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Control of diving responses by carotid bodies and baroreceptors in ducks

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LILLO, RICHARD S., AND DAVID R. JONES. *Control of diving responses by carotid bodies and baroreceptors in ducks*. *Am. J. Physiol.* 242 (Regulatory Integrative Comp. Physiol. 11): R105-R108, 1982.—The precise role of carotid body chemoreceptors and systemic baroreceptors in cardiovascular responses during experimental diving in ducks is controversial. The diving responses of chronically baroreceptor-denervated, chemoreceptor-denervated, and combined baroreceptor- and chemoreceptor-denervated White Pekin ducks, *Anas platyrhynchos*, were compared with those of intact and sham-operated birds. All three types of denervation elevated pre-dive heart rates on average by 100–150 beats/min. During submergence, the cardiac rate of the barodenervates quickly dropped and after 60 s stabilized at levels similar to those of submerged intact ducks for the remainder of a 2-min dive. However, arterial blood pressure declined drastically in the barodenervates. Ducks without functional carotid bodies showed significant bradycardia during submergence, although heart rate only fell to the pre-dive rate of intact animals. Birds with combined baroreceptor and chemoreceptor denervation exhibited the same degree of bradycardia as chemoreceptor denervates, and arterial blood pressure rose spectacularly during a dive. It is concluded that during experimental diving in ducks 1) cardiac responses are not baroreflexive in origin, 2) the major portion of bradycardia is due to stimulation of carotid body chemoreceptors, and 3) intact systemic baroreceptors appear essential for maintenance of blood pressure.

Anas platyrhynchos; apneic asphyxia; cardiovascular; diving bradycardia

THE PRECISE ROLE of carotid body chemoreceptors and systemic baroreceptors in cardiovascular responses during experimental diving in ducks is controversial. Combined carotid body and baroreceptor denervation has been reported to abolish the diving bradycardia response in ducks (10, 11). Jones and Purves (15), however, found that carotid body denervation substantially reduced but did not eliminate the cardiac decline during submergence. Diving bradycardia in ducks is believed by some investigators to be a baroreflex resulting from an increase in peripheral vascular resistance, which is mediated by chemoreceptor stimulation (1, 3, 4). Yet, chronically baroreceptor-denervated ducks exhibit a drop in heart rate comparable to that in normal animals, although blood pressure falls significantly in the denervates (12). On the other hand, the bradycardia response seems to be diminished and blood pressure usually rises in acutely barodenervated ducks (17).

Because of the above contradictions, it appeared appropriate to reexamine the role of carotid bodies and baroreceptors in cardiovascular responses during experimental diving in ducks. This investigation presents cardiovascular data from diving experiments with chronically baroreceptor-denervated, carotid body-denervated, and combined baroreceptor- and carotid body-denervated White Pekin ducks as well as intact and sham-operated birds.

METHODS

Data were obtained from 26 adult White Pekin ducks, *Anas platyrhynchos*, weighing 2.5–3.3 kg and acclimated to laboratory temperatures (18–23°C). Animal preparation, baroreceptor and carotid body denervation, and diving experiments were carried out as described in Lillo and Jones (19). In addition to these procedures, the electrocardiogram (ECG) was recorded bipolarly, one needle electrode placed into the left thigh, another just under the skin of the right side of the thorax. Heart rate was measured by triggering a ratemeter off the amplified ECG signal. Blood pressure was recorded by a pressure transducer connected to a cannula in the brachial artery. The transducer signal was amplified and displayed, along with the ratemeter output, on a chart recorder as well as being recorded on a four-channel tape recorder. Following experiments, the tape was replayed with the pressure signal led through an RC network with a long time constant to yield mean pressure.

