PART 1

THEORETICAL AND METHODOLOGICAL ISSUES

1

Acute exercise and psychological functions: a cognitive-energetic approach

Michel Audiffren

Feelings of efficiency or inefficiency are often reported by people practising a mental task during or following a physical activity. For instance, athletes know from experience that performing a warm-up exercise improves their reactivity to a start signal; soldiers carrying heavy loads complain about the debilitating effect of central fatigue on decision making while walking long distances; and the elderly are aware that regular physical activity improves mental health and autonomy. In spite of these popular and professional beliefs, the interactions between the physiological changes, induced by exercise and the psychological functions potentially affected by these changes were, and still are, the object of an extended debate. Today, a large number of scientific studies support a positive effect of exercise on psychological functions (for recent narrative and meta-analysis reviews see Colcombe and Kramer, 2003; Etnier *et al.*, 2006; McMorris and Graydon, 2000; Tomporowski, 2003b). The purpose of this chapter is to present different theories and methods drawn from cognitive and energetic approaches that explain the effects of exercise on psychological processes. In addition, we will attempt to determine the location of these effects in the cognitive-energetic architecture of the information processing system.

The chapter is organized as follows. The first section will be devoted to the proposal of common taxonomies for the effects of exercise on psychological and physiological variables. These taxonomies will guide the choice of adequate physiological interventions, cognitive tasks and theories or models, which can explain the different effects of exercise on psychological processes. In the second section, the cognitive psychology approach and the information processing paradigm will be briefly presented. This approach provides very powerful methods that allow the study of the effect of exercise on psychological functions. The energetic approach will be

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assessed in the third section, as it supplies a very useful theoretical framework from which to understand the acute effects of exercise on cognition. In the fourth section, four cognitive-energetic models explaining the facilitating and debilitating effects of acute exercise on information processing will be proposed. The fifth section will present six methods from cognitive psychology that explain the localization of the effects of exercise in the architecture of cognitive-energetic systems. Finally, in the sixth section, some limits of the cognitive-energetic approach will be discussed and complementary approaches that could give additional information on the mechanisms underlying the effects of exercise on cognition will be suggested.

1.1 Varieties of exercise effects on psychological variables

The literature on the effects of exercise on psychological functions is abundant. From 1960, several hundred experiments have been conducted throughout the world on this topic. Four kinds of results are generally reported: (1) an improvement in psychological functions; (2) an impairment of psychological functions; (3) a change in strategy to maintain psychological test performance; and (4) no effects on psychological functions. The fourth category is problematic because researchers cannot distinguish between two possible reasons for the failure: (1) there is no effect of exercise on psychological functions in the real world or (2) the methodology used in the experiment was not appropriate to show a significant effect of exercise on psychological functions. The three other categories of results are the most interesting because they lead to new questions: (1) what are the adequate conditions to observe these phenomena (intensity and duration of exercise, time of observation during or after exercise, age and cardiovascular fitness of participants, etc.); (2) which physiological mechanisms explain these positive or negative effects on psychological processes; and (3) which psychological processes are affected by these mechanisms. The aim of this first section is to propose taxonomies for the interaction between exercise and cognitive tasks, which can help scientists to conceptualize future research on the topic.

Aerobic versus anaerobic exercise

Studies that assessed the effects of exercise on psychological functions have used a large variety of exercise protocols (see Tomporowski and Ellis, 1986, for a narrative review). Physical exercises performed by the participants can be classified according to their mode of progress (constant or incremental load), their intensity and duration, and the two general metabolic pathways that supply the energy to the muscle (aerobic and anaerobic). According to the review by Tomporowski and Ellis, four categories of exercises can be distinguished (see Table 1.1).

The intensity of exercise is generally defined according to the capabilities of the participants. Different indices have been used by researchers to determine the same relative intensity of exercise for all participants: for instance, the percentage of

Table 1.1 Taxonomy of physical exercises as a function of duration and intensity of the physiological intervention.

Mode of exercise	Duration	Intensity	Metabolic pathway	Example
Constant-load exercise	Very brief <3 min	Supra-maximal >100% VO_2max	Anaerobic	Handgrip at maximal force
Ramp incremental exercise	Moderate 10 to 25 min	Up to maximal Up to 100% VO_2max	Aerobic and Anaerobic	VO_2max test
Constant-load exercise	Short to moderate 5 to 60 min	Sub-maximal 30 to 80% VO_2max	Aerobic	Walking on a treadmill
Constant-load exercise	Long > 60 min	Sub-maximal 30 to 80% VO_2max	Aerobic	Marathon race

maximal oxygen uptake (e.g. Delignières, Brisswalter and Legros, 1994; Travlos and Marisi, 1996), the percentage of maximal power output (e.g. Arcelin, Delignières and Brisswalter, 1998; Hogervorst *et al.*, 1996; McMorris and Graydon, 1996a; Paas and Adam, 1991), the percentage of ventilatory threshold (e.g. Davranche *et al.*, 2005a, Davranche, Audiffren and Denjean, 2006a), the percentage of lactate threshold (Chmura *et al.*, 1998; Kashihara and Nakahara, 2005), the percentage of maximal heart rate (e.g. McGlynn *et al.*, 1979), the percentage of heart rate reserve (e.g. Pesce, Casella and Capranica, 2004), or the rating of perceived exertion (e.g. Kamijo *et al.*, 2004b). In Table 1.1, the intensity of exercise is expressed in percentage of maximal volume of oxygen uptake (%VO_2max), a function of the cardiorespiratory system reflecting the total amount of oxygen that the individual can utilize. This index is commonly used in exercise physiology and exercise psychology.

Physiological mechanisms providing energy to the muscle and physiological states induced by exercise vary considerably from one category of exercise to the other. Very brief and intense exercise, described in the first line of Table 1.1, mainly involves the anaerobic metabolism. It may be localized, such as a handgrip at maximal force, or involve the whole body, such as in the 100 m sprint. The anaerobic metabolism does not require oxygen and yields small quantities of adenosine 5′-triphosphate (ATP) per mole of glucose or muscle glycogen. Three separate anaerobic mechanisms, initiated in parallel but varying markedly in duration, provide ATP to the muscle following the initiation of this type of exercise (Ward-Smith, 1999): (1) a small quantity of endogenous ATP molecules stored in muscle, which are depleted in approximately 5 s; (2) the breakdown of intramuscular phosphocreatine (PCr) that contributes to the production of ATP and lasts approximately 10 s; and (3) the oxygen-independent glycolysis that supplies predominantly the ATP from 10 to 100 s. Blood lactate and H^+ ions are the end products that are released into the blood by this oxygen-independent glycolysis. The availability of phosphagens (ATP and PCr), and blood acidosis are generally accepted to be two of the most likely limitations to anaerobic muscle performance. Very brief and intense exercise presents two problems for studying the effects of exercise on cognition. On the one hand, due to the short duration of the exercise, the number of trials recorded during the exercise for the cognitive task is necessarily small. On the other hand, peripheral fatigue mechanisms take place during this category of exercise. Studies not concerned with these peripheral fatigue phenomena should choose one of the other categories of exercise.

Graded exercise, described in the second line of Table 1.1, in which exercise intensity is progressively increased from light intensity to exhaustion, involves anaerobic as well as aerobic mechanisms. When exercise is sustained beyond 100 s, aerobic metabolism, which requires oxygen and yields large quantities of ATP per mole of glucose, progressively replaces anaerobic metabolism as the main source of energy. In a graded exercise, the aerobic mechanism provides the larger part of the energy until the anaerobic lactate threshold is reached. Anaerobic lactate threshold represents the critical point at which metabolic modifications bring about the energy-demand transition from aerobic to anaerobic exercise. Incremental exercise until exhaustion presents a serious limit for studying the effect of exercise on cognition because the participants' physiological state changes throughout the exercise. During the first minutes of the exercise, the energy is mainly supplied by aerobic mechanisms, and there is no fatigue nor any real mental effort required to sustain the relatively low intensity of exercise. By contrast, during the last minutes of this kind of exercise, the energy is mainly supplied by anaerobic glycolysis, participants generally feel peripheral fatigue and a high level of mental effort is required to continue the exercise.

Aerobic exercise of moderate duration, described in the third line of Table 1.1, seems to be the most interesting category of exercise to study the positive effect of exercise on cognition. There are three main reasons for this: (1) participants perform at steady-state throughout the entire exercise session and aerobic mechanisms are the main source of energy soon after the beginning and until the end of exercise; (2) a cognitive task involving a large number of trials can be performed simultaneously to the exercise; and (3) central as well as peripheral fatigue phenomena are limited, which is in contrast to the three other categories of exercise. Finally, aerobic exercise of long duration, described in the fourth line of Table 1.1, is more interesting for studying the effects of central fatigue on cognition. The last two categories of exercise generally require whole-body activation.

Acute versus chronic exercise

There is another very important distinction concerning the protocols used to study the effects of exercise on cognition. Both acute and chronic exercise have been extensively used, but they must be distinguished because they induce different changes in the organism (see Table 1.2). While acute exercise concerns itself with a single bout of exercise, chronic exercise concerns itself with the repetition of bouts of

Table 1.2 Taxonomy of physical exercises as a function of physiological changes they induce.

Type of effect	Mode of exercise	Type of physiological change	Type of brain mechanism underpinning the effect
Acute effect	Single bout of exercise	Transient	Modulation of the activity of a neural network
Chronic effect	Regular exercise	Durable	Anatomical changes in the brain structure

exercise over time, lasting from weeks to years (Audiffren *et al.,* 2007a). The behavioural and psychological changes induced by a single bout of exercise generally appear quite rapidly after the beginning of exercise (seconds to minutes) and disappear relatively quickly after its cessation (minutes to hours). Neurophysiological changes, which underlie the transitory behavioural and psychological changes induced by exercise, can be viewed as a transient modulation of the activity of the neural networks involved in the cognitive task or the mental state of interest. In contrast, chronic effects of exercise reflect structural and durable changes in the organism, like angiogenesis (e.g. Swain *et al.*, 2003), synaptogenesis (e.g. Chu and Jones, 2000) or neurogenesis (e.g. van Praag *et al.*, 1999).

The behavioural and psychological changes induced by the regular practice of a physical activity typically appear a few weeks after the beginning of the exercise programme and can be maintained several weeks after its termination. Neurophysiological changes underlying stable behavioural and psychological changes induced by exercise can be viewed as durable anatomical changes in the brain structure at different possible levels (e.g. neuroreceptor, synapse, neuron, neural network, brain structure). In this chapter, we will focus on theories and models which can explain the acute effects of exercise on cognitive processes.

Bottom-up versus top-down processes

Psychometric tasks used to examine the acute effects of exercise on psychological processes involve a large variety of sensorimotor and cognitive processes. According to Paillard (1986, 2005), it is useful to distinguish these two levels of information processing (see Figure 1.1). On the one hand, the sensorimotor level can be conceived as an interface between the brain and its environment. Ascending information gathered by sensory organs for further processing through attentional control and descending commands for self-generated movements require this sensorimotor interface. The sensorimotor level is mainly genetically pre-wired and supplies vital functions such as stretch reflex and orienting reaction. On the other hand, the cognitive level is underpinned by an apparatus endowed with the whole resources of neocortical and limbic structures and able to process a large variety of mental states that characterize higher brain functions. The sensorimotor level mainly functions in a reactive way, but possesses its own adaptive loops, whereas the

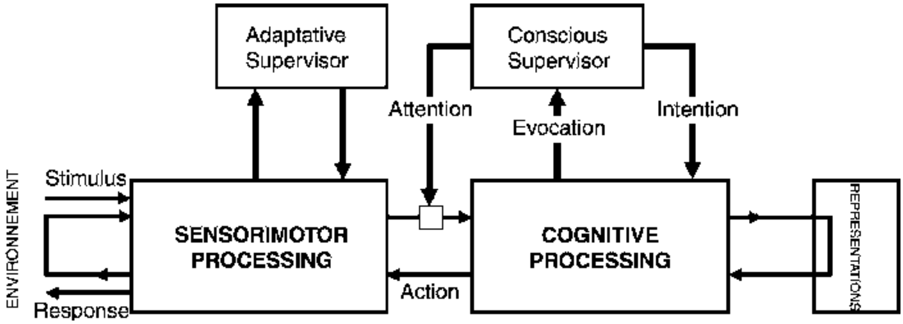

Figure 1.1 Sensorimotor and cognitive levels of information processing. (Modified from Paillard, 1986, 2005.)

cognitive level anticipates events and functions in a predictive way on the basis of abstract representations of internal and external worlds stored in long-term memory.

