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THE AIR HUNGER RESPONSE OF FOUR ELITE BREATH-HOLD DIVERS

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Abstract

Normal subjects terminate breath-holds due to intolerable ‘air hunger’. We hypothesize that competitive breath-hold divers might have increased tolerance of air hunger. We tested the air hunger (AH) response of 4 divers who could hold their breath for 6 - 9 min. Tidal volume and respiratory rate were controlled by mechanical ventilation (ventilation $\approx 0.16 \text{ L} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$). AH was induced by raising P_{CO_2} and rated using a visual analog scale whose maximum was defined as intolerable. SpO_2 was maintained at $>97\%$. Three divers reported the same uncomfortable urge to breathe as normal subjects; the slopes of their responses were within normal range. Both resting CO_2 and AH threshold were shifted to higher CO_2 in some divers. Diver 3 was unique amongst neurologically intact subjects we have studied: he denied feeling an urge to breathe, and denied discomfort. We conclude that elite divers' strategies to tolerate intense air hunger are a minor factor in their ability to tolerate long breath holds.

Keywords

hypoxia; hypercapnia; dyspnea; breathlessness; shortness of breath; urge to breathe; breath-hold diving; apnea; breaking point

1. Introduction

The use of voluntary breath hold as a probe to gain insight into the physiological mechanisms of shortness of breath dates to at least a century ago (Hill and Flack 1908; Flume et al. 1994; Nishino et al. 1996). Breath holds are normally terminated due to a perception of the need for air (‘air hunger’) that becomes intolerable; hence, breath hold time (taken conventionally as the time during which there is no airflow at the airway opening) has been used as a measure of air hunger tolerance (Lin et al. 1974). Competitive breath-hold divers can hold their breath substantially longer than untrained individuals. During “static apnea” competitions (competitor lies face down on the water surface) breath-holds lasting well over 8 minutes have been

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recorded. It is reasonable to hypothesize that, through training effects or specialized skills, these divers are less sensitive to air hunger than normal subjects. In an expanded case study we examined the response of four elite breath-hold divers to laboratory stimuli that evoked steady-state air hunger.

Voluntary breath hold is achieved by descending inhibition of respiratory pump motor activity at the level of the brainstem motoneurons (Orem and Netick 1986) and/or the final spinal motoneurons; in addition, closure of the larynx aids breath hold in many people when descending inhibition is insufficient to completely suppress pump muscle activity. During breathhold PaCO_2 increases and PaO_2 decreases; these stimuli increase brainstem respiratory center drive. An ascending copy brainstem motor output is thought to be the major stimulatory input for air hunger (corollary discharge) (Banzett and Lansing 1996). Input from slowly adapting pulmonary stretch receptors is thought to be a major afferent input inhibiting air hunger; this action occurs at both the brainstem (Kalia 1981) and above (Eldridge and Chen 1992). Air hunger builds throughout the duration of breath hold (Lin et al. 1974; Flume et al. 1994; Nishino et al. 1996). Maximal voluntary breath holds are terminated by a decision to breathe, or to return to the surface and breathe – they are not terminated by uncontrolled respiratory muscles. This decision is normally based on the individual's willingness to tolerate the increasing level of air hunger.

Breathhold training may alter these neural mechanisms, for example modification of chemoreceptor or pulmonary stretch receptor responses. Air hunger would be reduced by reduced response of chemoreceptors or brainstem motor centers to CO_2 (as manifested by reduced ventilatory response, e.g., Masuda et al. 1982; Grassi et al. 1994) or an increased response to lung stretch. Alternatively, repeated exposure to air hunger during breath hold training may lead directly to adaptation of the cortical and/or subcortical networks associated with air hunger generation, or to an ability to tolerate an increased level of air hunger. If any of these hypothesized neural adaptations exist they will reduce the air hunger response to CO_2 . We tested this prediction in a small sample of elite divers.