Barodenervates were allowed 2 mo to recover before diving experiments began; chemodenervates, combined baro- and chemodenervates, and sham-operated ducks were given approximately 2 wk. The effectiveness of the denervation operations was determined by various tests (19). Intact and barodenervated birds were subjected to 2-min dives. However, the less pronounced bradycardia of the chemodenervates and combined baro- and chemodenervates reduced the tolerance of these ducks to diving, so dives with these groups were only 1 min in length. Denervation of the carotid bodies depressed ventilation; and, therefore, pre-dive blood oxygen levels were lower and carbon dioxide levels higher than normal (19). This coupled with a reduced bradycardia in the chemodenervates resulted in quite extreme blood gas values in these animals after only a 1-min dive. Comparable blood gases are normally observed in intact birds only after much longer dives. Since diving responses generally take

40–60 s to develop fully in intact ducks, a 1-min dive was thought to be sufficient in duration to determine the cardiovascular responses to submergence in chemodenervates.

Heart rate and blood pressure data were independently compared using 2- and 3-factor analyses of variance (ANOVA) with repeated measures over time (BMDP8V, Univ. CA, Los Angeles). In cases of significant F values, pair-wise comparisons of means were performed with the least significant difference test (23).

RESULTS

Injection of 5–20 μg epinephrine HCl confirmed the absence of a baroreflex in the three barodenervates as well as in three of the eight chemodenervates. Chemosensitivity and lung inflation tests with all eight chemodenervates demonstrated that following denervation operations, the O_2 -chemoreflex drive of ventilation was eliminated and the inspiration-inhibiting reflex of lung inflation was accentuated. Test responses before and after sham operations appeared identical. After diving experiments, electrical stimulation of the peripheral ends of both cut vagi (at midcervical level) produced a bradycardia in all chemodenervates.

Figure 1 presents cardiovascular data from the diving experiments with the four groups of ducks: 1) intact and sham-operated animals, 2) barodenervates, 3) chemodenervates, and 4) animals with both baroreceptors and chemoreceptors denervated. The results from intact (10 birds) and sham-operated (5 birds) animals were combined as their responses were shown to be identical. All three types of denervation resulted in elevated pre-dive heart rates. Pre-dive rates (mean \pm SE) were: 150 ± 5 (intact), 300 ± 45 (barodenervated), 235 ± 25 (chemodenervated), and 250 ± 15 (combined baro- and chemodenervated) beats/min.

During submergence, the cardiac rate of the barodenervated ducks dropped very quickly and after 60 s stabilized at levels similar to those of submerged intact ducks for the remainder of the dive. Due to the elevated pre-dive heart rates of the barodenervates, on a percentage basis the bradycardia was much greater than that of intact animals. Ducks without functional carotid bodies showed significant bradycardia during submergence, although heart rate only fell to the pre-dive rate of intact birds. Combined baro- and chemodenervates exhibited the same degree of bradycardia as chemoreceptor denervates. In both denervated groups, bradycardia was diminished, in terms of absolute magnitude of decline as well as percent decline (Fig. 1), compared with that of intact ducks. Examining the cardiac responses of intact, chemodenervated, and combined baro- and chemodenervated animals, 20, 45, and 60 s of submergence was required, respectively, before heart rates declined significantly ($P < 0.05$). Due to the inequality of the variances associated with the barodenervated data, no results from ANOVA are reported from this group. The large variability connected with these ducks was due to the fact that one of the barodenervates had a heart rate and blood pressure similar to those of intact birds. All three