Each of these two levels of information processing can be separated into different modules, stages or functions (Fodor, 1983; Sternberg, 2001). For instance, information processing may be separated into sensory, perceptual, decisional and motor stages (Sanders, 1983), while executive processes can be separated into three basic functions, inhibiting pre-potent responses, updating working memory and shifting between tasks or rules (Miyake *et al.*, 2000). Recent empirical data suggest that steady-state aerobic exercise does not affect all these stages and functions, but influences some of them in different ways (Audiffren, Tomporowski and Zagrodnik, 2008; Davranche *et al.*, 2005a, 2006b; Dietrich and Sparling, 2004). Bottom-up stimulus-driven processes (see left column of Table 1.3) would be improved by acute aerobic exercise, whereas top-down effortful processes (see right column of Table 1.3) would be impaired. This idea of a bi-directional effect of arousing stimulation on information processing is not new, but

Table 1.3 The hypothetical bidirectional effect of acute bout of steady-state aerobic exercise on cognitive processes.

Improvement of performance	Impairment of performance
Bottom-up	Top-down
Stimulus-driven	Goal-driven
Automatic	Effortful
Implicit	Explicit
Unconscious	Conscious

Note: When participants perform a cognitive task while exercising, performance of the cognitive task may be either improved or impaired. Tasks which tap processes showing several characteristics described in the right column tend to be improved, whereas tasks which involve processes presenting several characteristics described in the left column tend to be impaired (see text for more explanations). Each line describes a bi-dimensional continuum (e.g. Automatic–Effortful). There is no dimensional overlap between the five bi-dimensional continua. For instance, a top-down process may be totally unconscious, or a stimulus-driven process may require allocation of effort.

similar to the distinction between sustained information processes and short-term memory processes made by Humphreys and Revelle (1984) and tested in exercise protocols by Paas and Adam, and their co-workers (Adam *et al.*, 1997; Paas and Adam, 1991). Currently, there is no general theory providing a synthesis for all these new data, approaches and hypotheses concerning the effects of acute bouts of aerobic exercise on cognitive processes. Several chapters of this book lay the foundation for a new theoretical framework explaining the multiple interactions between acute exercise and cognition.

The assessment of the effects of exercise on cognition should include: (1) the choice of an adequate physiological intervention; (2) the selection of tasks according to the sensorimotor and cognitive processes they involve; and (3) the separation of cognitive stages and functions within the same task. Different methods worked out by cognitive psychologists and cognitive neuroscientists in order to separate sensorimotor stages and cognitive functions will be presented later.

1.2 The cognitive psychology approach

Cognitive psychology emerged in the middle of the twentieth century. This branch of psychology is based on the theoretical framework of the cognitive sciences (i.e. artificial intelligence, mathematics, linguistics, philosophy, neurosciences and psychology). Therefore, mathematics inspired three main ideas of cognitive psychology (Andler, 1986). The first idea considers the language of the mind as a formal system. A formal system is a set of symbols that can be combined according to rules based on the shape of the symbols. Puzzles, alphabets and languages are all examples of formal systems. The mind uses these symbols to generate thoughts. The second idea considers the mind as a computing machine. The first universal computing machine was conceptualized by the English mathematician Alan Turing. A Turing machine is composed of an input/output system that can write and read a finite set of symbols, and of a memory system that can assume a finite set of states. According to Turing (1950), a machine could operate in the same way as the human mind. Thoughts, then, would simply be a combination of symbols. The third idea considers the mind as a channel of communication conveying information. This idea was inspired by the seminal paper entitled '*The Mathematical Theory of Communication*' published by Claude Shannon in 1948. In this article, Shannon proposed a linear system of information transmission and provided a quantitative definition of information, or uncertainty, measured in bits. Different laws predicting human behaviour, like Hick's law (Hick, 1952) or Fitts' law (Fitts, 1954), were formalized by cognitive psychologists thanks to Shannon's theory of communication. The quantitative definition of information is very useful to objectively determine the complexity of the task or the uncertainty the participants have to cope with.

These three main ideas led cognitive psychologists to conceptualize the information-processing paradigm. The term 'paradigm' is used here in the sense of Kuhn (1962), that is to say, the ideas, theories, methods, techniques and applications shared by a community of researchers to solve important scientific problems. Typically, a paradigm is first established by the publication of a revolutionary book or paper that sets out scientific problems and possible solutions. This chapter focuses on the information-processing paradigm because the larger part of studies interested in the effect of exercise on psychological functions used this specific approach.

Five basic assumptions underlie the information-processing paradigm and are shared by the community of cognitive psychologists: (1) there are mental states involved in mental processes; (2) mental states possess physical existence as physical states (i.e. they result from the electrochemical activity of neurons); (3) mental states cannot be reduced to physical states; (4) mental states take place in a computing system like the Turing machine (i.e. the mind is a symbol-processing system); and (5) a mental state corresponds to a representation and a mental process operates transformations of representations. One of the central concerns of cognitive psychology is to study these representations and mental processes. Because these objects are not directly observable, cognitive psychologists developed methods to infer some of their characteristics from the measurement of different variables, such as reaction time, and correct and incorrect response rates.

Behavioural psychologists assumed that scientific psychology must be based on directly observable facts such as stimuli and responses without any reference to hypothetical inner states. By contrast, cognitive psychologists are interested by states and processes that take place between sensory inputs and motor outputs of the information-processing system. These hypothetical inner states and processes are considered as intermediary or latent variables; intermediary because they take place between stimuli and responses, and latent because they are not directly observable, but inferred from variations of dependent variables.

Typical topics of cognitive psychology include attention, pattern recognition, memory, motor control, reasoning, problem-solving, language, decision-making, learning and, more recently, executive functions. Typical goals of cognitive psychology are to formulate general principles and laws concerning cognitive processes that are true for everyone; to separate the human information processing system into components; to identify the nature and duration of the component processes involved in the performance of a cognitive task; and to describe the architecture of the cognitive system in order to explain human mental performances in a large variety of situations. The information-processing paradigm was still dominant and considered by the majority of cognitive psychologists as the appropriate way to study human cognition in the last decades of the twentieth century (Eysenck and Keane, 1990). Today, thanks to the technological progresses in different branches of neurosciences, such as brain imagery, it becomes necessary to shift from a 'pure' cognitive psychology approach to a cognitive neuroscience approach to have a better understanding of cognitive functions.

Since the beginning of cognitive psychology, two major conceptual frameworks of human information processing were in competition: the resource-driven models and the data-driven models (Rabbitt, 1979; Sanders, 1983). Generally speaking, resource-driven models consider that performance of the human operator in a task requiring processing of information depends on three things: (1) the amount of available resources; (2) the amount of resources required to perform the task; and (3) the amount of resources actually allocated to the different processes involved in the task. Resources can be defined as energizing forces necessary to perform tasks (Gopher and Donchin, 1986). Human information processing and digital computers of the 1960s were conceived as limited capacity systems (Sanders, 1997), that is to say, systems which possess a limited amount of resources. In contrast, data-driven models consider that performance depends on the quality of the processing realized by a sequence of stages that transform input representations into output representations. A processing stage refers to an aggregate of computational processes that participate in the same mental operation, such as feature extraction or response selection (Gopher and Donchin, 1986). Pure data-driven models inspired by the computer metaphor do not explain variability of performance under different environmental or internal states of the organism (e.g. heat, stressful noise, emotion, effects of drugs, fatigue and arousal induced by exercise) (Hockey, Coles and Gaillard, 1986). In order to explain such variability in the information-processing system, it becomes necessary to combine resource- and data-driven approaches. The resource-driven approach shares several ideas with the energetic approach presented in the next section. For instance, the concept of resources is closely related to the concept of arousal.

Cognitive psychologists developed ingenious methods to infer mental processes, which take place between stimuli and responses, and the make-up of the architecture of the information-processing system (e.g. Sternberg's additive factors method, 1969a). Several of these methods can be also used to determine the locus of influence of aerobic exercise within the information-processing architecture and will be presented later in this chapter. The architecture of the information-processing system has been described in different models (e.g. Sanders' discrete/serial information processing model, Sanders, 1990). In the fourth section of this chapter, cognitive energetic models that synthesize the theoretical frameworks from cognitive and energetic approaches will be presented. They provide a very useful theoretical framework, which explains the different effects of exercise on cognitive processes.

1.3 The energetic approach

The energetic approach is concerned with the intensive or energizing aspects of behaviour as opposed to its directional or semantic aspects. Concepts such as arousal and activation were associated early with energy mobilization or energy release within the organism (Duffy, 1962) and their relation to performance can be traced to the earliest decades of experimental psychology and neurophysiology. For instance, Yerkes and Dodson (1908) observed an inverted-U shaped function of efficiency depending upon the degree of arousal of the organism. These findings led to the general supposition that under- or over-aroused individuals perform poorly, whereas optimal performance occurs in a moderately aroused state (Hebb, 1955). The U-shaped conceptualization of arousal has maintained a place in mainstream psychology and has been adopted by a number of applied researchers to explain performance in human factors and sport settings (e.g. Easterbrook, 1959; Oxendine, 1984; Raglin and Hanin, 2000). In this perspective, physical exercise has been considered an arousing stimulation of the organism (Cooper, 1973; Davey, 1973) and a U-shaped function between exercise and cognitive performance has been expected (Näätänen, 1973). However, empirical data did not support the hypothesis that performance is an inverted-U function of exercise intensity (for a review, see McMorris and Graydon, 2000). The view that acute aerobic exercise can be considered an arousing stressor is central in the present chapter.

Arousal and activation, terms often used interchangeably, were initially conceived by researchers as unidimensional constructs that ranged on a continuum from sleep to wakefulness (Duffy,1957, 1962; Malmo, 1959). Changes in arousal levels were often linked to the activity of the ascending reticular formation (e.g. Lindsley, Bowden and Magoun, 1949; Moruzzi and Magoun, 1949). According to the unidimensional perspective, there exists a general nonspecific pool of energetic resources that supports all cognitive functions and the amount of available resources allocated to a task depends, among other variables, on an individual's arousal level (e.g. Kahneman, 1973). The unitary perspective has been criticised, however. The low correlations among different measures of arousal obtained by researchers are inconsistent with a unidimensional view of arousal (Lacey, 1967; Eysenck, 1982; Thayer, 1989). The undifferentiated resource view is not compatible with perfect time-sharing of two resource-demanding tasks (Wickens, 1984). Further, neurophysiological evidence reveals that the reticular formation is not a homogenous system but, rather, one that is highly differentiated (Robbins and Everitt, 1995).

