Mental processes and breathing during exercise

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Abstract Breathing during exercise is an important physiological function for maintaining homeostasis of hydrogen ion concentration ($[H^+]$) in the internal environment. In general, ventilatory response during exercise is considered to be automatically (unconsciously) controlled depending on exercise intensity and the corresponding perturbation of neurohumoral factors. However, in awake humans, the act of performing physical exercise is coupled with conscious elements such as motivation, effort, and emotions. This means that ventilatory control during exercise is also inseparably linked to such mental processes. With regard to the indivisibility between ventilatory control and conscious elements, there has been increasing psychological and neurophysiological evidence supporting the importance of mental and behavior factors in addition to neurohumoral factors. Therefore, in this paper, previous studies, on the indivisibility of ventilatory control and conscious elements, were looked at, and the roles of mental processes in ventilatory control and $[H^+]$ homeostasis during exercise discussed.

Keywords : control of breathing, exercise hyperpnoea, hyperventilation, homeostasis, perception, behavior

Introduction

Regulation of hydrogen ion concentration ($[H^+]$) in the internal environment is a homeostatic mechanism necessary for optimal protein function at a given body temperature¹⁻⁴⁾. While both the kidneys and lungs operate to maintain $[H^+]$ homeostasis, an acute change of H^+ during exercise is taken care of by the latter function, CO_2 removal by pulmonary ventilation⁵⁻⁸⁾. In general, ventilatory control during exercise is regarded as a neural mechanism and/or humoral mechanism. A neural mechanism consists of activation of the respiratory center, induced, in parallel, by activation of the motor center, termed ‘central command’⁹⁾, and a neurogenic reflex via afferent nerve fibers from exercising muscle¹⁰⁻¹²⁾. The humoral mechanism is a feedback control in which central and peripheral chemoreceptors play a primary role¹³⁻¹⁵⁾. In this manner, breathing during exercise is automatically (unconsciously) controlled depending on exercise intensity and corresponding perturbation of neurohumoral factors.

However, in awake humans, the act of performing physical exercise is coupled with conscious elements such as motivation, effort, and emotions. This means that ventilatory control during exercise is also inseparably linked to such mental processes. With regard to the indivisibility between ventilatory control and conscious elements, there has been increasing experimental evidence supporting the importance of behavioral factors (e.g., arousal level and

mental activity) in addition to neurohumoral factors^{16,17)}. Furthermore, recent brain imaging techniques have shown the possibility that breathing (non-exercise condition in this case) is not only controlled by the bulbospinal pathway, but also modulated via corticospinal and corticolimbic circuits¹⁸⁻²¹⁾. This finding from neuroscience studies also encourages us to look more closely at the control of breathing that co-exists with mental processes such as cognition and emotional experience accompanying physical activity. Therefore, in this paper, previous studies, on the indivisibility of ventilatory control and conscious elements, were examined, and the roles of mental processes in ventilatory control and $[H^+]$ homeostasis during exercise discussed.

Indivisibility between ventilatory control and conscious elements

Perception of effort. Krogh and Lindhard²²⁾ observed the phenomenon that ventilatory response at exercise onset could be increased if the subject believed that he/she would be working at a higher intensity than was actually imposed²³⁾. They²²⁾ considered this phenomenon to be due to excitation of the respiratory center induced by ‘irradiation’ of impulses from the motor cortex. This conception was reinforced in later studies that used more empirical approaches such as injection of tubocurarine²⁴⁾ and vibratory stimulation⁹⁾ to manipulate the descending signals (central motor command) from the motor center, and this conception has become widely accepted as the ‘central

command' hypothesis. In this hypothesis, perception of effort is linked to the magnitude of central motor command^{9,24}). In other words, it means that in ventilatory control during exercise, perception of effort is an important factor for the generation of impulses in the primary motor cortex and for irradiation of impulses to the respiratory center.

Motor imagery. Later, some studies, by investigating the psychophysiological responses to imagined exercise, without actual physical exertion, have suggested the possibility that the effort-induced cardiorespiratory response during actual exercise does not necessarily require the parallel activation of central motor command. For example, Decety et al.²⁵) reported a covariation of respiratory activity with a degree of imagined effort during mental simulation of treadmill running. Furthermore, Thornton et al.²⁶) showed that hypnotized subjects increased their breathing during imagination of cycling uphill, but not during imagination of cycling downhill. In their study, significant activation was seen in brain regions such as the dorsolateral prefrontal cortex, supplementary motor areas, premotor area, and cerebellum, by using positron emission tomography (PET). Likewise, Williamson et al.²⁷) showed that the magnitude of cardiovascular response during imagined handgrip exercise could be dictated by an individual's effort sense that was estimated from ratings of perceived exertion (RPE). They²⁷) localized the insular and anterior cingulate cortices as key brain sites related to effort-induced response. Moreover, Fink et al.²⁸) demonstrated that the superolateral primary motor cortex, involved in volitional breathing, was activated during actual leg exercise, and even after the end of exercise during which there was no activation of the superomedial primary motor cortex involved in the execution of leg exercise. In this way, neuroanatomical evidence, supporting the possibility that effort-induced ventilatory response during exercise is not a simple 'central command' mechanism, has been provided. On the other hand, it is also a fact that there are reports showing that the primary motor cortex, related to the execution of exercise, was activated during imagined exercise²⁹⁻³¹). Actually, in studies by Thornton et al.²⁶) and Williamson et al.²⁷), activation of sensorimotor areas was detected during imagined exercise. In this regard, Williamson et al.²⁷) concluded that the activation of sensorimotor areas (as well as the thalamus and cerebellum), during motor activity, appears to be more related to execution of the movement itself, whereas activation of the anterior cingulate and insular cortices is more closely related to effort-induced response.

