Effect of Low-Concentration CO_2 on Stereoacuity and Energy Expenditure

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Background: Low-concentration CO_2 commonly exists in our living environment in such locations as airplanes and cars. Its effect on visual performance and energy metabolism (through O_2 uptake) has not been well studied, although several studies have shown that high-level CO_2 (6–10%) significantly impaired visual performance. ***Hypothesis:*** We felt that breathing CO_2 might also interfere with the energy expenditure pathway, partly due to the reduced O_2 fraction. Thus, we studied the effect of low-concentration CO_2 (2.5%) on human visual stereoacuity and energy expenditure. ***Methods:*** Computer-controlled Random Dot Stereograms and psychometric function were used for stereoacuity tests. A whole-room indirect calorimeter allowed for the accurate measurement of energy expenditure, and also served as a good testing environment. ***Results:*** Of 10 subjects tested, 8 had a slight increase in resting energy expenditure after exposure to 2.5% CO_2. The increase ranged from 0.4–6.1% ($p = 0.087$, paired *t*-test). In stereoacuity tests, the psychometric function curves of all three subjects tested shifted to the right when breathing 2.5% CO_2 and returned to baseline 2 h after breathing fresh air. Stereoacuity value, which is the reciprocal of stereoscopic threshold, was significantly lower ($p < 0.01$, 2-tailed z score test) after CO_2 exposure for all subjects tested. ***Conclusion:*** We conclude that CO_2 levels as low as 2.5% can cause temporary reduction in human stereoacuity, and also cause a persistent but small increase in energy expenditure.

IN MODERN LIFE, an increasing number of people are confined more frequently in enclosed environments with several other people, such as in an aircraft, a space shuttle module, a submarine, or a passenger car. The elevated CO_2 concentration in these environments may interfere with visual performance such as reading, detection of moving objects, and recognition of patterns. A subject's oxygen consumption and energy expenditure (metabolic rate) may also be elevated by the change in inspired air. This could impair the ability to perform strenuous activities, or impose concerns in special situations, such as in a space shuttle where the amount of oxygen and food storage is limited.

Animal studies have suggested that breathing higher than ambient CO_2 resulted in several changes in functions of the visual systems, such as the increase in latencies of electroretinogram (ERG) and evoked potentials (EP) when challenged with flash-light and pattern-reversal stimuli (9,14). In studying the response of cortical neurons of cats to visual stimuli, a significant reduction in the number of active neurons was found when the expired pCO_2 exceeded 4.5% compared with the normal range of 3.7 ~ 4.1% (Sun M, Bonds AB. Unpublished data.)

A few studies of the effect of CO_2 on human visual performance were conducted several decades ago, including scotopic vision, absolute visual threshold, and color vision (2,18,19). In general, results from these studies showed a reduced visual performance associated with the increase in CO_2 concentration. However, most of these studies used higher than normal CO_2 concentrations (5–8%). Almost all these studies were conducted in 1930's–1960's, with limited accuracies. We feel it is necessary to investigate the effects of moderate CO_2 concentration that is similar to the environments mentioned above on visual performance (such as stereoacuity).

The elevated tension of inspired CO_2 may also disturb various metabolic pathways and alter fuel oxidation and body energy expenditure (EE). We have not found conclusive data to support or oppose this hypothesis in the literature. Probably the main reason is the technical difficulties in measuring subtle changes in EE, as will be explained in the method section. We have not found any study done to investigate the influence of low-concentration CO_2 on energy expenditure.

In this paper, we have two specific aims: a) to determine if the elevated environmental CO_2 influences human stereoacuity; and b) to determine if this elevated tension of inspired CO_2 influences body oxygen consumption and EE. The testing environment was made as comfortable as possible for subjects and the ambient CO_2 tension was kept relatively low (2.5%) during the experiments in order to obtain CO_2 effects under situations that are similar to actual enclosed environments.

