Cardiac responses to first ever submergence in double-crested cormorant chicks (*Phalacrocorax auritus*)

Manfred R. Enstipp *, Russel D. Andrews, David R. Jones

Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC, Canada, V6T 1Z4

Abstract

Heart rates were recorded from double-crested cormorant chicks during their first ever and subsequent voluntary head submergences and dives, as well as during longer dives made after the chicks were accustomed to diving. Despite variation between chicks, the cardiac response to first ever and subsequent voluntary submergence (head submergences and dives) was similar to the response observed in adult cormorants. Upon submersion the heart rate fell rapidly when pre-submersion heart rate was high (325–350 beats min^{-1}). The heart rate established within the first second of voluntary submergence was between 230 and 285 beats min^{-1}, well above resting heart rate (143 beats min^{-1}). The same initial cardiac response occurred during longer dives performed after the chicks were accustomed to diving. In these dives the heart rate remained at the level established on submersion, unlike the response observed in shallow diving adult cormorants in which the heart rate declined throughout the dive. The heart rate was also monitored in a separate group of chicks in which the first exposure to water was during whole body forced submergence. Again, the observed response was similar to the adult response, although the cardiac response of chicks to forced submergence was more extreme than to voluntary submergence. Our results do not support the hypothesis that learning (by conditioning or habituation) is involved in the cardiac adjustments to voluntary submergence. It is suggested that the initial cardiac adjustments are reflex in nature and this reflex is fully developed by the first submergence event. Although the nature of this reflex pathway is obscure, cessation of breathing before submersion and the close linkage between breathing and heart rate might provide a plausible mechanism. © 1999 Elsevier Science Inc. All rights reserved.

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1. Introduction

In diving ducks and cormorants, there is a rapid fall in heart rate at the start of both voluntary dives and forced submergence [2,4,12,15,18]. In tufted ducklings (*Aythya fuligula*), the response to voluntary head or whole body submergence is variable but, in the majority of birds, similar to the adult response [16]. These ducklings had been held on land for about 2 weeks to allow implantation of heart rate transmitters and subsequent post-operative recovery. Unfortunately, of necessity, the ducks were offered water to drink during this period and repeated beak wetting may have triggered and reinforced heart rate responses displayed in first ever dives. In fact, ducklings did not dive immediately after being exposed to deep water, but performed beak dips and head submersions which precipitated marked falls in heart rate compared with the rate preceding these activities [16].

In nature, precocial chicks enter the water soon after hatching [19], whereas altricial young, like cormorants, remain in proximity of the nest for up to 6 or 7 weeks, before venturing onto water [17]. During this period chicks have no access to water other than the 'drinking water' supplied by the parents, which is placed into the chick's gular pouch (pers. observation). Consequently, in cormorant chicks, it is possible to monitor heart rate adjustments, not only to diving, but also to beak and head submergence, from their first ever exposure to open water.

* Corresponding author. Tel.: +1-604-8225043; fax: +1-604-8222416.

E-mail address: enstipp@zoology.ubc.ca (M.R. Enstipp)

Hence, the question we asked was whether the cardiac response to first ever voluntary head submergence or diving by cormorant chicks would be any different from those of experienced adults. To contrast the cardiac responses during first-ever-voluntary submergence with responses during first ever forced submergence, three chicks were subjected only to whole body forced submergences.

2. Material and methods

2.1. Birds

Nine double-crested cormorant chicks were collected from a breeding colony on Mandarte Island, BC, in September 1995, when chicks were approximately 5 weeks of age. Birds were housed in a sheltered outdoor pen with no access to water at the Animal Care Facilities of the University of British Columbia, Vancouver. Chicks were initially fed about 400 g of a mixed diet daily, which was reduced to about 10% of their body weight after a few weeks. Diet consisted of Pacific herring (*Clupea harengus*) and rainbow smelt (*Osmerus mordax*), supplemented with vitamin B1 tablets (Thiamine hydrochloride, Stanley Pharmaceuticals, North Vancouver, BC). After about 4 weeks in captivity the chicks 'fledged' (accompanied by marked behavioural changes) and the experimental trials started. At 'fledging', mean body mass of the chicks (2.33 ± 0.14 kg) had reached that of our adult birds (2.36 ± 0.17 kg, $N = 9$).

