THE RELATIONSHIP BETWEEN DIVE AND PRE-DIVE HEART RATES IN RESTRAINED AND FREE DIVES BY DIVING DUCKS

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SUMMARY

Dive heart rate was plotted against pre-dive heart rate in forced and voluntary dives and dabbles by restrained and free ducks. The relationship between pre-dive heart rate and the cardiac interval occurring just before or coincident with sub-mersion (first cardiac interval) and the heart rate after 2–5 s submergence (stabilized heart rate) was emphasized. Stabilized heart rate in forced dives by restrained ducks at rest and at the end of a bout of exercise, and heart rate in voluntary dives and dabbles were linearly related on a plot of dive heart rate against the logarithm of pre-dive heart rate. Even the heart rate occurring 2–5 s after ducks were 'trapped' under water, compared with the rate immediately before 'trapping', fitted on this line. The line was described by the equation $y = -451 + 246\log x$ where y is dive (or trapped) and x is pre-dive (or pre-trap) heart rate ($r^2 = 0.98$). The relationship was unaltered by β-blockade with propranolol. Furthermore, nasal blockade with Xylocaine, O_2 breathing before submersion, and arterial baroreceptor denervation had no marked effect on the relationship in voluntary and trapped dives. Implantation of stimulating electrodes bilaterally on the cut distal ends of vagal and cardiac sympathetic nerves suggested that in all these dives there is a similar increase in the level of efferent vagal activity during submersion. However, the first cardiac interval in voluntary dives represents a much lower heart rate and therefore higher level of vagal activity. The present data suggest that there is considerable psychogenic modulation of cardiac responses in voluntary diving and only in forced dives, by restrained animals, is cardiac control largely reflexogenic.

INTRODUCTION

Diving ducks show extremely different cardiac responses to submergence in voluntary compared with forced dives (Butler & Woakes, 1976, 1982a; Furilla & Jones, 1986). In forced dives, heart rate drops rapidly to around 20% of the pre-dive rate (Furilla & Jones, 1986). In contrast, dabbling ducks, such as the mallard (*Anas*

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platyrhynchos), exhibit a more slowly developing bradycardia in forced dives although, ultimately, heart rates again reach 10–20% of pre-dive rates (Hudson & Jones, 1986). In voluntary dabbles, on the other hand, the mallard shows little or no heart rate change associated with immersion, submergence or emersion (Gabrielsen, 1985; Furilla & Jones, 1986). In contrast, diving ducks show a number of cardiac adjustments to voluntary diving. A pre-dive tachycardia is followed by a marked fall in heart rate on submersion; heart rate then increases and in most cases exceeds that recorded from ducks at rest on the water surface (Butler & Woakes, 1982b).

This difference in the cardiac responses to voluntary and forced diving has led to considerable criticism of the concept of a 'diving response'. A number of authors have promoted the opinion that in forced dives the response is a product of, or is accentuated by, fear or stress (Kanwisher, Gabrielsen & Kanwisher, 1981; Kanwisher & Gabrielsen, 1985), depite claims that 'calm' or 'relaxed' ducks respond better in forced dives (Folkow, Nilsson & Yonce, 1967). Consequently, the lack of marked bradycardia in voluntary head submergences is viewed as the natural situation (Kanwisher *et al.* 1981). Obviously, these opinions imply that higher levels of the central nervous system modulate cardiac responses to submergence, especially in forced dives. This conflicts with the opinions of those who view cardiac events in forced dives as largely resulting from reflexogenic mechanisms (Huxley, 1913; Andersen, 1963; Gabbott & Jones, 1986).

No one, to our knowledge, has attempted to research the problem of the role of psychogenic and reflexogenic mechanisms in diving responses to see how one influences the other. One attempt has been made to quantify the extent of psychogenic modulation of the diving response in dabbling ducks (Blix, 1985), but this approach was literary rather than experimental. However, diving ducks display cardiac adjustments in association with the initiation and performance of voluntary diving behaviour (Butler & Woakes, 1982b) and therefore represent a means to explore the relationship between cardiac responses in voluntary and forced dives. Hence, we have tried to establish relationships between dive and pre-dive heart rates in dives by restrained and freely moving animals. Furthermore, we felt that it was important that any relationships be supported by our knowledge of both the afferent (Furilla & Jones, 1986) and efferent neural mechanisms involved in the response. To this end, we also report the results of a limited investigation of the efferent control of the heart rate in the duck.

MATERIALS AND METHODS

Eight redhead ducks (*Aythya americana*) and four lesser scaup (*Aythya affinis*) were used to monitor the heart rate response to voluntary and forced diving. Heart rate was obtained telemetrically using electrocardiogram (ECG) transmitters (Narco Biosystems, Downsview, Ontario, Canada). A midline incision was made in the skin and body wall over the abdomen after anaesthetizing the area by injection of local anaesthetic (Xylocaine, Astra Pharmaceuticals, Mississagua, Ontario). Bipolar loop electrodes were placed on the pericardium and the transmitter was placed in the

peritoneal cavity. Before insertion, the transmitter and electrodes were immersed in an antiseptic solution. The peritoneal cavity was then closed with surgical silk. After surgery, 125 mg of ampicillin (Penbritin, Ayerst Laboratory, Montreal, Quebec) was administered intramuscularly and the birds were allowed at least 1 day to recover before being used in any experiments. Recordings were made from an individual bird for up to 4 weeks and no differences were noted in the heart rate responses to submergence over this period. The ECG signals were received on a Narco FM-Biotelemetry receiver, stored on magnetic tape, and displayed on a pen recorder. On playback, heart rates were either determined from measurements of the cardiac intervals or by using a cardiotachometer.