METHODS

Subjects: We used only small samples of subjects in these preliminary experiments. Healthy adult subjects who are employees of the university (four male, six female; age, 34 ± 8.4 yr; height, 166 ± 9.1 cm; weight,

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67.2 ± 12.4 kg) volunteered in these experiments, which is part of a NIH sponsored study that has been approved by The Committee for the Protection of Human Subjects at Vanderbilt University (Assurance no. M1363). Informed consent was obtained before subjects participated in the experiment. All subjects participated in test 2 (the CO_2 vs. EE test). Among them three subjects (two male, one female) participated in test 1 (CO_2 vs. stereoacuity). These subjects had normal or corrected-to-normal visual acuity. Subjects participating in the stereoacuity tests were naive to the psychophysical tasks, which involved force-choice judgements with randomized order of conditions and criteria; this minimized expectation effects. All subjects were non-smokers, and did not have anemia or polycythemia.

Testing site: All the tests were conducted in an environmental room (3.4m × 2.5m × 2.4m = 20.4 m^3) which is part of the whole-room indirect calorimeter at Vanderbilt University. The room is airtight and large enough so that the expired air from a subject will not interfere with the desired ambient air components. This is further assured by additional fans that increase air mixing and circulation. The room also serves to isolate sound and light disturbance and to maintain a consistent and comfortable testing environment. Carbon dioxide is introduced to the fresh air inside the room prior to subject's entrance in order to bring ambient CO_2 in the room to 2.50%. This dilutes O_2 to approximately 20.4%, which is still close to fresh air O_2 (20.95%). Both CO_2 and O_2 are monitored by the Uras 3G and Magnos 4G differential gas analyzers (Uras 3G: 0 ~ 4% CO_2 range, Magnos 4G: 19 ~ 21% O_2 range; errors ± 0.02% for both instruments, Hartmann & Braun Instruments, Frankfurt, Germany). The CO_2 concentration is clamped at 2.5% throughout the experiment by a computer that reads CO_2% from the gas analyzer and controls the speed of a fan that purges the air out of the room to remove CO_2 produced by the subject.

O_2 consumption and energy expenditure measurement: One of the most accurate techniques for measurement of human energy expenditure is the whole-room indirect calorimeter (8,17). In humans, EE can be calculated using the following equation (6):

$$EE = \alpha \dot{V}O_2 + \beta \dot{V}CO_2 + \gamma N \qquad \text{Eq. 1}$$

where VO_2 is the oxygen consumption and VCO_2 carbon dioxide production in liters, and N is urinary nitrogen in grams. The parameters α, β, and γ are constants determining the energy equivalents of oxygen, carbon dioxide, and nitrogen. They change slightly depending on different diet. For a typical western diet, $\alpha = 3.866$, $\beta = 1.20$, and $\gamma = -1.41$. In an indirect calorimeter system, a gas-collecting system is required for collecting expired air from subjects for measurements of VO_2 and VCO_2.

We built a whole-room indirect calorimeter in 1989 for EE and substrate (carbon hydrate, fat, and protein) oxidation analysis (17). The gas exchanges of a subject in a calorimeter room (an air-tight room) are calculated according to the law of mass conservation. For any gas (G) to be measured, the rate of production V_G for the subject inside a room is

$$V_G = V_oF_{oG} - V_iF_{iG} + V\frac{dF_{oG}}{dt} \qquad \text{Eq. 2}$$

where the item $V_o \cdot F_{oG}$ is the product of outlet flow from the room and its gas concentration, $V_i \cdot F_{iG}$ the inlet flow times its gas concentration, and V the volume of the room. The first and second items in Eq. 2 are the outlet gas from the room and the inlet gas to the room, and the last item is the net change of the gas inside the room. Air is purged out of the room by a computer-controlled fan, and O_2 and CO_2 concentrations are measured by gas analyzers, as described previously. Flows are measured by mass flowmeters (Teledyne Hastings-Raydist, Hampton, VA). These parameters, together with temperature, barometric pressure, and humidity, are fed to an IBM PC compatible computer (80486-33, Mediage Co., Walnut, CA) through a high resolution (16-bit A/D converter, Analogic, Wakefield, MA) data acquisition system. A special multi-channel air sampling system was designed to ensure an even sampling of the expired gas by the subject.