2.2. Instrumentation

To record heart rate from the cormorants a purpose built data logging system was developed [1]. The data logger assembly consisted of a modified Tattletale Lite computer (Onset Computer, Pocasset, MA) connected to two electrocardiogram (ECG) electrodes and a small liquid level sensor (Model LL105100, Microswitch, Freeport, IL), used as an event marker (i.e. to sense submergence and emergence; for details see Ref. [1]). The data logger was programmed to sample the ECG at 100 Hz and the submergence sensor at 2 Hz. Before experimental application the data logger was glued onto a harness, made of rubber neoprene and Velcro straps, which was attached to the animal. This 'backpack' was tolerated extremely well by the birds. The ECG electrodes (stripped sections of insulated stainless steel biomedical wire (Cooner Wire, Chatsworth, CA)) were inserted subcutaneously, one placed 2 cm lateral to the posterior cervical region and one 4 cm lateral to the caudal end of the synsacrum, on opposite sides of the midline from one another. Adjacent to each insertion site, a 2-cm section of the ECG lead was sealed and glued to the feathers with 5-min epoxy. Before

every experimental trial chicks were caught, instrumented with the harness, and the data logger's ECG electrode leads were connected with the implanted ECG leads. Every effort was made to minimise handling time before trials.

2.3. Experimental trials

All double-crested cormorant chicks used in this study had never been exposed to water before the 'first ever voluntary submergence' and the 'first ever forced submergence' trials. Water temperature during the trials ranged from 4 to 9°C.

2.3.1. Voluntary submergences

Six chicks (~ 10 weeks old) were used to investigate the cardiac responses displayed during their first ever voluntary head submergence and during their early dives. At the beginning of a trial the instrumented chick was kept inside an enclosure for about 10 min, before opening a door, which allowed access to the dive tank (9 m long, 3 m wide, 1 m deep). Most chicks would not dive during the first trials but only submerged their heads. Since these head submergences were not detected by the data logger's submergence sensor, cormorants were filmed by a video camera equipped with an internal clock (0.1 s resolution). Data logger and VCR time was synchronised before every trial. At the end of a trial, which generally lasted around 30–60 min, birds were recaptured to disconnect the ECG leads and remove the harness. To avoid the initiation of 'escape dives' when catching chicks (especially in the early trials), chicks were gently encouraged into the enclosure and the door was closed. After each chick had completed five trials, ECG electrodes were removed and all chicks were housed inside the fenced dive tank. Chicks had to dive for their food daily and as they got accustomed to the tank, the surface of the tank was gradually covered during the training sessions, until only a small section (1 m × 1.5 m) at one end of the tank remained open. Birds would submerge here, swim underwater to the opposite end of the tank to pick up fish and return to the opening to swallow their prey. After about 2 weeks, five of the chicks were reinstrumented to monitor heart rate during the longer dives, which the chicks were now performing. Dive duration during these dives (chicks were ~ 16–17 weeks old) was typically between 10 and 20 s.

2.3.2. Forced submergences

To compare the cardiac response to voluntary dives with the response to forced submergence, a separate group of three chicks (~ 11 weeks old) was used in forced submergence experiments only. Chicks were held by an investigator and submerged to a depth of about 30 cm inside the diving tank. Submergence times of 3

and 10 s were matched for a total of 12 submergences, followed by a final forced submergence of 30 s. Between submergences chicks were given a 1-min period to recover.

