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Changes in rat respiratory behavior under varying P_{CO_2} levels and argon content in hyperbaric $Ar\text{-}O_2\text{-}CO_2$ atmospheres

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Friess, S. L., W. V. Hudak, and R. D. Boyer. 1976. Changes in rat respiratory behavior under varying P_{CO_2} levels and argon content in hyperbaric $Ar\text{-}O_2\text{-}CO_2$ atmospheres. Undersea Biomed. Res. 3(2):85-94. An anesthetized rat preparation has been used for breathing studies in hyperbaric $Ar\text{-}O_2\text{-}CO_2$ atmospheres in which total saturation pressure was varied in the range 1-19.1 ATA and P_{CO_2} was set at levels of 0.0, 0.05 or 0.10 ATA. The variables monitored were respiration rate and an isotonic measure of diaphragm-twitch amplitude during contracture/relaxation (twitch index). The results indicate that: (1) hyperbaric $Ar\text{-}O_2$ atmospheres are able to maintain the animal in stable condition for several hours; (2) elevation in P_{CO_2} level produces enhancements in respiration rate and twitch index that are markedly dependent on the P_{Ar} level; (3) successive increases in P_{Ar} are able to lower progressively the effects on both breathing parameters produced by either 0.05 or 0.10 ATA of CO_2, with full abolition of both effects of inhaled CO_2 in the P_{Ar} range 14-19 ATA; and (4) the intrinsic ability of hyperbaric argon to abolish respiratory enhancement by CO_2 is greater than that of hyperbaric helium. These results have been discussed in terms of possible CNS loci at which hyperbaric argon (or helium) is able to antagonize centrally induced effects from dissolved molecular species derived from inspired CO_2, and in relation to the broader task of control of excitatory/inhibitory centers of the CNS during diving by manipulation of the partial pressures of diluent components of breathing-gas mixtures.

hyperbaric argon
hyperbaric helium
diaphragm-twitch amplitude
CO_2-sparing effect
sparing mechanisms
Ar vs. He potency
respiration rate

In studies relating to the effects of inert gas partial pressures on excitable tissues, a growing body of evidence (Schreiner 1968; Small and Friess 1975) points to possible involvement of dissolved gas species (such as helium, argon, krypton etc.) with tissue receptors, leading to changes in physiological state or functionality of those tissues. In part, the observed changes in tissue function under saturation with atmospheres containing an inert gas in place of nitrogen may reflect a simple displacement/replacement of tissue-bound N_2 by *x* species, resulting in a new gas-saturation state of tissue sites in which the release of N_2-mediated depression may yield elements of response modification. An example of response modification would be amplification/depression in excised phrenic nerve-diaphragm preparation, independent of the chemical character of the displacing gas *x* (Friess, Durant, Martin, and Cowan 1970; Friess, Jefferson, and Durant 1971). A strong possibility exists, however, that the character of species x may well enter directly into the perturbation of tissue function when x replaces N_2 in tissue binding, by direct agonistic action of x on receptors.

Such a possibility has been probed in part in a recent in vivo study of respiratory tissues in the rat (Friess and Durant 1974) in which it was shown that elevated partial pressures of helium in $He\text{-}O_2\text{-}CO_2$ breathing-gas mixtures, in the total pressure range 1-91.1 ATA, are able to mitigate the well-known effects of inspired CO_2 in terms of increase in respiration rate and diaphragm-twitch amplitude. The degree to which this CO_2-sparing effect of elevated P_{He} in the rat is a particular function of specific helium-receptor interactions by virtue of the chemical character of helium, rather than a generalized effect of displacement and replacement of tissue-bound species by increasing partial pressures of a truly inert ligand, was unknown. Therefore, the present study was designed to probe this specificity problem by replacing the inert component helium in ternary hyperbaric breathing-gas mixtures $x\text{-}O_2\text{-}CO_2$ with the heavier atomic species argon (Ar). Experiments on the diving rat preparation were scheduled over the total pressure range 1-19 ATA afforded by a series of $Ar\text{-}O_2\text{-}CO_2$ mixtures.