Forced dives were performed by gently lowering the head of the duck into a container of water (10°C), and ducks were submerged for random times of not less than 15 s and not more than 2 min. To elevate the heart rate of ducks before a forced dive, one redhead duck was run on a treadmill and two others were allowed to run along a corridor until heart rate was over 400 beats min^{-1}. Immediately after exercise ceased, the duck's head was forcibly submerged into a beaker of water for 15 s. Voluntary dives were done on a man-made pond with a surface area of 3 m × 5·5 m. The bottom of the pond sloped so that the depth of the water ranged from 0·3 to 1·7 m. A platform (2·0 m × 1·5 m) with a Plexiglas enclosure (1·0 m × 1·5 m × 0·8 m high) was placed at the shallow end of the pond. Ducks entered the enclosure from the platform through an opening which could be closed off by a vertically sliding door. This door sealed the enclosure sufficiently so that oxygen levels in the enclosure could be elevated from air values to more than 80% oxygen. Also, the underwater entrance to the enclosure could be closed off by dropping a vertical panel from the side of the enclosure to the bottom of the pond. The surface of the water outside the enclosure was covered with netting stretched over wooden frames. Each frame was 1 m^2. The frames floated on the water and prevented the birds from surfacing anywhere but within the enclosure. However, the birds could lift the netting to take a breath if it became necessary. A feeding station with a chute through which food could be dropped into a receptacle at the bottom was placed at the corner of the pond furthest from the enclosure. Most voluntary dives occurred in the period after food had been delivered into the feeding chute. However, on some occasions the birds were made to submerge by banging on the lid of the enclosure with a stick or waggling a net at them (chase-induced dives) (Furilla & Jones, 1986). Four redhead ducks and four lesser scaup were prevented from surfacing at the end of voluntary or chase-induced dives by lowering the vertical panel to close off the underwater entrance to the enclosure just before the bird was to surface. The panel was usually lifted after an additional 10 s of diving; however, on one occasion each duck was forced to remain under water until it floated up under the netting and breathed.

The effects of various neural inputs on the diving responses in voluntary dives, especially where animals were prevented from surfacing, were investigated in eight birds. In three redheads, baroreceptors were denervated using methods similar to those described by Jones (1973), and diving responses were investigated after a 3-week recovery period. The efficacy of barodenervation was tested by measuring the

cardiac response to intravenous injection of the pressor agent, phenylephrine (25 μg in intact and 50 μg in barodenervated ducks). Four ducks (two redhead and two scaup) were allowed to breathe oxygen before unrestrained dives by flowing oxygen (at 20 l min^{-1}) through the enclosure. A fan mounted inside the enclosure mixed the gas with residual air. We assumed that this procedure would reduce arterial chemo-receptor stimulation in the dive. Nasal receptors were anaesthetized in two redheads using Xylocaine, as previously described (Furilla & Jones, 1986).

To reduce the sympathetic contribution to the increase in heart rate before a voluntary dive, 1·5 mg kg^{-1} of propranolol was injected into the muscles of three redhead ducks, and the animals were immediately returned to the pond. We also tried to reduce pre-dive heart rate by non-pharmacological means by encouraging three redhead ducks to dabble for food. The ducks were placed one at a time on a 25 cm deep pond with food on the bottom which the ducks reached by dabbling. To simulate the 'forced' dive response by unrestrained ducks, two redheads were presented with a 1-l beaker of water on the floating platform at the end of the pond. They voluntarily submerged their heads in the beaker to obtain food which covered the bottom.

In all dives, heart rate was determined from measuring the number of beats in the second before submersion, from the cardiac interval occurring just before or co-incident with submergence (first cardiac interval) and from cardiac intervals after the heart rate had stabilized, but not later than 5 s after submergence. However, when pre-dive heart rate was low (<150 beats min^{-1}) beats were counted over a 5-s, pre-dive period. Data were analysed by plotting the relationships between pre-dive heart rate and the heart rate at the first cardiac interval or heart rate in the first 2–5 s of diving. Regression analysis was performed on the data using a curve-fitting program on a microcomputer. When animals were trapped under water, the heart rate was measured 1 s before and 2–5 s after the partition had been closed. In this series of experiments n is the number of observations and N is the number of animals used.

To investigate the efferent neural pathway, we implanted stimulating electrodes, bilaterally, on the cut peripheral ends of the cardiac sympathetic and vagal nerves of three small white Pekin ducks (*Anas platyrhynchos*; body mass of approximately 1 kg). Ducks were anaesthetized by intramuscular injection of pentobarbital and the sternum was divided in the midline to expose the central cardiovascular area. Cardiac sympathetic and vagal nerves were identified as they coursed towards the heart and were sectioned 1–2 cm from the heart. Loop electrodes, similar to those described by Jones *et al.* (1983), were threaded onto the distal cut ends of the nerves. The electrodes were connected, one pair from each pair of nerves, to two stimulators *via* stimulus isolation units (Grass Model PSIU6D; Grass Instruments Corporation, Quincy, MA, USA). Rectangular wave stimulation pulses of 2·5 ms and 0·5 mA were used to excite the vagi and 1 mA current for the sympathetic cardiac nerves. These parameters were held constant and heart rate was caused to vary by changing the pulse frequency. For the cardiac nerves maximum heart rates were obtained at stimulation frequencies of 7–8 Hz while for the vagi frequencies up to 40 Hz were sometimes necessary before minimum heart rates were obtained. These stimulation
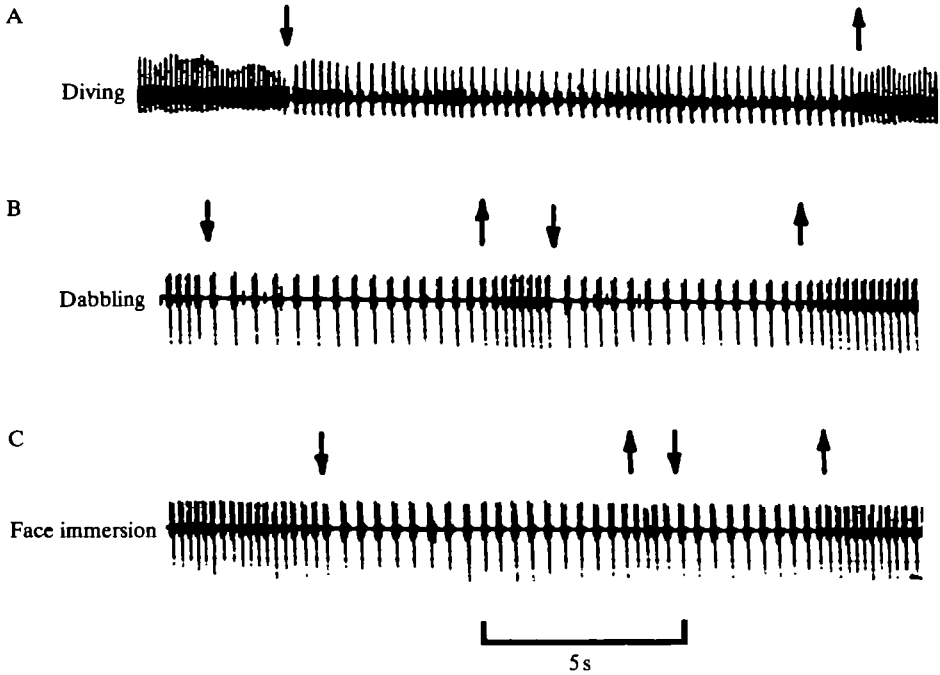
Fig. 1. Electrocardiogram traces of a redhead duck (A) diving voluntarily, (B) dabbling and (C) immersing its head into a beaker of water to retrieve food. The downward arrows are the approximate points of submergence and the upward arrows are the points at which the duck surfaced.

