



**European Journal
of Sport Science**
The Official Journal of the European College of Sport Science

Special Issue: Integrative Models of Exercise-Related Fatigue



ISSN: 1746-1391 (Print) 1536-7290 (Online) Journal homepage: <http://www.tandfonline.com/loi/tejs20>

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To cite this article: A. St Clair Gibson, J. Swart & R. Tucker (2018) The interaction of psychological and physiological homeostatic drives and role of general control principles in the regulation of physiological systems, exercise and the fatigue process – The Integrative Governor theory, *European Journal of Sport Science*, 18:1, 25-36, DOI: [10.1080/17461391.2017.1321688](https://doi.org/10.1080/17461391.2017.1321688)

To link to this article: <https://doi.org/10.1080/17461391.2017.1321688>



Published online: 06 May 2017.



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REVIEW ARTICLE

The interaction of psychological and physiological homeostatic drives and role of general control principles in the regulation of physiological systems, exercise and the fatigue process – The Integrative Governor theory

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Abstract

Either central (brain) or peripheral (body physiological system) control mechanisms, or a combination of these, have been championed in the last few decades in the field of Exercise Sciences as how physiological activity and fatigue processes are regulated. In this review, we suggest that the concept of ‘central’ or ‘peripheral’ mechanisms are both artificial constructs that have ‘straight-jacketed’ research in the field, and rather that competition between psychological and physiological homeostatic drives is central to the regulation of both, and that governing principles, rather than distinct physical processes, underpin all physical system and exercise regulation. As part of the Integrative Governor theory we develop in this review, we suggest that both psychological and physiological drives and requirements are underpinned by homeostatic principles, and that regulation of the relative activity of each is by dynamic negative feedback activity, as the fundamental general operational controller. Because of this competitive, dynamic interplay, we propose that the activity in all systems will oscillate, that these oscillations create information, and comparison of this oscillatory information with either prior information, current activity, or activity templates create efferent responses that change the activity in the different systems in a similarly dynamic manner. Changes in a particular system are always the result of perturbations occurring outside the system itself, the behavioural causative ‘history’ of this external activity will be evident in the pattern of the oscillations, and awareness of change occurs as a result of unexpected rather than planned change in physiological activity or psychological state.

Keywords: *Exercise regulation, fatigue, homeostasis, integrative governor*

Highlights

- Previously the regulation of physical activity has used the artificial constructs of central and peripheral mechanism to explain it.
- As part of the Integrative Governor theory, we suggest rather that competition between physiological and psychological homeostatic drives generates control in a dynamic manner.
- The general principles of homeostasis, negative feedback, information processing and comparison are the key components underpinning the new theory.
- Continuous dynamic oscillations across all systems are the signature of the working of these mechanisms and Integrative Governor Theory.

Introduction

The regulation of human performance has been an area of interest for researchers since antiquity, for the obvious reason that it is one of the fundamental requirements for the continued existence and survival

of the individual and therefore the human species. Too much physical activity, or athletic performance at too high an intensity, can damage the body’s organs or physiological systems, either acutely or chronically. Too low a level of physical activity can

lead to unsuccessful fulfilment of set tasks for which the physical activity was required, while insufficient exercise can also in the long term also lead to harmful effects on both organs and physiological systems (O’Keefe et al., 2012). Highly regulated control processes are therefore an absolute requirement of any physical activity or task performance requiring an increase in intensity of activity, to ensure optimal success in completing the task being performed while maintaining the level of activity within homeostatic-set boundary constraints in order to attenuate the possibility of a harmful outcome to the individual performing the activity.

Despite the efforts of researchers over the last few centuries across a wide number of research areas and disciplines, these regulatory control mechanisms, and how they co-ordinate and optimally manage physical activity, are still not well understood (Enoka & Duchateau, 2016). The fields of motor control and biomechanics have successfully developed an understanding of the motor programmes and efferent command outputs to individual and groups of muscles which regulate activity during simple tasks such as either single muscle movement, or simple tasks such as reaching for an object either during single or during repetitive occasions (Latash, 1998). The discipline of psychology is another area where there have been major developments in this area of the control of movement and action, particularly in our understanding of the motivations and reasons for performing a particular activity, and the underlying drives which set activity objectives and goals (Cabanac, 2006).

Exercise physiology as a discipline has developed substantially in the last three to four decades, and interest in how performance is regulated during both short- and long-term physical activity across different physiological systems has attracted increasing attention, with work initially examining regulation of activity in single physiological systems as discrete entities from a control perspective (Fitts & Holloszy, 1976). A more recent focus is that integrative regulation occurs, involving multiple physiological systems under the control of brain regulatory mechanisms, or as a complex interactive system where regulation occurs dynamically due to the continuous interaction of the different physiological systems across each of their boundaries (St Clair Gibson & Noakes, 2004; Ulmer, 1996).

