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Review

Physical activity and interoceptive processing: Theoretical considerations for future research

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ABSTRACT

Interoception, defined as the sense of the internal bodily state, plays a critical role in physical, cognitive, emotional and social well-being. Regarding physical well-being, contemporary models of exercise regulation incorporate interoceptive processes in the regulation of physical exertion. Top-down processes continuously monitor the physiological condition of the body to ensure allostasis is maintained, however, flagged perturbations also appear to influence these higher order processes in return. More specifically, enhancing one's physiological arousal by means of physical activity is a viable way of manipulating the afferent input entering the interoceptive system, appearing to optimise the integration of early sensory stimulation with later affective responses. Despite this, the relationship between physical activity and top-down regulation is underrepresented in interoceptive research. We here address this gap by integrating findings from different disciplines to support the overlapping mechanisms, with the hope of stimulating further research in this field. Developing our understanding of how interoceptive processes are shaped by physical activity could hold significant clinical implications considering the impact of interoceptive deficits to mental health and well-being.

1. Introduction

Interoception encompasses the afferent sensing, central processing, and mental representation of our internal bodily signals (Craig, 2003; Critchley and Garfinkel, 2017), occurring across all major biological systems, e.g., cardiovascular, gastrointestinal and thermoregulatory. The processing and perception of afferent interoceptive information has been found to be of particular importance for many physical, cognitive and emotional aspects of self-regulation and well-being (Ardizzi et al., 2016; Khalsa et al., 2018). This has led researchers to investigate methods to systematically measure and modulate interoception, with previous studies demonstrating that both cognitive e.g., focus of attention (Ainley et al., 2013) and physiological e.g., induced physiological arousal through physical activity (Durlik et al., 2014; Jones and Hollandsworth, 1981) manipulations can be effective in altering interoceptive ability. Considering the latter, it is clear that physical activity, defined as any bodily movement produced by skeletal muscles that results in energy expenditure (Caspersen et al., 1985), manipulates the afferent input entering the interoceptive system, such as by inducing cardiovascular activation (Hossack, 1987), initiating a cascade of hormonal and metabolic responses (Winder et al., 1979), or by altering resting cardiovascular dynamics (Gregoire et al., 1996). By contrast, the regulation of physical exertion is under the constant control of the central nervous system, where interoceptive mechanisms monitor the physiological condition of the body to achieve allostasis and influence goal-directed behaviour (Craig, 2003; Craig, 2006). Despite this suggested dynamic relationship, there is limited research examining the mechanisms by which physical activity interacts with interoceptive processes, and to the best of our knowledge, no paper to date has reviewed the current research by incorporating findings from varying disciplines. The aim of this paper, therefore, is to integrate findings from different lines of research in support of this relationship, with the hope of bringing together the disciplines of physiology, exercise science, cognitive psychology, and psychophysiology to stimulate further research. In doing so, we argue that physical activity and interoceptive processing interact in a feedback loop (Fig. 1), where a more efficient processing of interoceptive information aids the regulation of exertion during physical activity (Herbert et al., 2007), whilst in turn, physical

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activity holds the potential to influence interoceptive processing (Georgiou et al., 2015; Montgomery et al., 1984).

We will first discuss the main features of interoception, giving an outline of its significance and a brief review of current methodological issues. Second, we will review the literature supporting the top-down regulation of physical activity, discussing the moderating role of interoceptive mechanisms. Third, we will go on to outline the potential ways in which physical activity alters the neurobiology of interoceptive processing. Finally, future suggestions will be outlined regarding the next steps in the development of this field of research, directing attention towards the development of physical activity-based interventions with an interoceptive focus.

2. Interoception

Interoception encompasses the afferent sensing and central processing of change in the internal milieu of the body (Craig, 2003; Vaitl, 1996). Primarily functioning below the realm of consciousness, interoceptive processes can also be accessible to ones' awareness when allostasis is compromised e.g., noticing your heart beating faster when you are afraid. Whilst serving as a homeostatic regulator at the basic physiological level, the psychological significance of interoceptive processing can be seen in its implications to emotion, cognition and behaviour (Tsakiris and Critchley, 2016), where it plays a key role in many self-regulatory mechanisms e.g., emotion processing (Critchley and Garfinkel, 2017; Füstös et al., 2013), decision making (Dunn et al., 2010; Werner et al., 2009) and the regulation of physical exertion (Georgiou et al., 2015; Herbert et al., 2007). Aberrant interoception impairs associative learning between external cues and internal states, preventing the contextualisation of interoceptive signals. This is problematic considering that the integration of interoceptive signals with other sensory information is thought to be necessary for self-other distinction (Quattrocki and Friston, 2014). This lack of integration can therefore result in a decreased sense of embodied self, reduced sensory attenuation and social difficulties (Murphy et al., 2017). Accordingly, interoception has been suggested to play an underlying role in the aetiology of numerous somatic-based mental health conditions e.g., panic disorder and anxiety (Ehlers and Breuer, 1992; Garfinkel et al., 2016b; Khalsa et al., 2018; Murphy et al., 2017), a wide range of psychopathologies e.g., depression (Eggart et al., 2019; Paulus and Stein, 2010) and body-image disorders e.g., anorexia (Badoud and Tsakiris, 2017; Zamariola et al., 2017). In light of this, research interest directed towards interoceptive processing has increased significantly in recent years (Khalsa and Lapidus, 2016).

The cardiovascular system has been a key target of interoceptive research, with particular focus on the heart for pragmatic reasons; notably due to the ease of administration of behavioural tests where individual heartbeat intervals can be easily discriminated. Here, measures e.g., heartbeat evoked potentials [HEP] (Petzschner et al., 2018; Pollatos and Schandry, 2004) and heart rate variability [HRV] (Owens et al., 2018), and tasks e.g., heartbeat counting task [HCT] (Rainer Schandry, 1981) and the heartbeat discrimination [HBD] (Brener and Jones, 1974; Katkin et al., 1983; Whitehead et al., 1977), concerning predominantly cardiac processes have been frequently used in previous research. Despite the strengths and weaknesses reported for each method, with recent criticism being directed towards the HCT (Brener and Ring, 2016; Desmedt et al., 2018; Ring et al., 2015; Zamariola et al., 2018), important correlations have been found in domains which have

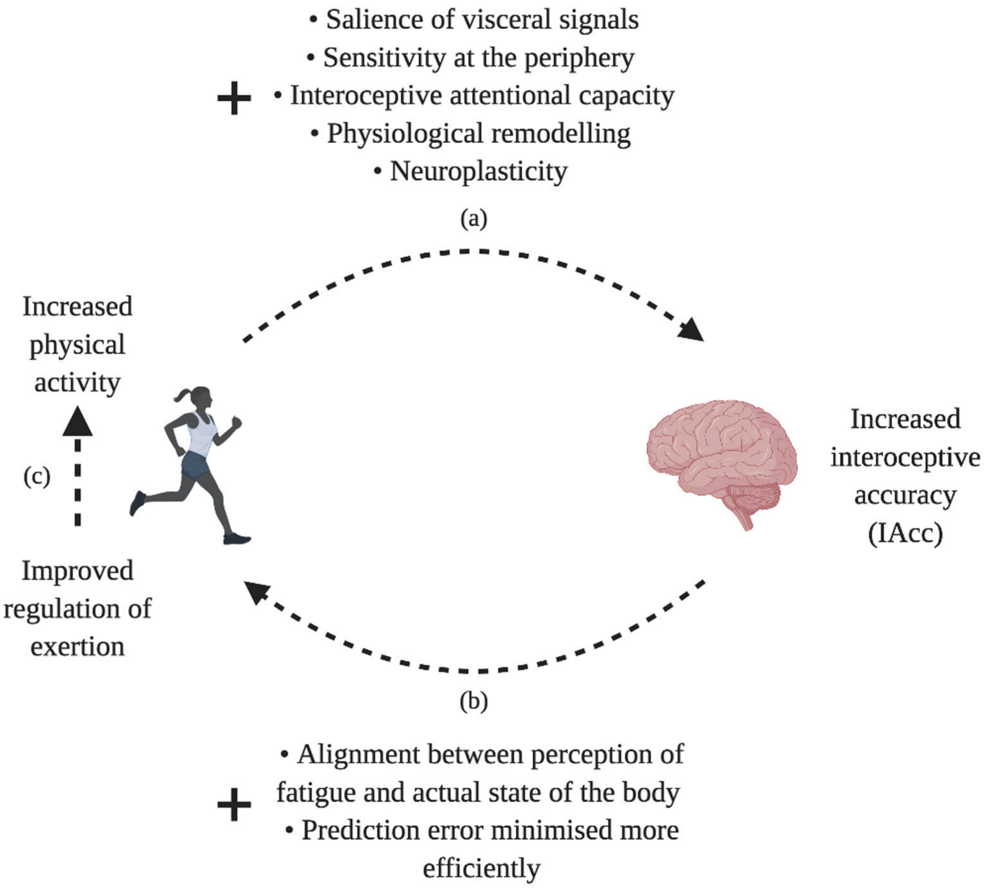

Fig. 1. Feedback loop between physical activity and interoceptive processes. This model displays (a) the main pathways by which acute and chronic physical activity influence interoceptive processes, (b) how interoceptive processes monitor the regulation of exertion during physical activity and (c) how increased ability to regulate oneself during physical activity is likely to encourage increased participation in physical activity over time.

previously been hypothesised as relevant to interoceptive processing, such as emotion processing (Critchley and Garfinkel, 2017; Durlik et al., 2014; Füstös et al., 2013), decision making (Dunn et al., 2010; Werner et al., 2009), and the prevalence of psychopathological conditions e.g., panic disorder, anxiety and depression (Ehlers and Breuer, 1992; Garfinkel et al., 2016b; Khalsa et al., 2018; Murphy et al., 2017).

When measuring interoception, there are three key dissociable dimensions which have been standardised by Garfinkel et al. (2016a): *Interoceptive accuracy* (IAcc) - reflecting the ability to correctly detect and track internal bodily sensations, *interoceptive sensibility* (IS) - being the self-evaluated assessment of how one experiences their internal bodily sensations, and *interoceptive awareness* (IA) - constituting the metacognitive awareness of ones' IAcc i.e. the extent to which ones' IS reflects their IAcc. Despite the importance of all dimensions, previous research has primarily focussed on IAcc as it provides the foundation for knowledge about ones' metacognitive awareness. Adding to this model, a fourth element has been proposed, constituting the very basic level of perception involved in the processing of internal bodily signals. Here, it is suggested that indices of visceral-afferent signal transmission e.g., heart rate, blood pressure, breathing rate, etc., act as a prerequisite for the subsequent central processing and mental representation of the physiological condition of the body (Forkmann et al., 2016). This is supported by the ability for both induced cardiovascular arousal (Pollatos et al., 2007a; Schulz et al., 2013) and indices of resting cardiovascular dynamics (Knapp-Kline and Kline, 2005; Schandry et al., 1993) to affect interoceptive performance in behavioural tasks. This fourth element, therefore, represents the importance of the transduction and encoding of the afferent input entering the interoceptive system at the periphery, providing the threshold necessary to initiate the cascade of subsequent communication along the brain body axis.

