Effect of Practice on the Voluntary Control of a Learned Breathing Pattern

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GALLEGO, J. AND P. PERRUCHET. Effect of practice on the voluntary control of a learned breathing pattern. PHYSIOL BEHAV 49(2) 315–319, 1991.—Changes in orientation of attention and ventilatory data were examined in three normal volunteers who practiced a learned ventilatory pattern over eight training sessions. The breathing task was a voluntary increase of inspiratory duration up to a given target with the aid of informative feedback on this variable. The orientation of attention was investigated through reaction time (RT) to auditory stimuli presented at different points in inspiration and expiration, during either automatic or voluntary control of breathing. Findings show that RTs are longer during voluntary than automatic breathing throughout the experiment, and that they decrease across sessions in both conditions. In the first sessions, RTs were longer during expiration than inspiration but this difference cancels out in the last sessions. The results are discussed in terms of attentional demands of control of breathing, automation, and the connection between automatic and voluntary control of breathing. This work shows that after eight practice sessions, the orientation of attention displays significant changes; however, the control of breathing remains attention demanding.

Breathing pattern Voluntary control Motor learning Automatization Reaction time

IN physiological research, what is usually termed the “behavioral component” of breathing covers a wide range of phenomena. Many ventilatory acts which are difficult to explain solely in terms of central pattern generator and adaptive control of breathing are often classified as behavioral, especially in research dealing with the control of breathing in conscious man. Conditioned anticipatory changes in breathing pattern before muscular exercise, voluntary breathing, ventilatory reactions to emotions, phonation, etc., are a few examples of what is usually classified as behavioral. Aside from several hallmark publications (11, 16, 17, 20), this behavioral component remains poorly defined and often ignored. Consequently, the results of many current studies are presented as though they were purely reflecting the activity of the central pattern generator, thus disregarding the fact that the activity of the respiratory system is controlled by the entire series of main descending systems, as noted by Von Euler (4).

An intriguing issue is the connection between automatic breathing, governed by the bulbospinal centers, and voluntary control of breathing, which is located in somewhat circumscribed areas of the cortex [see (6)]. A recent work has investigated cortical projections to respiratory muscles in man using the cortical stimulation technique (9). The authors conclude that there is a comparatively direct projection from the motor cortex to the diaphragm via mono- or oligosynaptic pathways. Further, despite the paucity of experimental data in man, there is a general consensus that the descending influences from the cortex also act on the bulbospinal generator via corticobulbar pathways. Several studies carried out on cats demonstrate that cortical stimulation inhibits inspiratory bulbospinal neurones (1), which supports the hypothesis that descending influences from the cortex excite both the respiratory motoneurones and the output stage of the respiratory bulbospinal oscillator, while inhibiting the latter’s oscillatory activity (11). This hypothesis assumes that the role of the pyramidal system in voluntary changes in breathing pattern is to bypass the prewired central pattern generator and play its own original kinetic melody on the spinal keyboard, rather than rearrange the existing bulbospinale programmes, to use the classic metaphor (15). However, as a general rule, if a voluntary act is often repeated, some learning occurs, and the neurophysiological and cognitive processes underpinning its control may change. This must also be true for breathing behavior, but this supposition has received little attention.

Because of its direct connection to both physiological research and clinical applications, an issue of particular interest is the integration of learned breathing acts into the automatic pattern. This concerns breathing therapies in chronic obstructive pulmonary disease (21), hyperventilation syndrome (10), and relaxation therapies. These therapies aim at learned modifications of the breathing pattern. Furthermore, recent investigations also suggest that certain learning processes affecting ventilatory movements during intrauterine life and up to several months after birth might be directly connected to the etiology of the sudden infant death syndrome (15). In keeping with previous studies on short-term effects of ventilatory pattern learning (5,7), the present study investigated learning over repeated sessions. The breathing task was to increase inspiratory duration with the aid of informative feedback on this variable. This prolonged training was expected to induce adaptive changes in the attentional control of the movement, as occurs with most motor skills. We tested this hypothesis by investigating the time course of the attentional control of breathing during the training sessions. The magnitude and the direction of attentional resources were analysed through reaction
time (RT) to a probe stimulus.

METHOD

Subjects

Three healthy males aged 24, 24, and 27 years took part in 9 experimental sessions (one reference and 8 training sessions). Subjects were paid for participation. All were unaware of the purposes of the experiment, and none had previous exposure to the task.