2.3.3. Resting heart rate

Resting heart rate was recorded from all of the chicks at ∼ 12 weeks of age. Birds were equipped with ECG leads and the data logger 'backpack' as described above, but then they were returned to their holding pens. Birds would perch immediately after release and return to their routine shortly after the investigator left. The heart rate was recorded during these trials and the birds were either observed from a blind or filmed by a video camera. Trials lasted for approximately 1 h. All trials were done during daylight hours with postabsorptive birds that were awake and perched in the upright position.

2.4. Data analysis and statistics

Submergence and emergence times were determined from the record of the data logger's submergence sensor. For the short head submergences, submergence periods were determined by visual analysis of the recorded video tapes. Cardiac interbeat intervals were derived from the ECG trace after identifying the QRS peaks by eye. The mean interbeat interval for each period of interest (e.g. an individual dive or forced submergence) was then converted to heart rate in beats per minute (beats min^{-1}).

Data were grouped into the following categories: (1) 'first' voluntary head submergence; (2) the 'six' following voluntary head submergences; (3) the 'first' voluntary dive; (4) the 'six' following voluntary dives; (5) the 'later' (longer) voluntary dives; (6) the 'first' forced submergence; and (7) the 'six' following forced submergences. The 'first' forced submergence lasted 3 s, while the 'six' following forced submergences were matched pairs of 3 and 10 s submergences.

As chicks in their early voluntary submergence trials apparently had to 'learn' how to submerge, a dive was defined as a complete head submergence, accompanied by forward propulsion. To allow comparison between the different submergence categories, heart rates before submergence, during submergence, and after surfacing were averaged over 1-, 2- or 3-s-intervals. Mean values (± S.D.) were calculated for all chicks for the different submergence categories (one and six submergences were taken per bird from the first and the following submergences, respectively). For each submergence category a grand mean was calculated from the means of the individual birds. Heart rates during 'later' (longer) dives were compared with heart rates obtained from four adult double-crested cormorants performing dives in the same dive tank (six dives were analysed for each

individual), lasting between 18 and 22 s (mean: 20.1 ± 0.8 s).

To calculate resting heart rates, instantaneous heart rate over the entire trial period was plotted against time. Heart rate was elevated due to handling at the beginning of the trial but fell to a baseline value within 10 min in all birds. After the heart rate had stabilised, a section of 20 min was chosen for the calculation of a single value, representing the resting heart rate. A mean value was calculated from all interbeat intervals during that period and converted into beats min^{-1}.

Heart rates during the different submergence categories were compared using one-way repeated-measures analysis of variance (ANOVA) with Student–Newman–Keuls pairwise multiple comparisons. When single comparisons were made, as in comparing values obtained from the chicks with values from the adult birds, Student's t-test was used. A significant difference was accepted at the level of $P < 0.05$.

3. Results

3.1. Resting heart rates, voluntary head submergences and dives

The grand mean for resting heart rate ($N = 9$ chicks) was 143.2 ± 24.6 beats min^{-1} and was less than half the rate recorded from chicks just before the start of voluntary head submergence or diving (Table 1). As can be seen from Table 1, for all five categories of voluntary head submergences and dives, heart rates during submergence were significantly different from heart rates before submergence and after surfacing. Heart rates (before submergence, during submergence and after surfacing), however, were not significantly different between the different voluntary submergence categories. In all categories of voluntary head submergence/dive, the heart rate fell immediately on submergence by 60–100 beats min^{-1}. The similarity in the immediate (first second) heart rate response in the first ever dive (mean dive duration: 2.3 ± 1.6 s) compared with that in the much longer (mean dive duration: 14.0 ± 3.0 s), later dives was particularly striking (Table 1).