Temperature, barometric pressure, and humidity of the room are controlled or monitored (temperature controlled within 22.5 ± 0.15°C by multiple sensors, pressure measurement range 500.0–765.0 mm Hg, errors within ±0.15 mm Hg, and vapor pressure 8–16 mm Hg, within ±0.2 mm Hg on a 24-h basis all year around). Data are collected by the on-line computer 60 times per second, and the computed EE and other parameters are stored in 1-min intervals. The accuracy of these measured parameters were evaluated by 56 propane and ethanol combustion tests under various conditions. The combustion process consumes oxygen and produces carbon dioxide and vapor similar to that of human breathing. VO_2 and VCO_2 can be accurately quantified during combustion in a controlled manner through their molecular weight. Results showed that the accuracy in VO_2 and VCO_2 measurements by our whole-room calorimeter were 99.4 ± 0.45% and 99.7 ± 0.53% (mean ± SD), respectively indicating this calorimeter is among the most accurate ones in the world.

Stereoacuity measurement: Human eyes are arranged with a lateral separation. This arrangement causes a slight difference (binocular disparity) in the relative positions between images on the left and right retina when we view two objects at different distances. The perception of relative depth from binocular disparity is called stereopsis, which is crucial in obtaining an awareness of distance, shape, and solidity of objects. Stereoacuity corresponds to the smallest binocular disparity at which a subject can reliably perceive depth.

Apparatus and stimuli: The details of our methods for stereoacuity measurement can be found elsewhere (4,20,21). Briefly, in stereoacuity tests, stimuli were random dot stereograms (RDS's) generated by a Macintosh IIsi computer and displayed on a 16-in gray-scale monitor (60 Hz frame-rate; 680H × 420V pixel resolution; P104 phosphor). **Fig. 1** shows an example of the random dot stereograms used in our experiments. The left and right images in the upper part of Fig. 1 are identical random-dot textures except for a rectangular area in the bottom of images, where random-dot textures are also identical but shifted relative to each other in the horizontal direction. Subjects viewed these displays through a mirror stereoscope, allowing each eye to see only one image on half of the screen. When these two images are fused

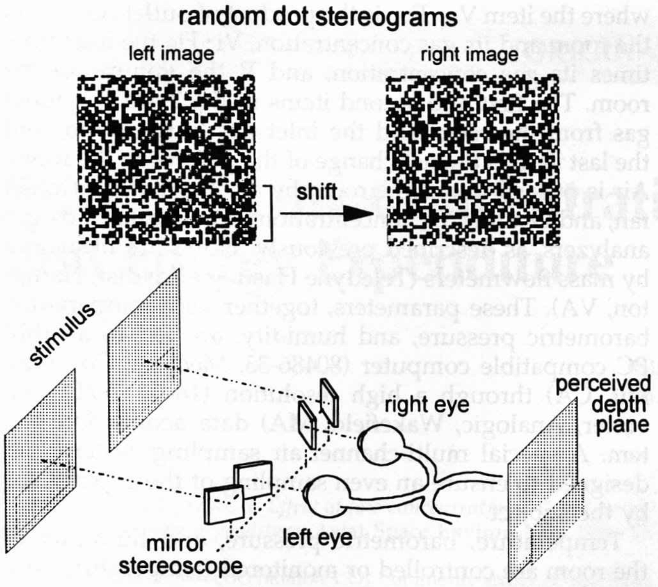

Fig. 1. Principle and experiment setup for stereoacuity tests. Fused stereograms were set for parallax disparity and depth perception at different thresholds. See text for more details.

through the mirror stereoscope, a rectangular plane defined by horizontal disparity can be perceived in a vivid depth above the background, as shown in the lower part of Fig. 1. Each half-image of the stereograms consisted of 100×100 white and black dots, with each dot being 2×2 pixels. The density of white and black dots was 50%, respectively. At a viewing distance of 2.45 m, the video screen subtended $5.84 \times 3.61^\circ$ of arc. Each pixel at this viewing distance subtended 30.91 s. Each half-image in the stereograms subtended $1.72 \times 1.72^\circ$. The shifted area that formed depth plane subtended $1.60 \times 0.52^\circ$. Multiple versions of stereograms were used in the experiments to avoid cues of micropattern of images.

Testing procedures: Before each test, the subject was required to sit quietly in a comfortable chair inside the room for 30 min and instructed to relax. This served several purposes: a) to enable the subject to adapt to the different gas concentrations; b) to adapt to the dark environment; c) to rest for the test of resting energy expenditure; and d) to familiarize the subject with the testing site. Subjects were requested not to eat or exercise 4 h prior to testing to avoid the synergistic effects of food and exercise on resting EE.