Apparatus

The experimental setup was composed of a heated Fleisch pneumotachograph (No. 2) with its pressure transducer (Schlumberger CH510510, No. 13, conditioner CA1065), an analog processing device built in the laboratory, an analog to digital converter (Selia PA300), a microcomputer (Olivetti M24) and an oscilloscope (Tektronix 5103N). The two inputs to the converter were tidal volume \((V_T)\) and a signal from a relay which tipped each time the flow crossed zero. The computer used this binary signal to compute inspiratory and expiratory times \((T_i\) and \(T_e\)). The sampling frequency for this signal was about 200 Hz. Volume was calibrated in ATS conditions (ambient temperature, pressure, and saturation) before each session with a stimuloid pump built in the laboratory. All volume measurements were then converted into ATS units (body temperature, . . .). Visual feedback used in the breathing task was presented on the computer monitor: immediately following the end of each inspiration, a horizontal segment moved up to a position corresponding to the mean duration of the ten preceding \(T_e\)'s (terminal, intermittent, and proportional feedback). Two horizontal lines (minimum and maximum values) represented the target. The screen resolution allowed 200 vertical steps corresponding to four seconds. The 50-millisecond auditory stimuli were generated by the computer at a comfortable audible volume and delivered binaurally to the subject via headphones. The interstimulus period varied randomly from 2 to 12 s. The RT task consisted of depressing one particular key of the computer keyboard placed near the right arm of the subject's chair whenever a sound was delivered through the headphones. Computer measures of time durations were electronically validated via the oscilloscope. Computer programs were written in Basic and compiled by Quick Basic Compiler.

Procedure

Subjects were tested individually. Each subject was seated in an armchair opposite the computer monitor with their right hand resting comfortably on a support. In a preliminary session, the subjects received instructions for the RT task. Ten practice trials were then run. A facial mask fitted with a pneumatic strip and attached to the pneumotachograph was then suspended at the appropriate height and fastened to the subject's head (no leakage was observed). Subjects were then instructed to read a text with no emotional impact. While they were reading, the experimenter monitored breathing signals via the oscilloscope, and the numerical values of \(T_i\), \(T_e\), and \(V_T\) on the computer display. After allowing a 10-min period for the subject to adapt to the apparatus, 120 reference values were collected for \(T_i\), \(T_e\), and \(V_T\).

The following eight experimental sessions were divided into 4 phases. After attaching the mask, subjects were given standardized instructions concerning Phases 1 to 4. During the 10-min familiarization period and Phase 1 (reference phase for ventilatory data; 20 cycles) subjects were instructed to read. Phase 2 (reference phase for RT; 20 RT trials) was devoted to the reaction time task. At the beginning of Phase 3, the moving segment corresponding to \(T_i\) and two horizontal lines defining the target appeared on the display. The distance between the lines corresponded to an interval of 0.2 s and the center of this interval corresponded to twice the reference \(T_i\) value. The subjects were informed of the significance of the visual feedback and were instructed to keep the moving segment inside the target delineated by the two horizontal lines. Subjects were warned against any excessive increase of \(V_T\). The phase began with a training period (15 cycles with continuous feedback). The subjects then carried out the ventilatory task and the reaction time task simultaneously (100 RT trials). The visual feedback only appeared every ten breathing cycles. Subjects were instructed to give priority to the breathing task over the RT task. The last phase (Phase 4, 20 cycles) was identical to Phase 1 (reading only). For each subject, the one-hour sessions were scheduled alternately in the morning and in the afternoon. Six hours were allowed to elapse between the two daily sessions and sixteen between the evening session and the first session the next day.

Performance Indices for the Breathing Task

The following three performance indices were used (18):

Absolute Error: \(AE = \Sigma (T_{ik} - T^*) / N\),

Constant Error: \(CE = \Sigma (T_{ik} - T^*) / N\),

Variable Error: \(VE = \text{Standard deviation of } T_i\),

where \(N\) is the number of cycles; \(T_{ik}, T^*\) value of the \(k\)-th cycle; and \(T^*\), target \(T_i\). AE is the average deviation from the target ignoring signs. This index expresses the amount of inaccuracy in the subject's movement timing. CE is the average algebraic deviation from the target. It represents directional biases in responding. VE indicates consistency in responding. For each subject, AE, CE, and VE were expressed as a percentage of each subject's target \(T^*\). Improvement in performance corresponded to a decrease in AE, VE, and the absolute magnitude of CE.