When making their first head submergence, three of the five chicks showed a noticeable decline in heart rate (Fig. 1(a)), while in the other two, this was not the case (Fig. 1(b)). The major difference between these two types of response was pre-submersion heart rate. When pre-submersion heart rate was high, the decline on submersion was accentuated. A similar picture holds for first ever dives (Fig. 1(c, d)). In two of the six chicks the pre-dive heart rate was in the range of 200–250 beats min^{-1}, and the decline associated with submersion, although present, was not particularly obvious

Table 1
Dive duration and heart rates of double-crested cormorant chicks associated with initial and later voluntary and forced submergence[a]

	Voluntary submergence					Forced submergence	
	First ever head submergence	Next six head submergences	First ever dive	Next six dives	Six later (longer) dives	First ever forced submergence	Next 6 forced submergences
Duration (s)	0.7 ± 0.2	0.8 ± 0.1	2.3 ± 1.6	2.5 ± 2.4	14.0 ± 3.0	3.5 ± 0.5	7.5 ± 0.2
Heart rate (beats min^{-1})							
Before submergence							
-3–0 s	327.2 ± 56.5	346.5 ± 43.0	338.7 ± 85.0	340.9 ± 26.4	333.9 ± 31.2	134.9 ± 53.7[c]	172.5 ± 79.5[c]
-1–0 s	328.6 ± 56.1	348.7 ± 39.0	341.1 ± 79.5	350.3 ± 26.8	345.3 ± 27.5	150.4 ± 39.3[c]	171.1 ± 63.4[c]
During submergence							
0–1 s	232.5 ± 42.9[b]	285.9 ± 41.8[b]	249.2 ± 44.9[b]	240.1 ± 18.4[b]	243.3 ± 17.2[b]	116.6 ± 4.8[c]	134.5 ± 47.7[b,c]
0–2 s		209.0 ± 34.0[b]		247.3 ± 27.1[b]	234.3 ± 12.8[b]	107.9 ± 44.9	119.7 ± 66.7[b]
0–3 s				224.2 ± 0.6[b]	222.6 ± 8.3[b]	143.8 ± 51.2	120.3 ± 64.4[b]
3–6 s					205.4 ± 14.4[b]		
6–9 s					203.4 ± 13.7[b]		
Mean	233.7 ± 40.4[b]	273.8 ± 39.5[b]	247.3 ± 45.6[b]	241.0 ± 20.4[b]	212.4 ± 16.9[b]	112.5 ± 66.2[c]	115.0 ± 60.1[b,c]
After surfacing							
0–1 s	318.8 ± 77.8	354.4 ± 31.4	366.9 ± 46.5	349.8 ± 16.5	350.6 ± 24.0	175.1 ± 32.4[c]	178.3 ± 52.9[c]
0–3 s	346.9 ± 54.2	358.8 ± 26.0	355.8 ± 50.4	350.2 ± 19.2	354.9 ± 27.3	198.7 ± 25.9[c]	210.3 ± 56.6[c]

[a] Values are presented as mean $\pm$ S.D. 'Mean' refers to the mean submergence heart rate. The 'next six forced submergences' were matched pairs of 3- and 10-s submergences. Heart rates during the first 3 s only were included in analysis. Number of double-crested cormorant chicks contributing to the mean values is six for the 'first ever dive', four for the 'later (longer) dives', and five for all other voluntary submergence categories. Three animals contributed to the forced submergence categories.

[b] Significantly different from 'before submergence (-3–0 s)' and 'after surfacing (0–3 s)' values.

