The Effect of Moderately Increased CO_2 Concentration on Perception of Coherent Motion

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Background: Several studies have shown that some aspects of vision are impaired when exposed to higher than normal CO_2 concentrations in air. The effect of moderately increased CO_2 concentration on coherent motion perception, however, has not been studied. ***Hypothesis:*** Studies in neurophysiology and cell biology have provided evidence that higher than normal CO_2 concentration in air affects cell activities from the retina to the cortex, including the V1 area in the visual cortex. We predicted that motion perception may be impaired by moderately increased CO_2, since the V1 area is a gateway for visual motion information processing. The purpose of the present work was to investigate the effect of 2.5% CO_2 concentration in air on coherent motion perception. ***Methods:*** Random dot cinematograms were generated by a computer and served as visual stimuli. A whole-room indirect calorimeter was used for the accurate measurement and control of CO_2 concentration in air, and served as the experimental environment. A two-interval-forced choice (2IFC) psychophysical procedure was employed to obtain psychometric functions. ***Results:*** For all three subjects, psychometric functions were shifted to the right when exposed to 2.5% CO_2 in breathing air, compared to those using fresh air. ***Conclusion:*** This finding implies that human ability in detecting coherent motion can be temporally impaired when CO_2 concentration in air is raised to 2.5%.

AN INCREASING NUMBER of people are frequently confined in enclosed environments such as passenger cars, aircraft, space shuttles. Normal atmospheric CO_2 levels are about 0.03%. However, in many enclosed environments without a good ventilation, CO_2 levels can reach 5% or higher. The question we address here is whether human motion detection, an important visual performance, is impaired by moderately increased CO_2 concentration in air.

A number of studies have investigated the effects of carbon dioxide (CO_2) on human visual performance. Generally, visual performance was impaired with acute exposure to air with a CO_2 concentration 5% or higher or chronic exposure to air with a lower CO_2 concentration (1.5%). For example, five decades ago, Wald et al. (15) showed that absolute visual threshold noticeably increased when CO_2 in air was increased to 5%. Shortly after, Alpern and Hendley (1) found that breathing a mixture of 7% CO_2 and 93% O_2 caused a decrease in critical flicker fusion. In 1969, Weitzman, et al. (16) investigated the effects of CO_2 on visual performance when the subject was repeatedly exposed to the inspired air containing higher than normal CO_2 content. They examined the chronic effects of CO_2 on various visual performance functions, such as visual acuity, lateral and vertical phoria, depth perception, area of visual field, color sensitivity, night vision sensitivity, and amplitude of accommodation. Their results showed that only scotopic sensitivity and color sensitivity (green) were impaired when the CO_2 content in air reached 1.5%. Recently, Perez and Silverman (8) reported a case study in which a 31-yr-old man worked in a dry ice factory and was poisoned by CO_2. His ability in visual-motor coordination was impaired. More recently, we reported that human stereoacuity was reduced by 2.5% CO_2 in air (13).

Few studies, however, have addressed the CO_2 effects on human motion perception. Motion offers useful information for visual perception. For example, motion informs us about direction and speed of a moving object, while speed and direction, in turn, guide our interactions with the environment. Motion can also offer information about the changes in our own positions in three-dimensional space. The combination of information about the direction and speed of other moving objects as well as about ourselves enables us to avoid collisions. Finally, motion can be used to segregate objects from their background and to specify three-dimensional shape and relative depth.

However, in many situations, such as in passenger cars, space shuttles, and airplanes, people have to live in an enclosed spatial environment where the CO_2 concentration may be higher than normal, and where motion perception plays an important role in people's activities and human-environment interactions. A number of studies (2,9,12) showed that cell activities can be affected by higher than normal CO_2 concentration in air from the retina to the cortex, including the V1 area, which is a gateway of motion information processing in the visual system (5,6). We, therefore, predicted that the elevated CO_2 concentration may impair human ability to perceive

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motion, and therefore hinder the completion of critical tasks (e.g., finding moving targets) in the situations mentioned above.