In response to these shortcomings, several researchers have proposed that arousal is a multidimensional construct. For instance, on the basis of many animal and human neuropsychological and psychophysiological data, (Pribram and McGuinness,1975; McGuinness and Pribram, 1980) suggested that there is an involuntary and a voluntary mode of attentional control. The involuntary mode involves two basal mechanisms: arousal, a phasic short-lived and reflex response to input; and activation, a tonic long-lasting and involuntary readiness to respond. A third mechanism, effort, coordinates arousal and activation, and allows a voluntary control of attention. Pribram and McGuinness restricted the use of the concept of arousal to be synonymous with the orienting reaction discovered by Sharpless and Jasper (1956), and Sokolov (1960). A response of the arousal mechanism occurs when an input change produces a measurable phasic change in a physiological or behavioural variable over a baseline. In accordance with studies by Berlyne (1960), arousal results when, in the history of the organism's experience, an input is surprising, complex or novel. Such a reaction involves the assumption that the input is matched against some residual of past experience in the organism, that is a residual neuronal model of events. Activation differs from arousal, therefore, in maintaining a tonic readiness to respond, reflected in an increase in cortical negativity (contingent negative variation – CNV) and tonic heart rate deceleration. Under many circumstances, arousal and activation appear to be forcibly linked. In stressful situations they share the function of reflex coupling input to output (e.g. startle reflex). In the absence of controlled arousal and activation, behaving organisms would be constantly aroused by their movements and moved by arousing inputs. One function of the effort mechanism is to uncouple arousal and activation in order to avoid undesirable reactions.

Recent advances in methods of assessing the structure and function of the brain have provided researchers the means to identify more precisely the neurophysiological components of arousal and activation. The reticular activating system has, for example, been shown to consist of several inter-related arousal systems that are differentiated by specific neurotransmitters (Robbins and Everitt, 1995). Three main systems of neuromodulators have been distinguished: the noradrenergic, the dopaminergic and the serotoninergic systems. Several studies conducted on animals and humans showed that acute physical exercise results in a releasing of brain catecholamines (noradrenaline and dopamine) and indolamines (serotonin or 5-hydroxytryptamine) (see Meeusen and De Meirleir, 1995, for a review). Therefore, a large part of acute and chronic effects of exercise on cognitive processes may be closely related to the catecholaminergic and indolaminergic neuromodulations of neural networks involved in information processing. The noradrenergic system originates from the locus coeruleus in the pons. Neural cell bodies send projections throughout a large part of the neocortex and the hippocampus. Fluctuations in locus coeruleus activity can be observed in cortical electroencephalograms (EEG) and in P300 event-related potentials. Tone, lights or tactile stimuli, as well as noxious or stressful events, result in an increase of the activity of the locus coeruleus, which has been linked to preservation of alertness that aids in detecting sensory signals under high levels of arousal (see Foote, Bloom and Aston-Jones, 1983; Berridge and Waterhouse, 2003; Posner, 1995; Pribram and McGuinness, 1975; Ramos and Arnsten, 2007; Robbins and Everitt, 1995; for reviews). The coeruleo-cortical noradrenergic system appears to have a protective function of maintaining an individual's capacity to maintain discrimination processes under stressful or arousing circumstances. An increase in brain noradrenergic transmission improves the signal-to-noise ratio of evoked responses to environmental stimuli, either by enhancing evoked responses, by suppressing 'background activity' or by a combination of these two effects in several cortical terminal regions, whatever the sensory modality (e.g. Kasamatsu and Heggelund, 1982; Foote, Freedman and Oliver, 1975; Hurley, Devilbiss and Waterhouse, 2004; Moxon *et al.*, 2007; Waterhouse and Woodward, 1980).

The dopaminergic system originates from cell bodies located in the substantia nigra pars compacta and from the ventral tegmentum. Projections from these areas modulate neural activity in (a) the dorsal and ventral striatum, which, in turn, affect the supplementary motor area, premotor area and primary motor cortex and (b) the frontal lobe, and more particularly the medial prefrontal cortex, that underlies

Table 1.4 Two energetical mechanisms activated by an acute bout of steady-state aerobic exercise.

Energetical mechanism	Neurotransmitter system	Brain localization	Main function	ERP index
Arousal	Noradrenaline	Locus coeruleus	Filtering inputs	P300
Activation	Dopamine	Substantia nigra pars compacta	Energizing outputs	CNV

Note: ERP: Event-related potential; P300: Positive cortical wave observed 300 milliseconds after the occurrence of response signal in a reaction time task; CNV: contingent negative variation.

executive functions. These pathways affect the activation or energization of behaviour and account for the vigour and frequency of behavioural outputs (Robbins and Everitt, 2007). Characteristics of noradrenergic and dopaminergic neuromodulator mechanisms are summarized in Table 1.4. The serotoninergic system originates from cell bodies located in the raphe nucleus. Neurons from this system dampen the actions of each of the two preceding systems and promote behavioural inhibition and cortical deactivation (see also Chapter 2).

We saw that exercise has been considered an arousing stressor (e.g. Davey, 1973; Näätänen, 1973; Thayer, 1987), but few investigators have provided a theoretical rationale for a causal link between exercise, arousal, brain catecholamines and improvement in cognitive performance. As stated by McMorris and Graydon (2000), Cooper (1973) was the first author to propose a set of clear arguments based on different studies conducted with animals and humans: (1) synthesis of noradrenaline increases in the brain of the rat during severe and prolonged forced exercise; (2) concentration of plasma catecholamines increases during exercise; (3) brain noradrenergic activity increases during cortical activation; (4) the level of cortical arousal is related to the level of activity of the reticular formation; and (5) exercise can increase the activation of the reticular formation via somatosensory feedback due to the movement of the limbs. Considerable research has provided support for these arguments and today, the peripheral and central arousing effects of exercise are well documented. Acute exercise is widely known to activate both the sympathetic nervous system and the hypothalamo-pituitary-adrenal system, resulting in a release of catecholamines and indolamines, both centrally and peripherally (e.g. Wittert, 2000; Meeusen and De Meirleir, 1995, for reviews). Models and methods presented in the two following sections are compatible with this hypothetical explanation of acute effects of aerobic exercise on cognition.

1.4 Exercise effects and cognitive-energetic models

During the second half of the twentieth century, several cognitive-energetic models synthesising the two main approaches were proposed (see Figure 1.2). In the present section, four of these models will be presented. They provide a heuristic framework for the study of the acute effects of exercise on cognition.

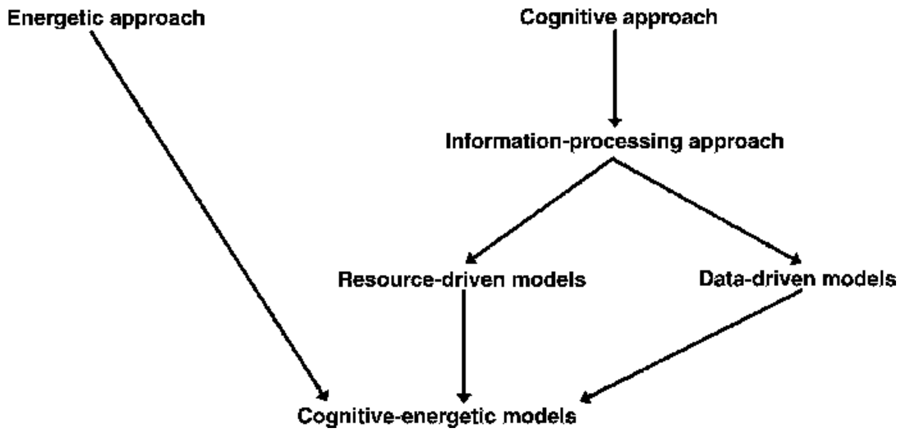

Figure 1.2 A schematic representation of the theoretical roots of cognitive-energetic models.

Kahneman's model (1974)

The first cognitive-energetic model can be found in Kahneman's book '*Attention and Effort*' (1973). Kahneman viewed the amount of resources available at any time as limited. The amount of available resources depends on the level of arousal, which is determined by two sets of factors: (1) the demands imposed by the activities in which the organism engages, or prepares to engage in; and (2) miscellaneous sources of arousal such as intensity of stimulations, psychostimulant effect of drugs, anxiety or acute effect of aerobic exercise. Resources are accumulated in a single undifferentiated pool of resources (see Figure 1.3). The amount of available resources and the effort invested performing a task can be measured through several measures of arousal (e.g. pupil dilatation, heart-rate variability). An allocation policy mechanism directs and supervises the allocation of resources. The strategy of allocation is influenced by enduring dispositions (e.g. pre-wired and automatic behaviours such as the automatic and involuntary orientation towards a novel stimulus), momentary intentions (e.g. reaching a task-related goal) and feedback from ongoing activities (e.g. feedback of success).

According to Kahneman, the level of arousal corresponds to the amount of available attentional resources, while effort is understood to be the voluntary attention allocated to a task. In this perspective, decrements in performance are due to demands of concurrent activities or processes which exceed the amount of available resources. The notions of 'processing limitations' and 'effort invested to perform a task' led Norman and Bobrow (1975) to introduce the very interesting concepts of data-limited and resource-limited processes. Whenever an increase in the amount of processing resources can result in improved performance, the performance on that task is said to be resource-limited; and whenever performance is independent of processing resources, the performance is said to be data-limited (see Figure 1.4). In the resource-limited region of the performance-resource function,

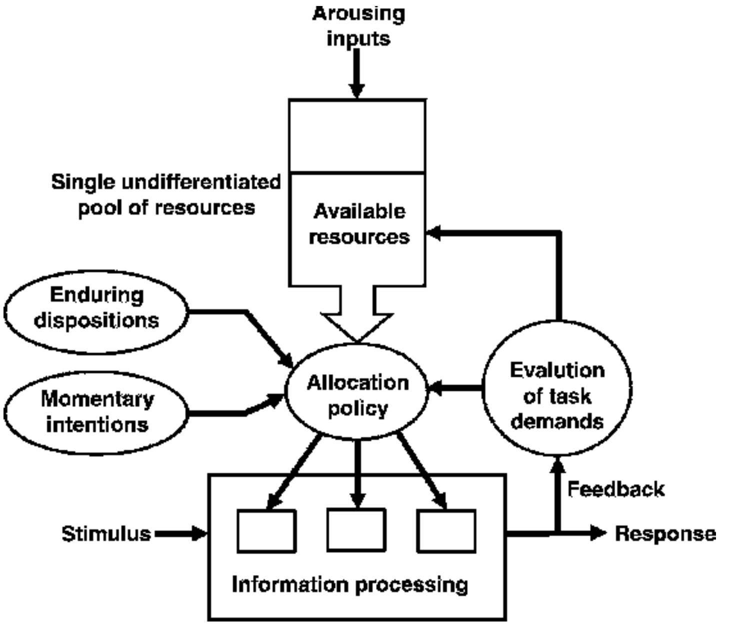

Figure 1.3 Kahneman's cognitive-energetic model. (Modified from Kahneman, 1973.)

performance is assumed to be a monotonically increasing function of the amount of allocated resources to perform the task. Norman and Bobrow distinguished two forms of data limitations: (1) signal data limitations, when the limit to performance depends primarily upon the signal-to-noise ratio and the quality of the input data

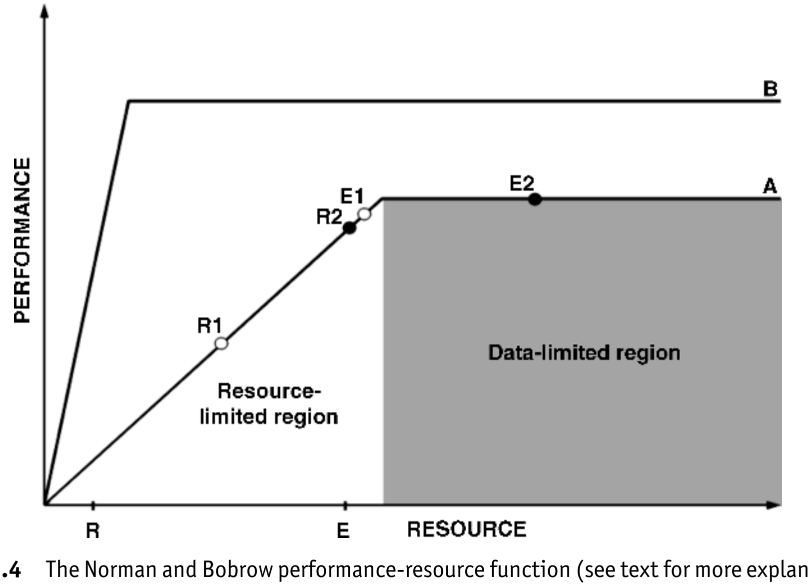

Figure 1.4 The Norman and Bobrow performance-resource function (see text for more explanation).

signal (e.g. detection of a very weak signal in a noisy environment); and (2) memory data limitation, when the limit to performance depends mainly upon the quality of the representation stored in memory (e.g. identifying which of two almost identically oriented presented lines has just been seen). Most tasks involve processes characterized by data-limited and resource-limited regions.