frequencies suggest that current intensity was maximal for the sympathetic but not for the parasympathetic nerves (Levy & Zieske, 1969), although increasing vagal stimulation current to 1 mA caused no obvious difference in the heart rate response at any given frequency of stimulation. Heart rate was recorded over a wide range of stimulation frequencies for each pair of nerves (although the frequency of stimulation was always the same for both vagal or both cardiac nerves). These heart rates were plotted against stimulation frequencies of vagal and sympathetic nerves using the method of presentation of Levy & Zieske (1969) except that the stimulation frequencies were normalized with regard to the frequency used in each animal, the maximum cardiac response being taken as 100 %. At the end of these experiments animals were killed with an overdose of pentobarbital.

RESULTS

Cardiac response to voluntary diving

Heart rates varied greatly during voluntary diving and dabbling, but there was a consistent pattern to the responses. Dives were usually performed in a series, and heart rate increased before the first dive and continued to do so in the pauses between dives. When diving, pre-dive and dive heart rates of redhead ducks were always nigher (Fig. 1A) than when dabbling (Fig. 1B) or retrieving food from the beaker of
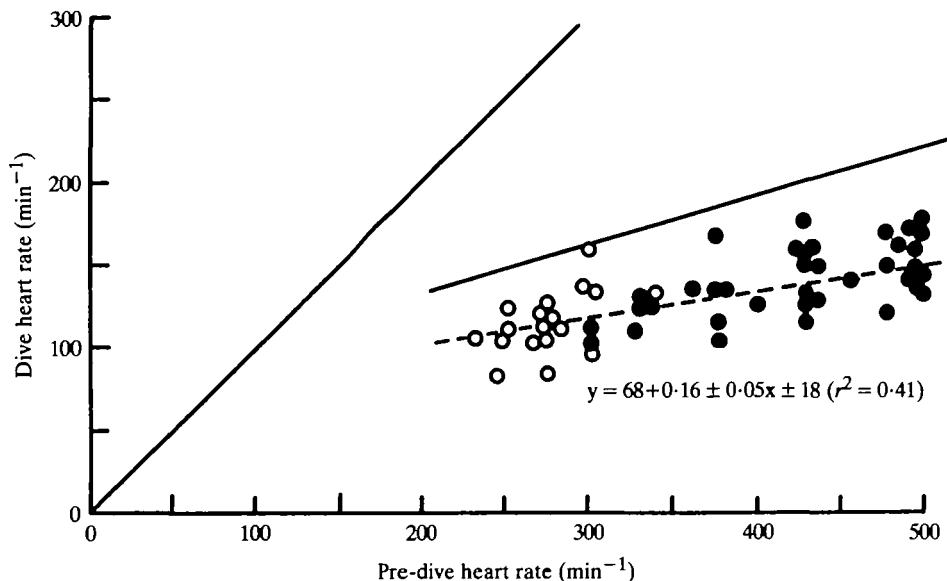
Fig. 2. The relationship between the pre-dive heart rate and the first cardiac interval at submergence. The broken line is the regression on these data and the regression equation includes the 95% confidence limits of the slope and the standard error of estimate. O, after β-blockade with propranolol; ●, untreated ducks. The short solid line is taken from Furilla & Jones (1986), and represents the stabilized heart rate occurring between 2 and 5 s after submergence. In this and all other similar figures the line through the origin represents the line of identity.

water (Fig. 1C). In all three situations heart rate dropped immediately upon submergence. The first cardiac interval in voluntary dives was usually the longest, and heart rates fell to between 100 and 140 beats min^{-1} (Fig. 2). Heart rate at the first cardiac interval was positively correlated with pre-dive heart rate. Pre-dive heart rate was more strongly correlated with heart rate after 2–5 s submergence (Fig. 2), and dive heart rate was significantly above that occurring at the first cardiac interval at all pre-dive heart rates over 250 beats min^{-1} (Fig. 2). β-Blockade prevented pre-dive heart rate from exceeding 300 beats min^{-1} even in a series of dives, but on submergence both the first cardiac interval and heart rate after 2 s and before 5 s fell in the same range as those obtained from untreated ducks with low pre-dive heart rates, i.e. before voluntary face immersion or dabbling. Blockade of nasal receptors with Xylocaine reduced the cardiac response to submergence by 10–30% (Furilla & Jones, 1986), although the heart rate response was unaffected by breathing 100% oxygen pre-dive or by chronic baroreceptor denervation.