In this study, we investigated the effect of moderately increased CO_2 concentration (2.5%) in air on coherent motion detection. We used a task that could measure the ability of the human visual system to discriminate coherent motion from random motion. Motion coherence can be perceptually defined as the degree to which elements move together. Physically, motion coherence depends on the correlation between patterns distributed over time and space (3,4). If a motion is completely coherent, the correlation between patterns distributed over time and space is one (e.g., the motion in a movie). If a motion is completely random, the correlation between patterns distributed over time and space is zero (e.g., the motion of dynamic snow on a TV screen). A subject's percentage of correct responses in discriminating coherent motion from random motion can be taken as an index of the degree of perceived motion coherence. The purpose of this research was to examine whether coherent motion perception would be affected by moderately increased CO_2 concentration via measuring detection thresholds of human subjects for coherent motion under normal atmospheric conditions and under conditions of 2.5% CO_2 concentration in air.

METHODS

Stimuli and Apparatus

Stimuli were random dot cinematograms (RDCs) generated on a Macintosh IIsi computer and displayed on a 16-in gray-scale monitor (60 Hz frame-rate; 680H X 420V pixel resolution; P104 phosphor). The detailed methods of generating textures of random dots in the RDCs was described elsewhere (17). Each motion stimulus consisted of 10 frames. **Fig. 1A** shows an example of one frame of a motion stimulus. **Fig. 1(B)** is a schematic of an animation sequence of a several-frame motion stimulus. Each frame image was a circular aperture filled with 50% black and 50% white dots. The luminance of the white dots was 74 cdm^{-2} and that of the black dots was 0.17 cdm^{-2}. The luminance of the gray background was 26 cdm^{-2}. The size of each dot was 2 pixels $\times$ 2 pixels, subtending 3.16′ arc $\times$ 3.16′ arc at a viewing distance of 0.8 m. The diameter of the circle, texture-filled region was 120 pixels, subtending 3.16° arc. These frame images were displayed on the computer screen in sequence for 830 ms. Subjects directly viewed the stimuli binocularly from this viewing distance.

All experiments were carried out in a dark environmental chamber where temperature, humidity, barometric pressure, and CO_2 concentration could be maintained at a desired level. The reader is referred to Sun et al. (13) for a detailed description of the chamber and the way in which it operates.

Motions of Dots

From one frame to the next, every black or white dot in a stimulus was displaced by six pixels (9.47′ arc). In a stimulus, a subset of the dots (termed "signal dots") moved non-randomly from frame to frame with a constant speed in an upward direction, and the remaining dots (called "noise dots") were redrawn randomly as either black or white from frame to frame. The signal dots and noise dots were independently and randomly chosen in each frame. The ratio of the number of signal dots to the number of noise dots was constant for each frame of a motion stimulus. The random motion of a noise dot was achieved by randomly assigning its luminance (black vs. white). A stimulus containing 100% noise dots was called "motion noise," while a stimulus containing a certain percentage of signal dots was called "motion signal."