In Figure 1.4, curves A and B represent performance-resource functions for two tasks, respectively task A and task B. Task A requires more resources to be performed than task B. The higher demands of task A can be caused either by a higher complexity, or by a lower familiarity of those performing this task. The resource-limited and data-limited regions are represented only for curve A. The asymptotic level in performance is different for curves A and B suggesting a better performance for task B. Points R and E represent the presumed level of arousal of participants, who were at rest (R) or who exercised (E), during an experiment on the facilitating effect of aerobic exercise on cognitive tasks. In the theoretical framework of Kahneman's model, it is assumed that exercise induces an increase in physiological arousal and then an increase in available resources. If participants perform tasks A and B at rest (R on Figure 1.4) and during exercise (E on Figure 1.4), we will observe a significant improvement in task A, but not in task B. We can conclude from this graph that tasks which require large amounts of resources (task A) are more sensitive to a facilitating effect of aerobic exercise than tasks which require fewer resources (task B). In addition, Humphreys and Revelle (1984) pointed out that stimulant drugs and other arousers (e.g. acute aerobic exercise) are most likely to improve performance of sustained information transfer tasks (e.g. choice reaction time task) when the participants are at a low level of arousal in the placebo or control condition. Imagine participants who perform task A at rest (R1 on Figure 1.4) and during a steady-state aerobic exercise (E1 on Figure 1.4). In this case, we will observe a significant improvement of performance. If, the same participants perform task A with a higher level of arousal at rest (R2 on Figure 1.4) and during exercise (E2 on Figure 1.4), the likelihood to observe a significant improvement is weaker. For that reason, participants involved in an experiment assessing the facilitating effect of aerobic exercise on cognition must be instructed to refrain from drinking stimulant beverages (e.g. coffee, tea, alcohol) just before the experiment. In the same way, it is important to lower the initial arousal level of participants, for example by conducting the experiment early in the morning or increasing time on task.

According to the Kahneman's model, interference between tasks is an increasing function of workload. Workload can be defined as the amount of resources necessary to perform a specific task for a specific participant. At low values of workload, there may be little or no interference between tasks, whereas at high values of workload, the interference may be severe. This interference phenomenon can explain why performance of cognitive tasks can be impaired during exercise. If the walking, running or cycling exercise competes with the cognitive task for resources, we will observe such interference. Knowles (1963) and Rolfe (1973) proposed a workload assessment technique named the 'dual-task' or 'secondary-task' technique, based on the measurement of interferences between two tasks (see Abernethy, 1988, for a review).

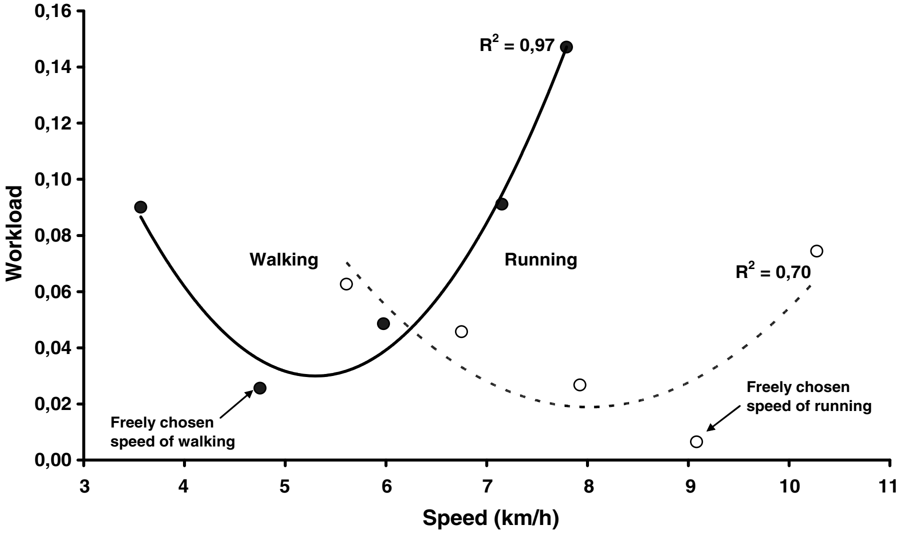

Figure 1.5 Workload of walking and running on a treadmill as a function of speed (Black circles: walking; White circles: running).

In this measurement paradigm, the workload associated with a given task, named the 'primary' task, is measured by assigning the human operator another task, named the 'secondary' task, to perform concurrently with the primary task. Impairment of the secondary task is assumed to be a linear function of workload. By using this dual-task method, it is possible to measure the workload of exercising. A study conducted by Dorgans and Audiffren (2003) showed that the workload of walking and running is the lowest for the freely chosen speed (see Figure 1.5). The primary task consisted of walking or running at specific speeds and the secondary task was a simple reaction time task. Similar results were obtained by Kurosawa (1994) and Brisswalter *et al.* (1995). These results show that it is important to instruct participants to walk, run or cycle at a freely chosen speed to lower the workload of exercise to a minimal value if researchers want to avoid risks of interferences between the cognitive task and physical exercise. Freely preferred locomotor speed can be defined as the speed to which humans adopt the most natural possible gait (Holt, Hamill and Andres, 1991). The speed adopted naturally by participants is related to the resonance frequency in which a human moves in order to optimize his/her efficiency while maintaining a weak energy demand. This speed is automatically adopted by quadrupeds when they change locomotor gait in order to minimize their energy expenditure (Hoyt and Taylor, 1981).

To summarize, Kahneman's model supports four important ideas concerning the effects of exercise on cognition: (1) if exercise increases the arousal level, it increases at the same time the amount of resources available to perform a concomitant cognitive task; (2) resource-limited processes are most likely to be improved by an arousing stressor such as an acute bout of exercise; (3) participants underaroused in the rest or control condition are most likely to show an improvement in performance in the arousing exercise condition; and (4) impairment of performance in cognitive tasks observed in some experiments assessing the effects of exercise on cognition can be explained by the too high mental workload required by physical exercise (e.g. monitoring the speed of cycling). The second summarized idea is not compatible with some results showing that effortful executive processes are impaired by acute aerobic exercise (Dietrich and Sparling, 2004; Pontifex and Hillman, 2007). This problem comes from the unidimensional modelling of resources reservoir used in the Kahneman's model, in which arousal and on-task effort are confounded. The two following models, which take place in a multidimensional approach of cognitive and energetic interactions, can explain the observation that some cognitive processes are improved by acute aerobic exercise, whereas other are impaired.

Sanders' model (1983)

In the beginning of the eighties, Sanders proposed a heuristic cognitive-energetic model of information processing (Sanders, 1981, 1983, 1998), in which arousal, activation and effort influence specific stages of information processing. Sanders proposed a synthesis of the two major approaches in mental chronometry described earlier: (1) a computational data-driven approach, which emphasizes the structural aspects of the reaction process (e.g. Donders, 1969; Sternberg, 1969b); and (2) an energetic resource-driven approach concerned with capacity limitations, resource allocation and strategic control (e.g. Kahneman, 1973). The Sanders' model includes three aspects of information processing: (1) a cognitive level composed of four processing stages; (2) an energetic level composed of three energetic mechanisms, which allocate processing resources; and (3) an evaluation level that corresponds to an executive process, which manages processing resources (see Figure 1.6). From a large number of reaction time experiments using the additive factors method of Sternberg (1969a, 1998), Sanders argued that arousal is linked to the feature

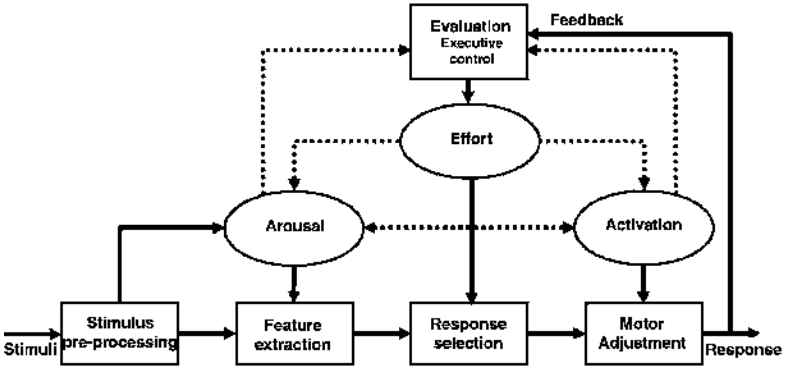

Figure 1.6 Sanders' cognitive-energetic model. (Modified from Sanders, 1983.)

extraction stage; activation influences the motor adjustment stage; and effort is involved in response selection (see Figure 1.6). Stimuli encoded by sensory organs have two dimensions, an energetical dimension, which arouses the organism, and an informational dimension processed by the different stages of information processing. The effort mechanism also serves the function of keeping the basal resources at an optimal level in order to satisfy the demands of the task. The main difference between Kahneman's and Sander's cognitive-energetic models is a shift from a unidimensional conception of resources (one unique reservoir of arousal) to a multidimensional perspective (three supply systems). The three energetic mechanisms bear a close resemblance to those described by Pribram and McGuinness (1975). The Sanders' model is particularly helpful to interpret facilitating or slowing effects of exercise on reaction processes.

In Sander's model, an acute bout of aerobic exercise may increase both arousal and activation mechanisms and then modulate input and output processes. Exercise may also influence decisional processes via the effort mechanism if both the cognitive task and the motor task (e.g. cycling at an imposed speed) consume mental effort. In this case, the amount of effort necessary to perform the cognitive task can be slightly insufficient and lead to a slowing of decisional processes. In the next section, we will see two methods allowing localizing of the acute effects of aerobic exercise in the architecture of the Sanders' cognitive-energetic model.

Humphreys and Revelle's model (1984)

Another cognitive-energetic model using a multidimensional approach of mental energy was developed during the 1980s: the personality, motivation and performance structural model of Humphreys and Revelle (1984). This model integrates two major approaches to the study of human mental performance: the cognitive approach and the differential approach. According to the metaphor of the digital computer used by cognitive psychologists, the human information processing system operates exactly in the same way for everyone. From this perspective, it is coherent and pertinent to study the average of the performances of dozens of subjects to infer general principles of functioning of the information processing system. In contrast, differential psychologists are interested in the variability due to the psychological differences among individuals. Based on the answers of hundreds of participants to questionnaires, they define different personality traits (e.g. high achievers versus low achievers, extroverts versus introverts, individuals who are high or low in trait anxiety). According to some authors using this approach (e.g. Eysenck,1967, 1992; Humphreys and Revelle, 1984), these stable characteristics of personality interact with situational factors (e.g. time of day, time on task, task difficulty) and modulate the information processing. For instance, personality traits can influence baseline arousal level (see Matthews, 1992 for a review) and selective attention (e.g. MacLeod and Matthews, 1988).