Cardiac responses to forced diving by restrained and free animals

Heart rate of restrained animals, in the laboratory, was usually 90–120 beats min^{-1}, although occasionally rates as high as 200 beats min^{-1} were observed. On submersion, heart rate fell rapidly to a stable level in approximately 5 s (Fig. 3A). In contrast to the situation in voluntary diving, the first cardiac interval was usually the shortest in forced dives (Fig. 3A). Pre-dive heart rates were considerably elevated
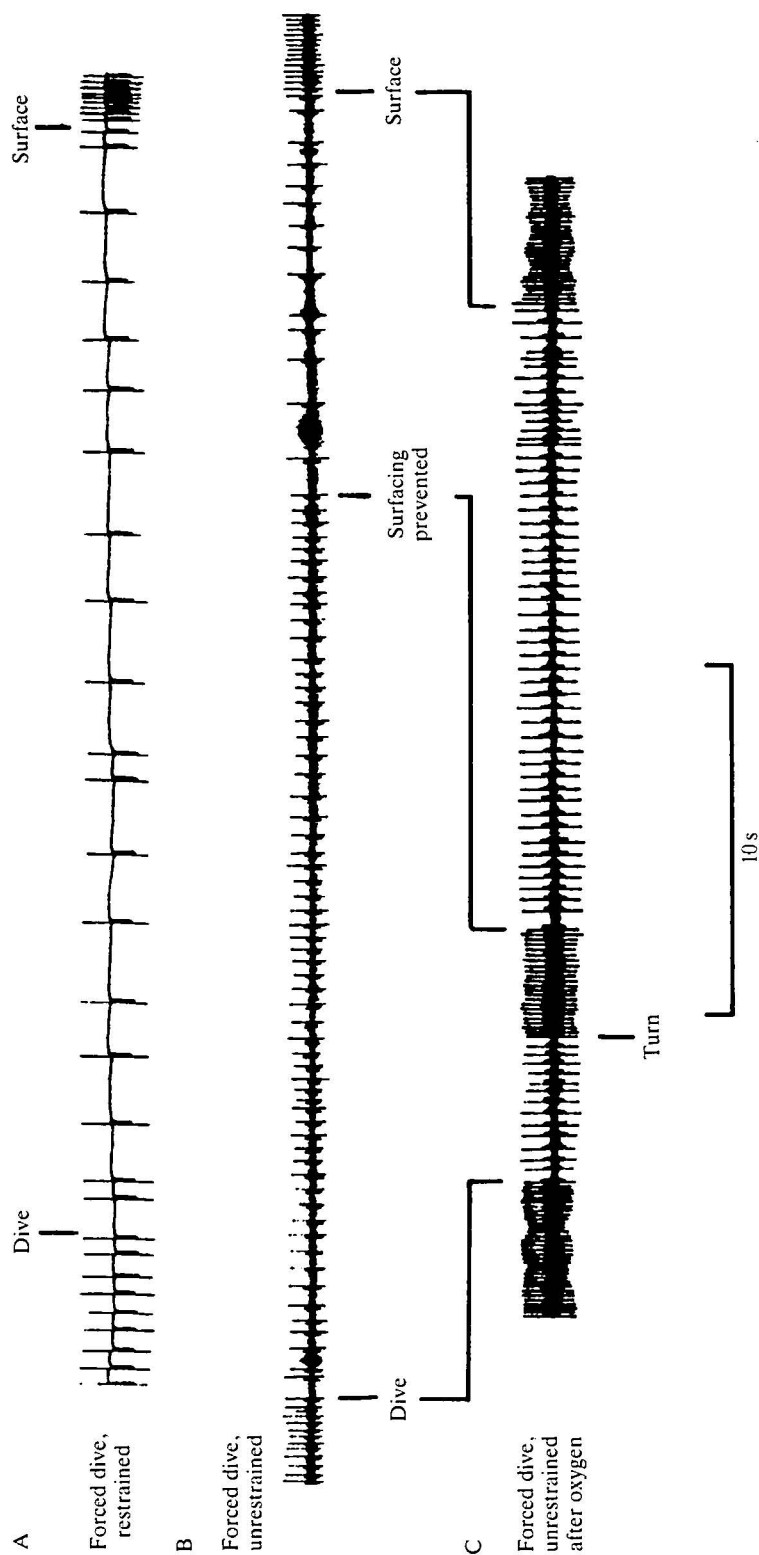
Fig. 3. Electrocardiogram traces of a redhead duck (A) forcibly submerged while under restraint, (B) prevented from surfacing at the end of a voluntary dive and (C) as in B but the duck had breathed oxygen before diving. The point marked 'turn' is the point at which the duck began to return to the enclosure.

in chronic barodenervates (179 ± 29 beats min^{-1}), but dive heart rates spanned the range seen in intact ducks. The ducks running on a treadmill had a pre-dive heart rate of over 300 beats min^{-1}, and heart rate fell on forced submergence but not as low as in restrained animals (Fig. 4). Ducks which ran along the corridor before being forcibly submerged had extremely high pre-dive heart rates (over 400 beats min^{-1}). Heart rate fell immediately and remained stable for 2–5 s, after which the rate began falling gradually but quickly over the remainder of the 15-s dive. It is only the first 5-s period that was used in the present analysis (Fig. 4). Unfortunately, it was not possible to obtain reliable estimates of the first cardiac interval in dives involving exercising animals and the regression line shown in Fig. 4 pertains only to forced dives in the laboratory.