In this review, we examine the different factors involved in these above-described regulatory mechanisms, how they are integrated by control processes in the brain and body, and how they usually, but not always, lead to optimal completion of an athletic event in the best possible time or at the fastest possible speed, while also maintaining physical

homeostasis and protecting the athlete’s physical integrity and safety. The control processes involved in the regulation of physical performance are also examined, in order to determine whether there are any unifying control theories that span across both physical and theoretical disciplines, in order to take forward our understanding of how physical activity is regulated in human physiological systems and body organs. Based on this information, we also propose a novel theory of the control of exercise performance, the Integrative Governor theory, which explains and brings together the different factors, processes and mechanisms associated with successful athletic performance and exercise activity, in an integrative model of the regulation of physical performance.

Single factor control theories of exercise regulation

The understanding of how exercise performance is regulated has been examined and described in physical terms, and mostly in single specific physical or anatomical systems, and at different levels of physiological function, from the bio-molecular to the bio-mechanical. For instance, a geneticist would describe associations between specific genes, or combinations of genes, and physical performance as the underlying determinant of successful exercise-related activity (Wang et al., 2013). For example, a relationship between the ACE (Puthuchearry et al., 2011) and other (Saunders, Posthumus, O’Connell, September, & Collins, 2015) genes and endurance capacity has been described, and it is suggested that a particular allele of this gene is important for the optimal regulation of performance of an endurance event. Similar or other genes have been suggested to be the principal regulator of sprint performance ability (Eynon et al., 2013). In contrast, a biochemist would suggest that the level of activity of a specific enzyme in individual muscle cells would be most important in the regulation of exercise performance, and the ability of the enzyme to either change a particular fuel into the basic energy source required to maintain cellular function (ATP), or to break up the metabolic by-products of other enzymatic pathways before they overwhelmed the system in which they operated in a physical concentration related manner would be the ultimate regulator of exercise performance (Fitts & Holloszy, 1976; Green, 1997). This enzymatic/biochemical conceptual framework of the regulation of exercise activity would be similar to that of the genetic theories, from the perspective that the regulation of activity is suggested to occur at a specific molecular/cellular level, and

would mean that this similar process must occur in a huge number of molecules and cells at the same time to allow overall physical activity function to occur, given how many cells are present in a single organ in the body, let alone the entire body itself. The function of these enzymes would also need to be similarly impaired across all cells if it was the principal determinant of the process which regulates exercise activity and which we describe as fatigue.

At a 'higher' systemic level of body function, it has been suggested that an organ's general function, rather than biochemical/cellular activity in each cell in the organ, may be responsible for regulating activity during an exercise bout. For example, a muscle physiologist would suggest that the specific make up of an individual's muscle fibres would be responsible for determining exercise performance and maximal capacity (Coyle, 1999; Harber & Trappe, 2008). A greater percentage of type I muscle fibres has been suggested to be associated with a more optimal performance in endurance athletic events (Coyle, 1999), while a greater percentage of type II muscle fibres has been suggested to be associated with greater success in shorter distance and ballistic athletic performance (Williams et al., 1997).

A cardiac/blood flow regulation researcher would suggest that the capacity of the heart to pump blood to the peripheral skeletal muscles, brain, and other organs would be the ultimate regulator of exercise performance, while a respiratory physiologist would suggest that the capacity of the lungs to extract oxygen from the air, and deliver it to the circulating blood and then muscles, would be the limiting regulator of performance, with fatigue developing in a 'catastrophic' manner (usually defined as 'peripheral' fatigue) when supply cannot keep up with demand (Amman, 2012; Bassett & Howley, 1997; Coyle, 1999). A researcher focused on nutrition and metabolism would suggest that muscle or liver glycogen depletion, or low levels of blood glucose, are the important determinants of performance, particularly during endurance-type exercise (Balsom, Gaitanos, Soderlund, & Ekblom, 1999; Coggan & Coyle, 1987). Similarly, a neuroscientist would say that physical circuitry in the brain is responsible for regulating exercise performance, with regulation related to either changes in the concentration of neuromodulators such as serotonin, dopamine, and glutamate, amongst other chemical agents (Khan, Evans, Hughes, & Smith, 2005; Meeusen, Watson, Hasegawa, Roelands, & Piacentini, 2006; Meeusen & Watson, 2007), or due to the algorithms in brain circuitry that in a computational manner are responsible for regulating the firing of and activity in peripheral skeletal muscles, as well as other body organ

functions, with down-regulation of these as part of the fatigue process (usually defined as 'central' fatigue) therefore being the ultimate regulator of exercise performance (Enoka & Stuart, 1992; Farina, Negro, Muceli, & Enoka, 2016; Gandevia, 2001; Goodall, Twomey, & Amann, 2014; Kennedy, McNeil, Gandevia, & Taylor, 2013; Klass, Duchateau, Rabec, Meeusen, & Roelands, 2016; St Clair Gibson, Lambert, Lambert, Hampson, & Noakes, 2001a; Taylor, Amann, Duchateau, Meeusen, & Rice, 2016).