In their model, Humphreys and Revelle (1984) showed the effect of three relatively independent personality constructs (impulsivity, achievement motive and trait

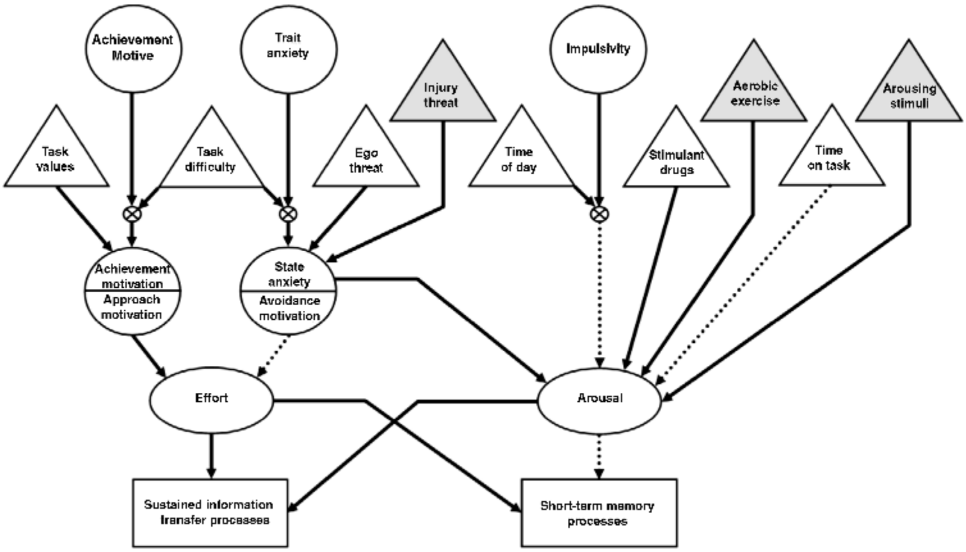

Figure 1.7 Cognitive-energetic model of Humphreys and Revelle (modified from Humphreys and Revelle, 1984). Solid lines represent positive influences and dashed lines represent negative influences. Circles represent latent variables, triangles represent situational variables, ellipses represent energetic mechanisms, and rectangles represent information-processing processes. Achievement motive, trait anxiety and impulsivity are dispositional variables. Circled Xs represent interactive effects. Interaction between dispositional variables and situational variables results in state variables, for instance, achievement motivation and state anxiety. Approach and avoidance motivations are motivational states related respectively to achievement motivation and state anxiety. Shaded triangles have been added to the original model.

anxiety) in combination with six situational moderators (incentives, feedback of success and failure, psychostimulant drugs, ego threat, time of day and time on task) on the two motivational constructs of arousal and on task effort. Figure 1.7 shows a slightly modified version of this model. Three situational moderators have been added: injury threat, aerobic exercise and arousing stimuli. These variables may influence inner states in sport situations. For instance, a young boxer may be simultaneously aroused by growing anxiety due to the threat of an injury caused by the punches of his brutal opponent, by his own movements in the ring and by the applause and cheers of the crowd. The name of several situational variables has been changed to carry meaning related to more recent motivation theories. The variable 'incentives' has been replaced with 'task values' in reference to the *expectancy-value* model (e.g. Wigfield, 1994; Wigfield and Eccles, 1992). In the same way, the variable 'feedback of success/feedback of failure' has been replaced with 'task difficulty' in reference to the theory of *motivational intensity* (e.g. Brehm and Self, 1989). Finally, the short-term memory processes described by Humphreys and Revelle are very similar to the working memory function of the central executive (e.g. Baddeley and Della Sala, 1996; Baddeley and Hitch, 1974). Humphreys and Revelle did not contest that there are different arousal systems or physiological ways of becoming aroused but, in contrast to Pribram and McGuinness (1979), they considered general arousal a higher-order construct common to various indicants of alertness.

Humphreys and Revelle (1984) distinguished between arousal at the micro and at the macro levels. At the micro level, arousal is very transitory, indexed in milliseconds, may be measured by pupil dilatation, changes in heart rate, changes in the EEG (Kahneman, 1973) and could be assimilated to Pribram and McGuinness (1979) arousal. At the macro level, arousal is of much longer duration, indexed in minutes or in hours, relates to the general feelings of alertness or activation (Thayer, 1989), body temperature (Blake, 1967), hormonal excretions (Frankenhaeuser, 1975), and could be assimilated to stress (Selye, 1976). The arousal mechanism shown in Figure 1.7 corresponds to the macro level arousal described by Humphreys and Revelle.

The theoretical framework developed in the cognitive-energetic model of Humphreys and Revelle (1984) makes two main contributions to the assessment of exercise effects on cognition. First, personality traits interact with situational moderators resulting in a change in arousal level. Two independent personality traits have been related to arousal: anxiety and impulsivity. On the one hand, people who are generally highly anxious have, on average, a higher level of arousal than people with low anxiety levels. On the other hand, low impulsives are more aroused in the morning than high impulsives. These two interactions suggest that people who are highly anxious and low on impulsivity should be less sensitive to the arousing effect of exercise in the morning. In other words, individual differences in personality traits related to arousal increase the inter-individual variability of the effect size of exercise. Researchers interested in the effects of exercise on cognition must be aware of this potential problem and take account of individual differences in their research protocols. Second, arousal seems to have opposite effects on tasks involving sustained information transfer processes (e.g. choice reaction time task) and tasks tapping short-term memory processes (e.g. letter memory task). The model predicts that an acute bout of aerobic exercise improves choice reaction time but impairs the number of recalled items in a working-memory task. This prediction is particularly important and may explain some controversial results in the literature. This prediction is also compatible with the hypofrontality theory developed by Dietrich (2003, 2006; Chapter 3 of this book) and merits more experimental testing.

Hockey's model (1997)

In the tradition of cognitive energetic models, Hockey (1993, 1997) proposed a compensatory control model, which accounts for the different patterns of effects on performance observed under stress and high workload (see Figure 1.8). The main contribution of Hockey's model is to distinguish two performance regulation loops: (1) an effort-based compensatory control mechanism, which maintains task performance under disturbance from stressors (e.g. noise, sleep deprivation) and prevents

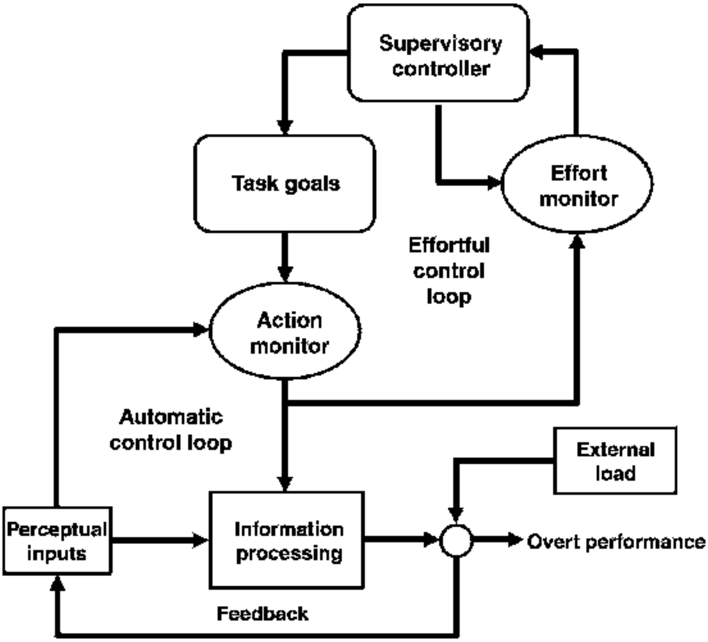

Figure 1.8 Hockey's compensatory control model of performance regulation. (Modified from Hockey 1993, 1997.)

the loss of task goals, particularly under high processing demands (e.g. a very difficult task) or competition for resources from other tasks (e.g. dual-task situation) (effortful control loop in Figure 1.8); and (2) an automatic control mechanism, which functions without effort and concerns the regulation of well-learned skills under the guidance of well-established goals (e.g. expert basketball player running while dribbling ball) (automatic control loop in Figure 1.8).

Hockey (1997) gave a central role to the compensatory effort as a main explanatory mechanism of performance under stress, which occurs when there is a mismatch between required and available resources. Hockey argued that the maintenance of performance stability under demanding conditions is an active process under the control of the individual (supervisory controller in Figure 1.8), requiring the management of cognitive resources through the mobilization of effort. The *action monitor* (see Figure 1.8) compares target outcomes with current outcomes. If a discrepancy is detected, adjustment in resource allocation, speed, timing and/or memory-use is carried out automatically until the discrepancy is reduced to keep it within acceptable limits. For instance, during incremental exercise, the action monitor adjusts the motor command to cope with the increase in workload. A disruption of equilibrium may be brought about either by unexpected surges in external load (e.g. a boar crossing the road just in front of a car while the driver speaks with his/her passenger) or a fall in internal resources (e.g. fatigue). It is assumed that the usual and frequent discrepancies within the normal range are managed through the use of an automatic routine correction mechanism (automatic control loop in Figure 1.8).

The *effort monitor* mechanism (see Figure 1.8) is assumed to be sensitive to increasing control demands in the lower loop ensured by the automatic control mechanism. An increase of control demands may happen when there is a failure to resolve the discrepancy between target and current outcomes, too slow a rate to solve the discrepancy or too high a variability of outcomes. The *supervisory controller* (see Figure 1.8) detects any failure to solve the discrepancy and selects a mode of regulation among several available strategies. Another important contribution of Hockey (1997) is to distinguish two control options for resolving the discrepancy between increasing demands and availability of effort: (1) in the first option, the allocation of effort is increased to cope with the new level of demand and the target outcome can be maintained; and (2) in the second option, task goal and target outcome are adjusted downward and the allocation of effort is maintained at its initial level.

According to Hockey (1997), it is very important to take into account the compensatory trade-off between cognitive goals and effort in order to understand the performance changes observed under stress and high workload. Hockey identified four latent breakdowns in performance, evidence of the manifestation of the same regulatory mechanism: (1) selective impairment of low-priority task components (e.g. narrowing of attention); (2) within-task shift to less effortful strategy (e.g. less use of working memory, shift in the speed–accuracy trade-off); (3) increase in activation of physiological systems and in affective response involved in emergency reactions (e.g. sympathetic and neuroendocrine stress reactions); and (4) post-task preference for low-effort strategies due to fatigue after-effects. The Hockey model is very interesting for studying the effects of exercise on cognition, because it allows for interpreting shifts in strategy that have been observed in several experiments (e.g. Audiffren, Tomporowski and Zagrodnik (2007b)).

Table 1.5 summarizes the contributions of the four cognitive-energetic models to the understanding of the different possible concomitants or after-effects of steady-state exercise on cognitive task performance.

1.5 Sensorimotor and cognitive functions affected by exercise

Localizing the effects of stressors, such as physical exercise, in the architecture of the information-processing system can be only addressed if researchers are able to divide the complex system into functionally distinct stages, processes and functions. In this section, five methods that allow us to identify the locus of influence of the effects of acute bouts of aerobic exercise are presented along with some examples. For a very interesting critical overview of several methods separating cognitive processes, readers are referred to Sternberg (2001). The five presented methods can be used either separately or simultaneously in the same experiment, and, in some cases, even in the same task.

Table 1.5 Contributions of cognitive energetic models to the understanding of effects of steady-state aerobic exercise on information processing.