Preventing access to the surface caused a pronounced fall in heart rate when the duck returned to the surface in the enclosure at the end of a voluntary dive. Heart rate fell immediately after the entrance to the chamber had been blocked. Mostly this new rate was maintained for the rest of the enforced submergence although, occasionally, it slowly increased (Fig. 3B). Heart rate 2 s after blocking the chamber was correlated with the rate immediately before blockade, and although the heart rates of restrained ducks before and after submergence were often lower than those of unrestrained ducks before and after access to the surface had been prohibited, there was considerable overlap of the dive:pre-dive relationship (Figs 4, 5). This overlap in the relationship was unaffected by β-blockade, baroreceptor denervation or
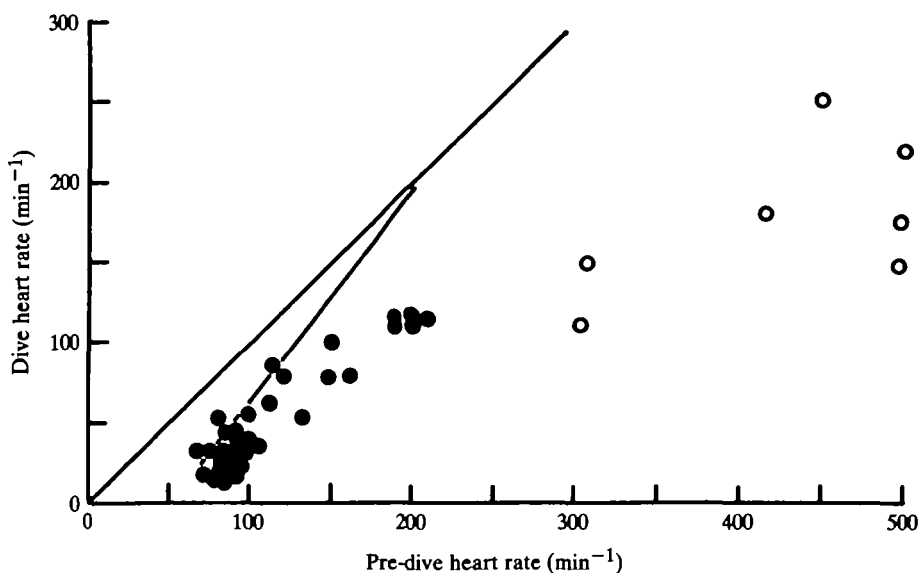

Fig. 4. The relationship between dive and pre-dive heart rates taken at the time when heart rate stabilized but before 5 s submergence in restrained dives. ●, data taken while the animals were immobilized on an operating table; ○, from one duck, exercised on a treadmill (the two points at 300 beats min^{-1} pre-dive) and from two ducks after being allowed to run along a corridor (above 400 beats min^{-1} pre-dive). The short line with slope >1 was drawn from the regression of the first cardiac interval for restrained dives not including those following exercise.

anaesthetization of nasal receptors with Xylocaine. In two scaup, breathing 100% O_2 before the dive had no effect on the dive:pre-dive heart rate relationship. In another two scaup and also in one redhead whose baroreceptors had been denervated, heart rate rose suddenly soon after the birds turned to return to the enclosure (Fig. 3C). When surfacing was prevented heart rate fell into the range of those in voluntary dives made from similar starting heart rates (Fig. 5).

On two occasions, with each duck, the entrance to the enclosure was not re-opened. Animals swam around the pond although wing propulsion replaced leg propulsion after about 40 s under water. Eventually all activity ceased and the ducks floated up under the netting covering the pond, and breathed. Heart rate remained low throughout these manoeuvres except when the breath was taken. The total period spent under water until activity ceased was around 60 s and this was extended by 10 s when the ducks breathed oxygen before the dive.

The relationship between the cardiac response to voluntary diving and those to forced diving by restrained and free animals

Linear, exponential, logarithmic, power and quadratic regressions were performed on a plot of stabilized dive (or trapped) heart rates against pre-dive (or pre-trap) heart rates for dabbles, for voluntary and chase-induced dives before and after propranolol and for forced dives by restrained animals at rest and after exercise. For combined data, the highest coefficient of determination (r^2) was obtained for the
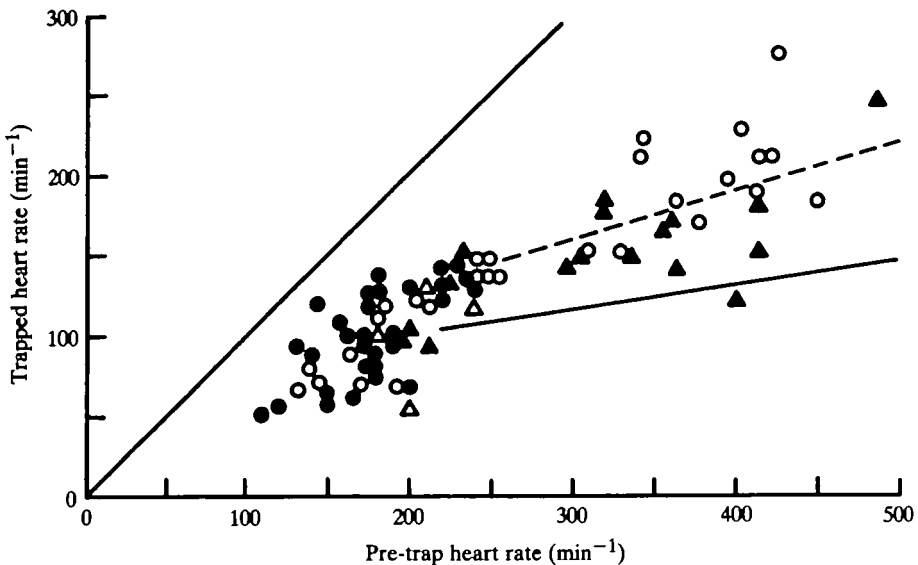