While the current lack of understanding of how mental function occurs in the brain mitigates against describing psychological processes as a strictly physical entity, similar to the physical processes described above, psychology researchers suggest that psychological drives and motivation are responsible for the regulating exercise performance, and it would be these psychological drives, and the reasons underpinning them, that would set both the goals for, and the limits of, performance (Cabanac, 2006; Deci & Ryan, 2000; Ekkekakis, Lind, Hall, & Petruzello, 2007; Jones, 2002; Marcora, Staiano, & Manning, 2009; Marcora, 2010; Raglin, 2001, 2007; Rhoden, West, Renfree, Corbett, & St Clair Gibson, 2014; Smith, Ntoumanis, & Duda, 2007; Solms & Turnbull, 2002; West, Rhoden, Robinson, Castle, & St Clair Gibson, 2016). While ostensibly a non-physical control mechanism, it is likely that in the future a clearer understanding of the relationship between psychological function and underlying physical brain activity will surely be determined. Since psychological theories of exercise regulation are ostensibly related to a single physical organ, namely the brain; therefore psychological control theories can perhaps be described as a type of the single organ control processes described above.

All of these different factors which have been suggested to regulate exercise almost certainly play a part in its control. Each involves a particular system or a particular mechanism or process at a bio-molecular, cellular, or organ level which is involved in controlling function and it is up- and down-regulation during exercise activity. However, it has also been suggested that to focus on one of these specific regulatory mechanisms is reductionistic, and the fact that there are so many very different putative control mechanisms which have been suggested to individually regulate exercise activity suggests that there is no strong evidence that any single one of them is the principal regulator of all exercise activity. Instead, a more complex explanation of 'higher order' control mechanisms is required to better understand how multiple systems, organs, and physiological activity are controlled during an exercise bout (Atkinson, Peacock,

St Clair Gibson, & Tucker, 2007; Hampson, St Clair Gibson, Lambert, & Noakes, 2001; Marino, 2004; Marino, Gard, & Drinkwater, 2011; Noakes, 1988, 1997; Noakes, St Clair Gibson, & Lambert, 2004; Noble, 2008; St Clair Gibson, Lambert, & Noakes, 2001b; Swart et al., 2009; Tucker, 2009; Ulmer, 1996).

Complex integrative factor control theories of exercise regulation

A more teleological, complex model of the control of activity, the central governor theory, which was based on teleoanticipation theory of Ulmer (1966), suggested that the level of activity required for a particular exercise bout is continuously modulated by an algorithmic regulatory system in the brain, which sets an anticipatory level of initial activity based on distance or duration of the exercise to be performed. The brain then modulates exercise intensity using feedforward commands to the motor system, in response to afferent feedback from peripheral physiological activity and fuel substrate levels (Rauch, St Clair Gibson, Lambert, & Noakes, 2005), from receptors monitoring the external environment (Tucker, Rauch, Harley, & Noakes, 2004), and from information generated by memory of prior events of similar duration (Kriel et al., 2007; Paterson & Marino, 2004), in order to protect the body from damage which could occur if the athlete pushed themselves too hard or too far during the exercise bout (Lambert, St Clair Gibson, & Noakes, 2005; Noakes et al., 2004; Noakes & St Clair Gibson, 2004; Noakes, St Clair Gibson, & Lambert, 2005; St Clair Gibson & Noakes, 2004).

Implicit in this proposed model was the principle of physiological homeostasis, and the model suggested that the teleological purpose of the regulatory governor process (in the brain) was to protect the peripheral physiological systems from catastrophic failure, which would result if exercise intensity or level of activity was set at too high a rate, or if it continued on for too long a duration. The regulatory systems were therefore suggested to be inhibitory in nature, and include the conscious sensation of fatigue, which arose from the subconscious brain regulatory systems, and would function teleologically as a conscious signaller indicating that peripheral physiological systems might be harmed if exercise were to continue at a given intensity (St Clair Gibson et al., 2003). In this central governor model, exercise activity was suggested to be performed to a level which would allow the individual to complete the activity in the optimal time, but not at a level where physical harm could occur. A pacing strategy was

thus identified as the operative controller of the level of activity in a strategic and tactical manner.