We measured the air-hunger response of elite breath-hold divers using a hypercapnic stimulus at fixed tidal volume and respiratory frequency. In addition to possible changes in neural mechanisms, competitive breathholders also use techniques that increase O_2 stores and decrease CO_2 stores prior to breathhold (e.g., lung over-inflation and hyperventilation). Our protocol did not allow divers to use the pre-dive maneuvers normally implemented to extend breath holds.

2. Methods

2.1 Subjects

Four competitive breath-hold divers, one woman (Diver 1), and three men, were tested. Diver 1 held several records for depth in breath-hold diving, including a dive of 160 meters. Diver 2 had been breath-hold training for 4 years and was about to enter his first competitive diving season. Diver 3 held records for dynamic apnea (breath-hold while swimming to depth). Diver 4 was the current World record holder for static apnea with both air (8mins 58secs) and oxygen (14mins 12secs). The study was approved by the Human Subjects Committee at Harvard School of Public Health. Subjects gave written informed consent. Subject details are shown in Table 1.

We used an air-hunger test that was similar to that previously used on normal subjects in our laboratory (Banzett et al. 1996) so that comparisons with normals could be made. The divers were tested on two consecutive days. The first day consisted of a practice session and measurement of resting end-tidal P_{CO_2} (PETCO_2). Data on air hunger stimulus-response were

gathered the second day. All studies were performed in the seated position (slightly reclined, thorax 80° from horizontal).

2.2 Psychophysical measurements

Subjects were given the following instructions regarding the sensation to rate: “pay attention to your breathing sensations, in particular, discomfort caused by your urge to breathe; in other words, a feeling of being short of breath, starved for air or out of breath” (Banzett et al. 1996). Subjects scored air hunger at the end of each expiration on a 100mm visual analogue scale (VAS). The bottom and top were labeled ‘None’ and ‘Extreme’ respectively, along with the annotations ‘Slight’, ‘Moderate’, and ‘Severe’ at 25%, 50%, and 75% of scale. They were informed we would reduce the stimulus if they rated ‘Extreme’. Subjects were asked after each experiment to describe the sensation they felt and to point out appropriate descriptors from a given list and indicate which two best described what they felt (see Figure 2 for descriptors). At the conclusion of the second day, subjects were interviewed about the sensations experienced in competitive breath holding and were asked to compare the laboratory experience to breath holding.

2.3 Physiological Measurements

Throughout the practice and test sessions we measured blood pressure every two minutes using an automated arm cuff, oxygen saturation using a finger probe, and three-lead ECG (Cardiacap II, Datex-Omeda). End-tidal gases (P_{CO_2} and P_{O_2}) were continuously sampled at the mouthpiece (Cardiacap II, Datex-Omeda). Tidal volume and respiratory rate were recorded from the output of the ventilator, as were the airway pressure and flow traces. All data were digitally recorded at 40 Hz (Powerlab, AD Instruments, Colorado Springs, CO), apart from the ECG, which was recorded at 200 Hz.

During the test session we also used respiratory inductive plethysmography (Respirace® Ambulatory Monitoring, Ardsley, NY) to measure respiratory movements of the thorax and abdomen. The Respirace® was calibrated using the standard gain ratio method previously described (Banzett et al. 1995).

2.4 Protocol

Practice sessions and introduction to laboratory air-hunger—During the practice session the divers were coached to relax while being mechanically ventilated (Siemens, 900C) via a mouthpiece. Volume-control ventilation was used with triggering threshold set at the maximum (−20 cmH₂O) so the subjects were unable to appreciably increase tidal volume or minute ventilation. As in our previous studies of normal subjects (Banzett et al. 1996; Moosavi et al. 2003), minute ventilation was set at $0.16 \text{ L} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ with a fixed rate of 12 breaths $\cdot \text{min}^{-1}$. Inspired gases were 30% O₂, variable (0-10%) CO₂ and balance N₂. Once the diver was capable of relaxing the respiratory muscles during mechanical ventilation (assessed by inspiratory pressure and expiratory flow traces) we proceeded to introduce the sensation of air-hunger. During mechanical ventilation, inspired P_{CO_2} was increased surreptitiously in steps of 3-4 mmHg at the end of each minute, while ventilation was maintained at the same level. When the subject reached extreme on the VAS (or P_{ETCO_2} reached 65 Torr, our IRB-approved limit), the subject was instructed to take out the mouthpiece and to breathe normally.