Quality of imagery. In a study by Porro et al.³¹), it was shown that the degree of activation of the primary motor cortex was lower during imagined exercise than during real movement. Furthermore, the activation of brain areas concerned with motor behavior seems to be greater

when an exercise task is imagined from a first-person perspective than when imagined from a third-person perspective^{32,33}). In a study in which the quality of imagery was examined, it was shown by Wang and Morgan³⁴) that effort sense and ventilatory response to internal imagery (kinesthetic imagery) more closely resembled actual exercise (dumbbell exercise) than external imagery (visual imagery). Moreover, Wuyam et al.³⁵) reported that ventilatory response to imagined exercise was greater in competitive sportsmen than in ordinary people who had little exercise experience. Thus, it is thought that effort-mediated ventilatory response during exercise is influenced by the exerciser's own exercise experience and situation recognition³⁶).

Awareness and attention. Bell et al.³⁷) reported that when subjects were instructed to start exercise (leg extensions) while performing a cognitive task in the background, exercise hyperpnea at exercise onset was significantly reduced. They proposed a 'division of attention' during the exercise task as a cause of the attenuated breathing^{17,37}). On the other hand, Yunoki et al.³⁸) showed that when subjects performed prolonged moderate incremental exercise, under the condition of being provided false prior information that the workload would remain constant, awareness of change in load and ventilatory response were significantly reduced compared to the control condition in which true prior information was provided (Fig. 1). Since magnitudes of RPE (or effort sense) and central motor command (estimated from an integrated EMG of exercising muscle) were similar between the two conditions, they concluded that ventilatory response during moderate exercise depends not so much on effort sense, but more on awareness or attention that is closely connected to information detection³⁸). Awareness or attention can be one of the stresses that elicit emotion. Such sensory information, for instance, a feeling of fear, is conveyed to the hypothalamus via the amygdala³⁹⁻⁴¹). Kuwaki et al.⁴²) and Zhang et al.⁴¹) demonstrated that orexin neurons in the hypothalamus play a significant role in emotional cardiorespiratory regulation. The insular cortex and anterior cingulate cortex, which have been shown by Williamson et al.^{27,43}) to be related to effort-mediated response, are also parts of the brain, along with the amygdala, involved in emotional reaction. Although the neuroanatomical structure is not clearly understood, emotional change induced by awareness or attention activate these brain sites and consequently affect the ventilatory response at exercise onset and even during prolonged exercise³⁸).

Role of the perception of effort in ventilatory regulation during heavy exercise

In actual exercise, unlike in the case of imagined exercise at rest, there are always feedback inputs to the central nervous system from the peripheral system. In heavy

Fig. 1 Effects of awareness of change in load on ventilatory response during moderate exercise ($N = 7$) (data from Yunoki et al.³⁸). (a) Prior information and actual exercise. The load was imperceptibly increased from 1.0 to 1.5 kp in steps of 0.1 kp every 3 min. In the control protocol, subjects were correctly informed that the load would be progressively increased. In the deception protocol, subjects were told that the load would be constant, while, in actuality, they were made to exercise in the same loading configuration as that of the control protocol. In both protocols, subjects were asked to press a button attached to the handlebar of the cycle ergometer when they were aware of or felt an increase in load. (b) This chart shows

the frequency of awareness of change in load during exercise under the two conditions in an individual subject. Dotted lines denote the time at which the load changed. Vertical solid lines denote the time at which the subject pressed the button. The first solid lines are marks to locate the start of the exercise. The subject pressed the button 23 times and 3 times in the control and deception protocols, respectively. There was a significant ($P < 0.05$) difference in the frequencies of awareness between the two protocols. (c) Relationship between ventilation and carbon dioxide output obtained during exercise performed under the two conditions. The relationship shown was obtained from mean values for the group. Slope of the relationship was found to be significantly ($P < 0.01$) lower in the deception protocol than in the control protocol.