A problem with the central governor model as it was described was that it was essentially a physiological homeostatic control model. While it described exercise-related modulatory control mechanisms, and explained their functions and mechanism of action, it did not explain why exercise is initiated, and that exercise from the perspective of these protective mechanisms would be counter-intuitive, given that these mechanisms were essentially inhibitory and designed to resist or reduce the 'desire' to continue the activity (Inzlicht & Marcora, 2016; St Clair Gibson et al., 2005). From the perspective of homeostatic control theory, the act of initiating activity, or desiring to continue activity in the face of a number of inhibitory warning signals and modulatory control processes, to the point where some athletes do indeed collapse during exercise, is paradoxical (St Clair Gibson et al., 2005). Therefore, either these suggested modulatory, homeostatic control processes are not completely successful, or some other control mechanism or competitive psychological drives are 'competing' with them during exercise, and causing these athletes to initiate and continue their activity to the potential, and occasionally actual, point of damaging their bodily function, despite the modulatory actions of these homeostatic inhibitory control processes (St Clair Gibson et al., 2013). An alternate scenario may be that these inhibitory control mechanisms are active in response to immediate or predicted threats to homeostasis but in the absence of such threats return to a quiescent state in which psychological drives are the primary determinants of activity levels (Swart, Lindsay, Lambert, Brown, & Noakes, 2012).

Developing the Integrative Governor theory – rules and principles underpin control processes regulating exercise performance

In the above sections, we have described the development of different models and theories explaining the regulation of exercise activity. Developing this theme, we propose a new theory, the Integrative Governor theory, which suggests that instead of regulation of activity being either 'centrally' or 'peripherally' based, or a combination of both, that regulation of activity is created by competition between psychological drives and physiological protection requirements, and that both of these are underpinned by similar basic control mechanisms such as homeostasis and negative feedback loop mechanisms. As part of the Integrative Governor theory, we suggest a number of rules that are fundamental both to the

theory and for the regulation of activity and exercise performance.

Rule 1. Rather than central or peripheral processes controlling exercise activity and the fatigue process, exercise regulation is the result of a pacing/power output choice strategy generated as a result of the competing requirements of physiological protective and psychological success-related drives, which are both paradoxically homeostatic, but in competition with each other, and the level of performance is the product of the relative 'weighting' of each in a dynamic 'decision-making' manner by regulatory factors and algorithmic processes yet to be determined (Renfree, Martin, Micklewright, & St Clair Gibson, 2014). Individuals who have a strong physiological protective drive will likely always complete the athletic event but are unlikely to achieve for what that individual would be an optimal performance individuals, while individuals who have too much psychological drive are in danger of collapsing either during or after the athletic event they participate in (St Clair Gibson et al., 2013) (Figure 1). As suggested by Sigmund Freud more than 100 years ago, 'the nervous system is an apparatus which has the function of getting rid of the stimuli that reach it, or of reducing them to the lowest possible level, or which if it were feasible, would maintain itself in an altogether unstimulated condition' (Ferris, 1997; Freud, 1923). His description can be used to describe both the initiation and performance of an athletic event in order by its successful completion to assuage unfulfilled psychological drives (St Clair Gibson et al., 2013), and the need to reduce exercise intensity (and the uncomfortable sensation of fatigue)

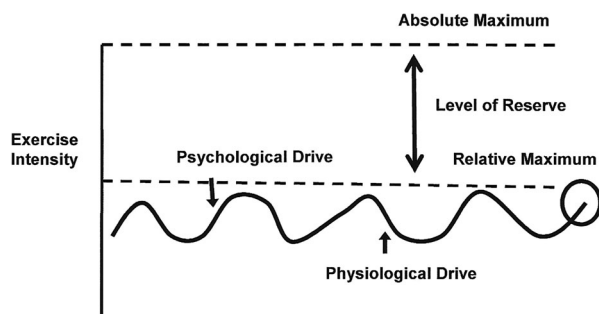


Figure 1. The relationship between physiological and psychological drives in the regulation of activity during exercise. A continuous dynamic interplay between the two occurs throughout the event, with the level of reserve maintained a product of the relative weighting between the two competing drives by the individual. The higher the relative weighting for psychological drive, the less the level of functional reserve, and the higher the relative weighting for physiological drive, the greater the level of functional reserve. The end-point (circled) and the distance and time duration to it would be an important factor in the relative weighting of psychological and physiological drives as the athletic event continues.

or terminate the exercise activity completely as a means of protecting peripheral physiological systems from complete system failure which may occur if the systems are pushed to complete failure during the exercise bout (St Clair Gibson & Foster, 2007). Indeed, while Freud called this desire to reduce psychological 'pressure' related to unfulfilled drives the 'constancy' theory (Freud, 1915; Kanzer, 1983), the early work on physiological homeostasis was similarly referred to as physiological 'constancy' rather than as homeostasis in its first iteration as a suggested theory (Woods & Ramsay, 2007). The power output generated during any event will be the final result of the competition between these physiological and psychological drives, and will alter dynamically throughout the event as the competition between them continues, increasing as a result of psychological drive requirements, and decreasing as a result of physiological protective mechanisms, and the oscillating power output trace which can be observed over an entire athlete event, which we call the pacing profile for the event (St Clair Gibson & Noakes, 2004; Tucker et al., 2006), is in effect the relative weighting of these competing drives, both of which are underpinned by the principle of homeostasis, as part of a decision-making process or structure in the brain (Renfree et al., 2014; St Clair Gibson et al., 2013).