One modality known to influence the afferent input entering the interoceptive network is physical activity, acting on the periphery to alter visceral-afferent signal transmission (Craig, 2006; Schandry et al., 1993). Conversely, the top-down regulation of interoceptive cues has been proposed as the underlying mechanism in contemporary models of exercise regulation (McMorris et al., 2018), reinforcing this dynamic interaction between the two constructs. In addition, the health benefits of physical activity for emotional and cognitive aspects of self-regulation have long been discussed (Asmundson et al., 2013; Hillman et al., 2008; Stathopoulou et al., 2006), where more recently, researchers have suggested the mediating role of interoceptive processes in such effects (Garfinkel et al., 2016a; Sabourin et al., 2015; Sabourin et al., 2016). Despite the strong supporting evidence, interest into the relationship between physical activity and interoception has been surprisingly under-weighted in interoceptive research (Table 1).

3. Interoceptive processes regulate physical exertion

In numerous contemporary models of exercise regulation, such as those relating to the somatosensory-cognitive overlap, interoception is postulated to play a central role (Noakes, 2012). It is thought that the processing of interoceptive information contributes to the rating of perceived exertion (RPE) during cardiovascular activity, signifying that exercise capacity is, to some degree, governed by psychophysiological mechanisms (Noakes and Gibson, 2004). Considering this, RPE has been proposed to represent the psychophysiological link between the subjective sensation of exertion and the physiological changes that occur during exercise, playing a key role in the regulatory protective system (Tucker, 2009). Distinct models of both exercise regulation and interoceptive processing provide insights into this hypothesised association, demonstrating the parallel and complementary nature of different research disciplines. For example, Tucker's (2009) anticipatory feedback model of exercise is analogous to models of interoceptive predictive coding when interpreting both with regards to the psychophysiological regulation of RPE. The anticipatory feedback model identifies a 'template RPE'; a theoretical concept generated by past experiences of exercise, representing a set point for comparison with the 'conscious RPE'. The conscious RPE thus reflects the subjective perception of the physiological condition of the body, influenced by numerous factors e.g., previous experience as well as current, contextually relevant information. This hierarchical model reflects the multidimensional nature of fatigue, where physiological and psychological mechanisms interact to inform perception (McMorris, 2020; McMorris et al., 2018). Similarly, the role of error units are discussed in interoceptive predictive coding models, where predictions (priors) are compared against incoming afferent information to generate regulatory error signals (prediction error), amounting from the discrepancy between the two (Seth et al., 2012). Successful mediation and minimisation of these error signals is then responsible for the effective interpretation of incoming stimuli, guiding the behavioural response to ensure allostasis is maintained (Seth and Tsakiris, 2018). The minimisation is achieved by either active inference i.e., performing actions to induce a physiological state aligned with one's predictions, or by modulation of the predictions themselves. Considering the latter, our internal mental representations of the bodily self are continuously modified when the perceptual experience from novel circumstances are compared against previous experience, constantly adapting to accommodate for new incoming stimuli and environments. In this way, predictions are described as hypotheses about the outside world that are tested against incoming sensory information (Barrett and Simmons, 2015). Both models could be applied to the regulation of self-paced exercise, where the brain integrates afferent information from multiple physiological systems, contextual information and prior knowledge of sensations of fatigue, generating a conscious RPE represented by an emotional response or feeling state. This mediates anticipatory adjustments in exertion to ensure that the task is completed optimally, yet safely. Such adjustments precede potentially dangerous physiological considerations during exercise, such as severe depletion of muscle glycogen and hyperthermia (Nybo et al., 2014). Here, however, problems may arise with regard to the precision weighting of information, biased in either a top-down or bottom-up direction (Clark, 2017a, 2017b). Regarding top-down bias, excessive precision weighting is placed on prior predictions at the sacrifice of afferent incoming stimuli, whereas the opposing explanation describes a hypersensitivity to afferent sensory information i.e. assigning too little weight to top-down predictions (Pellicano and Burr, 2012; Van de Cruys et al., 2014). This disrupted generation of accurate templates from prior experience causes much of the incoming sensory information to be perceived as novel and unfamiliar, reducing the individuals' ability to anticipate the consecutive events and react with the correct behavioural response to maintain allostasis (Clark, 2017a, 2017b; Sinha et al., 2014). Such impairments present dangerous implications to exercise regulation at both ends of the scale (Fig. 2).

With greater perceived fatigue in comparison to the actual state, one could terminate exercise prematurely, resulting in reduced participation in physical activity over time. On the other hand, impairments could result in the continuation of exercise to the point of dangerous physiological boundaries. This is demonstrated in how individuals with coronary heart disease significantly underestimate their heartbeats during physical activity, where disrupted sympathetic activation along the afferent pathway could result in increased weighting on top-down information (Kollenbaum, 1994). This mismatch between the template RPE and the actual state of the body results in an inaccurate conscious RPE; analogous to a low IAcc. In light of this, RPE measures should be interpreted with caution, where the subjective perception of fatigue is not a direct and completely accurate representation of the internal physiological condition of the body, instead it is dependent on ones' ability to accurately perceive and interpret their bodily signals. Novel interoceptive illusions demonstrate the malleability of the subjective perception of fatigue, where one study induced misperceptions of ones' physiological state by providing false cardiac feedback during physical activity (Iodice et al., 2019). Despite the intensity of exercise remaining constant, when the auditory tones were faster than the actual heart rate,

Table 1

A table of the empirical studies included in this manuscript supporting the relationship between physical activity and interoceptive processing. Papers vary in their design (acute vs chronic), testing methods, and also in the direction of the proposed relationship; physical activity to influence interoceptive processing, and alternatively, interoceptive processing to regulate physical activity.

Empirical studies linking physical activity and interoceptive processes				
Paper (author, year)	Participant characteristics (N, sex, $M_{age,}$ age range, BMI)	Activity (acute/chronic)	Measure of interoception	Summary of findings
		Acute		
Iodice et al., 2019	$N = 18$ M, $M_{age} = 22.15$ y, 20–26 y, $M_{BMI} = 24.1$	Acute; Interoceptive illusion: auditory feedback of heartbeats (congruent or faster/slower) during cycling task of different intensities	MAIA[b]	Auditory feedback of heartbeats faster than actual causes greater perception of effort. No effect when heartbeats are slower. No correlation between interoception and changes in perceived effort ratings.
Herbert et al., 2007	$N = 34$ (15M), $M_{age} = 26.4$ y, 20–40 y	Acute; Free-cycling task, instructed to cycle freely for 15 min	HCT[a]	There was a negative correlation between IAcc and covered distance, change in HR, stroke volume and cardiac output, suggesting a more finely tuned self-regulation of physical load in good heartbeat perceivers.
Machado et al., 2019	$N = 32$ M, 21–27 y, $M_{BMI} = 24.1$	Acute; Maximal incremental cycling test	HCT[a]	IAcc had no influence on physical, physiological and perceptual responses to maximal incremental exercise.
Tabor et al., 2019	$N = 38$ (19M), $M_{age} = 23$, $M_{BMI} = 22.07$, inactive	Acute; Wingate sprint cycling test	HCT[a]	Performance in the sprint task was determined by both IAcc and anxiety sensitivity.
Köteles et al., 2020a	$N = 47$ (42.2% M), $M_{age} = 21.4$, healthy	Acute; Preproduction of three different exercise intensities (25, 50, 75% or aerobic range)	HCT[a]	IAcc at rest is associated with reproduction of physical training load only at very low intensities
Köteles et al., 2020b	$N = 67$ (40M), $M_{age} = 20.67$, healthy	Acute; perceived exertion, arousal and valence measured during three physical loads (below, around and above the anaerobic threshold)	HCT[a]	IAcc at rest was associated with arousal but not valence.
Perakakis et al., 2017	$N = 37$ M, low fit ($N = 20$, $M_{age} = 22.55$, $M_{BMI} = 22.15$) vs high fit ($N = 17$, $M_{age} = 22.94$, $M_{BMI} = 23.66$)	Acute; submaximal incremental effort cycling task	HEP[c]	There was a significant difference in the neural processing of heartbeats (HEP) between individuals who exercise regularly and their sedentary counterparts.
Montgomery et al., 1984	$N = 24$ M, moderate ($N = 12$) vs high ($N = 12$) levels of fitness, 18–25 y	Acute; HBD performed whilst standing on treadmill, walking briskly on treadmill and during recovery from exercise	HBD[d]	There was no difference between groups in their cardiac awareness at rest. Both showed increased awareness during recovery, however only the moderate group increased awareness during exercise.
Antony et al., 1995	$N = 60$ (24M), $M_{age} = 30$, subjects with panic disorder, social phobia and no mental disorder	Acute; HCT performed at rest and following a period of exercise (2 min step-up task within individualised target range of HR)	HCT[a]	There was no significant difference in IAcc at rest. All groups showed significant improvements in IAcc following exercise. Despite no group differences, self-reported anxiety was positively related to IAcc.
Jones and Hollandsworth, 1981	$N = 36$, $M_{age} = 26$, 14–42 y, groups = sedentary, tennis and distance running	Acute; HBD measured at rest and following cycling where HR was increased by 75%	HBD[d]	Only the male distance runners had an elevated awareness at rest, however after exercise there were only improvements for the tennis and sedentary groups.
Williamson et al., 2003	$N = 16$ (12M), $M_{age} = 26$, healthy	Acute; Handgrip dynamometer and maximal voluntary contraction (MVC)	Neuroimaging; Insular activity	Cerebral blood flow in the insular cortex is related to central command during the exercise, independent of metaboreflex activation and rise in blood pressure.
Williamson et al., 1997	$N = 8$, $M_{age} = 28$, healthy	Acute; voluntary active and passive induced cycling	Neuroimaging; Insular activity	There was a significant increase in insular activation only during active/dynamic cycling.
Williamson et al., 1999	$N = 18$ (15M), $M_{age} = 25$, healthy	Acute; dynamic exercise protocol (cycling); low intensity, higher intensity and seated rest on bicycle. Static exercise protocol (handgrip); 25% of MVC for 1-, 3- and 5-min duration	Neuroimaging; Insular activity	Increases in insular activity during exercise are intensity-dependent.
		Chronic		
Hirao et al., 2020	$N = 32$, 17 long-distance runners (15M): $M_{age} = 19.65$ and 15 sprinters (13M): $M_{age} = 19.93$	Chronic; HCT, subjective interoceptive ability and stimulus-preceding negative (SPN) measured at rest	HCT[a], SPN insular activity	Sprinters displayed greater perceived interoceptive ability and larger insular activation compared to the long-distance runners.
Georgiou et al., 2015	$N = 49$ (29M), $M_{age} = 9.72$, $M_{BMI} = 17.33$	Chronic; accelerometery and 6 min run-performance task	HCT[a]	IAcc correlated positively to the degree of physical activity participation, and children with higher IAcc performed better in the performance task.
Mölbert et al., 2016	$N = 87$ (43M), 60 obese 28 and 27 normal-weight, 9–17 y	Chronic; Weight-reduction programme (physical activity, cognitive behavioural therapy and balanced diet), $M_{duration} = 38$ days	HCT[a]	Weight reduction after the programme was associated with improved IAcc.
Mehling et al., 2018	$N = 47$ war veterans (81% M), $M_{age} = 46.8$	Chronic; 12-week integrative exercise programme (aerobic and resistance exercise with mindfulness-based principles and yoga)	MAIA[b]	They found significant improvements in mindfulness, interoceptive bodily awareness, and positive states of mind in the experimental group compared to a waitlist group.
Sharp et al., 2018	$N = 86$, 18–44 y, BMI < 35	Chronic; 20-week cognitive + fitness + mindfulness intervention	Neuroimaging; Insular activity and MAIA[b]	There was a significant Increase in right insula activity only when mindfulness was included.

M = male, F = female.

[a] Heartbeat counting task (Schandry, 1981).