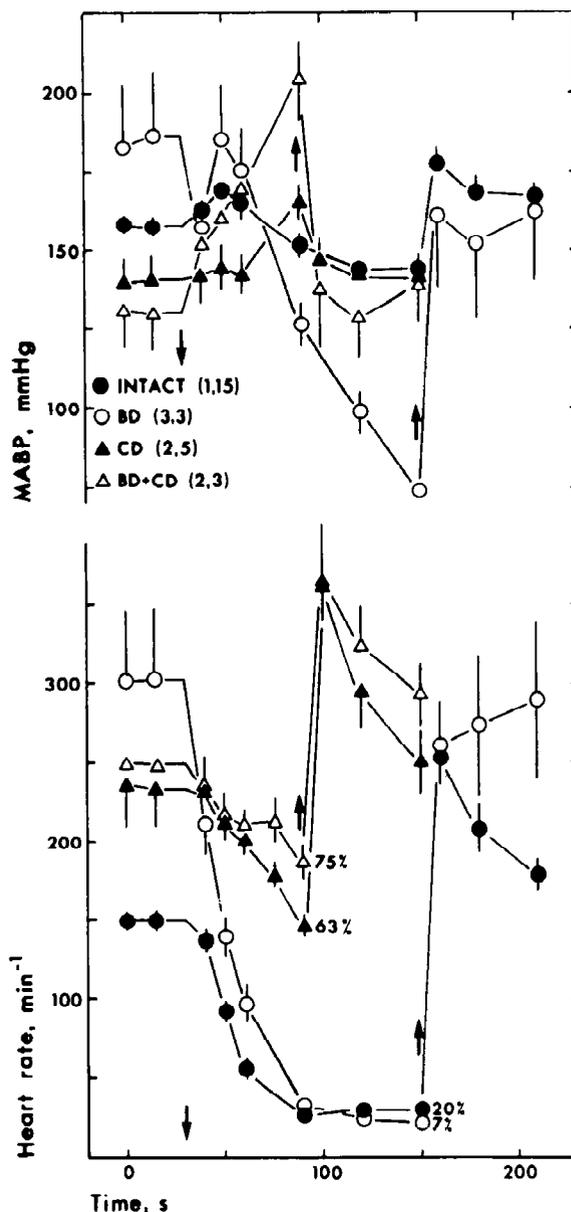


FIG. 1. Heart rate and mean arterial blood pressure (MABP) before, during, and after experimental dives with unanesthetized intact, barodenervated (BD), chemodenervated (CD), and combined baro- and chemodenervated (BD + CD) ducks. Symbols and bars represent means \pm SE derived from n dives with each of N animals, (n, N); 2-min dives, intact and barodenervated birds; 1-min dives, chemodenervated and combined baro- and chemodenervated birds. Downward arrows indicate submergence; upward arrows indicate emergence. Percentages beside heart rate symbols immediately before emergence indicate percentage of pre-dive level that end-dive value represents.

animals, nevertheless, exhibited comparable responses during diving.

Arterial blood pressure fell slightly during diving in intact ducks and decreased drastically during submergence in barodenervates. Ducks without intact carotid bodies exhibited a hypertensive response during diving that was more pronounced when the baroreflex had also been eliminated. Submergence of 90, 60, and 60 s was required before significant ($P < 0.05$) change occurred in

blood pressure in intact, chemodenervated, and combined baro- and chemodenervated animals, respectively.

DISCUSSION

Results from this investigation (Fig. 1) support the views that bradycardia during experimental diving in ducks is not baroreflexive in origin (12), and that the major portion of the response is due to stimulation of peripheral chemoreceptors (15). Nevertheless, intact systemic baroreceptors appear essential for maintenance of arterial blood pressure when heart rate falls during a dive.

A change in blood pressure induced by withdrawing or injecting blood (9, 14), by pharmacologic α -adrenoceptor blockade with phentolamine (1), or by sympathetic blockade with guanethidine or bretylium (18) seems to have little effect on diving bradycardia in ducks. In fact, only pretreatment with reserpine inhibits diving bradycardia when blood pressure falls in a dive (1, 18). Because reserpine appears to have a marked overall debilitating effect on the animals (18), one is reluctant to attribute the absence of bradycardia to a failure of the barostatic reflex particularly in light of the contradictory evidence provided by the other studies. The demonstration that injected norepinephrine causes hypertension and bradycardia in reserpinized ducks during diving (1) merely reveals that the baroreflex is present in the dive. In particular, the sensitivity of this reflex has been reported to decline during diving in ducks [(20); unpublished data]. However, it is questionable whether the sensitivity of the barostatic reflex during diving was correctly assessed in one of the investigations (20), since heart rate was simply compared to the prevailing blood pressure during diving without experimentally inducing changes in pressure. Thus, the change in sensitivity measured in this manner may largely be due to the chemoreceptor-driven reduction in heart rate occurring during a dive. Conversely, the sensitivity of the baroreflex in seals has been reported to increase during experimental diving (2).