Rule 2. The same homeostasis-related control mechanisms occur at any level of any physiological system or structure, and this system control apparatus is multiple cascades of negative feedback loops. Negative feedback regulates biochemical pathways, genetic development, single cell metabolic function, single organ and entire body function, as well as behavioural and social activity, in response to any requirement or perturbation (Carpenter, 2004;

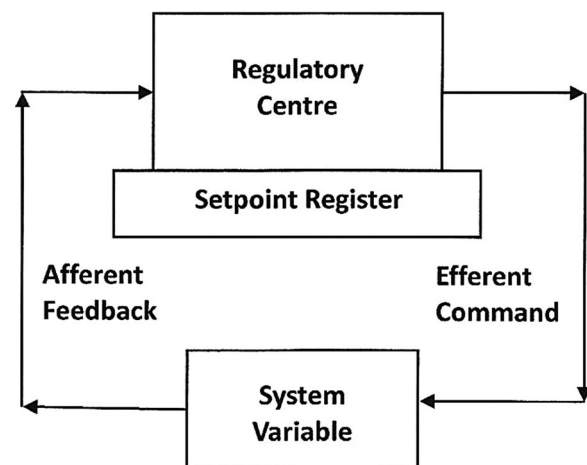


Figure 2. The basic structural components of a negative feedback loop.

Cooper, 2008; Lambert et al., 2005; Modell et al., 2015; St Clair Gibson et al., 2005; Woods & Ramsay, 2007). Negative feedback loops are the apparatus which the brain and body use to control all systems, and operate in any type of system in a similar manner (Figure 2). In order for a system to control any psychological or physiological system using homeostatic principles, three principal regulatory factors are required to be either components of the negative feedback system (Carpenter, 2004; Koeslag, Saunders, & Wessels, 1997; Lambert et al., 2005; Modell et al., 2015; Woods & Ramsay, 2007). The first is the presence of a sensory apparatus that can detect either changes in whatever substance or process being monitored, or changes in the internal or external environment or others systems which interact with or impact on the substance or process being monitored. The second is a control structure or process which would receive the information from the sensory apparatus, and would make a decision regarding whether to respond to the information or to ignore it as not relevant. The third would be an effector mechanism or process which would make the changes to the system decided upon by the control structure. In order to set initial pace for exercise activity, forecasting and anticipatory activity and behaviour at both physiological and psychological levels are created by prior feedback from similar or other earlier similar events, with strategic forecasting setting initial activity. The activity is then modified by tactical control mechanisms using afferent feedback from sensory systems to determine the level of change required and efferent control mechanism to enable the changes to be made (Atkinson et al., 2007; St Clair Gibson et al., 2013) as part of dynamic negative feedback loops. Negative feedback loops can occur within a particular system, or across different systems, and the greater the number of negative loops occurring in any system, the greater is that systems robustness and the greater is the complexity of its efferent output and overall function (Angelini et al., 2007; Costa & Goldberger, 2015; Peng et al., 1998).

Rule 3. Metabolic set points are required in order for negative feedback control systems to be able to compare the level of current activity against and to plan the level of response required to be initiated to return the physiological systems to, and indeed what these levels of response are. The human body is an extremely complex system to manage from a control perspective, because of the huge number of physiological processes continuously active and interacting with each other, all of which require regulation. Given the large number of different physiological processes active at any moment, one would expect large variability in the concentrations

of metabolites, substrates, or activity of physiological processes between different people. One would also expect this potential variability between different people to fluctuate over time. However, somewhat surprisingly, the actual values and range for any physiological variable, metabolic activity, or fuel concentration are very similar in different individuals. For example, in the example of glucose regulation described above, the blood glucose concentrations are usually maintained between 4 and 6 mmol/l in healthy subjects, and only go beyond these limits if the blood glucose regulatory mechanisms are impaired, as in the case of an individual suffering from diabetes mellitus (Saunders, Koeslag, & Wessels, 1998). Therefore, similar physiological system, metabolic activity and fuel concentration set points appear to be present in all individuals to enable such similarity across all individuals (St Clair Gibson et al., 2005), as part of the control requirements of the negative feedback loop mechanisms, and therefore are crucial both in the Integrative Governor model and for the regulation of activity in all physiological systems and therefore during exercise activity itself.