[b] Multi-dimensional assessment of Interoceptive awareness (Mehling et al., 2018).

[c] Heartbeat-evoked potential.

[d] Heartbeat discrimination task (Brener and Jones, 1974; Whitehead et al., 1977).

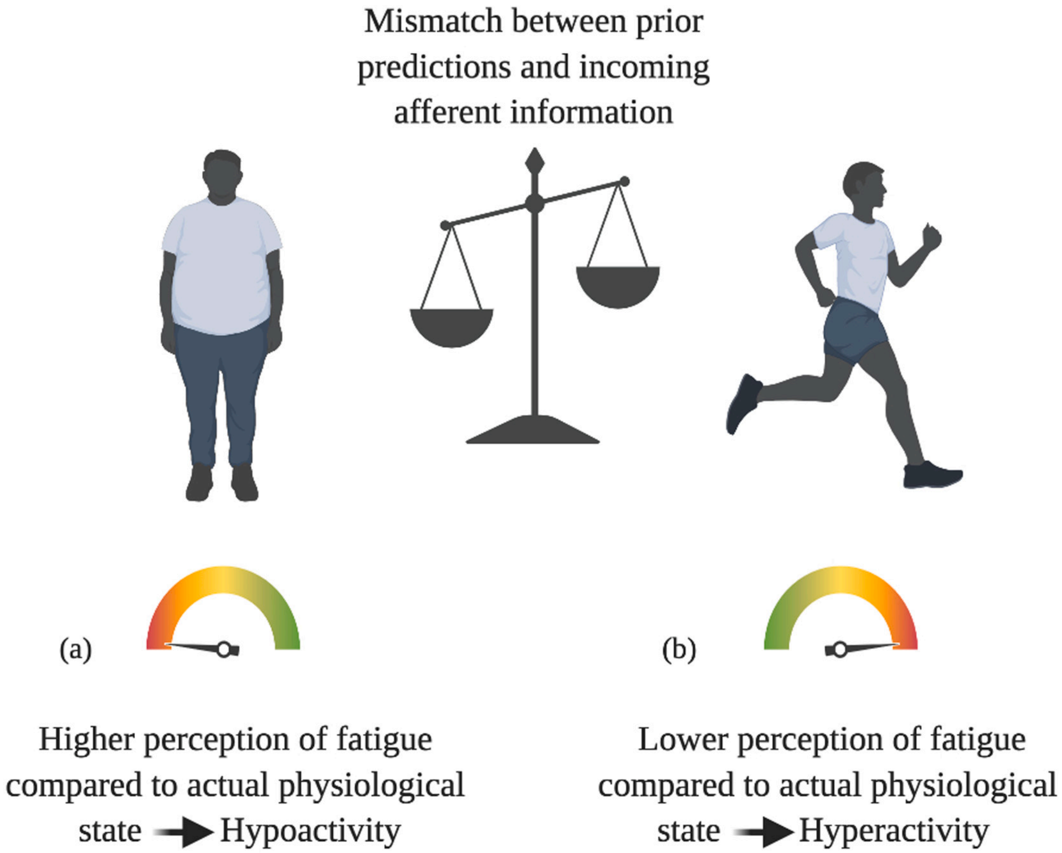

Fig. 2. The influence of interoceptive processing and exercise behaviour. A schematic showing the negative effects a mismatch between perceived fatigue and the actual physiological state can cause to exercise regulation at both ends of the scale; (a) hypoactivity and (b) hyperactivity.

the RPE was higher. Interestingly, however, the RPE was not influenced when the auditory tones were slower than the actual heartbeat, suggesting that in healthy individuals, risk-aversive strategies are in place to monitor the dangers of underestimating fatigue. Considering this, it could be of interest for future research to investigate whether individuals with a higher IAcc at baseline could have protection against such interoceptive illusions, improving their ability to efficiently minimise prediction error to regulate exertion when our perception of the body is compromised. That being said, previous studies found no relation between IAcc at rest and perceived exertion during physical activity below, around and above the anaerobic threshold (Köteles et al., 2020b). Instead of being interpreted as a lack of relationship, the authors speculated that different perceptual abilities exist between aroused and relaxed states, where individual differences become apparent during compromised homeostatic states. Taking this into consideration in further research could therefore reveal important individual differences that may be missed from assessing IAcc at rest. Aside from amplified sensations of fatigue, an inaccurate perception of the body may also lead to physical inactivity through increased negative affect towards one's own body and a sense of lack of control (Ley-Flores et al., 2019). This is in line with the affective-reflexive theory of physical inactivity and exercise, which states that when self-control resources are low, exercise-related stimuli trigger automatic associations and a resulting automatic affective valuation of exercise. When this automatic reflective response is negative, this stimulates an action impulse to remain physically inactive (Brand and Ekkekakis, 2018). Whilst touching on different constructs, both accounts explain how an inaccurate perception of the body can negatively impact exercise behaviour through stimulating negative subjective valuations of the activity.

Several studies have attempted to test the hypothesis that a better and more accurate perception of bodily signals provides the basis for improved regulation of physical exertion. For example, Herbert et al. (2007) found good heartbeat perceivers to regulate exertion more efficiently to reduce cardiovascular responses in a sub-maximal self-paced cycling task, demonstrating a more finely tuned regulation of exertion than poor heartbeat perceivers. A recent study, however, found no relationship between IAcc and the physiological and perceptual measures at maximal intensities of exercise (Machado et al., 2019), where it was concluded that the influence of IAcc might be dependent on the intensity, mode and design of the exercise task. Similarly, when looking at the influence of IAcc at rest on regulation during a variety of intensities, Köteles et al. (2020a) reported that there was only a moderate relation to replication performance under slight physical load (25% of the aerobic reserve e.g., walking), but not at higher intensities (50% and 75% of the aerobic reserve e.g., jogging or running). This is in line with previous research using the same protocol, showing a systematic bias for individuals to underestimate their HR at higher intensities (Kollenbaum et al., 1996). Here, the authors concluded that whilst theoretically sympathetic activation of cardiodynamics improves the perception of heartbeats (Schandry et al., 1993), different strategies and additional factors appear to be at play under states of increased arousal. This could be explained by the interoceptive model of central fatigue (McMorris et al., 2018), where it is proposed that at maximal intensities, it becomes difficult to produce a prediction based on past experience, compared to a task where you are instructed to reproduce a controlled speed or intensity. This would make it difficult to produce accurate templates to guide behaviour, reducing the potential for IAcc alone to mediate such actions, and opening up the potential for psychological indices to influence behaviour. This idea was supported in a similar study investigating the ability to regulate exertion during a sprint task, also assessing how IAcc influences self-regulation at higher intensities, but this time taking into account additional psychological characteristics (Tabor et al., 2019). Again, IAcc alone did not predict output in the high intensity performance task. Instead, however, physical output was only reduced in those participants who had both elevated IAcc and increased anxiety sensitivity. Anxiety sensitivity, being the fear of the predicted negative consequences of bodily sensations, could be one factor that moderates this relationship between our ability to accurately perceive internal bodily signals and self-regulation of exertion at maximal intensities. If true, this would highlight the importance in how we attend to and appraise such signals in determining the subsequent actions we choose, meaning less weighting would be placed on the accurate sensing of afferent physiological perturbations, representing a more balanced dynamic between physiological and cognitive processes. This is in line with the more recent clarification of distinct interoceptive dimensions by Garfinkel et al. (2016a); sensitivity, accuracy, sensibility and awareness. Whilst previously IAcc was used as an umbrella term for a complex multi-dimensional construct, it is now clear that distinguishing between independent dimensions is key, where facets other than IAcc may influence self-regulation.

In addition to relatively stable pre-determining factors that constitute our prior predictions e.g., previous experience of exercise and physical self-concept, perception can be influenced by motivation inducing environments, such as competition, training to improve performance, or in this case, a maximal performance task (McMorris et al., 2018). These additional contextual factors at play could therefore provide another valuable explanation as to why IAcc alone could not predict physiological and perceptual responses to maximal-intensity exercise. In a recent account of fatigue and physical performance, cognitive fatigue is proposed to alter predictions of sensory consequences i.e., increased cognitive fatigue results in inaccurate perceptions of physical effort during subsequent physical activity (McMorris, 2020). Theoretically, motivation has the capacity to override these perceptions of fatigue to prevent the premature cessation of exercise, where tonic activation of noradrenaline overrides cost-benefit analysis during tasks perceived as overly taxing. This is demonstrated to an exaggerated extent in high performance athletes in the way they push the boundaries of human performance, going purposefully beyond the homeostatic set points which guide the rest of us to terminate exercise to avoid exhaustion or injury (McCormick et al., 2015). Yet despite such theoretically sound accounts, research has failed to provide consistent evidence for the role of motivation in interoceptive mechanisms of fatigue. This could however be partly explained by the methods used, where more objective measures of motivation would reduce bias. Taken together, it appears that there are certain cognitive factors that could override, to some extent, the strength of the role interoceptive processes play in the regulation of exertion at higher intensities.

Whilst the suggested role of psychological factors at higher intensities is logical, it does in some ways contradict the dual-mode theory of affective responses to exercise (DMT), which states that whilst cognitive factors dominate at submaximal intensities, strong interoceptive cues dominate and override these individual differences once the anaerobic threshold (AT) has been exceeded (Ekkekakis et al., 2008). Here, bioenergetic optimisation models describe how we maximise distance vs energetic cost on a basis of pleasure-displeasure, where intensity is chosen based on what would elicit the optimal affective response, supported in the way preference for exercise intensity predicts variance in output in sub-maximal exercise (Ekkekakis, 2009; Ekkekakis et al., 2006). Yet whilst individual differences in psychological factors and cognitive appraisals are proposed to influence our response to physical activity at submaximal stages, their input is overridden past the point of the AT due to a general negative valence and thus a desire to terminate exercise. That being said, although generally a negative valence is reported past the AT, inter-individual differences still occur between the AT and the respiratory compensation point, after this proposed shift to interoceptive cues (Ekkekakis et al., 2020;Ekkekakis et al., 2011). This therefore suggests a possible learned ability to override these dominant signals in certain individuals, for example through increased fitness, previous experience of exercise and variability in psychological traits. As such, truth could be taken from both theories, where interoceptive cues clearly dominate at maximal intensities, however, certain psychological factors hold more strength in the ability to override these physiological processes. It could therefore be that more trait-like psychological factors (e.g., motivation, anxiety sensitivity etc.) have this overriding capacity, whereas the current cognitive state (e.g., cognitive fatigue) succumbs to the increased salience of physiological signals at maximal intensities. This is reflected in the way moderate to high effects of cognitive fatigue were only found at submaximal intensities, with either low or no effects found at maximal intensities (McMorris, 2020). More work is therefore needed to differentiate between such state- and trait-like psychological factors in their role in exercise regulation and perception of fatigue at higher intensities. Further, the nature of the exercise task (e.g., self-selected vs incremental stages) should be considered due to likely differences in the underlying mechanisms.