Cognitive energetic model	Direction of the effect	Explanation of the effect	Time of the effect
Kahneman's model	Improvement of performance	Aerobic exercise increases the amount of available resources	During and after
Kahneman's model	Impairment of performance	Exercise and cognitive task compete for resources	During
Kahneman's model	Impairment of performance	Exhaustion of resources in the case of very long exercise	During and after
Sanders' model	Improvement of sensory and motor processes	Aerobic exercises increases the level of arousal and activation	During and after
Sanders' model	Impairment of decisional processes	Exercise and cognitive task compete for effort	During
Humphrey and Revelle's model	Improvement of reaction processes	Aerobic exercise increases arousal	During and after
Humphrey and Revelle's model	Impairment of short-term memory processes	Aerobic exercise increases arousal	During and after
Hockey's model	Shift to an easier strategy	Exercise and cognitive task compete for effort	During and after

Note: The direction of the effect (column 2) concerns the performance of the cognitive task. The time of effect (column 4) indicates if the effect may be observed during, just after, or both during and just after exercise.

Task-comparison method

This method is the oldest method used by psychologists to measure the speed of mental processes. It is also used by neuropsychologists to determine which cognitive functions are deteriorated by brain lesions. The logic of this method is simple: if two tasks, A and B, involve different cognitive processes and a given factor X influences the performance of only one of them, for instance task A, then one can conclude that factor X selectively influences processes involved in task A and not those involved in task B. For example, Donders (1969) assumed that simple reaction time tasks (SRT) do not require stimulus discrimination or response selection, whereas choice reaction tasks (CRT) do. In the same way, Boutcher (2000) gave examples of cognitive tests used to study fitness effects on cognitive performance in ageing; he assumed that the Stroop colour test taps attentional processes, whereas the Sternberg number task involves memory processes.

The Donders (1969) subtraction method is certainly the most venerable task-comparison method. In the example above, by subtracting SRT from CRT we obtain the duration of all processes included in CRT but not in the SRT task. The subtraction method has been criticized by many authors (e.g. Pachella, 1974), but is still used in brain imagery and cognitive psychology. One limit of this method is the a priori assumption that a particular task taps a specific cognitive process.

It is important to distinguish the task-comparison method from the four other methods presented in the five following sub-sections. The goal of the task-comparison method is to show that a factor (e.g. aerobic exercise) has a selective influence on different tasks, each involving a different complex process. In contrast, the goal of the five other methods is to decompose or partition a complex process involved in a task into separate sub-processes (Sternberg, 2001). For that reason, task comparison can be considered as a less precise and rougher method of localizing the effect of exercise in the cognitive architecture. In addition, the task-comparison method requires a theory which can justify how the different tasks used in the experiment involve distinct complex processes.

Several studies have used the task comparison method to examine the effects of acute aerobic exercise on cognitive processes (e.g. Adam *et al.*, 1997; Audiffren, Tomporowski and Zagrodnik, 2008; Dietrich and Sparling, 2004; Paas and Adam, 1991). In these four studies, the authors predicted different patterns of results for the two tasks they selected. Results are summarized in Table 1.6. This set of experimental data suggests that tasks requiring sustained information transfer (Humphreys and Revelle, 1984), such as choice reaction time tasks, are improved by concomitant acute aerobic exercise, whereas tasks involving working memory processes, such as the Paced Auditory Serial Addition task, are impaired or require a shift toward a less effortful strategy. These results can be interpreted in the theoretical framework of cognitive energetic models and Dietrich's hypofrontality model.

Within-task subtraction method

The subtraction method was also used to compare two or more different conditions within the same task. In this case, the task involves a mixture of different kinds of trials. For instance, in an attempt to distinguish automatic and conscious orienting of attention, Posner and Snyder (1975) used a subtraction method to calculate the cost and benefit of attentional orienting. For this purpose, they developed a reaction time procedure in which the imperative response stimulus is preceded by a priming stimulus. This procedure was later used to study the covert orienting of visual attention. Covert attention corresponds to attending the location of a stimulus according to preliminary information (e.g. priming stimulus) without any change in eye or head position. When the priming stimulus occurs in a specific location, it leads to an automatic orienting of attention, which improves information processing and decreases reaction time if the response stimulus occurs within 50–150 ms after the occurrence of the priming stimulus. This covert and automatic shift of attention is

Table 1.6 Synthesis of studies using the task-comparison method to assess the effects of acute aerobic exercise on cognitive processes.

Tasks	Direction of effect	Time of measurement	Characteristics of exercise	Reference
Choice reaction time	Improvement			
Short-term memory	Impairment	During	20 min cycling at 75% MAP	Paas and Adam, 1991
Choice reaction time	Improvement	During	20 min cycling at 75% MAP	Adam *et al.*, 1997
Short-term memory	Speed-accuracy tradeoff			
Wisconsin card sorting	Impairment	During	45 min cycling or running at 70–80% HRmax	Dietrich and Sparling, 1994, exp. 1
Brief Kaufman intelligence	No effect			
Paced auditory serial addition	Impairment	During	65 min running at 70–80% HRmax	Dietrich and Sparling, 1994, exp. 2
Peabody picture vocabulary	No effect			
Choice reaction time	Improvement	During	35 min cycling at 90% VT	Audiffren *et al.*, 2008
Random number generation	Shift toward a less effortful strategy			

Note: MAP: Maximum aerobic power; HRmax: Maximum heart rate; VT: ventilatory threshold.

interpreted as a way of guiding the eyes to appropriate areas of the visual field (Posner, 1995).

The manipulation of the stimulus onset asynchrony (SOA) between the priming stimulus and the response stimulus allows one to study the efficiency of automatic orienting of attention. Conscious attention responds to the probabilities of different events, speeding up reactions when an expected event occurs. In the priming procedure, conscious attention can be manipulated by varying the probability of validity of preliminary information given by the priming stimulus. If the information given by the priming stimulus is valid, the imperative response stimulus occurs in the location indicated by the priming stimulus and reaction time is quicker. Inversely, if the information given by the priming stimulus is invalid, the response stimulus occurs in an unexpected location and the reaction is slowed. When there is a high probability that prime location matches response signal location (e.g. $p = 0.80$), two situations may happen: (1) if prime location really matches response signal, both automatic and conscious attention facilitates performance; and (2) if prime location does not match response signal location, only conscious attention is responsible for reorienting of attention and slowed performance. According to Posner and Snyder, facilitation of performance can be due either to conscious or to automatic orienting of attention, whereas impairment of performance is due only to conscious attention. By subtracting reaction time observed in the valid or neutral prime condition from the reaction time observed in the invalid prime, we obtain an index of the attention reorienting cost.

The priming procedure was used by Pesce and her co-workers to study the arousing effect of aerobic exercise on conscious and automatic orienting of attention (Pesce *et al.*, 2003). Probability of prime validity (0.80 or 0.20) and SOA (150 or 500 ms) were manipulated. Participants had to perform the reaction time task while cycling (50–60 rev.min^{-1}) at 60% heart rate reserve. Pesce and collaborators found interesting results in their first experiment. They observed a third-order interaction between prime-response signal matching, SOA and exercise level (at rest or while exercising). The interaction was mainly due to the fact that the mismatching condition led to slower reaction times at rest than during exercise only with longer SOA. This result strongly suggests that the arousing effect of aerobic exercise improves conscious reorienting of attention.

Posner's priming procedure used a subtraction method to isolate the conscious reorienting of attention process. In the same way, the subtraction method was used in the Stroop task and the Flanker task to isolate conflict or inhibiting processes (see Eriksen, 1995; MacLeod, 1991, for reviews), and in the switching task to isolate shifting processes (Rogers and Monsell, 1995; Vandierendonck, 2000). These three kinds of tasks were used in protocols assessing the effect of acute aerobic exercise on executive processes (Coles and Tomporowski, 2008; Hillman, Snook and Jerome, 2003; Hogervorst *et al.*, 1996; Sibley, Etnier and Le Masurier, 2006; Pontifex and Hillman, 2007; Tomporowski and Ganio, 2006). Results of these studies are summarized in Table 1.7. No clear tendency emerges from this set of experimental data, but executive functions seem to be improved by acute aerobic exercise.

Additive factors method

This method, conceived by Sternberg (1969a, 1998), is based on the discrete serial information processing model (Sanders, 1990). The additive factors method (AFM) considers reaction time as the sum of the duration of each of the processing stages that take place between the occurrence of the stimulus and the initiation of a response. For each stage, at least one computational factor (e.g. stimulus–response compatibility) exists that directly and selectively affects its duration without modifying processing quality. If assumptions of the AFM are respected, the following logic may be applied: (1) when two factors influence no stage in common, one can expect their effects to be additive; conversely, (2) when two factors influence at least one stage in common, one can expect their effects to interact in an overadditive manner. It is important to note that the logic of the AFM is compatible with other models of information processing such as the cascade model (McClelland, 1979) and other

Table 1.7 Synthesis of studies using the within-task subtraction method to assess the effects of acute aerobic exercise on cognitive processes.

Trials	Cognitive process	Direction of effect	Time of measurement	Characteristics of exercise	Reference
Valid vs invalid prime	Conscious reorienting of attention	Improvement	During	12 min cycling at 60% VO_2max	Pesce *et al.*, 2003
Colour naming vs colour-word interference	Inhibition processes	Improvement	After	60 min cycling at 75% MAP	Hogervorst *et al.*, 1996
Colour naming vs colour-word interference	Inhibition processes	Improvement	After	20 min jogging at 3–6 METs	Sibley *et al.*, 2006
Congruent vs incongruent	Inhibition processes	No effect on RT data	After	30 min running at 83.5% HRmax	Hillman, *et al.*, 2003
Congruent vs incongruent	Inhibition processes	No effect on RT data	During	6.5 min cycling at 60% HRmax	Pontifex and Hillman, 2007
Switch vs non switch	Switching processes	No effect	After	30 min cycling at 60% VO_2max	Coles and Tomporowski, 2008
Switch vs non switch	Switching processes	No effect	After	30 min cycling at 60% VO_2max	Tomporowski and Ganio, 2006

Note: RT: reaction time; VO2max: Maximum oxygen uptake; MAP: Maximum aerobic power; MET: Metabolic equivalent; HRmax: Maximum heart rate.

models with temporally overlapping processes (Miller, van der Ham and Sanders, 1995). On the basis of the literature on the additive stage structure of traditional choice reactions, Sanders (1983) distinguished four well-established stages resulting from the robust pattern of additivity between four computational factors: (1) pre-processing stage, influenced selectively by signal intensity; (2) feature extraction stage, influenced by signal quality; (3) response selection stage, influenced by stimulus–response compatibility; and, finally, (4) motor adjustment stage, influenced by foreperiod duration (see Figure 1.6). Several authors have used the additive factors method to localize the effects of acute bouts of aerobic exercise in the sequence of information processing stages (e.g. Arcelin, Delignières and Brisswalter, 1998; Davranche and Audiffren, 2004; Davranche *et al.*, 2005a) (see Table 1.8, for a synthesis). For instance, in the Arcelin *et al.* study, participants performed a choice reaction time task during a cycling exercise at 60% of maximal aerobic power or at rest. Three computational factors were manipulated in combination with exercise level (at rest versus while exercising): signal quality, stimulus–response compatibility and foreperiod variability. Arcelin and collaborators observed that the facilitating effect of exercise and the effects of the three manipulated computational factors are additive on mean reaction time and first quartile of reaction time distribution. However, they observed a significant interaction between the effect of exercise and foreperiod variability on the third quartile of reaction time distribution. The effect of acute aerobic exercise was larger for varied foreperiod duration than for fixed foreperiod duration. This overadditive interaction suggests that aerobic exercise improves motor preparatory processes. Results obtained with the AFM are summarized in Table 1.8.