Rule 4. Changes in the function or activity of any system is the result of changes occurring external to the system being controlled. An example of this is the concept that the known physical endpoint of the activity or exercise bout is used by the regulatory mechanisms to set the level of intensity or duration of a particular event at the start of an event in an anticipatory manner (though as described above, given this would be based on prior experience and would mean the anticipatory decisions were part of a 'higher level' negative feedback loop themselves (Woods & Ramsay, 2007). This is also known as 'teleoanticipation', a concept first proposed by Ulmer (1996), which suggests that knowledge of the endpoint of the event is the crucial necessary factor which sets the levels of activity for a particular event or exercise bout. For example, the pace set for a 10 km running bout would be very different to that for a 100 km running bout, and the energy requirements demanded by that pace would be very different for each of these distances. Because of this, the physiological activity in a particular system would be very different for a 10 km compared to a 100 km running bout, and thus the external requirement and set pace strategy would set the physiological activity in the exercise bout. During the exercise bout, unexpected changes in the external environment (such as a hotter day than expected) would impact on the physiological system, which would require a response to maintain system fidelity. Any change in the external environment that impacts on a physiological system causes changes to the internal environment of the

system. In contrast, if no external environmental change occurs, the physiological activity would be maintained consistently at its set point level. Ulmer's work (1996) therefore suggested that an external factor, in this case the execution of the task, was the regulating factor of the activity of the physical processes involved in completing the task, rather than some regulatory factor in the actual motor control system itself.

Rule 5. Because negative feedback is the ultimate control mechanism of all psychological and physiological systems, and a time delay occurs between receiving afferent information as a result of some external perturbation impacting on the system, making a decision to act on this afferent information, and putting into effect changes because of it, all systems and activity, physiological or social or psychological, will oscillate continuously, but with changing amplitude or frequency, depending on the particular circumstances in which the system is operating at a particular point in time (Goodner et al., 1977; Lambert et al., 2005; St Clair Gibson & Noakes, 2004; St Clair Gibson et al., 2006) (Figure 3). The level of oscillation (also described as a fluctuation) of a physiological variable or system is called its 'gain', and the time taken for the entire system to return to a state of zero fluctuation, although 'zero' fluctuation is essentially a theoretical concept as any variable in a living system fluctuates continuously, even if at a very low amplitude, is called the time constant of the gain of the system (Lambert et al., 2005).

It has been previously suggested that time delay related to the delay in information reaching the decision-making structures from the time point when an efferent command has generated a particular level of activity in a peripheral physiological system to

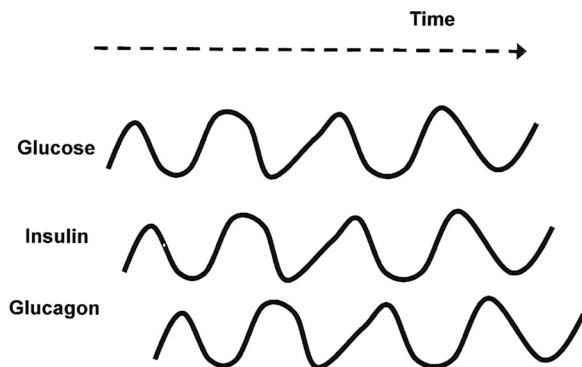


Figure 3. Oscillatory behaviour of insulin, glucagon, and glucose, with insulin and glucagon concentration changing in response to changes in glucose concentration, and by their actions either attenuating (insulin) or increasing (glucagon) the glucose concentration. There is of necessity due to communication requirements, a time lag between the change in concentration, and therefore oscillatory changes, of all three variables.

the time point when sensors can pick up these changes and relay the information about them through afferent pathways to the decision-making structures or mechanisms in the control system create a period of 'uncertainty' from an information knowledge perspective in the controlling structures (St Clair Gibson et al., 2006). During this period of 'uncertainty', no absolute knowledge of the current state of the physiological system can be evident to its controlling system, and no responses can be initiated by the control system during the uncertainty time period. Once the decision-making algorithms in the regulatory centre receive this information, a period of 'certainty' occurs, and the control system or processes make a decision whether to effect changes in the physiological system or maintain its current status, and send commands via efferent control pathways in order to make these changes. Periods of 'certainty' and 'uncertainty' will therefore alternate in a continuous and dynamic throughout an exercise bout and at rest/during activities of daily living, and the duration of each of these periods will be related to the requirements of the task being performed, the infrastructural composition of the negative feedback system controlling the physiological system and the changes of activity in it, and the 'hierarchical' level of the negative feedback loop involved in the control function. For example, the periods of certainty and uncertainty will be of short duration when associated with the negative feedback loop between insulin, glucagon, and glucose, and longer for negative feedback loops between glucose sensors which pick up changes in glucose concentrations in the bloodstream and the brain where behavioural changes would be initiated and managed in response to changes in the blood glucose concentration, and these different time durations for each period of certainty, uncertainty and decision at different hierarchical levels make overall regulation even more complex, and the oscillator patterns of any single negative feedback system more complex and potentially non-linear, even if more robust (St Clair Gibson et al., 2006).