Air-Hunger Test (second day)—Subjects were mechanically ventilated with the same parameters used during the practice session. Inspired P_{CO_2} was manipulated so that P_{ETCO_2} was at resting levels. In 5-minute intervals, we increased inspired P_{CO_2} to raise P_{ETCO_2} 5, 10, 15 or 20 mmHg above baseline level in a pseudo-random order. Each period of raised P_{ETCO_2} was followed by a 5-minute period at resting P_{CO_2} (see Figure 1).

During the test, subjects rated their air hunger as they did during the practice session. At the end of the test we repeated the debriefing that had been performed on the practice day with additional questions about how this laboratory experience compared to what the diver felt during a competitive breath-hold.

2.5 Additional Testing

For the measurement of resting PETCO_2 , subjects sat in a comfortable chair in a quiet room with a nasal catheter taped at the nostril. Measurements were made over 30 minutes while the subjects sat reading a magazine. The resting end-tidal PCO_2 was taken as the average of this period.

Hypercapnic ventilatory responses (HCVR) of Divers 3 and 4 were determined using the Read rebreathing technique with modifications introduced by Duffin (Read 1967; Duffin 1990). Briefly, subjects voluntarily hyperventilated for 5 min to reduce their CO_2 stores. Subjects were coached to maintain an end-tidal PCO_2 of 20 mmHg. Immediately following hyperventilation, subjects were instructed to hold their breath after inhalation so as to allow the experimenter to open the rebreathing circuit. The subjects took 3 slow and deep breaths from the rebreathing bag, containing a mixture of 5% CO_2 and balance O_2 , to allow for rapid equilibration of the CO_2 stores. Once equilibration was determined (i.e. once end-tidal/venous PCO_2 equaled inspired/arterial PCO_2) subjects were asked to relax and breathe at a rate and depth that was natural to them. The experiment ended when the subject reached a maximum end-tidal PCO_2 of 60 mmHg.

2.6 Data Analysis

In order to only use data that were gathered during steady state, the air-hunger scores during transitions in PETCO_2 (both increases and decreases) were not included (Banzett et al. 1996). We used the last ten breaths at each PETCO_2 to determine the mean steady-state PETCO_2 and corresponding mean air-hunger score. The resting PCO_2 was taken to correspond to zero air hunger. A linear regression of air hunger and PETCO_2 was performed for each diver as well as for the mean values for the normal subjects (Banzett et al. 1996).

3. Results

3.1 Resting PETCO_2

While Diver 1 had a normal resting end-tidal PCO_2 (39.5 mmHg). Divers 2, 3 and 4 had resting end-tidal PCO_2 somewhat higher than normal (46.0, 50.4 and 46.8 mmHg, respectively). It is very unlikely that these are overestimates, as sampling errors always result in underestimates. It should be noted that Diver 1 appeared to briefly fall asleep during the resting CO_2 measurement; the relevant data were removed from the analysis.

3.2 Quality of Sensations

Like normal subjects, Divers 1, 2 and 4 gave subjective descriptions of an uncomfortable urge to breathe, as reflected in their free descriptions (Table 2), and shown in their descriptor choices (Figure 2). Diver 3, however, denied feeling a sense of urge to breathe, and denied discomfort during repeated and detailed questioning.