During resting EE tests, subjects were instructed to sit motionlessly for 30 min. The chair was placed inside the room calorimeter on top of a large force platform ($2.5 \times 2.5\ m^2$, sensitivity range: $0.01 \sim 800$kg) that measures physical movement of the subject (16). The elevated EE due to minor activities during the test, if any, was removed from the measured EE to guarantee the accuracy in resting EE measurement. The subject was requested to repeat the test if there existed an accountable amount of physical activities.

A 2-alternative forced-choice (2AFC) procedure was employed to determine stereoacuity. In a 2AFC task, the location of a depth plane was randomized (top vs. bottom) from trial to trial. A subject must identify one spatial location from two possibilities at which a depth plane could be perceived. On each trial of the 2AFC procedure, a pair of stereograms was presented for 167 ms to the subject. A subject's task was to determine the location of depth plane (top or bottom) by pressing one of two keys. For each trial, one of six disparity values was randomly selected. At very small disparity values, the subject may not be able to determine the location of the depth plane. In this case, the subject was forced to guess, and the correct rate was close to 50%. At very large disparity, on the other hand, the subject could make 100% correct judgment. Other intermediate depths would have a correct rate between $50 \sim 100\%$.

The experiment was divided into four sessions to reduce the effect of fatigue. Each session consisted of 120 trials, with 20 for each of 6 disparity values. For each subject at the given CO$_2$ concentration, a total of 480 trials were used to generate a psychometric function, which is a plot of percent correctness in 2AFC against disparity values, as shown in **Fig. 2.** The disparity value corresponding to a 75% correctness is defined as the stereoscopic threshold. Three experiments: one baseline with fresh air, one with 2.5% CO$_2$, and one repetitive test after subjects had breathed fresh air for 2 h post CO$_2$ test, were performed for each of three subjects. Throughout this paper, the result obtained under the term *fresh air* refers to the result obtained by combining the fresh air data before and 2 h after the end of 2.5% CO$_2$ exposure.

RESULTS

Resting energy expenditure: **Fig. 3** shows the resting energy expenditure of 10 subjects who spent 2 1-h sessions inside the whole-room calorimeter. Data represented by the hatched bars were obtained when subjects breathed fresh air; those by the solid bars were obtained under 2.5% CO$_2$. During each experiment, 30 resting EE measurements were collected at 1-min intervals after subjects had stayed in the room calorimeter for 30 min. The error bars in Fig. 2 were the standard errors of the 30 measurements. Of the 10 subjects, 8 had a slight increase in resting EE during 2.5% CO$_2$ breathing, while the remaining 2 had a slight decrease in resting EE. During CO$_2$ exposure, the averaged resting EE increased from 76.5 ± 5.4 W (mean ± SD) to 78.2 ± 5.6 W. The highest increase for one subject was from 94.7 to 100.5 W, a 6.1% increase. However, paired *t*-test showed that the difference was close to but did not reach 0.05 significance level ($p = 0.087$).

Stereoacuity: Fig. 2 shows the psychometric functions from stereoscopic experiments for three subjects in fresh air ($pCO_2 < 0.2\%$) and in 2.5% CO$_2$. Each open circular symbol in Fig. 2 represents an averaged percentage of correctness from 80 2AFC trials at a given disparity in fresh air, and each solid dot was obtained with 80 additional trials in a 2.5% CO$_2$ environment was presented. When the disparity in RDS stimulus equals zero, the percent correctness in a 2AFC should be close to 50%. At zero disparity stimulus, the data in Fig. 2 were truncated to 50% if they were lower than 50%. The lowest value was 45% and the highest was 56% in these tests, indicating the variation in percent correctness in these stereoacuity tests was approximately 5% or less. From Fig. 2 it can be seen that for all three subjects, there is no significant difference in stereoacuity between fresh