Fractionation of reaction time

The locus of the effect of exercise can also be addressed by fractionating the reaction time, with respect to a change in electromyographic (EMG) activity of the response agonist muscle, into two components: the time interval between the onset of the response signal and the onset of EMG activity of the response muscle, termed premotor time (PMT), and the time interval between the onset of EMG activity and the onset of the required motor response, termed motor time (MT) (Botwinick and Thompson, 1966). MT reflects the duration of the electromechanical transduction within muscle fibres, whereas PMT reflects the duration of all earlier stages. The duration of MT is included in the motor adjustment stage described by Sanders (1990). By separating PMT and MT, it is possible to determine whether the facilitating effects of acute bouts of exercise on RT takes place before or after the onset of EMG activity and, therefore, whether it influences early cortical integration processes or late motor processes (Hasbroucq *et al.*, 2002). Three studies used the fractionation method to localize effects of exercise (e.g. Audiffren, Tomporowski and Zagrodnik, 2008; Davranche *et al.*, 2005a, Davranche, Audiffren and Denjean, 2006a). Results of these three studies are summarized in Table 1.8. Two of these studies are presented in Chapter 7.

Table 1.8 Synthesis of studies using a process decomposition method to determine the locus of influence of the facilitating effect of exercise in the information processing flow.

Inference method	Cognitive stage or function	Time of measurement	Characteristics of exercise	Reference
Additive factors method	Sensory processes	During	15 min cycling at 50%MAP	Davranche *et al.*, 2005, 2006
Additive factors method	Motor processes	During	10 min cycling at 60% MAP	Arcelin *et al.*, 1998
			15 min cycling at 50% MAP	Davranche *et al.*, 2005, 2006
RT fractionation	Motor processes	During	35 min cycling at 90% VT	Audiffren *et al.*, 2008
Signal detection theory	Sensory processes	After	30 min running at FCS	Audiffren, *et al.*, 2007
Factor analysis method	Inhibitory processes	During	35 min cycling at 90% VT	Audiffren *et al.*, 2008

Note: Column 1: Method of inference used to localize the effect; Column 2: Information processing stage or cognitive function affected by exercise; third column: time of measurement of the cognitive task; Column 3: Time of measurement of the cognitive task; MAP: Maximum aerobic power; VT: ventilatory threshold; FCS: Freely chosen speed.

Signal detection theory

This theory allows the separation of two hypothetical processes that underlie performance in many tasks: a sensory process and a decision process (Green and Swets, 1966). The measure of the sensory processes (e.g. d-prime or d′) is influenced by sensory factors, such as stimulus properties, but not by decision factors, such as rewards and penalties. Conversely, the measure of decision processes (e.g. bias or β) is influenced by decision factors but not by sensory factors. Signal detection theory (SDT) was initially applied whenever subjects had to detect a specific event within noise or to discriminate between two stimuli. Three tasks are usually used by SDT researchers to calculate SDT indices: yes/no tasks, rating tasks and forced-choice tasks. For instance, in yes/no tasks, a very weak visual signal is presented during 'signal + noise' trials and nothing at all during 'noise' trials. After each trial, the subjects indicate whether a signal was present or not. On 'signal + noise' trials, 'yes' responses are correct and are termed hits. On 'noise' trials, 'yes' responses are incorrect and are termed false alarms. The hit rate and the false-alarm rate fully describe performance in a yes/no task, and more generally in a SDT task. Sensory sensitivity (d′) and response bias (β) are calculated from hit and false-alarm rates (see Stanislaw and Todorov, 1999, for calculation formula).

Audiffren, Abou-Dest and Possamai (2007a) used the SDT to assess the effect of two aerobic exercises, walking and running for 30 minutes at a freely chosen speed on a treadmill, on sensory decision processes. Participants had to decide if they perceived the flickering of a light at rest, just after the end of exercise, and 30 minutes after the post-exercise test. For retinal reasons, humans do not perceive the flickering of a light above 46–50 Hz; this visual phenomenon is called fusion and is used for many purposes, such as for moving pictures. In half of the trials the light flickered at 50 Hz, and in the other half at 80% threshold of flickering perception. Audiffren and collaborators chose a critical flicker/fusion frequency task because it is well known to be very sensitive to psychotropic drugs (Hindmarch, 1982; Parrott, 1982). In addition, several studies showed that aerobic exercise improves flickering or fusion detection (Davranche and Audiffren, 2004; Davranche and Pichon, 2005) and contrast sensitivity (Woods and Thomson, 1995). In their study, Audiffren, Abou-Dest and Possamai (2007a) showed that sensory sensitivity increased just after the 30 minutes bout of walking or running and returned to baseline 30 minutes after cessation of exercise. These results confirmed that acute aerobic exercise influences early sensory processes; they are summarized in Table 1.8.

Factor analysis method

This method separates a latent variable (e.g. state anxiety) into several components with the help of exploratory or confirmatory factor analyses. For instance, using a confirmatory factor analysis (CFA), Miyake *et al.* (2000) showed that the latent variable 'executive function' can be separated into three sub-components, namely: (1) shifting between tasks or mental sets, (2) updating and monitoring of working memory representations, and (3) inhibition of dominant pre-potent responses. In other respects, Towse and Neil (1998), Towse and McLachlan (1999), Miyake *et al.* (2000) and Friedman and Miyake (2004) performed a principal component analysis (PCA) on a set of randomness indices used in random number generation (RNG) tasks and found that they loaded on three components. Two of these components matched with two of the sub-components extracted by Miyake and his colleagues. The first component had high loadings for the indices that seem to be more sensitive to the degree to which stereotyped sequences are produced (e.g. turning point index, adjacency index, variability of phase lengths) and was interpreted as reflecting the 'inhibition of pre-potent responses' process. The second component had high loadings for the indices that seem to assess the degree to which each number is produced equally frequently (e.g. redundancy index, coupon score, mean repetition gap) and was assimilated to the 'updating of working memory' process.

The use of these two groups of RNG indices that tap selectively different sub-components of the executive function allows localizing more accurately the effect of an arousing stressor on executive processes. This approach was used by Audiffren, Tomporowski and Zagrodnik (2007b) to study the effect of an acute bout of aerobic exercise on RNG indices. In their experiment, participants performed the RNG task at rest and while cycling at 90% of ventilatory threshold. Their study showed two interesting results: (1) aerobic exercise modulated the inhibition function but not the updating function; and (2) participants shifted toward an easier strategy during exercise in order to generate random sequence of numbers. The second result was larger in the starting period of exercise, suggesting an effortful monitoring of the motor task.

Other ingenious methods developed by cognitive psychologists are available but have not yet been used to localize the effects of acute aerobic exercise in the cognitive architecture, for instance Robert's multiplicative factor method (Roberts, 1987; Sternberg, 2001) and Jacoby's process dissociation procedure (Jacoby, 1991). Results presented in this section suggest that the arousing and facilitating effect of an acute bout of aerobic exercise influences selectively some, but not all, sensorimotor and cognitive processing stages and functions. Table 1.8 summarizes the main results obtained with the four methods. Further experiments must be conducted to delineate precisely which sensorimotor and cognitive functions are improved by acute exercise, which ones are impaired and which ones are not affected.

1.6 Limits of the cognitive-energetic approach and future perspectives

The examination of the effects of exercise on psychological functions is a good example of an interdisciplinary research topic. This kind of research needs the integration of concepts and methodologies that come from many different disciplines, such as cognitive psychology and exercise physiology. We saw in the preceding sections that cognitive psychology alone cannot explain the variability of performance under different environmental stresses (e.g. heat, hypoxia, hyperpressure) or internal states of the organism (e.g. emotion, sedative drugs, fatigue and arousal induced by exercise) (Hockey, Coles and Gaillard, 1986). Other disciplines such as energetic psychology and differential psychology are necessary to study the interaction between physical exercise and psychological functions. In this section, several proposals will be made in order to integrate other disciplines, such as neurosciences and related sub-disciplines such as psychopharmacology, psychobiology and psychophysiology. They should delineate the neurophysiological mechanisms that underlie improvements or impairments of performance and the shift in strategy observed during and following acute bouts of exercise.

Three main levels of integration between cognitive-energetic psychology and neurosciences can be distinguished (Requin, 1986): (1) at the first and lowest level, researchers observe a co-existence or temporal coincidence between one behavioural phenomenon and one physiological or neurophysiological phenomenon; (2) at the second level, researchers predict and test an isomorphic relationship between a structural model of information processing and the anatomo-functional organization of the nervous system; and (3) at the third and highest level, researchers can demonstrate the univocal nature of both cognitive-energetic and neurophysiological models. The work of Chmura, Nazar and Kaciuba-Uscilko (1994) is a good example of the co-existence between behavioural and physiological phenomena related to the effects of exercise on information processing (level 1 of integration). These authors showed a curvilinear relationship between speed of choice reaction time (CRT) and plasma noradrenaline level: CRT was significantly faster just after the adrenaline threshold than at rest and during exercise at maximal oxygen uptake. However, McMorris and Graydon (2000) stated that changes in plasmatic catecholamines concentration do not mirror changes in brain catecholamines concentration.

To my knowledge, there is no research devoted to the study of acute exercise and cognition that belongs to levels 2 and 3 of interdisciplinary integration of cognitive-energetic psychology and neurosciences. However, in order to illustrate these two levels of integration, I propose an example of possible future research for them. The first example is based on predictions made by the Sanders (1983) cognitive-energetic model and by the Robbins and Everitt (1995) neurophysiological and multidimensional model of arousal. One could test the following cascade of hypotheses in the same experiment: (1) aerobic exercise increases arousal via the locus coeruleus; (2) brain noradrenaline released by the locus coeruleus improves the signal-to-noise ratio in sensory processes; (3) sensory sensitivity in a signal detection task is improved during exercise by comparison to rest; and (4) efficiency of neural networks involved in sensory processes are improved during exercise by comparison to rest.

This experiment could be carried out by measuring simultaneously, while participants exercise or rest, the subjective feeling of arousal, the performance in a sensory detection task, the brain noradrenaline concentration and evoked potentials. One would expect an increase of the following behavioural and neurophysiological indices during exercise by comparison to rest: (1) subjective perception of arousal; (2) sensory sensitivity d' index, (3) brain noradrenaline concentration; and (4) amplitude of evoked potential. Such results would have strong explanatory implications for cognitive-energetic psychologists and neuroscientists concerning the understanding of the facilitatory effect of exercise on sensory processes. It would be more difficult to reach the third level of integration. This level proposes to manipulate the level of arousal induced by exercise (e.g. three levels of exercise intensity), to measure the signal-to-noise ratio in neural networks involved in the signal detection task and to show a univocal relationship between variations in physiological arousal and variations in signal-to-noise ratio at the neuronal level. This kind of experiment is currently possible in animals but not in humans. Such results would, however, settle much of the debate on the nature of the facilitating effect of exercise on sensory processes. The following sub-sections propose different interdisciplinary approaches which might contribute to the better understanding of neurophysiological mechanisms underpinning the facilitating and debilitating effects of exercise on cognitive processes.

Contributions of psychopharmacology

Psychopharmacology is the study of drug-induced changes in mood, sensation, information processing, cognitive functioning and behaviour. A major goal of psychopharmacology is to explain how psychotropic drugs alter mental states and mental processes by modifying neurophysiological and biochemical mechanisms in the central nervous system. Psychopharmacology has been extensively used in humans to study the effect of psychoactive drugs on attention, arousal and information processing (e.g. Clark, Geffen and Geffen, 1987; Coull *et al.*, 1995; Halliday *et al.*, 1994; Hou *et al.*, 2005; Mehta and Riedel, 2006; Müller, von Cramon and Pollmann, 1998). Few studies have combined the use of psychoactive drugs and exercise (e.g. Gualtieri *et al.*, 1986; Hogervorst *et al.*, 1999). The main interest of psychoactive drugs is that they can influence a specific neurotransmitter system selectively. For instance, it could be very interesting to use a psychopharmacological agent well known to decrease brain noradrenergic transmission and a placebo at rest and during exercise. If, the arousing effect of aerobic exercise is due to an increase in activity level of this specific neurotransmitter system, the effect size of the facilitating effect of exercise on cognitive processes would decrease, or the effect would disappear, in the drug condition by comparison to the placebo condition. In the same way, it could be interesting to combine the arousing effects of exercise and psychostimulant drugs to examine the pattern of their interaction in the light of the Sternberg's AFM. If an overadditive interaction is observed, one could conclude that both arousing affects have the same locus of influence in the information processing flow, suggesting a common energetic mechanism. In contrast, if an additive pattern is observed, one could conclude that both arousing agents affect different stages of processing and perhaps are underpinned by independent energetic mechanisms.