MATERIALS AND METHODS

The pharmacological procedures leading to the anesthetized rat preparation for hyperbaric study of respiration rate and an isotonic index of diaphragm-twitch amplitude have been described previously (Friess and Durant 1974). Male rats of the Long-Evans hooded strain weighing 200 ± 10 g were used throughout the study. Details of the surgical procedures leading to installation of the preparation in the miniature hyperbaric chamber, attainment of thermal equilibrium, and recording of control responses after equilibration with $Ar\text{-}O_2$ gas mixtures at any given pressure followed the previous helium studies precisely. Experimental animals were monitored for mean respiration rate at the beginning and end of the postsurgical equilibration period. Any decrease in rate to levels below 60% of preanesthesia values was taken as cause to terminate experiments with that particular preparation, in order to minimize complications due to anoxia.

In the hyperbaric experiments, the animals were successfully compressed in $Ar\text{-}O_2$ atmospheres at the same pressures and according to the same diving schedules previously specified for $He\text{-}O_2$ mixtures (Friess and Durant 1974). The animal preparations at saturation at each pressure exhibited remarkable stability of respiration rate and twitch-index parameters (5-10% variability) over the 30-min period prior to changeover to test-gas mixtures containing CO_2. The final 3 min of equilibration time furnished the interval of control respiratory behavior for subsequent comparisons with CO_2-perturbed responses.

Gas mixtures were prepared from cylinders of the pure components in a mixing manifold, using precision gauges, and checked for accuracy by instrument analysis of O_2 and CO_2 content. As in the helium studies, mixtures were prepared to yield a surface-equivalent content of 0.20 ATA of oxygen at all times and all total pressures. At each equilibration pressure, a slow gas flow to discharge plus matched input removed atmospheric contaminants from the chamber in the course of the 30-min equilibration period. Following switchover to $Ar\text{-}O_2\text{-}CO_2$ mixture from a given equilibration with $Ar\text{-}O_2$ at the same total pressure, changes in respiratory rate and twitch-amplitude index were followed during a test period of 4-5 min. Blood samples were taken via a carotid artery cannula following the test interval, decompressed rapidly, and monitored for pH depression. Exposure intervals in atmospheres containing high P_{CO_2} levels (e.g. 0.10 ATA) were kept brief by design, to avoid systemic response perturbations from progressive acidosis.

The composition of each respiratory gas mixture employed in the present study is summarized in Table 1, with indications of P_{CO_2} and total pressure P_t for each mixture and a notation of the total-pressure equivalent in terms of feet of sea water depth.

RESULTS

For convenience of tabulation and comparison of new findings with those from the previous study using He-O_2-CO_2 mixtures, the present results with Ar-O_2-CO_2 breathing mixtures furnished to the rat preparation will be summarized in a set of figures and tables. The tables will compare relative respiration rates and twitch-index parameters at times 1.0, 2.0, and 4.0 min into the test interval, with mean values tabulated as responses relative to a reference index = 100 for the 3-min control interval just prior to switchover to the test gas.

TABLE 1

Composition of Ar-O_2 and Ar-O_2-CO_2 gas mixtures* employed in rat respiration experiments

Total pressure, P_t		P_{CO_2}	Equivalent seawater depth
ATA	psig	ATA	ft
1.0	0	0.00	0
		0.05	
		0.10	
4.4	50	0.00	112
		0.05	
7.8	100	0.00	225
		0.05	
		0.10	
14.6	200	0.00	449
		0.05	
		0.10	
19.1	266	0.00	598
		0.05	
		0.10	

*P_{O_2} fixed at 0.20 ATA in each mixture.

For general illustration of the effects of hyperbaric Ar in altering the course of CO_2-perturbation of breathing rates and diaphragm-twitch amplitudes, Figs. 1 and 2 display a selection of rat-response data for the two respiratory variables under: (1) an $Ar\text{-}O_2$ atmosphere, P_t = 19.1 ATA, P_{CO_2} = 0; (2) an $Ar\text{-}O_2\text{-}CO_2$ atmosphere, P_t = 1.0 ATA containing 0.10 ATA CO_2; and (3) an $Ar\text{-}O_2\text{-}CO_2$ atmosphere, P_t = 19.1 ATA containing 0.10 ATA CO_2.