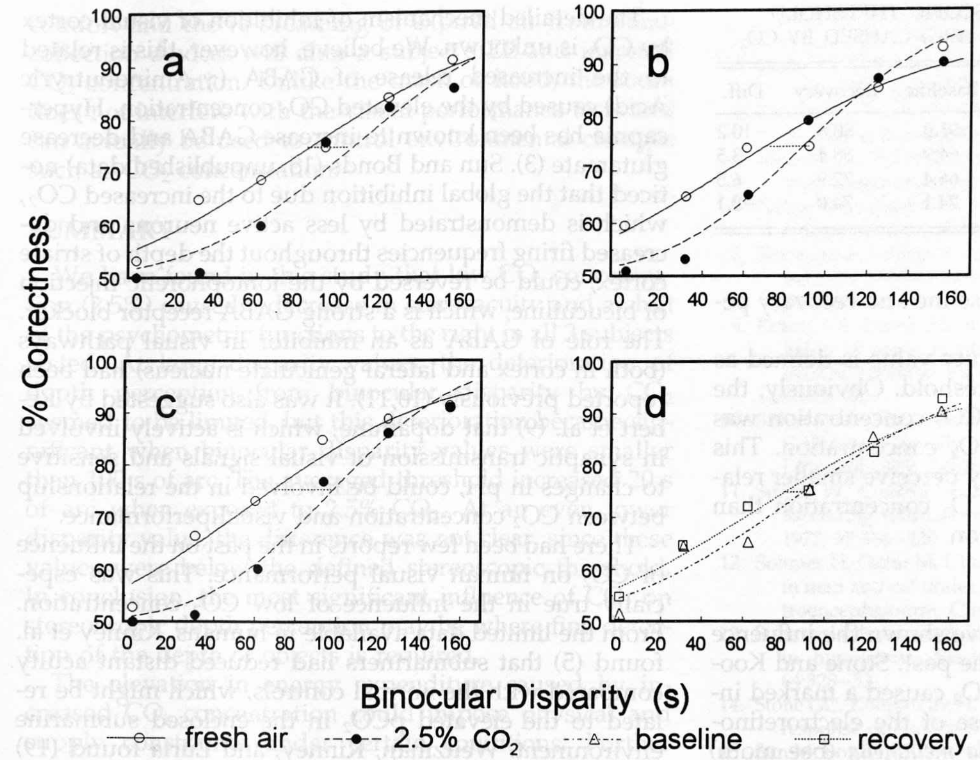

Fig. 2. Subjects' psychometric functions of stereoacuity tests. Results show that the curves tend to shift to the right after breathing 2.5% CO_2 (dashed lines vs. solid lines in a, b, and c). The stereoscopic threshold also increased (see the dotted horizontal line). In d, on the contrary, the threshold decreased when subject data after fresh air recovery was compared with the baseline.

air and 2.5% CO_2 tests when the disparity value is greater than 120 s of arc. When the disparity value decreases so that the 2AFC task becomes more difficult, an apparent separation in % correctness appears between the fresh air and CO_2 tests. The largest separation is found to be at 30 s. At this point, the difference in percent correctness reaches 13.8%. The differences become smaller again (averaged 3%) at zero disparity which is lower than the stereoscopic threshold.

Theoretical and experimental studies showed that subjects' responses (i.e., a psychometric functions) in a 2AFC procedure should be closely approximated by a cumulative Gaussian curve (1). In order to obtain the stereoscopic threshold, the data points were fitted by cumulative Gaussian curves to form psychometric functions using a nonlinear curve fitting (7). The disparity value corresponding to 75% correct rate on the fitted psychometric function in Fig. 2 is then taken as the measure of stereoscopic threshold. The solid lines in Fig. 2 (a, b, and c) represent subjects' psychometric functions when breathing fresh air, while the dashed lines are the psychometric functions when breathing 2.5% CO_2.

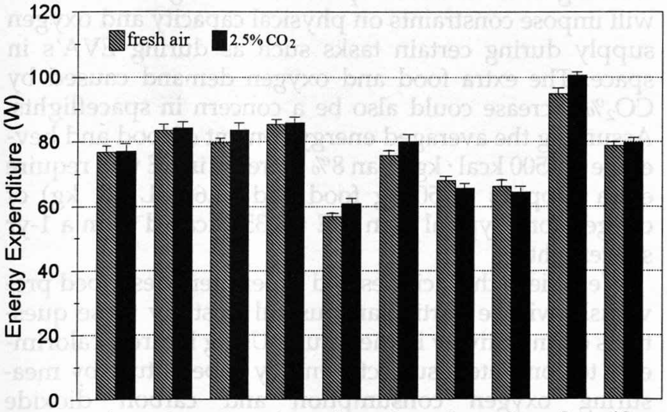

Fig. 3. Difference in resting EE (energy expenditure) of 10 subjects who breathed fresh air (hatched bar) and 2.5% CO_2 (solid bar) inside a whole-room calorimeter. Most of the subjects had a slight increase in EE during CO_2 test.