When contemplating the interaction between cognitive and interoceptive processes in the regulation of exertion, one must also consider the role of attentional focus. Attentional strategies have been found to augment the perception of fatigue, with associative attention towards the body proposed to increase the precision in perception of physiological signals, whereas dissociative attention is considered to improve the affective response by taking focus away from the body. This is in line with the competition of cues hypothesis (Pennebaker and Lightner, 1980), where it is suggested that interoceptive and exteroceptive mechanisms compete for attentional resources, with heightened attention to one source diminishing attention to the other. As such, both methods have been associated with different benefits dependent on intensity and duration of the task (Razon et al., 2010); associative attention is linked with increased time on task and improved regulation during higher intensities, and dissociative with a decreased perception of effort during submaximal exercise (Lohse and Sherwood, 2011; Razon et al., 2014). This emulates the core principles of the DMT, in that dissociative strategies appear effective at low to moderate intensities, with their effectiveness diminishing nearing maximal intensities i.e., beyond the AT where interoceptive cues dominate (Lind et al., 2009; Nethery, 2002). In future research, an inter-disciplinary approach including psychophysiological measures of interoception would help to confirm these underlying mechanisms and support the different uses of attentional strategies in different contexts.

Whilst it is clear that top-down interoceptive processes play a crucial role in the regulation of physical exertion, research also suggests that the psychophysiological characteristics of physical activity could in turn help to improve the efficiency and accuracy of interoceptive processing (Georgiou et al., 2015; Montgomery et al., 1984). Here, it is possible that exercise-induced changes at a neurochemical, structural and behavioural level modulate interoceptive processes, for example by acutely increasing the salience of signals, increasing the attentional capacity, stimulating physiological remodelling or supporting neuroplasticity. The potential of physical activity to alter the perception of bodily signals in this way suggests its suitability for interoception-based interventions. First, however, the underlying mechanisms must be better understood before advancing with therapeutic designs.

4. How physical activity influences interoceptive processing

4.1. Acute physical activity

The ability to accurately perceive interoceptive signals has been shown to have high re-test reliability (Mussgay et al., 1999), leading to the conclusion that IAcc is a relatively stable trait variable. In addition to functioning as a trait-like variable, however, research suggests the potential for state-dependent fluctuations, where it is possible that IAcc is influenced by context-dependent triggers in a transient pattern of activation (Edwards et al., 2018; Meyerholz et al., 2018). Considering this, a number of physiological, affective and cognitive manipulations have been tested in attempt to acutely modulate IAcc, and one modality known to do so by manipulating the physiological state is physical activity (Craig, 2006). The notion that interoception can be manipulated immediately following a single bout of physical activity is not novel, where numerous studies have demonstrated increases in state IAcc immediately following physiological arousal (Antony et al., 1995; Jones and Hollandsworth, 1981; Schandry et al., 1993). It is proposed that the perception of interoceptive signals is enhanced due to the salience of the afferent signals entering the interoceptive system (Montgomery et al., 1984). Alternative explanations, however, attribute the increases in IAcc down to increased attention regulation towards interoceptive cues, thus increasing the accuracy in perception. Here, acute physiological arousal may narrow attentional resources and favour attention to task-relevant stimuli (Schulz and Vögele, 2015), thus increasing precision in perception of the specific sensory channel in question.

At the neurochemical level, several neurotransmitters have been found to have a neuromodulatory role important to interoceptive processing; dopamine, for example is involved in the reward-motivated pathway (Bromberg-Martin et al., 2010). Here, the sensitivity of dopamine to predictive error signals strengthens neural pathways and promotes learning (Atzil and Barrett, 2017). Interestingly, dopaminergic systems have been found to be activated in a feed-forward pattern both before and during exercise (Björklund and Dunnett, 2007). More specifically, exercise has been demonstrated to increase striatal D2 receptor binding potential, as well as elevate striatal dopamine metabolite levels in the dorsolateral striatum (Lin and Kuo, 2013), where findings have been replicated in both animal (Chen et al., 2018) and human studies (Foley and Fleshner, 2008; MacRae et al., 1987; Robertson et al., 2016). It is therefore possible that the increase in dopaminergic activity brought about by physical activity increases the accuracy and sensitivity of the interoceptive network. By increasing the ability to detect prediction error signals, it could prevent misinterpretation and thus reduce the mismatch between bottom-up and top-down processing.

The same could be applied to the expression of oxytocin, a neurotransmitter which plays an important role in social cognition and behaviour (Yatawara et al., 2016). Oxytocin has been postulated to mediate encoding of the strength of interoceptive signals (Quattrocki and Friston, 2014). Furthermore, oxytocin levels have also been shown to rise in response to acute physical activity (de Jong et al., 2015; Martins et al., 2005), increasing oxytocinergic projections (Hew-Butler et al., 2008). It is therefore possible that physical activity modulates interoceptive processing by stimulating the expression and projection of oxytocin towards the posterior part of the insula, an area specifically responsible for the primary detection of interoceptive signals (Grinevich and Stoop, 2018). Increasing sensitivity to interoceptive signals in this way would improve the detection of primary physiological cues, albeit, evidence of the causal relationship between physical activity and oxytocin is inconclusive (Chicharro et al., 2001), therefore results should be understood with awareness of limitations. Nevertheless, in studies looking at the effects of acute intranasal oxytocin administration on interoceptive processing, it is hypothesised that the administration of oxytocin works by increasing the flexibility of resource allocation between internal and external cues (Betka et al., 2018). This could hold relevance when considering the neuromodulatory response to physical activity, however, future research would have to test this hypothesis explicitly, looking at the direction of observed effects in response to the physical activity-induced rise in oxytocin.

One cannot discuss the influence of neurochemical responses of acute physical activity on interoceptive processes without considering adrenal stress hormones such as epinephrine and cortisol. More specifically, stress-activation of the sympathetic autonomic nervous system and the hypothalamic–pituitary–adrenal axis causes a cascade of hormonal responses coordinating the release of epinephrine and cortisol, resulting in physiological responses such as an increase in blood pressure and heart rate (Berntson and Khalsa, 2021; Tsigos and Chrousos, 2002). Effective communication between descending stress signals and ascending interoceptive processing of peripheral organs is therefore essential to ensure optimal regulation of the body (Schulz and Vögele, 2015). It is therefore possible that interoceptive processing of the adrenal response to physical activity causes activation of the interoceptive domain, which is supported by studies showing increases in IAcc in response to an acute stressor to be mediated by the cortisol response (Maeda et al., 2019). Whilst such studies use psychosocial stressors, the multidimensional stress response proposes that the body has specific responses to any perceived stressor that threatens homeostasis (e.g., emotional, psychological, physical; Childs and de Wit, 2014). Therefore, the same could be expected in response to physiological stressors, in this case physical activity. Further research should however empirically test this by assessing the mediating role of adrenal hormones in physical activity-induced elevations in IAcc.

The acute effects of physical activity on interoceptive processes are further demonstrated in neuroimaging studies investigating the neural responses to exertion. Here, overlapping mechanisms are supported by functional magnetic imaging studies, demonstrating the shared activation of neural correlates during both participation in physical activity (Williamson et al., 2003; Williamson et al., 1997) and interoceptive tasks (Critchley et al., 2004; Pollatos et al., 2007b); the anterior insular and anterior cingulate cortex. Further investigation also found insular activity to increase proportionally to the incremental increases in intensity of exercise (Williamson et al., 1999), suggesting that there is an intensity-dependent relationship. Such studies not only demonstrate that the regulation of physical exercise involves the insula and anterior cingulate cortex, but they also support the possibility of physical activity to produce acute perturbations of interoceptive processing.

The DMT becomes relevant again when considering the intensity of acute physical activity required to cause adaptations to interoceptive processes. In this way, as there is a proposed shift from descending cognitive processes to ascending interoceptive cues at around the point of the AT, it would suggest that only physical activity of an efficient intensity appears to significantly benefit interoceptive processing (Paulus et al., 2013). This is supported in the aforementioned studies of Williamson et al. (1997, 1999, 2003), demonstrating an intensity-dependent activation of the interoceptive domain. This importance of intensity is also demonstrated in the way sprinters showed greater insular activity and subjective interoceptive ability relative to long-distance runners, which may be a result of more frequent training within higher boundaries of intensity (Hirao et al., 2020). The importance of the salience of elicited physiological signals should therefore be taken into consideration in the design of physical activity-based interventions for interoceptive processing.

4.2. Chronic physical activity

Repetition of the aforementioned acute mechanisms holds the potential to stimulate and contribute to the neuroplasticity necessary to support interoceptive processing. It is likely that repeated exposure to periods of increased visceral-afferent signal transmission improves the accuracy in detection overtime, developing more accurate internal mental representations. This idea is suggested in previous research, where higher levels of physical activity and greater physical fitness were found to positively correlate with IAcc scores in children, suggesting that increased participation in physical activity might favour the development of a better ability to accurately identify internal bodily signals (Georgiou et al., 2015). Here it is possible that repeated physical activity of a sufficient intensity acts as a form of interoceptive exposure, where through non-associative learning one can become familiarised with their bodily signals (Garfinkel et al., 2016a). This has been suggested as the mechanism responsible for physical activity interventions aiming to improve well-being in individuals with varying somatic mental health conditions e.g., anxiety and post-traumatic stress disorder, where the elicited heightened physiological arousal is proposed to act as a form of interoceptive exposure to improve the familiarity of physiological cues of arousal, and thus reduce the propensity to negatively attribute autonomic changes through a better ability to accurately identify internal bodily signals (Sabourin et al., 2015, 2016). A number of studies have reported successful modulation of interoception following long-term interventions incorporating a physical activity element (Mehling et al., 2018; Mölbert et al., 2016; Sharp et al., 2018), however, varying methodological differences persist and obstruct the generalisability of their findings. Firstly, there is a lack of consistency with the way in which interoception is measured and deduced, with different results referring to different dimensions of interoception, i.e., methods include self-report, neuroimaging data (increased insula connectivity) and objective tests (HCT). Secondly, the combined and integrative nature of the intervention designs make it difficult to deduct the main factor driving the changes, where interventions often include additional components alongside physical activity e.g., mindfulness, cognitive behavioural therapy and a balanced diet, for example. Whilst promising, the significant lack of studies objectively and systematically measuring changes in interoception following chronic physical interventions needs to be addressed.

Athletic individuals make a suitable population to examine the hypothesis that chronic physical activity supports interoceptive processes, as they are repeatedly exposed to salient afferent signals over long periods. This has led to the suggestion that athletic individuals hold an advantage regarding the development of accurate mental models, leading to an enhanced perception of the physiological condition of the body. Research reinforces this hypothesis, where in a study by Jones and Hollandsworth (1981), trained athletes were found to outperform sedentary counterparts in heartbeat perception at rest, which was concluded to be a result of a learned sensitivity to cardiac activity through training. However, this could also be explained by the fact that athletes tend to have a lower resting heart rate, and lower resting heart rates have been found to negatively correlate with IAcc (Zamariola et al., 2018). Future research should therefore assess differences in perception during periods of allostatic disturbance rather than at rest e.g., during physiological arousal, where such confounding factors have less influence on perception. Albeit, the significance of this learning process was again highlighted in another study where reduced heart-beat evoked potentials (HEP) were recorded during an attention task, comparing scores from highly-trained individuals to sedentary counterparts (Perakakis et al., 2017). Despite the methodological considerations acknowledged by the authors, the lower HEP recorded at frontocentral sites may indicate the effects of greater IAcc, acquired through learning. This is in line with the findings of a study by Canales-Johnson et al. (2015), where a similar pattern of HEP responses were reported in participants who underwent an auditory interoceptive feedback training. These findings suggest that physical activity of a sufficient intensity and frequency may alter anticipatory representations of interoceptive sensations, playing an important role in maintaining allostasis in response to physiological perturbations.