Fig. 5. The relationship between 'trapped' and 'pre-trap' heart rate. Trapping was effected by preventing surfacing at the end of voluntary or chase-induced dives. ●, intact animals having breathed air before the dives; ○, ducks that had breathed oxygen before the dive; ▲, barodenervated ducks; △, ducks with nares anaesthetized with Xylocaine. The short solid line is from the regression of the first cardiac interval in voluntary dives, and the broken line describes the stabilized rate after 2 s but before 5 s submergence (from Furilla & Jones, 1986).
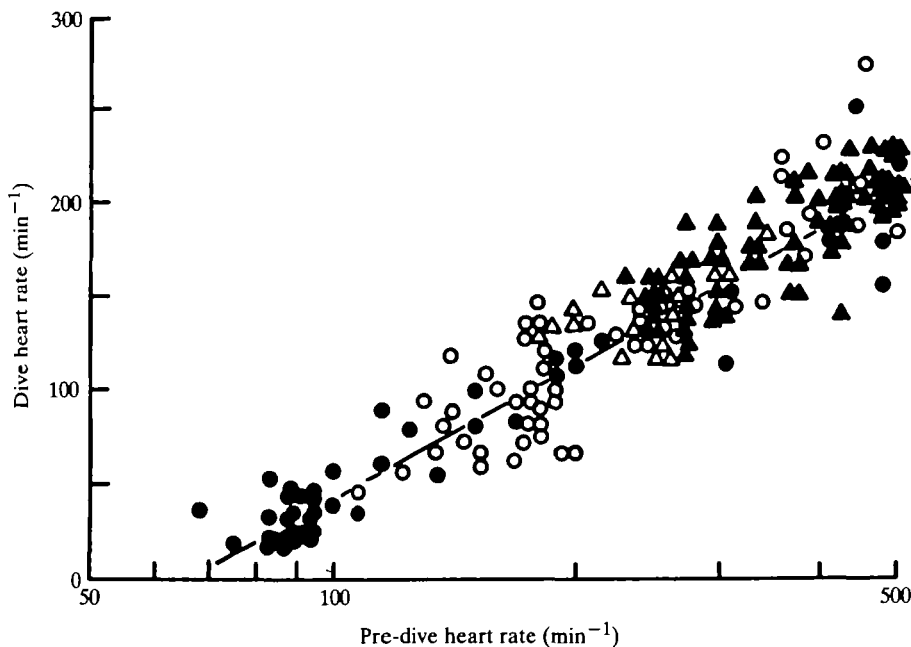
Fig. 6. The relationship between dive (or trapped) heart rate and the logarithm of pre-dive (or pre-trap) heart rate for all dives. ●, restrained dives including those after exercise; ○, all trapped dives; ▲, all voluntary dives including β-blocked dives; △, dabbles and voluntary face immersion.

regression of dive heart rate against the logarithm of pre-dive heart rate (Fig. 6; Table 1). The slope of the line was not significantly different from slopes obtained using a similar regression analysis on each group of data alone (Table 1).

Cardiac control by vagal and cardiac sympathetic nerves

Heart rate was 283 ± 28 beats min^{-1} ($n = 9$; $N = 3$) after bilateral section of the vagal and cardiac sympathetic nerves of Pekin ducks. This was also the heart rate

Table 1. Regression coefficient (b) and coefficient of determination (r^2) for general non-linear fitting to the model $y = a + b \log x$ where y is dive heart rate (or heart rate after trapping) and x is pre-dive (or pre-trap) heart rate

Condition	N	n	b (±S.E.)	r^2
Voluntary dives and dabbles (unrestrained)	5	75	234 ± 19	0·99
Trapped dives (unrestrained)	8	71	251 ± 20	0·98
Forced dives (restrained)	6	38	220 ± 11	0·96
All above dives	19	184	246 ± 7	0·98

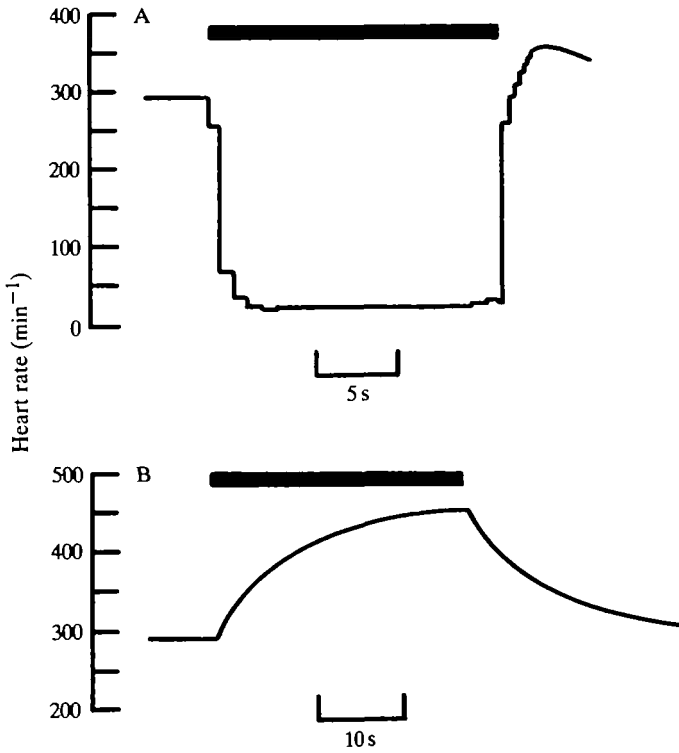N, number of ducks; n, number of observations.

