. Psychol.* 2017; 42(2):162–73.

47. Ludyga S, Schilling R, Colledge F, Brand S, Pühse U, Gerber M. Association between cardiorespiratory fitness and social cognition in healthy adults. *Scand. J. Med. Sci. Sports*. 2020; 30(9):1722–8.
48. Ludyga S, Gerber M, Brand S, Möhring W, Pühse U. Do different cognitive domains mediate the association between moderate-to-vigorous physical activity and adolescents' off-task behaviour in the classroom? *Br. J. Educ. Psychol.* 2022; 92(1):194–211.
49. Zhang Y, Fu R, Sun L, Gong Y, Tang D. How does exercise improve implicit emotion regulation ability: preliminary evidence of mind-body exercise intervention combined with aerobic jogging and mindfulness-based yoga. *Front Psychol.* 2019; 10:1888.
50. Aguirre-Loaiza H, Arenas J, Arias I, et al. Effect of acute physical exercise on executive functions and emotional recognition: analysis of moderate to high intensity in young adults. *Front. Psychol.* 2019; 10:2774.
51. Bernstein EE, McNally RJ. Acute aerobic exercise helps overcome emotion regulation deficits. *Cogn Emot.* 2017; 31(4):834–43.
52. Brand S, Gerber M, Colledge F, Holsboer-Trachsler E, Pühse U, Ludyga S. Acute exercise and emotion recognition in young adolescents. *J. Sport Exerc. Psychol.* 2019; 41(3):129–36.
53. Edwards MK, Rhodes RE, Loprinzi PD. A randomized control intervention investigating the effects of acute exercise on emotional regulation. *Am. J. Health Behav.* 2017; 41(5):534–43.
54. Giles GE, Eddy MD, Brunyé TT, et al. Endurance exercise enhances emotional valence and emotion regulation. *Front Hum Neurosci.* 2018; 12:398.
55. de Jaegher H, Di Paolo E, Gallagher S. Can social interaction constitute social cognition? *Trends Cogn. Sci.* 2010; 14(10):441–7.