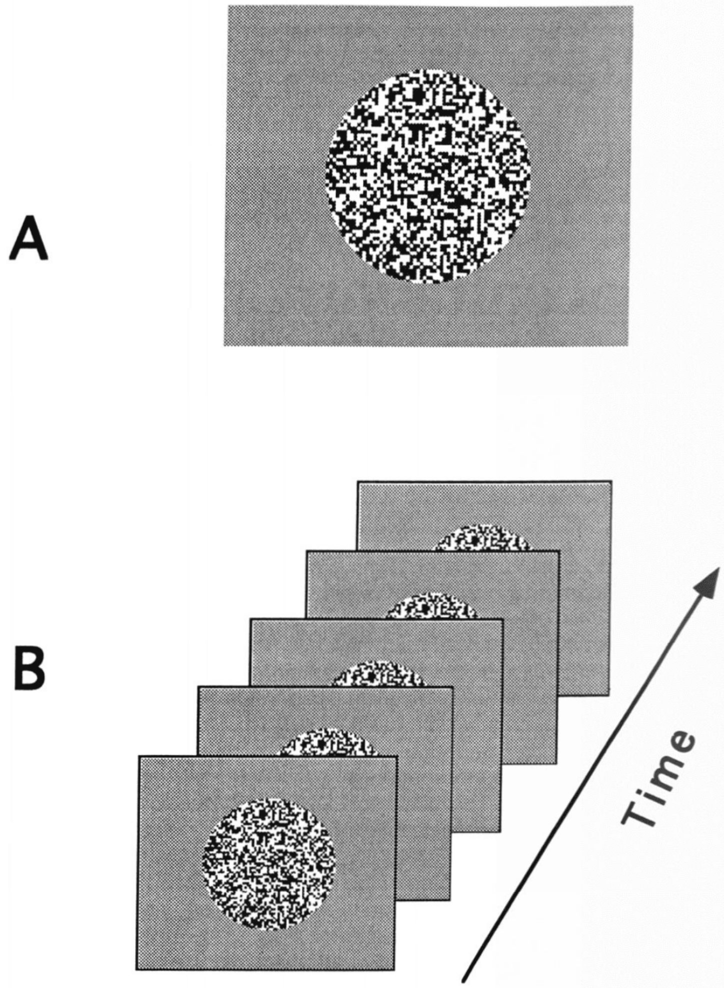

Fig. 1. A. An example of one frame of a random dot motion stimulus. B. A schematic example of an animation sequence of a several-frame motion stimulus.

The ratio of the number of motion signal dots to the total number of dots in a stimulus provides a measure of the strength of coherent motion in that stimulus. We term this ratio motion signal intensity (MSI). If all dots in the stimulus move upwards, MSI is 100%. If 50% of the dots move upwards, and the rest of the dots move randomly, the MSI is 50%, and so forth. The minimum MSI at which a subject can detect coherent motion with 75% probability is taken as the detection threshold for coherent motion. For more details about the motion stimuli, the reader is referred to Yang and Blake (17).

Subjects

Three subjects with normal or corrected-to-normal vision participated in these preliminary experiments,