exercise, there is not only a large increase in perception of effort, but also severe perturbation of neurohumoral factors stemming from the peripheral system. How are these central and peripheral factors involved in ventilatory control during heavy exercise? There have been some studies about their interrelation in ventilatory control. For instance, an essential role for muscle afferent feedback in respiratory regulation has been suggested by the observation that blocking somatosensory feedback by fentanyl injection caused hypoventilation during a cycling time trial⁴⁴. Furthermore, using a similar pharmacological method, Amann et al.⁴⁵ demonstrated that blocking somatosensory feedback substantially attenuated the ventilatory and also perceptual responses to heavy exercise. These findings by Amann et al.^{44,45} raise the possibility that input of groups III and IV muscle afferents contributes to the central motor command driving respiration during exercise⁴⁶. In contrast, Marcora et al.⁴⁷ demonstrated that muscle fatigue per se enhances ventilatory response during heavy exercise, independent of metabolic stress, and they^{47,48} argued that ventilatory response during exercise is mediated by the perception of effort, which is derived from corollary discharge⁴⁹⁻⁵¹ of central motor command, independent of peripheral signals. Likewise, it has been reported that ventilatory response to heavy exercise does not depend on acid-base conditions⁵²⁻⁵⁴ and Yamanaka et al.⁵⁴ have shown a strong link between effort sense and ventilatory response. In addition, Yamanaka et al.⁵⁵ have demonstrated that during repeated heavy exercise performed after glycogen depletion, hyperventilation was increased in accordance with the augmentation of effort sense despite attenuation of blood pH (Fig. 2). This suggests that in heavy exercise, blood pH does not play a significant role for ventilatory control but rather is controlled by ventilation. If ventilatory response is weakened with attenuation of metabolic stress, blood and/or muscle pH will decrease due to inhibition of CO₂ removal and, as a result, the subject may not be able to complete the assigned task. Therefore, in heavy exercise, respiratory regulation independent of blood pH is important for sup-

porting pH homeostasis and exercise performance.

Some early studies using glycogen depletion^{56,57)} and tubocurarine^{24,58)} introduced the notion that the increase in central motor command, induced by muscle fatigue or weakness, is a major mediator of the increase in ventilatory response. However, in some recent studies, in which muscle fiber recruitment (EMG) was examined, it was confirmed that, during exercise performed after muscle glycogen depletion, integrated EMG, which reflects central motor command, remained unchanged⁵⁹⁾ or de-

creased^{55,60)} (Fig. 2). Therefore, although hyperventilation during heavy exercise is related to perception of effort, it may be an event independent of the traditional model of 'central command' that drives breathing via parallel activation of motor and respiratory centers. Thus, these recent studies^{44-48,54,55)} collectively emphasize the importance of a cognitive process such as perception of effort in respiratory regulation during heavy exercise. However, the formation mechanism of effort sense during heavy exercise and the role of effort sense in ventilatory control are still not clear⁶¹⁾.

Conclusion

In this review, many case examples of breathing during imagined exercise or actual exercise, being modulated by mental processes such as cognition and emotional experience, have been described. Furthermore, in some cases, a neurophysiological mechanism that exists between ventilatory response and the mental processes has been proposed. These findings suggest that 1) perception of effort is involved in ventilatory control during exercise by a mechanism that perhaps differs from traditional 'central command', 2) ventilatory response during moderate exercise depends not so much on effort sense but mainly on attention to or awareness of self-motion, and 3) ventilatory response to heavy exercise is independent of metabolic stress and mainly associated with perception of effort. These findings emphasize again that the control of breathing, that co-exists with mental processes during exercise, should not be overlooked, and that mental processes are an important function for $[H^+]$ homeostasis by breathing. However, with regard to the relationship between ventilatory response and perception of effort, there are still some issues to be resolved. For instance, more direct examination of the relationship between an increase in effort sense and excitation of the primary motor cortex will be needed to clarify the involvement of 'central command'. Furthermore, $[H^+]$ homeostasis compensated by an increase in hyperventilation would compete with locomotor muscle fatigue by constricting blood flow^{62,63)}. Therefore, to understand the purpose and overall strategy of breathing during exercise, investigation from an integrated systems perspective may be needed^{17,64)}.

Fig. 2 Effects of reduced muscle glycogen on blood pH, ventilation, and integrated electromyogram (EMG) of exercised muscle during and after repeated heavy exercise (Ex.1, filled rhombics; Ex.2, open squares; Ex.3, open triangles) ($N = 8$; data from Yamanaka et al.⁵⁵⁾). Subjects performed heavy exercise (100-105% of peak O_2 uptake, 2 min) three times at 100-120-min intervals. Each interval consisted of 20-min passive recovery, 40-min submaximal exercise at ventilatory threshold intensity (in order to reduce muscle glycogen content), and a further resting recovery for 40-60 min. Data presented are means $\pm$ SD. *Significant difference between Ex.1 and Ex.3 ($P < 0.05$).

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