Learning

In keeping with a widely accepted distinction between learning and performance (18, 19), within-session variations in perfor-
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![Diagram showing reaction times to auditory stimuli and ventilatory data during four phases of each session.](image)

Results

Learning of the Breathing Task

Dependent measures for each subject were the AE, CE, and VE values computed for each individual target value (3700, 3563, and 3849 ms). Figure 1 shows that subject performance improved globally across sessions. This was confirmed by an analysis of variance on the group of three subjects, with session as the within-subject factor. This analysis showed a significant main effect of session for AE and VE, F(7,14) = 3.77 and 3.40, respectively, p < 0.025. A significant decreasing linear trend of these two indices across sessions was observed [for AE: F(1,2) = 20.01, p < 0.01, and for VE: F(1,2) = 27.95, p < 0.01]. This clearly confirmed the improvement in performance across sessions. On the other hand, CE did not vary significantly, which indicates that learning mainly affected response variability rather than mean deviation from the target. This significant session effect for both AE and VE revealed a retention effect over sessions providing evidence for learning. However, performance varied considerably over successive sessions, as shown by the serrated curves of Subjects 2 and 3 in Fig. 1. These variations in performance might have resulted from the shorter interval (and consequently the better retention) from the morning to the evening session than for the evening to next morning session. But nonspecific factors such as diurnal changes in the vigilance level may well have affected both the learning of the breathing task and the reaction times (Fig. 2).

Figure 3 shows the mean variations in ventilatory parameters (T1, T2, Vr, and V) for each phase of the eight sessions. These data were analyzed with a separate analysis of variance for each parameter, using session (1 to 8) and experimental phase (1 to 4) as within-subject factors. Both factors displayed significant main effects for T1, F(3,6) = 33.49, p < 0.001, for T2, F(3,6) = 29.33, p < 0.001, and for VT, F(3,6) = 12.99, p < 0.005. This is due to the fact that when subjects performed the breathing task (which consisted of increasing T1), they also tended to increase T2 and Vr. On the other hand, the mean flow rate V was not significantly affected by the breathing task, as though the subjects had spontaneously adjusted T1 and Vr to compensate for the voluntary increase in T1. In the last phase (Phase 4, reading) the T1s (averaged over the three subjects) remained slightly higher than their baseline values (calculated in Phase 1). This finding shows that the subjects tended to maintain the breathing pattern they adopted during training, at least for a short while, but this effect did not reach significance and cannot be unambiguously attributed to learning.

Reaction Time

The raw data for each subject and each session were the 20 RTs in Phase 2 (RT only) and the 100 RTs in Phase 3 (RT and breathing task). The session (1 to 8) and the experimental phase (2 to 3) were the within-subject factors of the analysis of variance. Both main effects were significant. As shown in Fig. 2, RTs differed across sessions, F(7,14) = 3.02, p < 0.05, and were higher in Phase 3 than in Phase 2, F(1,2) = 57.61, p < 0.025. For both phases, the decrease in RT across sessions exhibited a marginal linear tendency [F(1,2) = 13.84, p = 0.065, and F(1,2) = 16.78, p = 0.054, respectively]. The difference between phases reflects the considerable interference between RT and the breathing task. Partial comparisons showed that the session effect in RT was significant in Phase 3, F(7,14) = 2.82, p < 0.05, whereas the corresponding session effect in Phase 2 was not significant. This might reflect a slight reduction of interference, but no firm conclusion can be drawn because the Session x Phase interaction did not reach significance.

Reaction times were further analyzed as a function of the respiratory phase (inspiration or expiration) during which the auditory stimulus occurred. These times are shown in Fig. 2. During spontaneous breathing (Phase 2), there was no difference between the RTs to the stimuli delivered during inspiration or expiration. However, during voluntary control of breathing (Phase 3) the
mean RTs tended to be shorter during inspiration than expiration in the first five sessions, whereas this tendency was no longer apparent on the three last sessions. This was confirmed by a reliable Session × Respiratory Phase interaction, F(7,14) = 3.22, p < 0.05. This effect shows gradual orientation of attention toward the whole breathing cycle.

DISCUSSION

Accuracy in controlling inspiratory duration improved significantly across sessions. This finding, which clearly demonstrates the retention of the target timing, was taken here as a proof of learning. However, this result does not indicate what exactly was learned, given that the breathing task involved various components. Two of these were the estimation of time and the control of the breathing muscles. The adaptive changes in amplitude of breathing pattern associated with the change in frequency might also be considered as a component of the task, since respiratory comfort during the session is a necessary precondition for performing the task. The evidence for learning, based on overall performance, does not indicate whether these components were differentially affected by learning. The time course of attentional demands during the learning process may provide some insights.