Fig. 7. The heart rate response to bilateral stimulation of the (A) vagus (0·5 mA, 2·5 ms, 35 Hz) and (B) cardiac sympathetic nerves (1 mA, 2·5 ms, 7 Hz). The horizontal bar represents the duration of the stimulus.

observed in two redhead ducks after pharmacological blockade of cardiac sympathetic and vagal nerves (propranolol, 1·5 mg kg^{-1}, and atropine, 2·5 mg kg^{-1}). Bilateral stimulation of the vagal nerves resulted in a rapid fall in heart rate, a stable rate usually being achieved within 1 or 2 s (Fig. 7). Restoration of pre-stimulation heart rate was equally rapid when stimulation was stopped. In contrast, heart rate only rose slowly in response to bilateral stimulation of the cardiac sympathetic nerves. Usually it took about 30 s for heart rate to stabilize even in response to the maximum stimulus frequency we used (8 Hz). When stimulation stopped, heart rate fell slowly and reached pre-stimulation levels within 20–30 s. Heart rates *versus* normalized stimulation frequencies of vagal and sympathetic nerves are shown in Fig. 8, and the surface in Fig. 8 predicts all heart rates that can be produced by any combination of sympathetic and vagal stimulation.

DISCUSSION

The present data have shown that in diving ducks heart rates after 2 s but before 5 s submergence are linearly related to the logarithm of heart rate in the immediate pre-dive period for a wide range of diving behaviour. This relationship holds for unrestrained ducks making voluntary dives, chase-induced dives, dabbles and even
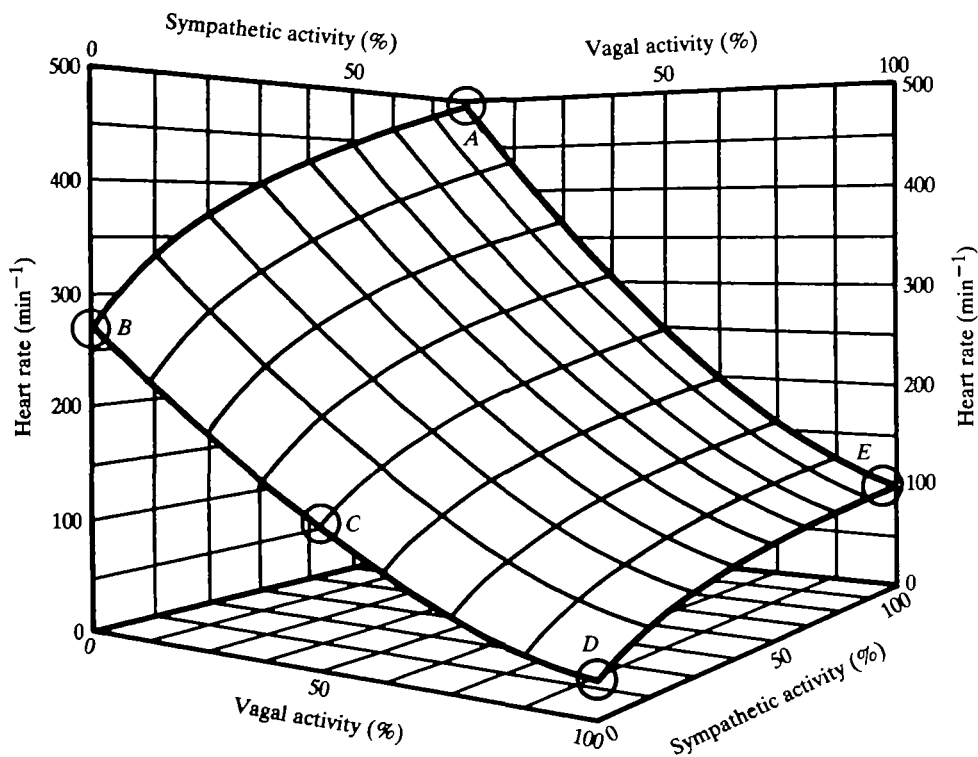
Fig. 8. The relationship of heart rate to bilateral stimulation of the distal cut ends of the vagus and cardiac sympathetic nerves. 100% represents the frequency of stimulation above which no further changes in heart rate occurred with increases in stimulation frequency. The heart rate caused by a given level of vagal and sympathetic stimulation was plotted on 'perspective' graph paper and the surface was drawn, by eye, to encompass all heart rates obtained in the stimulation experiments. See the text for an explanation of points *A–E*.

while immersing their head in a beaker of water. The relationship also holds for restrained ducks forcibly submerged while at rest and immediately after an exercise bout. Furthermore, even heart rates 2–5 s after ducks are 'trapped' under water, compared with the rates immediately before 'trapping', fit this relationship. This is the first demonstration of a relationship between the cardiac response in forced and natural diving behaviour, but whether this relationship can be supported by our knowledge of the efferent and afferent neural mechanisms affecting cardiac control remains to be demonstrated.

Little new information about cardiac efferent neural control in diving ducks has been obtained directly from these studies. β-Blockade with propranolol indicated an important role for the cardiac sympathetic innervation in the elevation of pre-dive heart rate which occurs with time as a diving bout progresses. On the other hand, there seems to be little sympathetic influence on heart rate in birds at rest before forced dives. Furthermore, stimulation experiments suggest that there would not be time for changes in sympathetic activity to affect heart rate significantly in voluntary dives. In fact, this suggestion is supported by the observation of Butler & Woakes

(1982a) showing that heart rate in unrestrained ducks diving after atropine injection did not change, even when pre-dive heart rate was as high as 400 beats min^{-1}. Also, no heart rate changes accompany forced submergence by restrained redheads after atropine injection (R. A. Furilla, unpublished results). Hence, it seems reasonable to conclude that cardiac responses in both free and forced dives are caused by changes in cardiac vagal activity.