For all subjects tested, the psychometric function curve shifted to the right after breathing with higher CO_2 concentration. From Fig. 2, it can be seen that stereoscopic thresholds under 2.5% CO_2 were higher than those under fresh air for all three subjects tested. The differences between these 2 thresholds are plotted as an horizontal dotted line in Fig. 2. To validate the reproducibility of the testing method, subjects were given an additional test which was identical to those with baseline fresh air and 2.5% CO_2 but performed after subjects had been breathing fresh air 2 h post CO_2 exposure. Results obtained during baseline period and 2 h after the end of CO_2 exposure of a subject are given in Fig. 2d. The curve shifted slightly leftward during recovery, suggesting some degree of learning/adaptation might exist. This, however, further confirms that CO_2 exposure increases the stereoscopic threshold. We calculated stereoscopic thresholds of three subjects under all conditions, and put them into Table I, which clearly shows the above conclusions. We applied the statistical analysis to the stereoscopic thresholds to test if the differences in stereoscopic thresholds between fresh air and 2.5% CO_2 and between baseline and recovery were significant. Result from the 2-tailed z scores of the means of 2 cumulative curves indicated that the differences in thresholds between fresh air and 2.5% CO_2 were significant ($p < 0.01$) for all three subjects. On the other hand, no significant

TABLE I. CHANGES IN STEREOSCOPIC THRESHOLD (VIEWING ANGLE IN SECONDS OF ARC) CAUSED BY CO_2.

	Fresh air	2.5% CO_2	Diff.	Baseline	Recovery	Diff.
Subject 1	86.4	107.5	21.1	91.0	80.8	−10.2
Subject 2	67.7	91.1	23.4	64.9	68.4	3.5
Subject 3	70.1	98.1	28.0	66.4	72.9	6.5
Mean	74.7	98.9	24.2	74.1	74.0	−0.1

difference was found between baseline and recovery periods for these subjects.

As mentioned above, stereoacuity value is defined as the reciprocal of stereoscopic threshold. Obviously, the stereoacuity value with normal CO_2 concentration was higher than that with higher CO_2 concentration. This suggests that human subjects may perceive smaller relative depth in air with normal CO_2 concentration than that with higher CO_2 concentration.

DISCUSSION

A number of investigations have shown the influence of CO_2 on the visual system in the past. Stone and Koopowitz (14) demonstrated that CO_2 caused a marked increase in latency and time course of the electroretinogram (ERG) of the moth *Galleria mellonella* (bee moth) during flash-light stimuli. It also abolished the phasic negative component of ERG. The authors suggested that the changes in time course and latency of ERG were probably due to the shifting of pH in the eye, while the abolition of the phasic negative component was due to a CO_2-specific reaction. In their studies of multiple sensory evoked potentials (EP) in Long-Evans rats, Rebert et al. (9) found that after breathing $8 \sim 16\%$ CO_2 for 20 min, the animals had significant increases in the latencies of several EP components (P1, N2, P2) of pattern-reversal evoked potentials. The latencies of N2, P3, P4, and especially N4 of the flash-light evoked potentials also increased at these CO_2 concentrations.

Similar results were found in single neuron recordings of cats' visual cortex (area 17) while animals were exposed to drifting sine-wave gratings stimuli (Sun M, Bonds AB. Unpublished data.) An apparent reduction in the number of active neurons a micro-electrode could encounter during one complete penetration (2.5 mm) of visual cortex was found when the expired P_{CO_2} exceeded 4.5%, compared with the normal range of $3.7 \sim 4.1\%$. The firing frequency responding to drifting sine waves with various frequencies, orientation and contrast also decreased for the neurons encountered at higher P_{CO_2}, suggesting the existence of a global inhibition. Considering that the activation of an action potential and thus the firing rate are controlled by the membrane potential, which is in turn further regulated by the ion channels across the membrane and the ionic balance, the disturbance of inter- or intracellular pH values/cell metabolism by CO_2 could certainly interfere with the neuronal activities and thus the visual information processing. This had been directly and indirectly supported by several studies (9,12,13). These studies also indicated that CO_2 inhibits visual functions at different sites (retina and visual cortex) and on various species, at least when the concentration is relatively high (8–16%).