It has been further suggested that each period of discrete 'certainty' of activity in each physiological system creates a 'quantal unit' of information which can be used to understand the control processes of a system and is used in this manner to regulate physiological systems (St Clair Gibson et al., 2006). Any trace of any physiological system recorded at high capture rates that capture one entire cycle of change in a physiological system during dynamic exercise activity, or example heart rate (Palmer, Hawley, Dennis, & Noakes, 1994) or power output (Terblanche, Wessels, Stewart, & Koeslag, 1999; Tucker et al., 2006), has been

shown to be non-monotonic, with each recorded point usually being different to that recorded immediately before or after it. Each of these differing power output or heart rate levels must be associated with a different level of efferent command generated by whatever control system regulates its activity (Balague, Torrents, Hristovski, & Kelso, 2017; St Clair Gibson et al., 2006), and therefore when one records a trace of for example power output or heart rate during an entire athletic event, if captured at a high enough rate, a record of ‘quantal units’ of information which has been generated by the control system in order to effect changes in the physiological system being studied. That these traces are always usually non-monotonic indicates that changes are continuously being made to the system being studied in a deterministic manner (Terblanche et al., 1999; Tucker et al., 2006), and they are created by tactical ‘decisions’ associated with maintaining the strategic plan for the entire athletic event the individual is participating in, related we suggest to the weighting of the competing requirements of psychological and physiological homeostasis (St Clair Gibson et al., 2013). Whether this is the case or not, whatever underpins them, oscillations occur in a dynamic manner in all physiological systems, and are a ‘signature’ of the negative feedback control mechanism which underpin them (Maeda & Kurata, 2014; Novak & Tyson, 2008; St Clair Gibson et al., 2006).

Rule 6. The unifying concept underlying all systems is comparison. A system cannot create any “knowledge” or “awareness” without comparison, and feedback cannot be initiated without comparison between variables or system states (St Clair Gibson et al., 2003, 2006). If a change in a variable occurs,

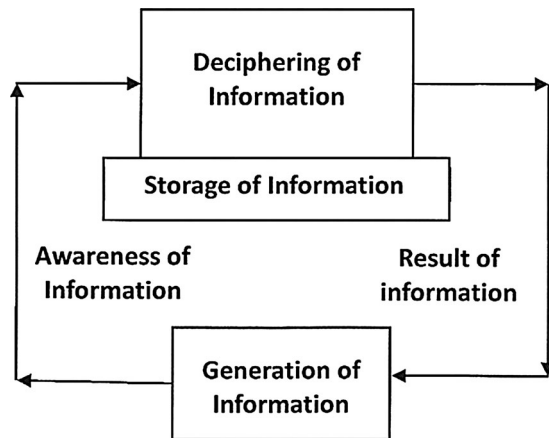


Figure 4. The integral requirement of information processing to the function of the negative feedback loop regulatory mechanism. Information flow occurs continuously through the body and brain regulating all activity and function.

it cannot be made sense of unless it is compared against something else, be that the set point level of the variable, or its level or concentration at a prior point in time, or against current or future requirements of the variable to enable the system to continue to function, or again a template of the expected activity (Paterson & Marino, 2004; St Clair Gibson et al., 2003; Swart et al., 2009; Tucker, 2009). For a response to either occur or not to occur, a decision based on comparison is also required (Renfree et al., 2014). Essential to the Integrative Governor theory, and the regulation of activity, therefore, is the notion or concepts of comparison and decision-making, and without comparison the regulatory processes can never make a “decision” and enact changes via efferent control mechanisms.

Rule 7. Information processing is the universal interactive language and requirement of different anatomical, physical, psychological or social systems, and also between these different systems (St Clair Gibson et al., 2006), and is an absolute requirement for comparison and decision-making by control mechanisms involved in negative feedback loops. All changes in any variable in a system generate information, which thus becomes the “language” of communication which operates across different types of systems. The most obvious example of this is in the rate of firing in the brain neurons and efferent nerves to the muscles in the body related to motor command signals (Debanne, 2004; Laurent, 2002; Scott, 2004). This rate of firing increases or decreases dependent on the calculated requirement for either more or less power output generation from muscles during any particular task, and in that increase or decrease is an information code which relays the exact requirement to the muscles. If the rate of firing in an efferent nerve is recorded, by examining the recorded trace one could state with a degree of certainty which spike trains were associated with more or less power output according to their observed firing rate (St Clair Gibson et al., 2006). Similar information code is generated by afferent nerves from sensory receptors in the body detecting changes in glucose, oxygen and other physiological variables and relayed to either the brainstem or brain itself (Richerson, 2004), and must be processed by an algorithm which is able to understand, process, and determine the information in the firing rate form it is generated and received (Figure 4). There is a piezoelectric nature to the transfer of information between systems in the body, as for example the firing rate information code in brain neurons transfers discretely and correctly across synapses using chemical neurotransmitters to transfer the information across the synapse (Montague et al., 2004), and bio-molecular activity, for example the activity