From these figures, and the more detailed summaries in Tables 2 and 3 of progressive changes in effects with systematic increase in pressure by raising P_{Ar}, it can be seen that an increase in P_{Ar} has a profound effect on the respiratory response of the animal to the imposition of a 0.10 ATA CO_2 loading in the inspired-gas stream. In general, the effects on breathing frequency are clear-cut: at 1 ATA $Ar\text{-}O_2$ the imposition of 0.10 ATA CO_2 (Fig. 1) produces an abrupt but modest ($\sim$ 20%) increase in breathing frequency, which gradually and only partially decays in the course of the next 4 min, and the imposition of sufficient P_{Ar} to raise the total pressure to 19.1 ATA completely wipes out the respiratory rate increase from 0.10 ATA CO_2. The general effects on twitch-amplitude index (Fig. 2) are equally impressive and even greater in magnitude. Loading of 0.10 ATA CO_2 in $Ar\text{-}O_2$ at 1 ATA total pressure causes a progressive increase in twitch index amounting to about a 150%

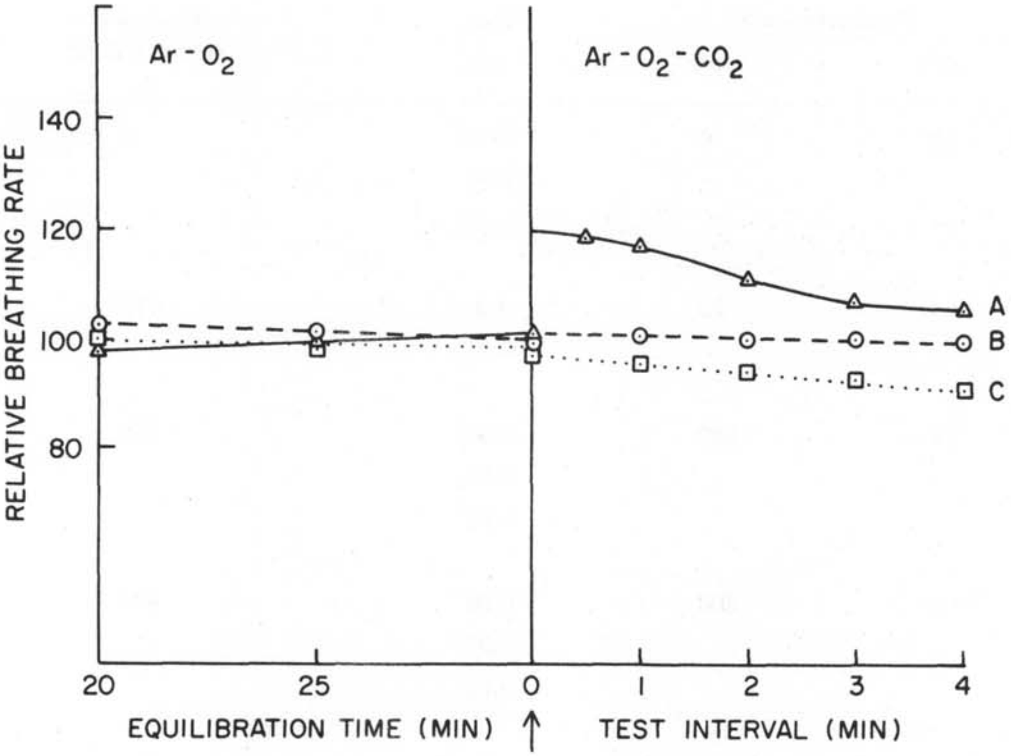

Fig. 1. Respiration rate for the rat preparation, relative to control index = 100 for the 3-min interval at the end of the equilibration period, vs. exposure time during equilibration with $Ar\text{-}O_2$ and later on switchover to $Ar\text{-}O_2\text{-}CO_2$ test gases. Values are means from the experiments summarized in Table 2. Curve A, P_t = 1.0 ATA, P_{CO_2} = 0.10 ATA; Curve B, P_t = 19.1 ATA, P_{CO_2} = 0.0 ATA; Curve C, P_t = 19.1 ATA, P_{CO_2} = 0.10 ATA.