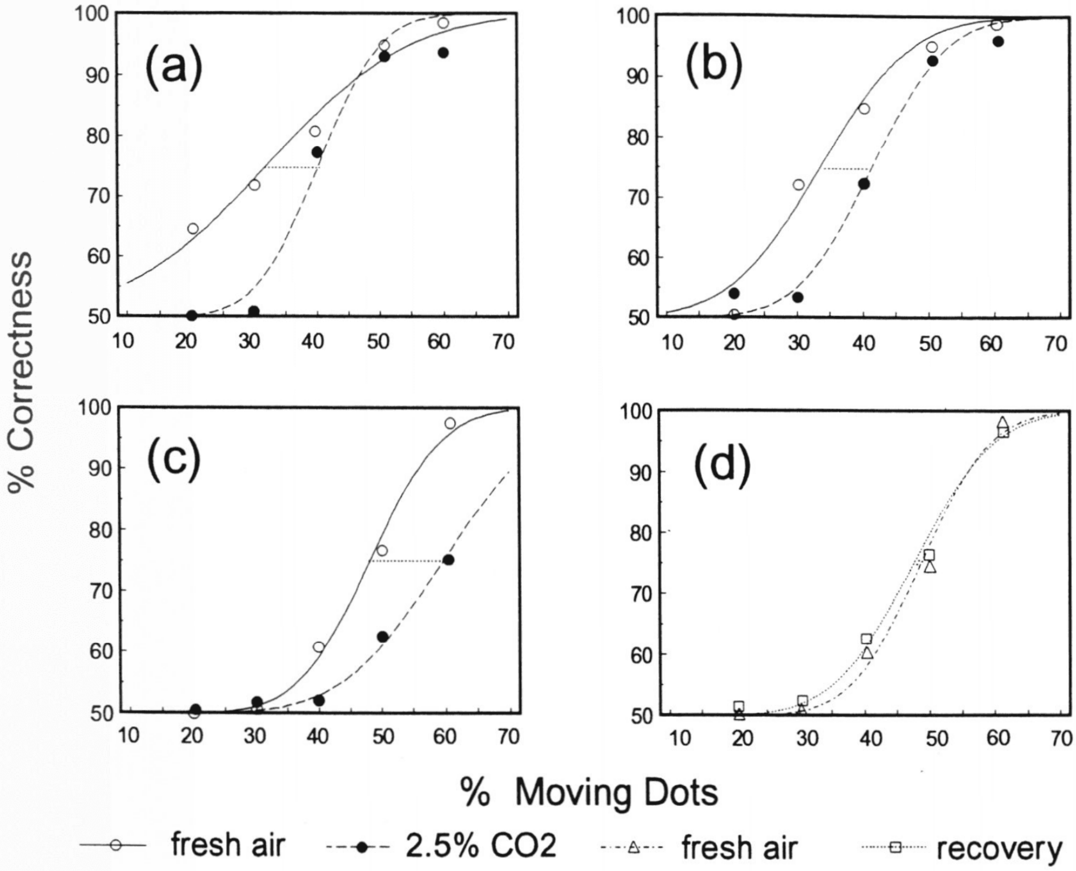

Fig. 2a, b, and c. The original data points and best-fitted psychometric functions under the fresh air condition (open circles) and the condition that applied 2.5% CO_2 (solid circles) for subjects 1, 2, and 3, respectively. **Fig. 2d.** The psychometric functions under fresh air before applied CO_2 (open triangles) and under fresh air after 1 h recovery from applying CO_2 (open squares). The data were averaged over the three subjects.

which is part of an 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 received from all three subjects before they participated in the experiments. All three subjects were naive about this psychophysical task and procedure. Two of them had no prior experience on visual psychophysics. Since the tasks involved forced-choice judgments with randomized order of conditions, criterion and/or expectation effects were minimized.

Procedure

Detection thresholds for coherent motion were determined for RDCs using a two-interval-forced choice (2IFC) procedure. On each trial, the subject viewed a motion noise stimulus (motion stimulus with a 0% MSI; i.e., no motion signal dots in the stimulus) in one interval and a motion signal stimulus in the other interval. The order of motion noise and motion signal stimulus was randomly chosen for each trial. The MSI value of the motion signal on a given trial was chosen from five values ranging from 20% to 60% in steps of 10%, and varied randomly from trial to trial. The subject's task was to judge in which interval—first vs. second—the motion signal stimulus was presented. Presentation duration for each interval was 0.84 s, with a 1-s interval intervening.

At least 150 trials of this 2IFC procedure were carried out for each subject to obtain a psychometric function. Each subject completed three sessions of the experiment under different conditions. That is, each subject first completed 150 trials under normal atmospheric conditions, followed by 150 trials under the condition with 2.5% CO_2 concentration in the air. Finally, each subject ran 150 trials under the normal conditions again. There was a 30- to 60-min rest period for subjects between sessions.

RESULTS

Fig. 2 shows the psychometric functions under different conditions obtained from the three subjects. The abscissa of the psychometric functions obtained from the 2IFC procedure was MSI (i.e., the percentage of coherent moving dots) and the ordinate was the percentage of correct responses. A cumulative Gaussian curve was fitted to the resulting psychometric function by probit analysis, and the MSI value corresponding to the 75% correct point on psychometric function defined the detection threshold for that condition. We applied a probit analysis method to obtain the best fittings.

From Fig. 2a, b, and c, we can see that, for all three subjects, psychometric functions under 2.5% CO_2 concentration were shifted to the right relative to those under the fresh air condition. We defined the proportion value of moving dot corresponding to 75% correct rate as a measure of motion detection threshold, and plotted these thresholds into **Fig. 3.** We can see that, for the three subjects, motion detection thresholds in the 2.5% CO_2 condition are about 1.3 times higher than thresholds obtained under the fresh air and recovery conditions. Under the fresh air conditions, the fresh air data and recovery data were very similar. We applied Z-score statistic test to our data to examine if motion detection thresholds under the fresh air and recovery conditions were significantly different from each other, and thresholds in 2.5% CO_2 condition were significantly different from that in the normal (i.e., the average over fresh air and recovery) conditions.