When asked to choose from a list, Divers 1, 2, and 4 chose descriptors associated with air hunger as in earlier studies of normal subjects (e.g. (Banzett et al. 1996). There was a notable exception, no diver chose “like breath hold” as a best descriptor. In fact, these divers volunteered comments that the discomfort they felt during this protocol was more unpleasant than that experienced at the break point of competition breath hold. – see further comparisons with breath holding in Discussion.

3.3 Air-hunger Ratings

Divers 1, 2, and 4 reported that they had been rating “discomfort”, “breathlessness”, “need to breathe”, “urge to breathe”; i.e., descriptors fitting the definition of air hunger (Diver 3 is discussed below). The stimulus response relationship between air-hunger and P_{CO_2} of the divers was compared to that of normal individuals in two similar studies (Banzett et al. 1996; Moosavi et al. 2003); these two studies showed similar normative responses in 16 and 11 subjects respectively. The three studies used the same definitions of air hunger and of the scale endpoints. A post-hoc analysis of several studies has shown that air hunger stimulus-response curves for normal subjects are nearly identical given these scale definitions (Lansing et al. 2003). The air hunger ratings of the three divers who experienced air hunger were within the range of the normal air hunger response to CO_2 . The slopes of the air hunger responses of divers 1, 2, and 4 were 7, 5, and 4% full-scale $\bullet$ Torr⁻¹ (compared to normals with a mean slope of 7% full scale $\bullet$ Torr⁻¹, range 5-14% full scale $\bullet$ Torr⁻¹ (Banzett et al. 1996; Moosavi et al. 2003)). The zero air hunger intercepts were 39.2Torr, 43.9Torr and 47.9 for divers 1, 2 and 4 respectively (compared to normals with a mean intercept of 39.8Torr). The r^2 values for the linear regressions of air hunger and $P_{ET}CO_2$ ranged from 0.86 to 0.98. The air hunger responses of these divers are shown with in Figure 3, with comparison to the normal response.

Diver 3, who felt no air hunger throughout the test, elected to rate instead the growing sensation of involuntary muscle contraction (“urge to take over [from the ventilator]...unrelated to discomfort or urge to breathe”). In further questioning he again specifically denied feeling discomfort despite “looking for it”.

Several of the expected non-respiratory symptoms of hypercapnia were reported: Restlessness, salivation, and headache were reported by two subjects; sweating, flushed or warm, numbness, dizziness, visual effects, hearing effects, taste, irritability and heart pounding were each reported by one subject.

3.4 Perceptual experience of prolonged breath hold

When asked to describe the sensations during a competition breath hold, Divers 1, 2, and 4 described the experience as beginning with little sensation, followed by a struggle to tolerate discomfort of air hunger that builds until 80-90% of the breath hold time. They reported using distraction techniques through this portion of the breath hold to overcome air hunger. They reported that air hunger then fades, while signs of declining cerebral function become more prominent. (Diver 3 did not report the buildup of air hunger during breath hold.) All our divers reported using self-checks of cerebral function towards the end of their 6 to 9 min breath holds to avoid loss of consciousness; these checks include tests of cerebral and retinal function such as mental arithmetic and loss of color vision. All 4 divers reported that breath hold is ordinarily terminated due to concern over impending loss of consciousness (which would disqualify them in competition), rather than inability to tolerate air hunger.

3.5 Hypercapnic Ventilatory Response

The HCVR of Divers 3 and 4 showed blunted responses that were shifted rightward. The slope of the ventilation vs $P_{ET}CO_2$ curve was 1.1 and 0.6 L $\bullet$ min⁻¹ $\bullet$ Torr⁻¹ for Divers 3 and 4 respectively, which is lower than the mean in normal subjects studied with this protocol, but falls within the range of normal individuals (Duffin et al. 2000; Vovk et al. 2000; Pandit et al. 2003). The threshold of the ventilatory response (i.e., the end-tidal P_{CO_2} value when ventilation begins to increase) was 53 and 48 mmHg for Divers 3 and 4 respectively, well above the normal subject mean (Duffin et al. 2000; Vovk et al. 2000; Pandit et al. 2003). HCVR of Divers 1 and 2 were not measured. This is consistent with previous data from competitive breath-hold divers (Grassi et al. 1994).