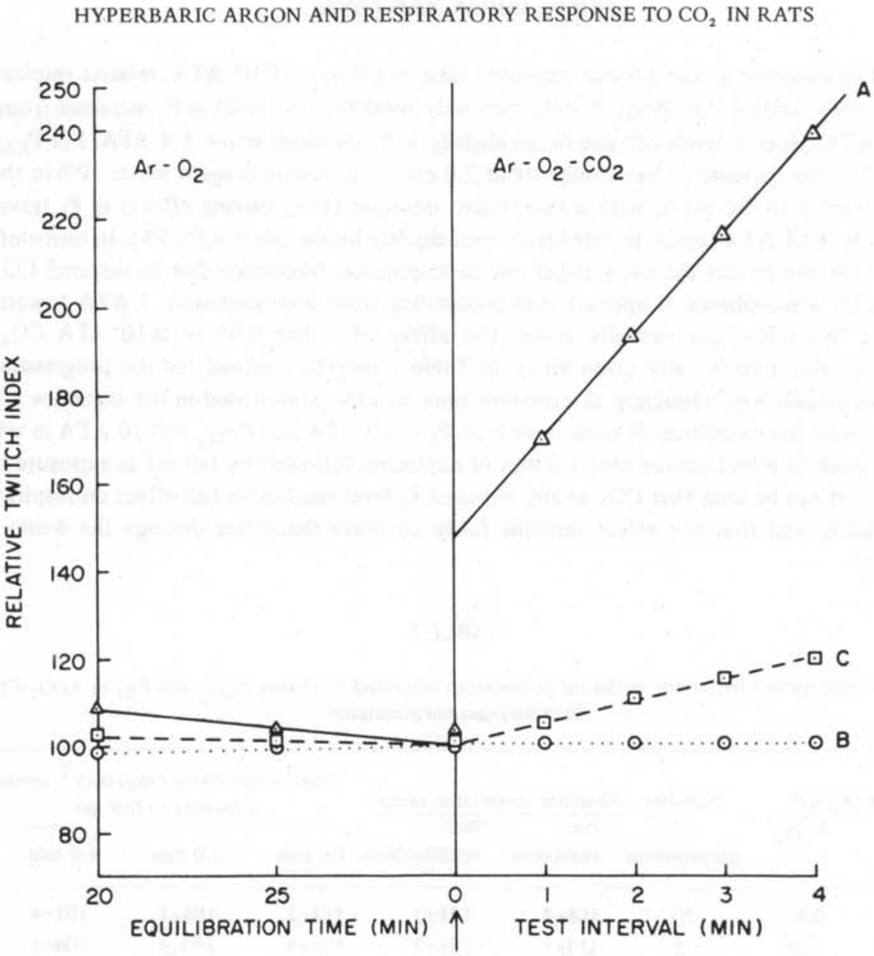

Fig. 2. Relative diaphragm-twitch index for the rat preparation in Ar-O_2 (equilibration) and Ar-O_2-CO_2 (test-gas) atmospheres. Curves A-C refer to the conditions specified in Fig. 1 and consist of mean values from the experiments summarized in Table 3.

increment over the course of 4 min. An increase in P_{Ar} sufficient to raise P_t to 19.1 ATA virtually abolishes the CO_2 effect. These general results mirror in part the effects previously seen with hyperbaric helium and CO_2, but there are also significant variations in argon vs. helium perturbations of CO_2 responses that will be noted subsequently.

The detailed responses of the rat respiratory preparation to increased loading of CO_2 and increased partial pressures of Ar are summarized in Tables 2 and 3. Table 2 presents respiratory-frequency data, relative to control = 100 for mean values at the end of the Ar-O_2 pressure-equilibration period. Table 3 summarizes the corresponding information for the same preparations on changes in the twitch-amplitude index at the same time points.

Effects on respiration rate

From Table 2, the effects of change in P_{CO_2}, P_{Ar} and P_t on respiration rate are clear; they can be illustrated best by following the change in magnitude of the frequency index with increasing P_t, at a fixed level of P_{CO_2}, down the vertical column of any exposure-time point. For example, at the 2.0-min exposure time and $P_{CO_2} = 0.05$ ATA, relative respiration rate vs. zero control (i.e. $P_{CO_2} = 0.0$) rises only modestly ($\leq 10\%$) as P_t increases from 1.0 to 4.4 ATA; then it levels off and drops slightly as P_t increases above 4.4 ATA. For $P_{CO_2} = 0.10$ ATA, the increase in breathing rate at 2.0 min of exposure is again about 10% in the P_t region from 1 to 7.8 ATA, with a subsequent decrease (*CO_2-sparing effect*) as P_t traverses the 7.8- to 19.1-ATA region to rate levels even slightly below control ($\sim 5\%$). In terms of the P_{Ar}, which damps out the early slight rise in respiration frequency due to inspired CO_2 in Ar-O_2-CO_2 atmospheres, it appears that proceeding from approximately 7 ATA toward 14 ATA of this noble gas virtually erases the effect of either 0.05 or 0.10 ATA CO_2 on breathing rate. Finally, any given entry in Table 2 may be scanned for the progression of effect on respiration frequency as exposure time to CO_2 is increased in the sequence 1.0 to 4.0 min; with the exception of experiments at $P_t = 1.0$ ATA and $P_{CO_2} = 0.10$ ATA in which a slight peak in effect occurs near 1.0 min of exposure, followed by fall-off as exposure time increases, it can be seen that CO_2 at any elevated P_t level reaches its full effect on respiration rate quickly and that the effect remains fairly constant thereafter through the 4-min test interval.