In their recent review, Keele and Ivry (12) provide both experimental and neurological support for the hypothesis that the different components of a skill, especially timing, are processed by different neural systems. In particular, observation of neurologically impaired patients provides some insight into the separate location of the time estimation process and the motor response itself. The present data indicate that in the first session, RTs were longer during expiration than inspiration and that this difference tended to level out in the last sessions. The finding that longer RTs occurred during expiration confirms previous results on a larger group of 27 subjects who performed a similar breathing task during a single session (8). RTs in this study were particularly high at the beginning of expiration and gradually decreased up to the middle of expiration. Appropriate analyses indicated that this variation was not due to interference with the processing of visual feedback which appeared at the beginning of expiration on every tenth cycle as in the present study. Rather, it was hypothesized that the peak RTs at the inspiration-expiration transition might be due to transient difficulties in the voluntary control of breathing muscles, especially the diaphragm (3). Given that the variation of RT closely paralleled the antagonist activity of diaphragm in the first half of expiration, the high RTs at this stage of the breathing cycle were attributed to the subjects’ difficulty in controlling the diaphragm during the shift from agonist (inspiratory) to antagonist (expiratory) activity. A similar interpretation of the difference in RT during inspiration and expiration could be made here. The present results show that this difference tended to disappear with practice, which reflects a change in the way the subjects controlled their diaphragm. Possibly, the attentional resources initially focused on the transition from inspiration to expiration spread from this stage to the whole breathing cycle. This change did not notably reduce the global demands of the breathing task, as revealed by the comparison of RT during the breathing task to reference RT. Rather, as performance improved, the subjects may have shifted from terminal control of inspiratory duration to concurrent control of the whole cycle, thus assigning sensory information a continuous monitoring function.

Although the metabolic and behavioral components of breathing are often contrasted, it must be stressed that the voluntary control of breathing does not necessarily disturb respiratory homeostasis. Our results indicate that the voluntary increase in inspiratory duration was associated with an increase in inspiratory duration and in tidal volume, but the mean flow remained roughly steady. The subjects, who were explicitly warned against any excessive increase in tidal volume during the breathing task, adjusted their breathing pattern to avoid any breathing discomfort. A previous experiment (5) has shown that subjects instructed to increase inspiratory duration tend to override tidal volume and hyperventilate. Accordingly, the observed adjustments of breathing pattern may be seen as a voluntary adaptation rather than a consequence of chemical control of breathing.

A general feature of sensory-motor learning is the processing of information from different internal and external sources (14). In the learning of the breathing pattern investigated here, the sources were the information feedback provided by the apparatus, the afferent information from different sets of receptors located in the lungs, the upper airways, the joints, the skin, all the muscles involved in the act of breathing, and possibly information feedback from the efferent pathways. To date, the primacy of any of these sources of information is a controversial issue but it is likely that all these sources of information contribute to the genesis of respiratory sensation, and hence, to the learning of a breathing pattern. Both sources of information, internal and external, are necessary for the learning of a breathing pattern. If information feedback had been given continuously, subjects would have relied too heavily on this external information, and they may not have learned to detect their own errors on the basis of internal sensations. This is why the subjects in the present study were given intermittent feedback. The close ties between efficient training and forms of informative feedback must be stressed.

The acquisition of new motor skills implies an attentionally controlled phase involving all the resources of cognitive processing, followed by a progressive delegation of action control to processing modes on the sensory-motor level (15). In conditions of extended and consistent practice, this process may lead to a global reduction of the attentional resources devoted to the movement, termed automatization. Some of these automatic skills involve the breathing effector, especially during phonation (20). However, there is no experimental evidence that initially conscious ventilatory responses can become automatic, and so fail to reach awareness, as is sometimes assumed [e.g., (2)]. Clinical data on breathing retraining, and traditional practices such as yoga do not provide any evidence for automatization either. However, this issue has rarely been addressed with appropriate methodology. Reaction time tasks provide a suitable means of revealing attentional control of breathing and assessing the automaticity of the breathing pattern. The present findings do not indicate a reliable convergence of reaction times collected during spontaneous and voluntary breathing across sessions. Even after eight practice sessions, the control of breathing remains attention-demanding. This provides some insights into the practice time necessary to effect changes in automatic breathing.

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