Alternative explanations for altered interoceptive processing in athletic individuals, however, could come from a purely physiological perspective, rather than through incorporating higher-level processing. Structural exercise-induced changes, such as “athlete's heart syndrome”, for example, could be responsible for the altered processing of interoceptive signals in highly trained individuals. In this way, regular training causes physiological remodelling, such as enlargement of the left ventricular cavity and increased wall thickness (Cantwell, 1987). Such structural changes result in modulation of cardiovascular dynamics, thus altering the salience of visceral-afferent signal transmission. As such, several parameters have been suggested to influence the increase in heartbeat perception observed following both acute and chronic exercise (Jones and Hollandsworth, 1981; Montgomery et al., 1984), including stroke volume, contractility, ejection volume, and momentum (Schandry et al., 1993). In addition, the interoceptive channel responsible for blood pressure regulation via the baroreflex has been found to be modulated by physical activity, where both acute and chronic increases in baroreflex sensitivity have been reported (Gomes et al., 2017; La Rovere and Pinna, 2014; Laterza et al., 2007; Masson et al., 2014). Here, it is clear that the underlying physiology of the organ system under investigation is undoubtably connected (Tsakiris et al., 2019), reflecting the intertwined nature of cardiac activity and the perception of cardiac activity.

In reviewing the influence of chronic physical activity on interoceptive processes, it is equally as important to consider the effects of chronic physical inactivity, in the case of accidents, illness or lifestyle choice, for example. Whilst this pattern is discussed in the previous section looking at this relationship from the opposing direction; impaired interoceptive processing causes a higher perception of fatigue compared to the actual state thus leading to hypoactivity, it could also be that hypoactivity is causing disruption to interoceptive processes. More specifically, from an absence of the positive adaptations discussed previously (e.g., increased salience of visceral signals, physiological remodelling, positive neuroplasticity etc.), hypoactivity could limit increases in interoceptive ability. In other words, if previous findings showing that interoceptive processes can be acquired through training are true (Canales-Johnson et al., 2015), lack of activity could also means a lack of interoceptive training. This can be seen in previous research demonstrating altered neural processing of cardiac afferent signals in sedentary individuals compared to their physically trained counterparts (Perakakis et al., 2017). It is however more likely to be a feedforward process working in both directions, where like demonstrated in Fig. 1 referring to physical activity, physical inactivity blunts development in interoceptive processes, which in turn perpetuates the issue in a viscous cycle by reducing participation in physical activity.

Taken together, research into both acute and chronic effects of physical activity indicates that exposure to heightened physiological arousal supports the sensing and processing of interoceptive cues, however, further research is needed to systematically investigate the mechanisms involved. Further, it remains unclear how and to what extent cognitive factors, e.g., attention and motivation, play a role in this process. A greater understanding of the underlying mechanisms could help to explain the neurobiology behind the benefits of physical activity interventions to both emotional and cognitive processes, which would hold clinical implications for the development of physical activity-based interventions with an interoceptive focus.

This review does not come without some limitations and hurdles faced. Firstly, whilst the interdisciplinary approach of this manuscript is one of its main merits, it is difficult to encapsulate and incorporate all findings from all fields, meaning this review includes a synthesis of only the most significant findings from each discipline. Further, as this is a narrative review, it should be noted that the included papers were chosen based on relevance to the manuscript without any systematic selection process. Finally, due to the lack of integration between fields in previous research, it is possible that some relevant papers could have been missed due to differing terminologies between disciplines. We hope however that an increased congruence between different research disciplines in the future will provide a more cohesive field of interoceptive research.

5. Conclusions and future directions

The different lines of research reviewed in this paper support the hypothesis for a dynamic relationship between physical activity and interoception, whereby interoceptive processes help regulate exertion during physical activity, and in turn physical activity supports the processing of internal bodily signals. Whilst this suggests overlapping, or possibly identical responsible neural systems, many open questions remain. For example, whilst evidence advocates integration to some extent, we are unsure of the underlying mechanisms by which physical activity acts on the neural substrates integral to interoceptive processing, and the limited number of studies into context-dependent changes in interoception prevent strong conclusions being drawn. Acknowledging the accumulating evidence discussed in this review, it is surprising that this association is seldom considered in interoceptive research, particularly in contemplating the therapeutic potential of physical activity (Lubans et al., 2016). As such, advancing on the current findings to incorporate physical activity further into interoceptive training programmes could be extremely valuable, particularly when considering the potential benefits of such training programmes to individuals with maladaptive self-regulatory behaviour e.g., mood disorders. The somatovisceral model of emotion (SAME; Cacioppo et al., 1992), which states that the same pattern of visceral afferents may be associated with different emotions, could help explain how physical activity interventions improve emotion processing via interoceptive mechanisms. In this model it is considered that visceral afferent stimulation is primarily perceived functionally, where later integration of the context and the cognitive state influences how those signals are interpreted. Through increasing the salience of afferent signals via physical activity, precision weighting can be shifted away from prior predictions and towards incoming stimuli at the periphery. This becomes important when we have inaccurate and inflexible prior expectations, where through increasing the salience of stimulus intensity in this way, the ability of afferent stimuli to attract attention increases to override maladaptive top-down predictions. Whilst top-down interoceptive appraisal is needed to reduce the ambiguity of afferent signals, improving the initial sensitivity at the periphery could increase the probability for accurate subsequent appraisal by reducing error (Farb and Logie, 2019). In other words, whilst interoceptive appraisal most consistently determines subjective well-being, IAcc determines the extent to which such appraisals are provoked by real physiological fluctuations.

Recent papers hypothesise on the mediating role of interoception in the beneficial effects of physical activity-based interventions for both emotional (Garfinkel et al., 2016a; Goldstein et al., 2018; Mehling et al., 2018; Sabourin et al., 2015; Sabourin et al., 2016) and cognitive processes (Zarza et al., 2019). Nevertheless, such hypotheses need to be empirically tested, with an initial focus on understanding the underlying mediating mechanisms before addressing the direction of the interactions. Moreover, more rigorous testing of interventions using crossover designs would tease apart any results elicited by integrative interventions i.e., a combination of physical activity, balanced diet and cognitive training etc.

An update on the research regarding state-dependent fluctuations in interoceptive processes elicited by physiological manipulations would also be of interest, helping to identify any individual differences in psychological characteristics which could be important protagonists in altering the neural response to physical activity e.g., motivation, anxiety sensitivity and attention regulation. Additionally, it is also important to consider which populations would benefit most, where we might see differences in age (Murphy et al., 2017) or gender (Grabauskaitė et al., 2017), for example. Detailed understanding of these mechanisms will not only allow for the development of physical activity-based interventions to modulate interoception, but also improve the understanding of the role interoception plays in the regulation of sport and exercise activities, which could serve to help reach existing health and performance goals. Further, populations with co-occurring compromised interoceptive abilities and maladaptive exercise behaviour could particularly benefit from such research e.g., Autism spectrum conditions (DuBois et al., 2016; Srinivasan et al., 2014).

Despite the clear and defined role of interoceptive processes in the response to and regulation of physical activity, the study of possible cross-model interactions across sensory systems would also benefit future research. For example, although generally considered distinct and dissociable constructs (Vaitl, 1996), there is a clear interrelatedness between interoception and proprioception, particularly when considering the relationship to fatigue. For instance, proprioception (the perception of the position and movement of the body) is also heavily involved in the bodily response to physical activity, where increased muscle fibre recruitment and motor command contribute to the conscious sensations of fatigue (Proske, 2019). In addition, proprioceptive feedback has been found to be disturbed by physical activity, where our sense of limb position can be altered by fatigue (Zabihhosseinian et al., 2015). This emulates the aforementioned feedback loop, where interoceptive processes are proposed to influence, and be influenced by, physical activity. Despite their independence, together this suggests that their interaction contributes to the subjective perception of fatigue, where valuable information could be gained by considering the complimentary and parallel nature of both processing systems, rather than studying them in isolation.

Finally, despite such promising findings, a level of consistency needs to be established with the measures used when considering the success of such manipulations. For example, findings from different tasks are used correspondingly, despite the possibility that different neural correlates are employed. In light of this, further research is needed to determine which measures are most appropriate, and the best way to elucidate differences in factors such as accuracy and attention, for example (Murphy et al., 2019). Methodological improvements would allow for greater comparison between findings and eradicate any uncertainty regarding which dimension of interoception is being measured by each task.

To recapitulate, beyond the scope of mechanistic advancements, further research in this field could inform evidence-based intervention and prevention programmes to modulate interoception. This could hold clinical implications considering the associations of interoceptive processing to physical, cognitive and emotional health. Moving from how physical activity interacts with interoceptive processes at the basic physiological level, to understanding how individual differences can affect higher level processing of visceral-afferent signals is of critical importance to create a holistic understanding of this relationship.

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Declarations of interest

None.

References

Ainley, V., Maister, L., Brokfeld, J., Farmer, H., Tsakiris, M., 2013. More of myself: manipulating interoceptive awareness by heightened attention to bodily and narrative aspects of the self. Conscious. Cogn. 22 (4), 1231–1238. https://doi.org/10.1016/j.concog.2013.08.004.

Antony, M.M., Brown, T.A., Craske, M.G., Barlow, D.H., Mitchell, W.B., Meadows, E.A., 1995. Accuracy of heartbeat perception in panic disorder, social phobia, and nonanxious subjects. J. Anxiety Disord. 9 (5), 355–371. https://doi.org/10.1016/0887-6185(95)00017-I.

Ardizzi, M., Ambrosecchia, M., Buratta, L., Ferri, F., Peciccia, M., Donnari, S., Gallese, V., 2016. Interoception and positive symptoms in schizophrenia. Front. Hum. Neurosci. 10 (11), 379. https://doi.org/10.3389/fnhum.2016.00379.

Asmundson, G.J.G., Fetzner, M.G., Deboer, L.B., Powers, M.B., Otto, M.W., Smits, J.A.J., 2013. Let's get physical: A contemporary review of the anxiolytic effects of exercise for anxiety and its disorders. Depress. Anxiety 30 (4), 362–373. https://doi.org/10.1002/da.22043.

Atzil, S., Barrett, L., 2017. Social regulation of allostasis: commentary on “Mentalizing homeostasis: the social origins of interoceptive inference.”. Neuropsychoanalysis 19 (1), 29–33. https://doi.org/10.1080/15294145.2017.1295214.

Badoud, D., Tsakiris, M., 2017. From the body's viscera to the body's image: is there a link between interoception and body image concerns? Neurosci. Biobehav. Rev. https://doi.org/10.1016/j.neubiorev.2017.03.017. Elsevier Ltd.

Barrett, L.F., Simmons, W.K., 2015. Interoceptive predictions in the brain. Nat. Rev. Neurosci. https://doi.org/10.1038/nrn3950. Nature Publishing Group.

Berntson, G.G., Khalsa, S.S., 2021. Neural circuits of interoception. Trends Neurosci. https://doi.org/10.1016/j.tins.2020.09.011. Elsevier Ltd.

Betka, S., Gould Van Praag, C., Paloyelis, Y., Bond, R., Pfeifer, G., Sequeira, H., Critchley, H., 2018. Impact of intranasal oxytocin on interoceptive accuracy in alcohol users: an attentional mechanism? Soc. Cogn. Affect. Neurosci. 13 (4), 440–448. https://doi.org/10.1093/scan/nsy027.

Björklund, A., Dunnett, S.B., 2007. Dopamine neuron systems in the brain: an update. Trends Neurosci. 30 (5), 194–202. https://doi.org/10.1016/j.tins.2007.03.006.

Brand, R., Ekkekakis, P., 2018. Affective–reflective theory of physical inactivity and exercise: foundations and preliminary evidence. Ger. J. Exerc. Sport Res. 48 (1), 48–58. https://doi.org/10.1007/s12662-017-0477-9.