The detailed mechanism of inhibition of visual cortex by CO_2 is unknown. We believe, however, this is related to the increased release of GABA (γ-Aminobutyric Acid) caused by the elevated CO_2 concentration. Hypercapnia has been known to increase GABA and decrease glutamate (3). Sun and Bonds (15; unpublished data) noticed that the global inhibition due to the increased CO_2, which is demonstrated by less active neurons and decreased firing frequencies throughout the depth of striate cortex, could be reversed by the iontophoretic injection of bicuculline, which is a strong GABA receptor blocker. The role of GABA as an inhibitor in visual pathways (both in cortex and lateral geniculate nucleus) had been reported previously (10,11). It was also suggested by Rebert et al. (9) that dopamine, which is actively involved in synaptic transmission of visual signals and sensitive to changes in pH, could be involved in the relationship between CO_2 concentration and visual performance.

There had been few reports in the past on the influence of CO_2 on human visual performance. This was especially true in the influence of low CO_2 concentration. From the limited data available in humans, Kinney et al. found (5) that submariners had reduced distant acuity compared with the normal controls, which might be related to the elevated pCO_2 in the enclosed submarine environment. Weitzman, Kinney, and Luria found (19) a moderate reduction in scotopic and color sensitivities when one subject breathed 1.5% and 3.0% CO_2 compared with fresh air. To our limited knowledge, we have not found reports concerning the influence on stereoacuity of low CO_2 concentration environment that is often encountered in our daily life.

The averaged resting energy expenditure also increased slightly (2.8%, or $43.2\ \mathrm{kcal \cdot d^{-1}}$) during CO_2 exposure. In general, this slight increase during resting period may not have significant meanings. However, the increase would be much higher during exercise or physical activities. A moderate exercise or physical activity such as climbing stairs will increase energy expenditure to $400\% \sim 650\%$ of the resting EE (17). The extra energy and oxygen requirements could be even higher if the inspired CO_2 concentration is greater than 2.5% when working in an enclosed space or wearing a mask. This will impose constraints on physical capacity and oxygen supply during certain tasks such as during EVA's in space. The extra food and oxygen demand caused by $CO_2\%$ increase could also be a concern in spaceflights. Assuming the averaged energy content of food and beverage is $1500\ \mathrm{kcal \cdot kg^{-1}}$, an 8% increase in EE will require extra supplies of 50 kg food and 14,600 L (21 kg) of oxygen for a typical man (EE = $2350\ \mathrm{kcal \cdot d^{-1}}$) in a 1-yr spaceflight.

We believe the facilities and experiment described previously will be particularly useful to study these questions quantitatively in the future. Using indirect calorimetry to compute a subject's energy expenditure by measuring oxygen consumption and carbon dioxide production is significantly faster (<1 min) than the direct calorimetry, which measures body heat dissipation. This enables quantifying dynamic EE requirement during work/exercise. Employing a room instead a facial mask or a mouth piece to collect expired gas from subjects makes the experiment much more comfortable. The discomfort and the re-breathing of expired air from small collection devices will alter a subject's EE and inspired CO_2 concentration. Unlike the mask or hood, the room does not interfere with the visual performance tests and can actually be used to control environmental changes such as CO_2 concentration.

SUMMARY

We have found in this study that low CO_2 concentration (2.5%) caused a decrease in stereoacuity and a shift of the psychometric functions to the right in all 3 subjects tested. At large disparity values, the deterioration of depth perception from binocular disparity by CO_2 seemed to be limited, but this deterioration became significant when binocular disparity values were smaller than 100 s of arc. The averaged threshold increased 20 s of arc when exposed to 2.5% CO_2. At an even lower disparity value, the difference was not clear, since these values were below the defined stereoscopic threshold. In conclusion, the most significant influence of CO_2 on stereoscopic depth perception may be where fine detection of the depth of objects is required.

The elevation in energy expenditure caused by increased CO_2 concentration could impose physical and supply constraints under certain conditions. Further studies are needed to quantify the increase in EE during various work/exercise loads under various CO_2 concentrations.

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