Cardiovascular responses of long-term barodenervated ducks in the present investigation agree well with those found by Jones (12). The decline in heart rate during submergence in intact ducks is apparently accompanied by a compensatory increase in peripheral vascular resistance mediated by the systemic baroreceptors, since little change occurs in stroke volume (9, 13). The reason for the hypertensive response during diving in acutely barodenervated ducks (17), as compared with the hypotension in the present chronically denervated birds, is not clear. However, the difference in response indicates that a significant physiological change occurs with time after barodenervation. The rapid and extreme drop in heart rate in the barodenervates during the initial part of the dive appears to be similar to that previously seen in intact ducks with abnormally high cardiac rates (Lillo and Jones, unpublished observations). In these instances, heart rate generally dropped within 10 s after initial submergence to levels that resembled those normally seen in intact animals after 10 s under water. If this initial phase (the first 10 s) of the bradycardia response in the

barodenervates is overlooked, the remaining heart rate profile corresponds well with that of intact birds. Clearly, the actual heart rate of the denervates is higher during the 1st min of the dive, but the rate of decline is much greater, and the minimal rate is reached at about the same time in both groups. Such comparisons between these two groups seem justified, since their pre- and end-dive blood gas values were not very different (19).

Because chemodenervated ducks with or without intact baroreceptors displayed similar diving responses, the discrepancies between the carotid body denervation data from this study (i.e., indicating a substantial diving bradycardia) with those of Hollenberg and Uvnas (10) and Holm and Sorensen (11) cannot be due to their denervating the baroreceptors as well as carotid bodies. However, both these groups of investigators did not test the effectiveness of their denervations by checking the functional state of either the chemoreceptors or baroreceptors. Furthermore, since denervation procedures involve cutting neural fibers branching off the nodose ganglion of both right and left vagi, it seems extremely important to confirm whether the vagal efferents to the heart were still intact following denervation. In fact, the excessively high heart rates associated with the denervates of Holm and Sorensen (11) could very possibly reflect cardiac vagal damage.

The chemosensitivity, lung inflation, baroreflex, and vagal stimulation tests conducted in the present study accomplished the goal of determining the precise effects of the carotid body denervation operations and, thus, provide credibility to the conclusions. The carotid bodies appeared to be effectively denervated, since the ventilatory responses to hypoxia as well as hyperoxia were eliminated (6, 7, 16). However, no apparent damage to pulmonary vagal afferents or cardiac vagal efferents was evident.

The nature of the cardiovascular responses observed during submergence in chemodenervates is not entirely clear. When forcibly submerged, ducks exhibit an immediate but rather modest decline in heart rate that is apparently independent of chemoreceptor influence and related to cessation of breathing (1, 5). However, most of the bradycardia associated with the denervates was gradual in development and greater in magnitude than the typical initial response normally seen on submergence. This bradycardia was not the result of a baroreflex, stimulated by the increase in blood pressure, since the chemodenervated birds without functional baroreceptors displayed similar cardiac responses. Since blood pressure rose in chemodenervates, then a proportionately greater amount of the increase in peripheral resistance, compared with bradycardia, must be mediated by pathways other than those involving the carotid bodies. This increase in peripheral resistance, however, is much smaller in magnitude compared with that usually seen, since in normal dives bradycardia will reduce cardiac output to 10–20% of the pre-dive value, whereas mean arterial pressure is largely unchanged. Thus, vascular resistance must go up 5–10 times (8). However, because heart rate only falls by 25% during a 1-min dive in chemodenervated ducks, the increase in mean arterial pressure cannot

reflect more than a doubling of peripheral vascular resistance. Birds have other chemoreceptors, supplied by the cerebral circulation that contribute to the ventilatory response to CO₂ (21, 22); and, as blood CO₂ increases during a dive, they may effect this small proportion of the cardiovascular responses to submergence.

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