TABLE 2

Relative respiration frequency in the rat preparation subjected to change P_{CO_2} and P_{Ar} in Ar-O_2-CO_2 breathing-gas environments

Pressure (ATA)*		Number of preparations	Absolute respiration rates†		Relative breathing frequency‡ during exposure to test gas		
P_t	P_{CO_2}		Pre-anesthesia	Post-equilibration	1.0 min	2.0 min	4.0 min
1.0	0.0	10	108±4	101±2	101±2	105±1	101±4
	0.05	5	112±5	101±2	105±4	103±4	104±5
	0.10	5	96±3	97±3	117±7	110±9	108±9
4.4	0.0	5	121±3	103±2	98±3	102±1	104±2
	0.05	5	107±6	99±3	110±3	110±1	111±2
7.8	0.0	5	91±5	100±6	93±3	90±4	93±3
	0.05	6	103±3	101±2	104±2	105±3	108±2
	0.10	7	93±3	102±4	108±4	109±5	111±6
14.6	0.0	5	91±4	96±3	105±3	106±4	107±6
	0.05	4	101±8	100±2	98±2	97±2	99±3
	0.10	5	99±2	100±1	93±2	94±2	96±2
19.1	0.0	4	96±6	100±1	101±3	99±2	98±1
	0.05	7	104±3	103±2	99±4	103±2	100±2
	0.10	5	104±4	104±2	95±3	93±3	91±3

* P_{O_2} fixed at 0.20 ATA in all experiments.
† Mean values ± SE, respirations /min.
‡ All responses are mean values ± SE, relative to response reference index = 100 just prior to switchover to test gas containing CO_2.

These effects of elevated P_{CO_2} and increased levels of P_{Ar} on breathing rate in the rat preparation mirror in part those previously seen in He-O_2-CO_2 atmospheres (Friess and Durant 1974), but there are some quantitative differences in the response pattern. Specifically, (1) the early peak elevation of breathing frequency for the condition P_{CO_2} = 0.10 ATA, P_t = 1.0 ATA is only about 20% in an argon atmosphere, whereas it amounts to approximately 30% in a helium atmosphere; and (2) the CO_2-sparing action of the diluent gas with respect to breathing rate seems to be somewhat more potent for argon than for helium, since the rate rise is fully negated in Ar-O_2-CO_2 at $P_t < 14.6$ ATA, but the rate is still slightly elevated above control at P_t = 19.1 ATA in He-O_2-CO_2.

Effects on twitch-amplitude index

The effects of P_{Ar} and P_t on depression of twitch-amplitude elevations produced by 0.05- and 0.10-ATA levels of CO_2 are much more dramatic than the corresponding effects on breathing rate (Table 3). Again selecting the 2.0- min exposure-time column for comparison samples, at P_{CO_2} = 0.05 ATA an elevation of amplitude occurs which is of the order of 30-50% in the P_t interval 1.0-4.4 ATA, and further increases in P_{Ar} lead to a CO_2-sparing

TABLE 3

Respiratory twitch index response in the rat preparation subjected to changes in P_{CO_2} and P_{Ar} in Ar-O_2-CO_2 breathing-gas environments

Pressure (ATA)*		Number of preparations	Relative twitch index† during exposure to test gas		
P_t	P_{CO_2}		1.0 min	2.0 min	4.0 min
1.0	0.0	10	101±4	100±4	105±6
	0.05	5	126±6	128±3	139±8
	0.10	5	166±23	197±21	248±22
4.4	0.0	5	96±8	98±10	91±8
	0.05	5	133±7	150±8	163±14
7.8	0.0	5	103±3	96±7	106±5
	0.05	6	115±3	116±5	125±6
	0.10	7	119±6	133±11	132±10
14.6	0.0	5	95±3	100±1	95±2
	0.05	4	104±5	112±4	115±6
	0.10	5	128±8	128±6	128±8
19.1	0.0	4	100±4	106±2	102±4
	0.05	7	101±3	106±3	109±4
	0.10	5	107±5	114±5	117±10

* P_{O_2} fixed at 0.20 ATA in all experiments.