Brener, J, Jones, J. M, 1974. Interoceptive Discrimination in Intact Humans: Detection of Cardiac Activity. Physiology and Behavior 13 (6), 763–767. https://doi.org/10.1016/0031-9384(74)90259-5.

Brener, J., Ring, C., 2016. Towards a psychophysics of interoceptive processes: the measurement of heartbeat detection. Philos. Trans. R. Soc. B Biol. Sci. 371 (1708) https://doi.org/10.1098/rstb.2016.0015.

Bromberg-Martin, E.S., Matsumoto, M., Hikosaka, O., 2010. Dopamine in motivational control: rewarding, aversive, and alerting. Neuron 68 (5), 815–834. https://doi.org/10.1016/j.neuron.2010.11.022.

Cacioppo, J.T., Berntson, G.G., Klein, D.J., 1992. What is an emotion? The role of somatovisceral afference, with special emphasis on somatovisceral “illusions”. Emot. Soc. Behav. 1, 63–98 (doi:tbd).

Canales-Johnson, A., Silva, C., Huepe, D., Rivera-Rei, Á., Noreika, V., Del Carmen Garcia, M., Bekinschtein, T.A., 2015. Auditory feedback differentially modulates behavioral and neural markers of objective and subjective performance when tapping to your heartbeat. Cereb. Cortex 25 (11), 4490–4503. https://doi.org/10.1093/cercor/bhv076.

Cantwell, J.D., 1987. The athlete's heart syndrome. Int. J. Cardiol. https://doi.org/10.1016/0167-5273(87)90027-1.

Caspersen, C J, Powell, K E, Christenson, G M, 1985. Physical activity, exercise, and physical fitness: definitions and distinctions for health-related research. Public Health Reports 100 (2), 126–131.

Chen, Y.H., Kuo, T.T., Kao, J.H., Huang, E.Y.K., Hsieh, T.H., Chou, Y.C., Hoffer, B.J., 2018. Exercise ameliorates motor deficits and improves dopaminergic functions in the rat hemi-Parkinson's model. Sci. Rep. 8 (1), 3973 https://doi.org/10.1038/s41598-018-22462-y.

Chicharro, J.L., Hoyos, J., Bandrés, F., Gómez Gallego, F., Pérez, M., Lucía, A., 2001. Plasma oxytocin during intense exercise in professional cyclists. Horm. Res. 55 (3), 155–159. https://doi.org/10.1159/000049988.

Childs, E., de Wit, H., 2014. Regular exercise is associated with emotional resilience to acute stress in healthy adults. Front. Physiol. 5 https://doi.org/10.3389/fphys.2014.00161.

Clark, A., 2017a. A nice surprise? Predictive processing and the active pursuit of novelty. Phenomenol. Cogn. Sci. 1–14. https://doi.org/10.1007/s11097-017-9525-z.

Clark, A., 2017b. Busting out: predictive brains, embodied minds, and the puzzle of the evidentiary veil. N. US 514, 727–753. https://doi.org/10.1111/nous.12140.

Craig, A.D., 2003. Interoception: the sense of the physiological condition of the body. Curr. Opin. Neurobiol. 13 (4), 500–505. https://doi.org/10.1016/S0959-4388(03)00090-4.

Craig, A.D., 2006. Physical activity and the neurobiology of interoception. In: Ekkekakis, P., Acevedo, E. (Eds.), Psychobiology of Physical Activity. Human Kinetics, Illinois, pp. 15–28.

Critchley, H.D., Garfinkel, S.N., 2017. Interoception and emotion. Curr. Opin. Psychol. 17, 7–14. https://doi.org/10.1016/j.copsyc.2017.04.020.

Critchley, H.D., Wiens, S., Rotshtein, P., Öhman, A., Dolan, R.J., 2004. Neural systems supporting interoceptive awareness. Nat. Neurosci. 7 (2), 189–195. https://doi.org/10.1038/nn1176.

Desmedt, O., Luminet, O., Corneille, O., 2018. The heartbeat counting task largely involves non-interoceptive processes: evidence from both the original and an adapted counting task. Biol. Psychol. 138, 185–188. https://doi.org/10.1016/j.biopsycho.2018.09.004.

DuBois, D., Ameis, S.H., Lai, M.-C.C., Casanova, M.F., Desarkar, P., 2016. Interoception in autism spectrum disorder: a review. Int. J. Dev. Neurosci. 52, 104–111. https://doi.org/10.1016/j.ijdevneu.2016.05.001.

Dunn, B.D., Galton, H.C., Morgan, R., Evans, D., Oliver, C., Meyer, M., Dalgleish, T., 2010. Listening to your heart: how interoception shapes emotion experience and intuitive decision making. Psychol. Sci. 21 (12), 1835–1844. https://doi.org/10.1177/0956797610389191.

Durlik, C., Brown, G., Tsakiris, M., 2014. Enhanced interoceptive awareness during anticipation of public speaking is associated with fear of negative evaluation. Cognit. Emot. 28 (3), 530–540. https://doi.org/10.1080/02699931.2013.832654.

Edwards, D.J., Young, H., Johnston, R., 2018. The immediate effect of therapeutic touch and deep touch pressure on range of motion, interoceptive accuracy and heart rate variability: a randomized controlled trial with moderation analysis. Front. Integr. Neurosci. 12, 41. https://doi.org/10.3389/fnint.2018.00041.

Eggart, M., Lange, A., Binser, M.J., Queri, S., Müller-Oerlinghausen, B., 2019. Major depressive disorder is associated with impaired interoceptive accuracy: a systematic review. Brain Sci. 9 (6), 131. https://doi.org/10.3390/brainsci9060131.

Ehlers, A., Breuer, P., 1992. Increased cardiac awareness in panic disorder. J. Abnorm. Psychol. 101 (3), 371–382. https://doi.org/10.1037/0021-843X.101.3.371.

Ekkekakis, Panteleimon, 2009. Let them roam free?: physiological and psychological evidence for the potential of self-selected exercise intensity in public health. Sports Med. 39 (10), 857–888. https://doi.org/10.2165/11315210-000000000-00000.

Ekkekakis, Panteleimon, Lind, E., Joens-Matre, R.R., 2006. Can self-reported preference for exercise intensity predict physiologically defined self-selected exercise intensity? Res. Q. Exerc. Sport 77 (1), 81–90. https://doi.org/10.1080/02701367.2006.10599334.

Ekkekakis, Panteleimon, Hall, E.E., Petruzzello, S.J., 2008. The relationship between exercise intensity and affective responses demystified: to crack the 40-year-old nut, replace the 40-year-old nutcracker! Ann. Behav. Med. 35 (2), 136–149. https://doi.org/10.1007/s12160-008-9025-z.

Ekkekakis, Panteleimon, Parfitt, G., Petruzzello, S.J., 2011. The pleasure and displeasure people feel when they exercise at different intensities: decennial update and progress towards a tripartite rationale for exercise intensity prescription. Sports Med. 41 https://doi.org/10.2165/11590680-000000000-00000.

Ekkekakis, Panteleimon, Hartman, M.E., Ladwig, M.A., 2020. Affective responses to exercise. In: Handbook of Sport Psychology. Wiley, pp. 231–253. https://doi.org/10.1002/9781119568124.ch12.

Farb, N., Logie, K., 2019. Interoceptive appraisal and mental health. In: Tsakiris, M., Preester, H. (Eds.), The Interoceptive Mind: From Homeostasis to Awareness. Oxford University Press, New York, pp. 227–239.

Foley, T.E., Fleshner, M., 2008. Neuroplasticity of dopamine circuits after exercise: implications for central fatigue. NeuroMolecular Med. 10 (2), 67–80. https://doi.org/10.1007/s12017-008-8032-3.

Forkmann, T., Scherer, A., Meessen, J., Michal, M., Schächinger, H., Vögele, C., Schulz, A., 2016. Making sense of what you sense: disentangling interoceptive awareness, sensibility and accuracy. Int. J. Psychophysiol. 109, 71–80. https://doi.org/10.1016/j.ijpsycho.2016.09.019.

Füstös, J., Gramann, K., Herbert, B.M., Pollatos, O., 2013. On the embodiment of emotion regulation: interoceptive awareness facilitates reappraisal. Soc. Cogn. Affect. Neurosci. 8 (8), 911–917. https://doi.org/10.1093/scan/nss089.

Garfinkel, S.N., Manassei, M.F., Hamilton-Fletcher, G., den Bosch, Y.I., Critchley, H.D., Engels, M., 2016a. Interoceptive dimensions across cardiac and respiratory axes. Philos. Trans. R. Soc. B Biol. Sci. 371 (1708), 20160014 https://doi.org/10.1098/rstb.2016.0014.

Garfinkel, S.N., Tiley, C., O'Keeffe, S., Harrison, N.A., Seth, A.K., Critchley, H.D., Critchley, H.D., 2016b. Discrepancies between dimensions of interoception in autism: implications for emotion and anxiety. Biol. Psychol. 114, 117–126. https://doi.org/10.1016/j.biopsycho.2015.12.003.

Georgiou, E., Matthias, E., Kobel, S., Kettner, S., Dreyhaupt, J., Steinacker, J.M., Pollatos, O., 2015. Interaction of physical activity and interoception in children. Front. Psychol. 6 (4), 502. https://doi.org/10.3389/fpsyg.2015.00502.

Goldstein, L.A., Mehling, W.E., Metzler, T.J., Cohen, B.E., Barnes, D.E., Choucroun, G.J., Neylan, T.C., 2018. Veterans group exercise: a randomized pilot trial of an integrative exercise program for veterans with posttraumatic stress. J. Affect. Disord. 227, 345–352. https://doi.org/10.1016/j.jad.2017.11.002.

Gomes, M.F.P., Borges, M.E., Rossi, V. de A., de Moura, E. de O.C., Medeiros, A., 2017. The effect of physical resistance training on baroreflex sensitivity of hypertensive rats. Arq. Bras. Cardiol. 108 (6), 539–545. https://doi.org/10.5935/abc.20170065.

Grabauskaitė, A., Baranauskas, M., Griškova-Bulanova, I., 2017. Interoception and gender: what aspects should we pay attention to? Conscious. Cogn. 48, 129–137. https://doi.org/10.1016/j.concog.2016.11.002.

Gregoire, J., Tuck, S., Yamamoto, Y., Hughson, R.L., 1996. Heart rate variability at rest and exercise: influence of age, gender, and physical training. Can. J. Appl. Physiol. 21 (6), 455–470. https://doi.org/10.1139/h96-040.

Grinevich, V., Stoop, R., 2018. Interplay between oxytocin and sensory systems in the orchestration of socio-emotional behaviors. Neuron 99 (5), 887–904. https://doi.org/10.1016/j.neuron.2018.07.016.

Herbert, B.M., Ulbrich, P., Schandry, R., 2007. Interoceptive sensitivity and physical effort: implications for the self-control of physical load in everyday life. Psychophysiology 44 (2), 194–202. https://doi.org/10.1111/j.1469-8986.2007.00493.x.

Hew-Butler, T., Noakes, T.D., Soldin, S.J., Verbalis, J.G., 2008. 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. 159 (6), 729–737. https://doi.org/10.1530/EJE-08-0064.

Hillman, C.H., Erickson, K.I., Kramer, A.F., 2008. Be smart, exercise your heart: exercise effects on brain and cognition. Nat. Rev. Neurosci. 9 (1), 58–65. https://doi.org/10.1038/nrn2298.