of NADPH in macrophages, which can be similarly increased by both electrical current and IL-6 acting on it (Adachi, Kindzelskii, Ohno, Yadomae, & Petty, 1999). Information must be generated and reacted to from more complex behavioural and social environments, for example the passing of time, the need for food or fluid ingestion, or the effect of competition or rivalry with other competitors in a race on one's own personal performance (St Clair Gibson et al., 2006, 2013). Indeed, at the root of any response to a system perturbation is the requirement for receiving information, deciphering the information, and responding to it (Figure 4). In the Integrative Governor theory, therefore, information processing is an absolute requirement of physiological and behavioural regulation, and underpins all activity and is a unifying factor related to both physiological function and its regulation.

Rule 8. "Awareness" of systems occurs because of unexpected changes in any system or other system acting on that system, or because of awareness of discrepancies between the strategy and tactics employed by the system governor (Swart et al., 2009; Tucker, 2009). It was previously suggested (Hampson et al., 2001; St Clair Gibson et al., 2003) that the sensation of fatigue is the conscious awareness of changes in subconscious homeostatic control systems, and is derived from a temporal difference between subconscious representations of these homeostatic control mechanisms in neural networks that are induced by changes in the level of activity. It was subsequently proposed that the sense of effort acts as such a signal in response to increases in exercise intensity that are perceived to be sustainable by the complex, dynamic subconscious teleological pacing control mechanisms (Swart et al., 2012). These researchers (Swart et al., 2012) demonstrated that the sense of effort can be distinguished as an independent sensory modality which was distinct from any physical sensations. The sense of effort was shown to rise to near maximal levels in response to acute increases in exercise intensity, despite physical sensations remaining submaximal. In addition, the sense of effort was abolished when the exercise intensity fell significantly below that which had been achieved for the same exercise task as a maximal voluntary effort, despite the persistence of physical sensations related to the exercise task, such as breathlessness and muscle pain, amongst other sensations. These conscious inhibitory regulatory signals may therefore occur intermittently and only in response to potential threats to physiological homeostasis, whether imminent or predicted by subconscious pacing mechanisms. These findings of Swart et al. (2012) suggest that the sense of effort acts as an intermittent inhibitory sensation, which

would compete with psychological drives to continue exercise, the outcome being either: (1) a willful disregard for the inhibitory sense of effort; (2) a conscious reduction of exercise intensity to correct to correct the pacing strategy to a potentially successful plan; or (3) in extreme cases, the cessation of the exercise altogether. It was further suggested that if one anticipated the fatigue level for an event, and this anticipation is exactly right, you should not theoretically be "aware" of the sensation of fatigue (Swart et al., 2012; Tucker, 2009).

Summary and conclusions

For several decades, research into the control mechanisms regulating exercise activity has been 'straight-jacketed' by theories of peripheral versus central control mechanism models, or a combination of both in integrative models. In this article, we have suggested that this may not be the appropriate focus for understanding the regulation of exercise activity, and have developed a new theory, the Integrative Governor theory, which hypothesizes that competition between psychological and physiological homeostatic drives, which are antagonistic but underpinned by the same general mechanisms, and the relative 'weighting of each' by a decision-making function or structure in the brain, is what regulates exercise activity, the fatigue process, and the outcome of a particular athletic event for the individual competing in it. At the root of both psychological and physiological drives is the general principle of homeostasis, or constancy, as homeostasis used to be described. How an individual performs in an event is a composite of the relative weighting of each of these antagonistic drives, and the level of 'pressure' related to each drive, and the power output during the athletic event is the behavioural 'trace' of this dynamic 'weighting' and decision-making function of the control processes which regulate it, and further research should perhaps attempt to understand how this relative 'weighting' processes occurs and the reasons its similarities and differences in different individuals.

The Integrative Governor theory further suggests that underpinning the homeostatic control mechanisms of both psychological and physiological drives is the negative feedback loop, with forecasting and feedforward control being components of reflex loop iterative behaviour, and that metabolic setpoint levels are necessary for the negative feedback loop control mechanisms, wherever and however these metabolic set points are determined. Information processing is the universal 'language' of communication of the regulatory processes, and the unifying

control concept is that of comparison of system variable concentration, activity, or state. Because negative feedback loop is the ultimate control mechanism underpinning system homeostasis, and has time delays in information associated with them, all physiological and psychological system variables and activity will continuously oscillate, and oscillatory activity is therefore a hallmark of both the Integrative Governor theory and evidence of dynamic control processes occurring throughout all systems in any individual performing exercise activity. It is a major future challenge to understand how these processes and decision-making activity are 'operationalized' in control structures and mechanisms still to be elucidated in the brain and body.

Disclosure statement

No potential conflict of interest was reported by the authors.

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