† All twitch-index responses are mean values ±SE, relative to reference response index = 100 just prior to switchover to test gas containing CO_2.

action in which the elevation at lower pressure is progressively damped out, with return to near control amplitude levels by the application of $P_{Ar} \sim 19$ ATA. At a P_{CO_2} exposure level of 0.10 ATA, the increments in response amplitude at low pressure are even greater (∼ 100%), and the damping-out effect of additional P_{Ar} is equally prominent, with a return to slightly above control response levels at $P_{Ar} \sim 19$ ATA. At any given condition of elevated P_{CO_2} and hyperbaric Ar, the effect of CO_2 in progressive exposure time is seen either to increase steadily or, in a few instances, to level off in the course of the total 4-min exposure.

Comparison of the present twitch-amplitude results in Ar-O_2-CO_2 atmospheres with those previously observed for He-O_2-CO_2 atmospheres in the same total pressure range reveals that the patterns of response are quite similar; increased levels of either P_{Ar} or P_{He} in breathing gas cause a sparing or damping-off of the direct effect of CO_2. However, the sparing effect exerted by argon at any given P_t level seems to be greater than that yielded by helium, since the magnitudes of residual amplitude enhancement by CO_2 at $P_t = 7.9$ and 19.1 ATA are much higher in He-O_2-CO_2 atmospheres (Friess and Durant 1974) than presently noted in Ar-O_2-CO_2 environments. For example, although the damp-out of the $P_{CO_2} = 0.10$ ATA effect is almost complete at added $P_{Ar} \sim 19$ ATA, it was only approximately 65% complete in the He-O_2-CO_2 at $P_{He} \sim 19$ ATA.

DISCUSSION

The present results add some valuable insights into the nature of the process by which major effects of elevated P_{CO_2} on breathing performance in the rat can be damped-out or eliminated by a sparing action of the diluent component x in hyperbaric x-O_2-CO_2 breathing-gas mixtures. It has now been shown that argon $= x$ can exert the sparing action with regard to CO_2-induced increase in breathing rate and amplitude of diaphragmatic contracture, and that the qualitative relationships involving P_{Ar}, P_{CO_2} and P_t for the sparing action by hyperbaric argon are quite similar to those previously documented for hyperbaric helium as the breathing-gas diluent (Friess and Durant 1974). Therefore, it is likely that the breathing gas components argon and helium may exert their interesting and important sparing action by equivalent types of agonistic or antagonistic interactions at tissue receptors in the rat. The speed with which the sparing process occurs and the fact that both breathing rate and amplitude of diaphragmatic contracture are affected implicates a respiratory center in the CNS as one of the most likely sites for potential competition of dissolved x and CO_2-derived species, leading to mitigation of the physiological effects of elevated CO_2. In this interpretation of events, increase P_{Ar} in the hyperbaric breathing gas would result in increased partial pressure of dissolved Ar in fluid reaching the respiratory center and, by mass action at the receptor loci, would produce a competitive displacement of bound CO_2 species from their agonistic interactions with tissue. Less likely—but still possible—would be an argon binding to and activation of inhibitory receptors at the respiratory center able to overcome the excitation initiated by CO_2-moieties acting as agonists at nearby loci.

Under the competitive model for central actions of argon leading to the observed CO_2-sparing effects on respiration in the rat preparation, it is now possible to accommodate the new finding that argon is somewhat more effective than helium in the mitigation process. Viewing argon and helium as competitive binding agents at central loci that also bind dissolved CO_2 species as agonists, the relative efficacy pattern $Ar > He$ in CO_2-sparing may simply reflect the order of binding strengths of the two noble gas species to the CO_2-sensitive loci. Such an order, with the heavier argon species more effective than the lighter helium in this biological action, is very much in accordance with the body of information available on the increase in clathrate-forming capability, increase in anesthetic potency, etc. (Schreiner 1968) as the noble gases increase in atomic weight in the series He, Ne, Ar, Kr, Xe. Further, the fact that the CO_2-sparing action (which increases with partial pressure of the diluent) is quantitatively different for argon and helium clearly implies that the action is at least in part due to the chemical character of the gas component, and not solely a function of increased pressure pre se.