Hirao, T., Vogt, T., Masaki, H., 2020. Difference in interoception between long-distance runners and sprinters: an event-related potential study. Med. Sci. Sports Exerc. 52 (6), 1367–1375. https://doi.org/10.1249/MSS.0000000000002248.

Hossack, K.F., 1987. Cardiovascular responses to dynamic exercise. Cardiol. Clin. 5 (2), 147–156. https://doi.org/10.1016/S0733-8651(18)30542-3.

Iodice, P., Porciello, G., Bufalari, I., Barca, L., Pezzulo, G., 2019. An interoceptive illusion of effort induced by false heart-rate feedback. Proc. Natl. Acad. Sci. 116 (28), 13897–13902. https://doi.org/10.1073/PNAS.1821032116.

Jones, G.E., Hollandsworth, J.G., 1981. Heart rate discrimination before and after exercise-induced augmented cardiac activity. Psychophysiology 18 (3), 252–257. https://doi.org/10.1111/j.1469-8986.1981.tb03029.x.

de Jong, T.R., Menon, R., Bludau, A., Grund, T., Biermeier, V., Klampfl, S.M., Neumann, I.D., 2015. Salivary oxytocin concentrations in response to running, sexual self-stimulation, breastfeeding and the TSST: the Regensburg Oxytocin Challenge (ROC) study. Psychoneuroendocrinology 62, 381–388. https://doi.org/10.1016/j.psyneuen.2015.08.027.

Katkin, E.S., Reed, S.D., Deroo, C., 1983. A methodological analysis of 3 techniques for the assessment of individual-differences in heartbeat detection. Psychophysiology 20 (4), 452.

Khalsa, S.S., Lapidus, R.C., 2016. Can interoception improve the pragmatic search for biomarkers in psychiatry? Front. Psychiatry 7 (JUL), 1–19. https://doi.org/10.3389/fpsyt.2016.00121.

Khalsa, S.S., Adolphs, R., Cameron, O.G., Critchley, H.D., Davenport, P.W., Feinstein, J. S., Zucker, N., 2018. Interoception and mental health: a roadmap. Biol. Psychiatry Cogn. Neurosci. Neuroimaging 3 (6), 501–513. https://doi.org/10.1016/j.bpsc.2017.12.004.

Knapp-Kline, K., Kline, J.P., 2005. Heart rate, heart rate variability, and heartbeat detection with the method of constant stimuli: slow and steady wins the race. Biol. Psychol. 69 (3), 387–396. https://doi.org/10.1016/j.biopsycho.2004.09.002.

Kollenbaum, V.E., 1994. A clinical method for the assessment of interoception of cardiovascular strain in CHD patients. J. Psychophysiol. 8 (2), 121–130.

Kollenbaum, Volker Edward, Dahme, B., Kirchner, G., 1996. "Interoception" of heart rate, blood pressure, and myocardial metabolism during ergometric work load in healthy young subjects. Biol. Psychol. 42 (1–2), 183–197. https://doi.org/10.1016/0301-0511(95)05154-6.

Köteles, F., Éliás, I., Szabolcs, Z., Körmendi, J., Ferentzi, E., Szemerszky, R., 2020a. Accuracy of reproduction of physical training load is not associated with resting heartbeat perception in healthy individuals. Biol. Psychol. 150 (4), 107831. https://doi.org/10.1016/j.biopsycho.2019.107831.

Köteles, F., Teufel, B., Körmendi, J., Ferentzi, E., Szemerszky, R., 2020b. Cardioceptive accuracy is associated with arousal but not with valence and perceived exertion under physical load. Psychophysiology 57 (9). https://doi.org/10.1111/psyp.13620.

La Rovere, M.T., Pinna, G.D., 2014. Beneficial effects of physical activity on baroreflex control in the elderly. Ann. Noninvasive Electrocardiol. 19 (4), 303–310. https://doi.org/10.1111/anec.12170.

Laterza, M.C., De Matos, L.D.N.J., Trombetta, I.C., Braga, A.M.W., Roveda, F., Alves, M.J. N.N., Rondon, M.U.P.B., 2007. Exercise training restores baroreflex sensitivity in never-treated hypertensive patients. Hypertension 49 (6), 1298–1306. https://doi.org/10.1161/HYPERTENSIONAHA.106.085548.

Ley-Flores, J., Bevilacqua, F., Bianchi-Berthouze, N., Taiadura-Jimenez, A., 2019. Altering body perception and emotion in physically inactive people through movement sonification. 2019 8th international conference on affective computing and intelligent interaction. ACII 2019. https://doi.org/10.1109/ACII.2019.8925432.

Lin, T.W., Kuo, Y.M., 2013. Exercise benefits brain function: the monoamine connection. Brain Sci. 3 (1), 39–53. https://doi.org/10.3390/brainsci3010039.

Lind, E., Welch, A.S., Ekkekakis, P., 2009. Do "mind over muscle" strategies work?: examining the effects of attentional association and dissociation on exertional, affective and physiological responses to exercise. Sports Med. 39 (9), 743–764. https://doi.org/10.2165/11315120-000000000-00000.

Lohse, K.R., Sherwood, D.E., 2011. Defining the focus of attention: effects of attention on perceived exertion and fatigue. Front. Psychol. 2 (11), 1–10. https://doi.org/10.3389/fpsyg.2011.00332.

Lubans, D., Richards, J., Hillman, C., Faulkner, G., Beauchamp, M., Nilsson, M., Biddle, S., 2016. Physical activity for cognitive and mental health in youth: a systematic review of mechanisms. Pediatrics 138 (3), e20161642. https://doi.org/10.1542/peds.2016-1642.

Machado, D.G. da S., Farias Junior, L.F. de, Nascimento, P.H.D. do, Tavares, M.P.M., Anselmo da Silva, S.K., Agrícola, P.M.D., Okano, A.H., 2019. Can interoceptive accuracy influence maximal performance, physiological and perceptual responses to exercise? Physiol. Behav. 204, 234–240. https://doi.org/10.1016/j.physbeh.2019.02.038.

MacRae, P.G., Spirduso, W.W., Cartee, G.D., Farrar, R.P., Wilcox, R.E., 1987. Endurance training effects on striatal D2dopamine receptor binding and striatal dopamine metabolite levels. Neurosci. Lett. 79 (1–2), 138–144. https://doi.org/10.1016/0304-3940(87)90686-0.

Maeda, S., Ogishima, H., Shimada, H., 2019. Acute cortisol response to a psychosocial stressor is associated with heartbeat perception. Physiol. Behav. 207, 132–138. https://doi.org/10.1016/J.PHYSBEH.2019.05.013.

Martins, A.S., Crescenzi, A., Stern, J.E., Bordin, S., Michelini, L.C., 2005. Hypertension and exercise training differentially affect oxytocin and oxytocin receptor expression in the brain. Hypertension 46 (4), 1004–1009. https://doi.org/10.1161/01.HYP.0000175812.03322.59.

Masson, G.S., Costa, T.S.R., Yshii, L., Fernandes, D.C., Soares, P.P.S., Laurindo, F.R., Michelini, L.C., 2014. Time-dependent effects of training on cardiovascular control in spontaneously hypertensive rats: role for brain oxidative stress and inflammation and baroreflex sensitivity. PLoS One 9 (5), e94927. https://doi.org/10.1371/journal.pone.0094927.

McCormick, A., Meijen, C., Marcora, S., 2015, July 20. Psychological determinants of whole-body endurance performance. Sports Med. https://doi.org/10.1007/s40279-015-0319-6. Springer International Publishing.

McMorris, T., 2020. Cognitive fatigue effects on physical performance: the role of interoception. Sports Med. 50 (10), 1703–1708. https://doi.org/10.1007/s40279-020-01320-w.

McMorris, T., Barwood, M., Corbett, J., 2018. Central fatigue theory and endurance exercise: toward an interoceptive model. Neurosci. Biobehav. Rev. 93, 93–107. https://doi.org/10.1016/j.neubiorev.2018.03.024.

Mehling, W.E., Chesney, M.A., Metzler, T.J., Goldstein, L.A., Maguen, S., Geronimo, C., Neylan, T.C., 2018. A 12-week integrative exercise program improves self-reported mindfulness and interoceptive awareness in war veterans with posttraumatic stress symptoms. J. Clin. Psychol. 74 (4), 554–565. https://doi.org/10.1002/jclp.22549.

Meyerholz, L., Irzinger, J., Witthöft, M., Gerlach, A.L., Pohl, A., 2018. Contingent biofeedback outperforms other methods to enhance the accuracy of cardiac interoception: A comparison of short interventions. J. Behav. Ther. Exp. Psychiatry. https://doi.org/10.1016/J.JBTEP.2018.12.002.

Mölbert, S.C., Sauer, H., Dammann, D., Zipfel, S., Teufel, M., Junne, F., Mack, I., 2016. Multimodal body representation of obese children and adolescents before and after weight-loss treatment in comparison to normal-weight children. PLoS One 11 (11), 1–14. https://doi.org/10.1371/journal.pone.0166826.

Montgomery, W.A., Jones, G.E., Hollandsworth, J.G., 1984. The effects of physical fitness and exercise on cardiac awareness. Biol. Psychol. 18 (1), 11–22. https://doi.org/10.1016/0301-0511(84)90022-X.

Murphy, J., Brewer, R., Catmur, C., Bird, G., 2017. Interoception and psychopathology: a developmental neuroscience perspective. Dev. Cogn. Neurosci. 23, 45–56. https://doi.org/10.1016/j.dcn.2016.12.006.

Murphy, J., Catmur, C., Bird, G., 2019. Classifying individual differences in interoception: implications for the measurement of interoceptive awareness. Psychon. Bull. Rev. (June) https://doi.org/10.3758/s13423-019-01632-7.

Mussgay, L., Klinkenberg, N., Rüddel, H., 1999. Heart beat perception in patients with depressive, somatoform, and personality disorders. J. Psychophysiol. 13 (1), 27–36. https://doi.org/10.1027//0269-8803.13.1.27.

Nethery, V.M., 2002. Competition between internal and external sources of information during exercise: influence on RPE and the impact of the exercise load. J. Sports Med. Phys. Fitness 42 (2), 172–178.

Noakes, Timothy David, 2012. Fatigue is a brain-derived emotion that regulates the exercise behavior to ensure the protection of whole body homeostasis. Front. Physiol. 3 (4), 82. https://doi.org/10.3389/fphys.2012.00082.

Noakes, T.D., Gibson, A.S.C., 2004. Logical limitation to the "catastrophe" models of fatigue during exercise in humans. Br. J. Sports Med. 38 (5), 648–649. https://doi.org/10.1136/bjsm.2003.009761.

Nybo, L., Rasmussen, P., Sawka, M.N., 2014. Performance in the heat-physiological factors of importance for hyperthermia-induced fatigue. In: Comprehensive Physiology, vol. 4. John Wiley & Sons, Inc, Hoboken, NJ, USA, pp. 657–689. https://doi.org/10.1002/cphy.c130012.

Owens, A.P., Friston, K.J., Low, D.A., Mathias, C.J., Critchley, H.D., 2018. Investigating the relationship between cardiac interoception and autonomic cardiac control using a predictive coding framework. Auton. Neurosci. Basic Clin. 210, 65–71. https://doi.org/10.1016/j.autneu.2018.01.001.

Paulus, M.P., Stein, M.B., 2010. Interoception in anxiety and depression. Brain Struct. Funct. 214 (5–6), 451–463. https://doi.org/10.1007/s00429-010-0258-9.