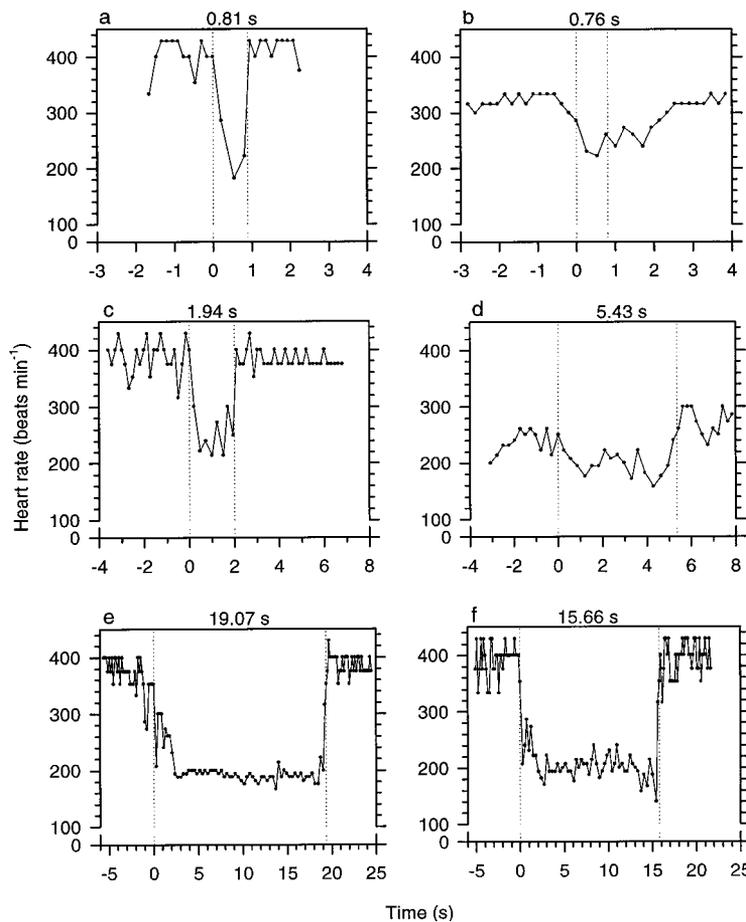[c] Significant difference between forced submergence and voluntary submergence values.

Fig. 1. Cardiac responses of double-crested cormorant chicks to first ever voluntary head submergence (a, b), first ever voluntary dive (c, d), and later (longer) voluntary dives (e, f). Figures are instantaneous heart rate records of individual chicks. Submergence periods are indicated by the dashed lines, with the negative time values referring to the pre-submergence period and zero indicating submersion. Submergence duration is shown on top of figures (a–f).

(Fig. 1(d)). In the next six dives, the variability in pre-dive heart rate was reduced (Table 1) and all animals showed a pronounced immediate decline in heart rate on submersion.

When tested later, after having learnt to dive for food, the heart rate was high in the pre-dive period and declined immediately on submersion to about 220–240 beats min^{-1} (Fig. 1(e, f)). The heart rate levelled off and remained stable at around 200 beats min^{-1} throughout these longer dives, before increasing in the period just before surfacing. Voluntary dives of four chicks (later, longer dives) were compared with dives of four adult cormorants (Fig. 2). The pre-dive heart rate was significantly lower (333.9 ± 31.2 beats min^{-1}) in chicks than adults (389.1 ± 12.2 beats min^{-1}). Over the first 3 s of submergence, mean heart rate in chicks and adults was identical (Fig. 2). The heart rate declined very slowly in chicks but much more rapidly in adults and, after 9 s into the dive, heart rate in adults was 50 beats min^{-1} below that in chicks. This difference was significant as was the difference in mean dive heart rate (chicks: 212.4 ± 16.9 beats min^{-1}; adults: 169.0 ± 13.1 beats min^{-1}).