4. Discussion

4.1 Air Hunger responses

The sensory quality, unpleasant urge to breathe, that these three divers described was in all respects similar to the descriptions given by normal subjects under similar conditions. The three divers who experienced air hunger in the laboratory remarked that it was more unpleasant than the sensation they routinely experience at the end of competitive breath hold. The magnitude of the air hunger response to CO_2 can be described by a slope and an intercept. Surprisingly, the slopes of the divers' air hunger responses was not outside the range of normal. Two of these three divers (Divers 2 & 4) had a rightward shift in their air hunger response curves, i.e., air hunger zero intercept and maximum tolerable level were at higher PETCO_2 . Air hunger responses have previously been shown to adapt to prevailing resting PCO_2 (Bloch-Salisbury et al. 1996); such adaptation could explain the change in resting PCO_2 and shift in air hunger response in these two divers.

Our data from two divers (3&4) shows that the ventilatory response to CO_2 occurs at a higher PETCO_2 compared to normals, while the slopes of their responses were within the normal range. Thus, the atypical air hunger response of Diver 4 is adequately explained by a change in chemoreceptor/brainstem response. Previous studies have also shown that the ventilatory response to CO_2 in divers is "blunted" (Masuda et al. 1982; Grassi et al. 1994), but there is insufficient information to determine whether this was a reduction in slope or a right shift of intercept.

4.2 Diver 3: Absence of air hunger

Diver 3 denied experiencing discomfort despite insistent questioning and clear understanding of the task. Although only a single example, Diver 3 is an intriguing case. The only subjects who have previously been shown to lack perception of air hunger under these conditions are those with congenital central hypoventilation syndrome ('CCHS' or 'Ondine's curse'); CCHS subjects fail to breathe during sleep, lack any ventilatory response to hypercapnia, and can hold their breath without discomfort (Shea et al. 1993). Diver 3 reported that as an infant he had been taken to the hospital after his parents observed an apneic episode, and that as an adult he has been observed to cease breathing for up to one minute during sleep. Diver 3, however, did not lack the reflex ventilatory response to CO_2 , as evidenced both by his HCVR and by the airway pressure fluctuations caused by involuntary contractions of his respiratory muscles during the air hunger test. He was aware of these contractions, and his ratings of their intensity were proportional to PETCO_2 , but they were not a source of discomfort. This disjuncture between respiratory center drive and air hunger suggests that either the ascending pathways from medulla or cortical areas responsible for appreciation of air hunger are dysfunctional (Eldridge and Chen 1992; Evans et al. 2002).

4.3 Comparison of laboratory air hunger test with competitive breath holding

During breathhold arterial PCO_2 rises at about 2-3 torr per minute in completely relaxed humans (Frumin et al. 1959); concomitant fall in PO_2 further stimulates air hunger. Improved air hunger tolerance alone does not seem sufficient to explain the extraordinary breath hold times of these divers during 'static apnea', but the interview data provide further information. The divers all reported to us that they hyperventilate for at least two minutes; PETCO_2 of 15 Torr has been observed in these divers (Ferrigno et al, personal communication). The divers also reported they distend their lungs beyond TLC through glossopharyngeal inspirations (Lindholm and Nyren 2005; Seccombe et al. 2006; Loring et al. 2007); this provides some additional O_2 reserve, and presumably stimulates pulmonary stretch receptors. Lung volume was controlled throughout our present study, so divers were unable to take large breaths and achieve relief from air hunger.