Paulus, M.P., Stewart, J.L., Haase, L., 2013. Treatment approaches for interoceptive dysfunctions in drug addiction. Front. Psychiatry 4, 137. https://doi.org/10.3389/fpsyt.2013.00137.

Pellicano, E., Burr, D., 2012. When the world becomes "too real": a Bayesian explanation of autistic perception. Trends Cogn. Sci. 16 (10), 504–510. https://doi.org/10.1016/j.tics.2012.08.009.

Pennebaker, J.W., Lightner, J.M., 1980. Competition of internal and external information in an exercise setting. J. Pers. Soc. Psychol. 39 (1), 165–174. https://doi.org/10.1037/0022-3514.39.1.165.

Perakakis, P., Luque-Casado, A., Ciria, L.F., Ivanov, P.C., Sanabria, D., 2017. Neural responses to heartbeats of physically trained and sedentary young adults. BioRxiv 156802. https://doi.org/10.1101/156802.

Petzschner, F.H., Weber, L.A., Wellstein, K.V., Paolini, G., Do, C.T., Stephan, K.E., 2018. Focus of attention modulates the heartbeat evoked potential. NeuroImage 186, 595–606. https://doi.org/10.1016/j.neuroimage.2018.11.037.

Pollatos, O., Schandry, R., 2004. Accuracy of heartbeat perception is reflected in the amplitude of the heartbeat-evoked brain potential. Psychophysiology 41 (3), 476–482. https://doi.org/10.1111/1469-8986.2004.00170.x.

Pollatos, O., Herbert, B.M., Kaufmann, C., Auer, D.P., Schandry, R., 2007a. Interoceptive Awareness, Anxiety and Cardiovascular Reactivity to Isometric Exercise. https://doi.org/10.1016/j.ijpsycho.2007.03.005.

Pollatos, O., Schandry, R., Auer, D.P., Kaufmann, C., 2007b. Brain structures mediating cardiovascular arousal and interoceptive awareness. Brain Res. 1141 (1), 178–187. https://doi.org/10.1016/j.brainres.2007.01.026.

Proske, U., 2019. Exercise, fatigue and proprioception: a retrospective. Exp. Brain Res. https://doi.org/10.1007/s00221-019-05634-8. Springer Verlag.

Quattrocki, E., Friston, K., 2014. Autism, oxytocin and interocpetion. Neurosci. Biobehav. Res. 47, 410–430.

Razon, S., Basevitch, I., Filho, E., Land, W., Thompson, B., Biermann, M., Tenenbaum, G., 2010. Associative and dissociative imagery effects on perceived exertion and task duration. J. Imagery Res. Sport Phys. Act. 5 (1) https://doi.org/10.2202/1932-0191.1044.

Razon, S., Mandler, K., Arsal, G., Tokac, U., Tenenbaum, G., 2014. Effects of imagery on effort perception and cycling endurance. J. Imagery Res. Sport Phys. Act. 9 (1), 23–38. https://doi.org/10.1515/jirspa-2013-0011.

Ring, C., Brener, J., Knapp, K., Mailloux, J., 2015. Effects of heartbeat feedback on beliefs about heart rate and heartbeat counting: a cautionary tale about interoceptive awareness. Biol. Psychol. 104, 193–198. https://doi.org/10.1016/j.biopsycho.2014.12.010.

Robertson, C.L., Ishibashi, K., Chudzynski, J., Mooney, L.J., Rawson, R.A., Dolezal, B.A., London, E.D., 2016. Effect of exercise training on striatal dopamine D2/D3 receptors in methamphetamine users during behavioral treatment. Neuropsychopharmacology 41 (6), 1629–1636. https://doi.org/10.1038/npp.2015.331.

Sabourin, B.C., Stewart, S.H., Watt, M.C., Krigolson, O.E., 2015. Running as interoceptive exposure for decreasing anxiety sensitivity: replication and extension. Cogn. Behav. Ther. 44 (4), 264–274. https://doi.org/10.1080/16506073.2015.1015163.

Sabourin, B.C., Watt, M.C., Krigolson, O.E., Stewart, S.H., 2016. Two interventions decrease anxiety sensitivity among high anxiety sensitive women: could physical exercise be the key? J. Cogn. Psychother. 30 (2), 131–146. https://doi.org/10.1891/0889-8391.30.2.131.

Schandry, Rainer, 1981. Heart beat perception and emotional experience. Psychophysiology 18 (4), 483–488. https://doi.org/10.1111/j.1469-8986.1981.tb02486.x.

Schandry, R., Bestler, M., Montoyo, P., 1993. On the relation between cardiodynamics and heartbeat perception. Psychophysiology 30 (5), 467–474. https://doi.org/10.1111/j.1469-8986.1993.tb02070.x.

Schulz, A., Vögele, C., 2015. Interoception and stress. Front. Psychol. 6 (7), 1–23. https://doi.org/10.3389/fpsyg.2015.00993.

Schulz, A., Lass-Hennemann, J., Sütterlin, S., Schächinger, H., Vögele, C., 2013. Cold pressor stress induces opposite effects on cardioceptive accuracy dependent on assessment paradigm. Biol. Psychol. 93 (1), 167–174. https://doi.org/10.1016/j.biopsycho.2013.01.007.

Seth, A.K., Tsakiris, M., 2018. Being a beast machine: the somatic basis of selfhood. Trends Cogn. Sci. 22 (11) https://doi.org/10.1016/j.tics.2018.08.008.

Seth, A.K., Suzuki, K., Critchley, H.D., 2012. An interoceptive predictive coding model of conscious presence. Front. Psychol. 3 (1), 1–16. https://doi.org/10.3389/fpsyg.2011.00395.

Sharp, P.B., Sutton, B.P., Paul, E.J., Sherepa, N., Hillman, C.H., Cohen, N.J., Barbey, A.K., 2018. Mindfulness training induces structural connectome changes in insula networks. Sci. Rep. 8 (1) https://doi.org/10.1038/s41598-018-26268-w.

Sinha, P., Kjelgaard, M.M., Gandhi, T.K., Tsourides, K., Cardinaux, A.L., Pantazis, D., Held, R.M., 2014. Autism as a disorder of prediction. Proc. Natl. Acad. Sci. 111 (42), 15220–15225. https://doi.org/10.1073/pnas.1416797111.

Srinivasan, S.M., Pescatello, L.S., Bhat, A.N., 2014. Current perspectives on physical activity and exercise recommendations for children and adolescents with autism spectrum disorders. Phys. Ther. 94 (6), 875–889. https://doi.org/10.2522/ptj.20130157.

Stathopoulou, G., Powers, M.B., Berry, A.C., Smits, J.A.J., Otto, M.W., 2006. Exercise interventions for mental health: a quantitative and qualitative review. Clin. Psychol. Sci. Pract. 13 (2), 179–193. https://doi.org/10.1111/j.1468-2850.2006.00021.x.

Tabor, A., Vollaard, N., Keogh, E., Eccleston, C., 2019. Predicting the consequences of physical activity: an investigation into the relationship between anxiety sensitivity, interoceptive accuracy and action. PLoS One 14 (3), e0210853. https://doi.org/10.1371/journal.pone.0210853.

Tsakiris, M., Critchley, H., 2016. Interoception beyond homeostasis: affect, cognition and mental health. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 371 (1708) https://doi.org/10.1098/rstb.2016.0002.

Tsakiris, M., Ainley, V., Pollatos, O., Schulz, A., Herbert, B.M., 2019. Comment on "Zamariola et al., (2018), interoceptive accuracy scores are problematic: evidence from simple bivariate correlations" - the empirical data base, the conceptual reasoning and the analysis behind this statement are misconceived and do not suppor. PsyArXiv. https://doi.org/10.31234/OSF.IO/WDEHR.

Tsigos, C., Chrousos, G.P., 2002. Hypothalamic-pituitary-adrenal axis, neuroendocrine factors and stress. J. Psychosom. Res. 53, 865–871. J Psychosom Res. https://doi.org/10.1016/S0022-3999(02)00429-4.

Tucker, R., 2009. The anticipatory regulation of performance: the physiological basis for pacing strategies and the development of a perception-based model for exercise performance. Br. J. Sports Med. 43 (6), 392–400. https://doi.org/10.1136/bjsm.2008.050799.

Vaitl, D., 1996. Interoception. Biol. Psychol. 42, 1–2, 1–27. https://doi.org/10.1016/0301-0511(95)05144-9.

Van de Cruys, S., Evers, K., van der Hallen, R., van Eylen, L., Boets, B., de-Wit, L., Wagemans, J., 2014. Precise minds in uncertain worlds: predictive coding in autism. Psychol. Rev. 121 (4), 649–675. https://doi.org/10.1037/a0037665.

Werner, N.S., Jung, K., Duschek, S., Schandry, R., 2009. Enhanced cardiac perception is associated with benefits in decision-making. Psychophysiology 46 (6), 1123–1129. https://doi.org/10.1111/j.1469-8986.2009.00855.x.

Williamson, J.W., Nobrega, A.C., McColl, R., Mathews, D., Winchester, P., Friberg, L., Mitchell, J.H., 1997. Activation of the insular cortex during dynamic exercise in humans. J. Physiol. 503 (2), 277–283.

Williamson, J.W., McColl, R., Mathews, D., Ginsburg, M., Mitchell, J.H., 1999. Activation of the insular cortex is affected by the intensity of exercise. J. Appl. Physiol. 87 (3), 1213–1219. https://doi.org/10.1152/jappl.1999.87.3.1213.

Whitehead, W. E, Drescher, V. M, Heiman, P, Blackwell, B, 1977. Realtion of heart rate control to heartbeat perception. Biofeedback Self Regul. 2 (4), 317–392.

Williamson, J.W., McColl, R., Mathews, D., 2003. Evidence for central command activation of the human insular cortex during exercise. J. Appl. Physiol. 94 (5), 1726–1734. https://doi.org/10.1152/japplphysiol.01152.2002.

Winder, W.W., Hickson, R.C., Hagberg, J.M., Ehsani, A.A., McLane, J.A., 1979. Training-induced changes in hormonal and metabolic responses to submaximal exercise. J. Appl. Physiol. Respir. Environ. Exerc. Physiol. 46 (4), 766–771. https://doi.org/10.1152/jappl.1979.46.4.766.

Yatawara, C.J., Einfeld, S.L., Hickie, I.B., Davenport, T.A., Guastella, A.J., 2016. The effect of oxytocin nasal spray on social interaction deficits observed in young children with autism: A randomized clinical crossover trial. Mol. Psychiatry 21 (9), 1225–1231. https://doi.org/10.1038/mp.2015.162.

Zabihhosseinian, M., Holmes, M.W.R., Murphy, B., 2015. Neck muscle fatigue alters upper limb proprioception. Exp. Brain Res. 233 (5), 1663–1675. https://doi.org/10.1007/s00221-015-4240-x.

Zamariola, G., Cardini, F., Mian, E., Serino, A., Tsakiris, M., 2017. Can you feel the body that you see? On the relationship between interoceptive accuracy and body image. Body Image 20, 130–136. https://doi.org/10.1016/j.bodyim.2017.01.005.

Zamariola, G., Maurage, P., Luminet, O., Corneille, O., 2018. Interoceptive accuracy scores from the heartbeat counting task are problematic: evidence from simple bivariate correlations. Biol. Psychol. 137, 12–17. https://doi.org/10.1016/j.biopsycho.2018.06.006.

Zarza, J.A., Sanabria, D., Perakakis, P., 2019. Can increased interoception explain exercise-induced benefits on brain function and cognitive performance? Exp. Psychol. 1–16.