A given heart rate results from the interplay of vagal and sympathetic activities (Fig. 8). Nevertheless, there seem to be regions on the surface shown in Fig. 8, obtained from anaesthetized Pekin ducks, that can be extrapolated with confidence to intact or alert diving ducks. Heart rates in cardiac denervated Pekin ducks and pharmacologically denervated redheads were equivalent. This region is identified as area *B* on the surface in Fig. 8. β-Blockade with propranolol resulted in heart rates around 300 beats min^{-1} in redheads before voluntary dives so that area *B* must also represent the interplay of vagal and sympathetic activities to produce this heart rate. In Pekin ducks, maximal sympathetic activation in the absence of vagal stimulation resulted in heart rates of 500 beats min^{-1} (area *A* in Fig. 8) which was also the highest rate observed in divers before voluntary dives. This and the previous observation suggest that by using small Pekin ducks we minimized mass-specific influences on such parameters as maximum heart rate. Finally, before restrained dives heart rate was between 90 and 140 beats min^{-1}, and since β-blockade did not lower heart rate further we believe that cardiac efferent control in these animals is described by the region around point *C* on Fig. 8. If areas *A*, *B* and *C* actually represent the vagosympathetic interplay to elicit pre-dive heart rates in voluntary, β-blocked and forced dives, respectively, then it can be seen from Fig. 8 that a like increase in vagal activity, of about half maximal, will give the dive heart rates between 2 and 5 s under water. Furthermore, heart rates in all other dabbles and dives, including heart rate changes when ducks are trapped under water compared with pre-trapped rates, appear to be the result of a similar increase in vagal activity. The curvilinear relationship between sympathetic and vagal activity and heart rate, alone or in combination (Fig. 8), is obviously linearized by taking the logarithm of pre-dive heart rate in the dive:pre-dive heart rate relationship. Support for this conclusion was obtained by re-analysing our stimulation data. A series of stepped increases in vagal activity representing an increase of about 50% of maximal vagal activity (from 0 to 50%, 20 to 70%, 50 to 100%, for example, on Fig. 8), at any given level of sympathetic stimulation, gave points which also lay around the same line as that which describes the dive:pre-dive heart rate relationships.

A 50% increase in vagal activity in forced dives by restrained ducks will result in maximal vagal activity (Fig. 8). In voluntary dives, the first cardiac interval is usually the longest and could also represent the heart rate at maximal vagal activity. However, it may be that there is insufficient time for full expression of the brady-cardia, because even during vagal stimulation the lowest, stable heart rates were not attained for at least 2 s (Fig. 7). Nevertheless, it might be expected that these points would be related on a plot of dive:pre-dive heart rate but it is difficult to predict what form the relationship would take. However, this relationship could be similar to that

describing the influence of sympathetic activity on heart rate at maximal vagal activity (Fig. 8). The relationship is illustrated by the curve DE in Fig. 8.

It seems unlikely that a single afferent mechanism could provide the necessary vagal activity in all types of dive, if only for the fact that there may be maximum vagal activity, although declining rapidly, at the start of all voluntary submersions, whether dives or dabbles. Surprisingly, Butler & Woakes (1979) claimed that the tufted duck shows no heart rate changes when freely dabbling; yet nine out of 10 of the dabbling episodes, as seen in their fig. 5A, are associated with rapid changes in heart rate and in three cases these changes are greater than 100 beats min^{-1}. Some of the heart rates associated with dabbling and emerging in the tufted duck resemble those depicted in Fig. 1B of this paper for a redhead duck dabbling voluntarily. The termination of hyperventilation at the onset of a dive or dabble (Butler & Woakes, 1976, 1979) could enhance vagal outflow and reinforce an increase in vagal activity concomitant with the onset of submergence, giving a prolonged initial cardiac interval. There is no pre-dive tachycardia or hyperventilation in forced dives, however, and in these dives heart rate declines rapidly and progressively. Certainly, the description of the first cardiac interval in free and forced dives by two separate linear regression equations seems entirely appropriate.

However, it does not seem implausible that a common afferent mechanism may produce a similar maintained level of vagal activity in all types of dive. Unfortunately no support for such a mechanism can be derived from our previous investigation of the role of afferent reflexogenic neural mechanisms in the diving response (Furilla & Jones, 1986). We showed that all of the cardiac response in restrained dives could be attributed to nasal receptors, but only between 10 and 30 % of the response was due to nasal stimulation in voluntary or chase-induced dives. Hence another mechanism must be involved in voluntary dives, but we do not believe that this other mechanism has anything to do with peripheral chemoreceptors. Breathing elevated or reduced levels of oxygen in the air before diving had no effect on the dive: pre-dive heart rate relationship up to 5 s submergence (Furilla & Jones, 1986). So, although chemoreceptors undoubtedly influence heart rate in longer dives (Butler & Woakes, 1982a), any influence is not expressed in the first 5 s of a dive. Certainly, in some ducks that had breathed oxygen before diving, heart rate increased markedly after they turned round to begin the return trip to the enclosure, suggesting a chemo-receptor influence on heart rate in long dives.

The response to forced diving in unrestrained animals is of considerable interest. As soon as the animal became aware that it was not going to be allowed to surface, heart rate fell to levels which would have been seen in forced dives by restrained ducks, depending on the heart rate immediately before surfacing was prevented. A similar response was described by Butler & Woakes (1982b) in tufted ducks, although they described it as 'progressive', as opposed to the sudden fall seen in our redhead ducks. This, then, may be an expression of the 'classical' dive response in unrestrained diving, but we are unable to suggest what mechanisms are involved in generating this response.

The fact that we have been unable to show any major reflexogenic influences on heart rate in voluntary dives leads us to propose that psychogenic influences are much more likely to be expressed in free than in restrained dives in diving ducks. For instance, psychogenic influences affect dive heart rate both initially, and after 2–5 s submergence, through their influence on the pre-dive rate. Anticipation of the dive response, described in voluntary dives by Butler & Woakes (1976, 1982*b*), also implies a profound psychogenic influence. Finally, the fact that heart rate can immediately drop when the normal diving pattern is disrupted, in unrestrained animals, suggests that, in free dives, processes of integration occur which are well above the brainstem level. These conclusions appear to be in conflict with those obtained from studying restrained and free head submersions by dabbling ducks (Kanwisher *et al.* 1981; Blix, 1985) in that psychogenic influences are claimed to affect the former but not the latter. Obviously this conflict can only be resolved, if at all, by further research.

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