The present finding on $Ar > He$ efficacy in CO_2-sparing may also have a recognizable consequence in the future as saturation diving practice takes account of the depletion of natural helium resources and adjusts to its replacement by a more abundant non-narcotic diluent gas such as H_2. Diving in H_2-O_2, or H_2-containing trimixes, etc. could then raise an interesting problem in requirements for CO_2 control if the major diluent H_2 is even less effective than helium in damping out central CO_2 effects. This point will be studied experimentally using the rat diving model. If it indeed turns out that the CO_2-sparing effect is a general inverse function of the atomic/molecular weight of the diluent gas, and that the efficacy series runs $H_2 < He < Ne < Ar$ . . . . ., it may then be necessary to consider trimixes, etc. in which a proportion of heavier diluent is added to the H_2-O_2 breathing gas specifically to control the central processes underlying respiration, under the influence of whatever levels of CO_2 result from the engineering solutions to atmosphere control in hyperbaric life support systems.

One further implication of the present picture of sparing interactions of helium, argon, and CO_2-derived species at respiratory-control centers has to do with the possibility that a fraction of heavier diluent gas in any diving-gas mixture may be generally useful in damping-out undesirable central effects. This possibility is already tacitly acknowledged in the diving community by the empirical utilization of trimixes (He-N_2-O_2) in saturation diving as a means of repressing tremors and borderline convulsive behavior constituting the high pressure nervous syndrome at diving depths in excess of 600-800 fsw (Bachrach and Bennett 1973; Hunter and Bennett 1974). The fractional use of diluent-breathing N_2 to relieve centrally mediated phenomena, seen as another aspect of the relative inability of light helium species to operate effectively in binding at CNS loci and regulating excitatory output, may be just the first approach to compensate for CNS inadequacies of light diving gases. The problem of uncontrolled excitation at CNS loci under high total pressure may be amenable to more quantitative manipulation in the future by the addition of small partial pressures of higher molecular weight species such as argon to the breathing-gas mixtures, balancing off excitation control by species of high efficacy in CNS binding/depression against the need to keep the major fraction of the mixture low in molecular weight and highly diffusible.

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Friess, S. L., W. V. Hudak, and R. D. Boyer. 1976. Modifications du comportement respiratoire du rat au cours de variations de la P_{CO_2} et du taux d'argone en atmosphères hyperbares $Ar\text{-}O_2\text{-}CO_2$. Undersea Biomed. Res. 3(2):85-94.—Des paramètres respiratoires ont été etudies chez le rat anesthesie en atmospheres hyperbares $Ar\text{-}O_2\text{-}CO_2$, dans lesquelles la pression totale à saturation a varié entre 1 et 19,1 ATA et la P_{CO_2} était à 0,0; 0,05; ou 0,10 ATA. La fréquence respiratoire et une mesure isotonique de l'amplitude des contractions diaphragmatiques pendent la contraction-relâchement (Twitch index) ont ete surveillees. Les résultats montrent: (1) qu'un animal peut être maintenu dans une condition stable en atmosphères hyperbares $Ar\text{-}O_2$ pendant plusieurs heures; (2) que l'augmentation de la P_{CO_2} provoque des augmentations de la fréquence respiratoire et de l'amplitude des contractions diaphragmatiques qui dépendent de la P_{Ar} d'une façon remarquable; (3) que des augmentations successives de la P_{Ar} abaissent progressivement les effets de CO_2 à 0,05 ou à 0,10 ATA sur les paramètres respiratoires, avec une abolition complète des deux effets du CO_2 inspiré quand la P_{Ar} se situe vers 14-19 ATA; et (4) que la capabilité inhérente de l'argone pour abolir les effets respiratoires de CO_2 est plus grande que celle de l'hélium. Le site du SNC auquel l'argone hyperbare exerce ses effets d'antagoniste des effets respiratoires du CO_2 est discuté, ainsi que le rapport entre ces résultats et la plus large tâche de contrôle des centres excitateurs-inhibiteurs du SNC pendant la plongée par la manipulation des pressions partielles des composants des mélanges respiratoires.

l'argone hyperbare
l'hélium hyperbare
la frequence respiratoire
respiration chez le rat
l'amplitude des contractions diaphragmatiques

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