Table 1.9 provides a list of psychoactive drugs used in human research, which enhance or impair brain noradrenergic and dopaminergic systems.

Contributions of psychobiology

Psychobiologists are interested in measuring biological variables (e.g. the concentration of some molecules synthesized in the brain) in an attempt to relate them quantitatively or qualitatively to psychological or behavioural variables. For instance, if acute effects of aerobic exercise on information processing are due to brain noradrenergic and/or dopaminergic modulation of neural networks involved in sensory, motor and associative cortices, it would be useful to measure the brain noradrenaline (NA) and dopamine (DA) concentrations during or following exercise. Different techniques measuring the concentration of catecholamines directly in the

Table 1.9 Drugs commonly used in human to enhance or impair brain noradrenergic and dopaminergic systems.

Type of psychoactive drug	Brain noradrenergic system	Brain dopaminergic system
Stimulant	Desipramine, Yohimbine, Modafinil	Bromocriptine, Levodopa, Methamphetamine, Methylphenidate, Pergolide
Sedative	Clonidine	Chlorpromazine, Droperidol, Haloperidol, Sulpiride

brain are available in animals, but are too invasive to be used in humans. In man, evaluation of central NA metabolism is based on the measurement of 3-methoxy 4-hydroxyphenylglycol (MHPG) in blood or urine. This molecule is the major metabolite of brain NA. It is able to cross the blood–brain barrier and is excreted in urine. However, urinary MHPG may also be derived from peripheral NA. Several studies have shown that two forms of urinary MHPG can be differentiated: (1) a sulfate form, which can be considered a good index of brain NA; and (2) a β-glucuronide form, which can be considered a more sensitive indicator of peripheral NA metabolism (e.g. Peyrin, 1990; Peyrin and Pequignot, 1983; Peyrin *et al.*, 1985; Yao *et al.*, 1997). However, it is important to note that more recently, Goldstein, Eisenhofer and Kopin (2003) suggested that MHPG sulfate metabolites derive mainly from noradrenaline release in the periphery rather than in the brain.

Two studies have assessed the relationship between exercise, mental performance and MHPG (McMorris *et al.*, 2008a; Peyrin *et al.*, 1987). The study conducted by McMorris and co-workers measured the plasma concentration of MHPG and 4-hydroxy 3-methoxyphenylacetic acid, well known as homovanillic acid (HVA), while performing cognitive tests at rest and during exercise at 40 and 80% maximum power output. Their results suggest a positive relationship between MHPG concentration and cognitive performance; however they did not differentiate sulfate and glucuronide MHPG. Peyrin and collaborators measured urinary sulfate and glucuronide MHPG prior to and following a mental test alone, an exercise bout alone and a combined condition in which participants performed the cognitive tasks while exercising. The three conditions were carried out in different sessions. Peyrin *et al.* showed a positive correlation between cognitive performance in a discrimination test and increases in MHPG sulfate. These two results are very encouraging and further studies measuring plasma MHPG sulfate, while exercising, are needed to test more carefully the catecholaminergic hypothesis.

Contributions of electroencephalography

Electroencephalography (EEG) measures electrical activity produced by the brain as recorded from electrodes placed on the scalp. EEG has a high temporal resolution compared to techniques such as functional magnetic resonance imaging (fMRI) or positron emission tomography (PET); it permits the detection of electrical activity changes in the brain on a millisecond timescale. Recording of EEG requires some methodological precautions, such as removing muscle and eye movement artefacts. Therefore, conducting an experiment which combines exercise and EEG is particularly difficult. In this case, researchers generally prefer cycling rather than treadmill walking or running and post-exercise testing rather than testing during exercise. However, a few authors have made the choice to record EEG concomitantly to exercise (e.g. Pontifex and Hillman, 2007; Yagi *et al.*, 1999). Two approaches with EEG can be found in the literature: (1) the analysis of raw EEG; and (2) the use of summation techniques to analyze evoked potentials (EP) or event-related potentials (ERP). Both approaches have been used to study the effects of exercise on cognition.

Raw EEG can be typically described in terms of rhythmic activity. Most of the cerebral signal observed in the scalp EEG falls in the range of 1–30 Hz. EEG activities below or above this range are generally considered as artifacts. Four frequency bands are distinguished in this range: (1) delta waves (up to 3 Hz) characteristic of slow wave sleep; (2) theta waves (4–7 Hz) observed in drowsiness or meditation states; (3) alpha waves (8–12 Hz), observed when the subject closes his/her eyes or relaxes; and (4) beta waves (12–30 Hz), observed for active or anxious subjects. Several studies assessed the EEG changes induced by acute aerobic exercise. Recordings were carried out either during or following the cessation of exercise. According to the traditional arousal theory (e.g. Duffy, 1962), a decrease in cortical arousal should be evidenced by a shift in power from the faster to the slower frequency bands, whereas an increase in cortical arousal should be evidenced by the opposite tendency (Kubitz and Pothakos, 1997), that is to say, a decrease in alpha activity and an increase in beta activity (Kubitz and Mott, 1996). A meta-analysis conducted by Crabbe and Dishman (2004) reporting 58 effects from 18 studies concluded that compared to before exercise, all frequency bands were increased by one-half a standard deviation during and immediately after exercise. These results do not support either a selective influence of acute exercise on a specific frequency band nor a shift from slower to faster frequency bands induced by physiological arousal. Other physiological phenomena which take place during exercise may also contribute to shifts in EEG frequency bands. For instance, the elevation of core and brain temperature observed during exercise may increase central fatigue and reduce alertness (Rasmussen *et al.*, 2004). Future studies examining the putative mechanisms underpinning the changes in spontaneous EEG activity induced by exercise are required.

The use of the EP/ERP technique seems more promising than the analysis of EEG power spectral densities. EPs and ERPs are electrical positive or negative brain waves time-locked to certain events as stimuli and responses (Picton and Hillyard, 1988). EPs always follow a stimulus whereas ERPs may both precede or follow it. Cognitive psychologists and some neurophysiologists assume that EPs reflect sensory processes elicited by the stimulus whereas ERPs reflect endogenous predictive or reactive cognitive operations involved in information processing. Raw EEG contains background activity which masks EPs/ERPs and represents ongoing brain processes. The use of averaging techniques permits isolation of EPs/ERPs from this background activity. Latency and amplitude of ERP are generally used as indices of cognitive functions or the efficiency of stages of information processing in reaction time protocols. Two ERP components are particularly interesting in the examination of facilitating effects of acute aerobic exercise on cognition, the P300 wave and the contingent negative variation (CNV).

The P300 is a positive wave recorded around 300 ms after the occurrence of the response signal. According to (Polich and Criado, 2006; Polich, 2007), P300 can be separated into two components: (1) P3a reflecting a stimulus-driven frontal attention mechanism during reaction process; and (b) P3b reflecting the allocation of attentional resources for memory updating in temporal and parietal cortices. Brain catecholamines would contribute to the generation of P3a. The CNV is a negative slow wave that takes place during the foreperiod duration of a reaction time, that is to say, between the warning signal and the response signal. It was first detected by Walter *et al.* (1964) and was separated into two components: (1) an early CNV reflecting an orienting response (e.g. Loveless and Sanford, 1974); and (2) a late component interpreted as indexing motor preparation (e.g. Vidal, Bonnet and Macar, 1995).

If acute aerobic exercise increases arousal and activation, more resources should be available for stimulus-driven attention and motor preparation, and the following hypotheses can be made: (1) P300 and CNV amplitudes should be larger in the exercise than in the rest condition; and (2) P300 latency should be shorter in the exercise than in the rest condition. Seven studies measured P300 during or following exercise (Kamijo *et al.*,2004b, 2007; Magniè *et al.*, 2000; Grego *et al.*, 2004; Hillman, Snook and Jerome, 2003; Pontifex and Hillman, 2007; Yagi *et al.*, 1999). Six out of seven studies observed an increase in P300 amplitude during (Grego *et al.*, 2004; Pontifex and Hillman, 2007) or following exercise (Hillman, Snook and Jerome, 2003; Magniè *et al.*, 2000; Kamijo *et al.*, 2004b; Kamijo *et al.*, 2007) by comparison with rest. However, it is important to note that the increase in P300 amplitude was observed only during the first 2 hours of a 3 hour bout of cycling exercise in the Grego *et al.* (2004) study, and only for light- (RPE = 11) and medium-intensity exercises (RPE = 13), but not for high intensity exercise (RPE = 15) in the Kamijo *et al.* (2004a) study. Only one study observed a decrease in P300 amplitude, but this was during a 10 minute moderate intensity cycling exercise (Yagi *et al.*, 1999) and with a speed-accuracy trade-off between rest and exercise in the RT task. For that reason, I did not consider this last study in the review of exercise effect on P300 latency.

Three studies out of six observed a decrease in P300 latency (Hillman, Snook and Jerome, 2003; Kamijo *et al.*, 2007; Magniè *et al.*, 2000), whereas two out of six observed an increase (Grego *et al.*, 2004; Pontifex and Hillman, 2007). Only one study examined the effect of an acute bout of aerobic exercise on CNV amplitude (Kamijo *et al.*, 2004a). The authors found lower CNV amplitude following high-intensity exercise in comparison to moderate-intensity exercise and rest conditions, but no difference was observed between rest and moderate-intensity exercise. Taken together, these studies confirm the importance of carefully controlling the intensity and duration of exercise in order to obtain facilitating effects of exercise on cognitive processes and neuroelectric mechanisms. More studies are needed to examine the effect of acute bouts of steady-state exercise on ERPs in different cognitive tasks.

Brain imagery techniques such as fMRI, PET and magnetoencephalography (MEG) could also be very useful to examine the effects of acute exercise on cognitive processes. However, these techniques have been only employed to examine the hemodynamical and metabolic adaptations of the human to acute exercise (e.g. Hollman *et al.*, 1994, for a review; see also Chapter 8 of this book) or the effects of chronic bouts of exercise on brain structure or brain functioning, particularly in ageing people (e.g. Colcombe *et al.*, 2004; Colcombe *et al.*, 2006). The use of these brain imagery techniques during cycling exercise would require the elaboration of specific apparatus allowing leg motions without any motion of the head. To my knowledge, such study has not yet been conducted.

1.7 Conclusion

This chapter is an attempt to give useful theoretical and methodological frameworks for researchers interested in the effects of acute bouts of exercise on sensorimotor and cognitive processes. A large set of experimental data led exercise and cognitive neuroscientists to consider that acute aerobic exercise acts like an arousing psychostimulant drug via brain noradrenergic and dopaminergic pathways. In addition, several lines of evidence suggest that increases in arousal and activation induced by exercise do not have a general facilitating effect on cognition but rather a selective influence on specific stages of information processing, such as sensory and motor processes. Some cognitive processes such as executive functions may be impaired by acute aerobic exercise. Future research integrating cognitive and energetic approaches and combining different methodologies presented earlier are needed to elucidate more precisely the neurophysiological mechanisms which underlie the effects of acute exercise on cognition, that is which psychological functions are improved by exercise and which ones are impaired. There is also a need for an innovative and heuristic cognitive-energetic model of exercise and cognition which would take into account data collected since 1995.