All of the divers in the present study exceed 6 min breath hold; breath holds of this length result in $P_{ET}O_2$ of 26 Torr or less (Overgaard et al. 2006); a level expected to impinge on cerebral function, cited by all divers as the proximal reason to end breath hold. Air hunger is therefore not the determining limit. One diver, however, reported having performed breath holds after breathing 100% O_2 (Apneamania 2006). In this case, the breath hold duration was longer (14 min 12 sec) and was indeed terminated due to air hunger of similar intensity and unpleasantness as in our laboratory test, rather than by loss of cerebral function.

4.4 Summary

The competitive breath-hold divers we studied showed air-hunger response 1) whose slope ranged from the mean to the lower bound of the range of normal slopes, 2) whose threshold relative to resting $P_{ET}CO_2$ was normal. (The resting $P_{ET}CO_2$ in most of the divers was elevated.) The slight differences between the air hunger response of these divers and that of normal subjects is paralleled by the differences in ventilatory response. These findings are consistent with the hypothesis that the major excitatory input to air hunger is respiratory center activity (Wright and Branscomb 1954; Banzett et al. 1989). They also show that even intensive training, repeated exposure, and selection of participants have essentially no effect on the relationship between the excitatory input and resultant perception; i.e., cortical mechanisms of air hunger generation or tolerance have not been altered. This stands in contrast to the perception of pain; prior conditioning with pain stimuli can lead to endogenous analgesia that reduces pain sensation on subsequent exposures (Price 1999). While adaptively diminished pain perception may have selective advantage, we speculate that adaptively diminished air hunger perception would put the animal at mortal risk.

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Figure 1.

Data from an air hunger test (Diver 2). The figure shows one 5 minute increase in PETCO_2 causing a rise in air hunger followed by a recovery when PETCO_2 was returned to baseline levels.

Figure 2.

Descriptors chosen as best 2 for the air hunger experiment (Session 2) shown as filled bars. Open bars show descriptors given by normal subjects in earlier study (Banzett et al. 1996). Subject 3, in contrast to all other subjects chose no descriptors, and denied discomfort (thus total % for divers adds to 150 rather than 200%).

Figure 3.

The air-hunger response of competitive breath-hold divers and values for normal subjects (solid line) (Banzett et al. 1996). Because D3 reported that he felt no discomfort throughout the test, his ratings are not shown (see text). The dotted lines represent the mean normal subject response ± 2 SD. Open symbols represent resting $P_{ET}CO_2$. The relationship between air-hunger and P_{CO_2} of the divers was compared to that of normal individuals (Banzett et al. 1996).

Table 1
Subject and ventilatory response details for both divers and the group of normal subjects. Best breath holds are given from competition and practice (latter in parentheses).

Subject	Age $\pm$ SD (years)	Height (cm)	Weight (kg)	Resting $P_{ET}CO_2$ (Torr)	Best breath hold (sec)
Normals	31.3 $\pm$ 5.2SD	171 $\pm$ 8SD	64.8 $\pm$ 8.2SD	39.1 $\pm$ 2.2SD	
Diver 1 F	32	168	56	39.5	(376)
Diver 2 M	30	182	70	46.0	(405)
Diver 3 M	28	193	79	50.4	538* (608)
Diver 4 M	28	178	74	46.8	486 (495)

* Current World record.

Table 2

Volunteered descriptions of sensations during air hunger test, Session 2

Diver 1	"Not getting enough breath." "Wanted to breathe deeper and faster." "Rating how uncomfortable with breathlessness and need to breathe."
Diver 2	"Needed to breathe. Not getting enough air." "Not like static [breath hold] because I am breathing." "Rating how much I needed to breathe."
Diver 3	"Was feeling how much my body wants to take over during inspiration." "Felt sleepy and inattentive." "Rating urge to take over, unrelated to discomfort or urge to breathe - Felt in diaphragm" "It was not discomfort. I really was looking for discomfort. It was the need to focus on the task of controlling breathing."
Diver 4	"short of breath, air hunger, tense --not fearful." "Rating urge to breathe (indicated substernal location)."