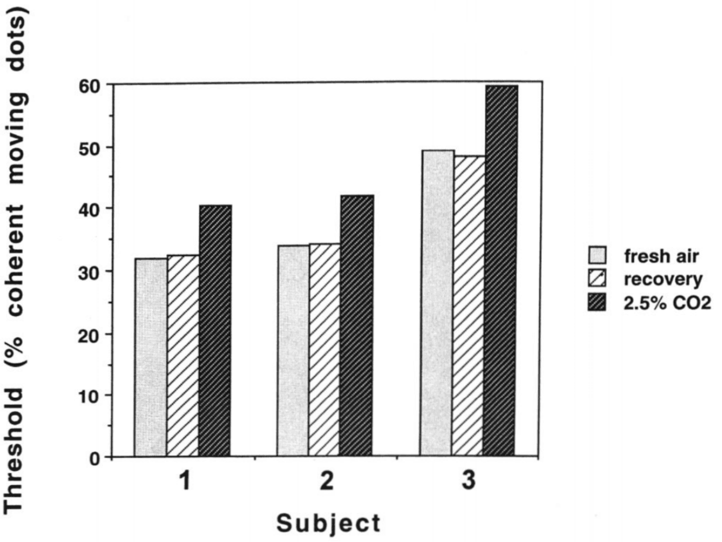

Fig. 3. Thresholds of coherent motion dection taken from the best-fitted psychometric functions shown in Fig. 2.

Z-score is defined by the following formula:

$$Z = [(X1 - X2)\cdot\sqrt{N}]/\sqrt{\sigma_1^2 + \sigma_2^2}$$

where X1 is the threshold for one condition and X2 is the threshold for the other. σ_1 is the standard deviation of the data from one condition, and σ_2 is the standard deviation of the data from the other condition. N is the total number of trials in each session of the experiments. For two-tailed tests the 99% confidence limits (i.e., $p < 0.01$) are −2.58 and 2.58. If Z-score is between values −2.58 and 2.58, then thresholds X1 and X2 are not significantly different. Otherwise, if Z-score is greater than 2.58 and smaller than −2.58, then X1 and X2 are significantly different. Applying the above formula, we obtained the Z-score values shown in **Table I.** From the values shown in the table, we can see that motion detection thresholds for fresh air and recovery conditions were not significantly different; however thresholds in 2.5% CO_2 condition were significantly different from those in normal conditions for all three subjects. We conclude that human ability in detecting coherent motion can be impaired when CO_2 concentration in air is raised to 2.5%.

DISCUSSION

As noted above, several studies found evidence that acute and chronic exposure to CO_2 can impair visual performance. In another research project (13), we found that stereoscopic sensitivity of the human visual system was decreased significantly at 2.5% CO_2 concentration in air. Interestingly, the results obtained from the present research show that coherent motion detection threshold increased significantly when CO_2 concentration in air was 2.5%. This implies that the sensitivity of the human visual system for coherent motion detection is decreased at 2.5% CO_2 concentration in air as well. Logically, if perceptual performance is affected by CO_2 concentration in air, as demonstrated in the present research and previous work, this motion detection effect most likely implies a neural origin. That is, the CO_2 effects on visual perception performance should originate from the CO_2 effects on activity of neuro-mechanisms underlying motion detection.

What is the neural basis for motion detection? From anatomical and physiological research on the visual system of primates, it is believed that different aspects of the visual scene are analyzed within several separate pathways (processing streams), organized hierarchically (19). There are two major pathways in the visual system originated within the retina. One is the parvocellular (P) pathway and the other is the magnocellular (M) pathway (5,14). Each pathway contributes to the performance of specific visual tasks. P cells primarily encode information about luminance contrast, color, and form while M cells mainly encode information about motion, stereopsis, and phase. About 10% of retinal ganglion cells are magnocellular projecting to the M layers of lateral geniculate nucleus (LGN). From LGN, M pathway continues in the striate cortex (the visual cortical area V1), the visual cortical area V2, the visual cortical area V3, the middle temporal visual area (MT), the medial superior temporal area (MST), and some posterior parietal areas. A number of studies have provided evidence (6,11) that V1, MT, and MST are involved in the processing of visual motion information. The neural activities in these areas form the neural basis for visual motion perception (5).

Several studies provided evidence that higher CO_2 concentration in air indeed affects cell activities from the retina to the cortex. For example, Stone and Koopowitz (12) found that the latency and time course of the electroretinogram (ERG) of the moth Galleria mellonella (bee moth) were dramatically increased by CO_2 during flash light stimuli, which was probably due to the change of pH in the eye. Shortly after, Rebert (9) found that 19% CO_2 increased latencies of both early and late components of flash-light evoked potentials (EPs). Recently, Sun and Bonds found that 4.5% expired pCO_2 (normal range is 3.7–4.1%) could reduce the firing rate of cortical neurons (in V1 area) and the number of active neurons in the cat, suggesting the existence of a global inhibition (Sun M, Bonds AB. Personal communication.). The research on cell level and molecular level provided evidence that the change of EPs by CO_2 could be interpreted as interference with the change of neural inhibitory transmitter caused by hypercapnia (2). Hypercapnia has been known to increase γ-aminobutyric acid (GABA) and decrease glutamate, while GABA has been confirmed to be an inhibitor in the visual pathways. Other work suggested that dopamine, which is involved in synaptic transmission of visual signal and sensitive to changes in pH, could be related to the effect of CO_2 on visual information processing (9).

In this study we applied two-interval forced-choice (2IFC) techniques with the methods of constant stimuli.

TABLE I. Z-SCORE VALUES OF TWO-TAILED TESTS FOR DIFFERENCES OF THRESHOLDS.

Subject	Z-score Normal vs. 2.5% CO_2	Z-score Fresh Air vs. Recovery
#1	8.4	0.22
#2	11.1	0.11
#3	14.8	1.20
Average of 3 subjects	—	0.51

These techniques are very common in modern psychophysical studies (10). In these studies, only a small number of subjects are needed (2, 3, or 4 subjects) because the studies are related to early stages (or lower levels) of neural systems, where the mechanisms being studied (e.g., color vision) are essentially uniform across subjects (aside from special disorders); thus in our methods sections, we often note that all subjects have normal acuity, excellent stereopsis, and so on. Given the assumption that we are studying aspects of vision that do not vary from person to person, it is preferable to collect a large amount of data on a relatively small number of subjects. Of course, if there are individual differences in result patterns among those few subjects, we must test more individuals. Now in medical research, however, investigators are often interested in comparing patients or some treated group with a control group, and they are studying problems where individual differences are routine. This calls for a between-subjects design with many participants. Of course, the exceptions are case studies, where a single individually is studied extensively.

Theoretical analysis (7) has shown that if the total number of trials in a two-alternative forced-choice (2AFC) task [the same as in a two-interval forced-choice (2IFC) task] run by a subject is more than 100, data distribution is close to a normal distribution, and probit analysis can provide a valid estimate on the threshold of a psychometric function via fitting the data by probit analysis equations. In this study, each subject ran at least 150 trials in each condition. Therefore, from the above discussion, the estimated thresholds in our results were very valid and the findings can be generalized.

From the methods section, we can see that subjects were given an additional test, which was identical to those with fresh air before applying 2.5% CO_2, but performed after subjects had been breathing fresh air 1 h post-CO_2 exposure. This was to validate the reproducibility of the testing methods. Fig. 2d shows the results obtained during fresh air period before applying CO_2 (i.e., "fresh air" condition) and 1 h fresh air breathing after the end of CO_2 exposure (i.e., "recovery" condition). From Fig. 2d, we can see the psychometric function for the recovery condition was shifted leftwards slightly relative to that of the fresh air condition, implying that the threshold for the recovery condition was a bit smaller than that for the fresh air condition. This might suggest some degree of learning or adaptation effects involved in our results. However, we have proved from a Z-score test that the difference between the thresholds of fresh air and recovery conditions shown in Fig. 2d was not significant, meaning that learning did not play a role in our experiments.

Normal atmospheric CO_2 levels are 0.03%, however, in enclosed environments, CO_2 concentrations are usually higher than normal. In order to learn how we pollute air by expiring CO_2, in another experiment, we tested 20 subjects, each of whom spent 24 h inside the whole-room indirect calorimeter. During 8 h of day time, even sedentary subjects produced CO_2 at an average rate of 0.3–1.2 $L \cdot min^{-1}$. At this rate, if a pilot were confined in a 3 m^3 cockpit for 8 h with a poor ventilation, CO_2 concentration in the air would increase to 5% or more. In many circumstances, controlling the CO_2 level becomes an important and crucial issue because requiring for too low a CO_2 level would impose too strong a demand on the CO_2 removal/O_2 supply system, while too high a CO_2 level would impair the visual performance, as we and other researchers have demonstrated. Therefore, our findings that 2.5% CO_2 concentration in air can impair visual motion detection ability provides useful information for the design and operation of vehicles such as space shuttles, airplanes, or submarines, where oxygen supplies may be limited, and where clear vision and excellent visual performance are required because of the complexity of structure and operation of those types of vehicles.

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