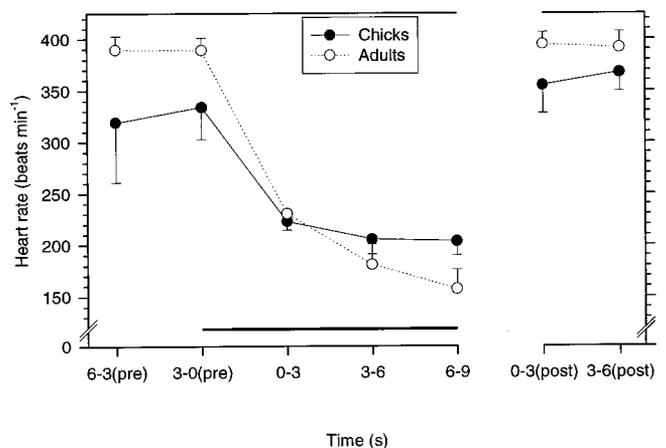
Fig. 2. Heart rates (beats min^{-1}) associated with the first 9 s of voluntary shallow diving in double-crested cormorant chicks and adults. Values are means $\pm$ S.D. ($N = 4$), averaged over 3-s intervals (six dives were analysed per individual). Mean dive duration for chicks and adults was 14.0 ± 3.0 and 20.1 ± 0.8 s, respectively. Dive period is indicated by the solid bottom line. 'Pre' and 'post' refer to the pre- and post-dive period, respectively.
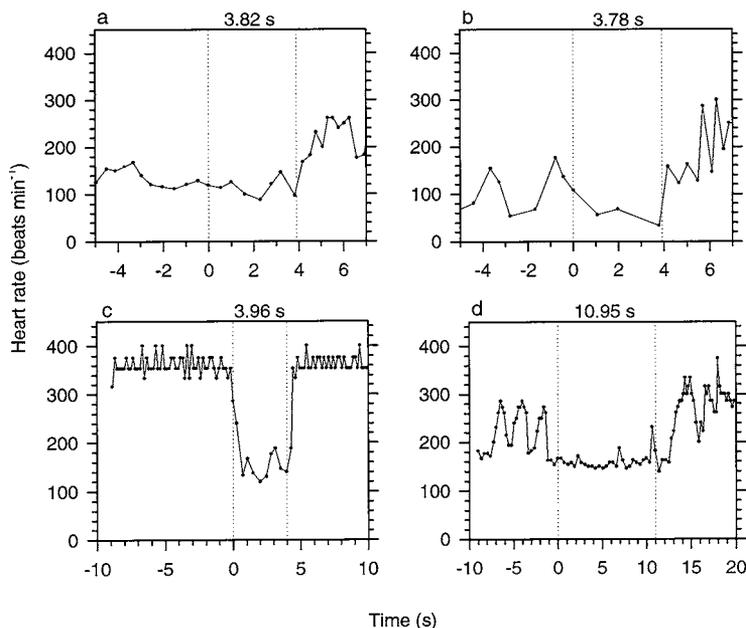
Fig. 3. Cardiac responses of double-crested cormorant chicks to forced submergence. Figures are instantaneous heart rate records of individual chicks during their first ever forced submergence (a, b) and during forced submergence after being subjected to repetitive forced submergences (c, d). Submergence periods are indicated by the dashed lines, with the negative time values referring to the pre-submergence period and zero indicating submersion. Submergence duration is shown on top of figures (a–d).

3.2. Forced submergence

The heart rate was extremely low (134.9 ± 53.7 beats min^{-1}) before the first ever forced submergence and an immediate decline in heart rate was not obvious (Table 1, Fig. 3(a, b)). The mean heart rate during 3 s of forced submergence (112.5 ± 66.2 beats min^{-1}) was not significantly different from the pre-submergence value. Pre-forced submergence heart rate increased with repetitive submergences (172.5 ± 79.5 beats min^{-1}) and a marked fall in heart rate (to 134.5 ± 47.7 beats min^{-1}) occurred upon submersion (Table 1, Fig. 3(c)). Chicks displayed sinus arrhythmia, which was especially prominent in one chick, and the forced submergence heart rate profile was established often before the actual act of submersion (Fig. 3(d)). The last forced submergence in each bird was extended to 30 s and in all chicks, the heart rate was between 50–100 beats min^{-1} during the last few seconds of submergence.

4. Discussion

4.1. Voluntary submergence

In adult birds, diving in shallow water, the heart rate plummeted on submersion. Pre-dive heart rate was about three times the resting heart rate (137.8 ± 17.4 beats min^{-1}; Enstipp et al., in preparation) and halved on submersion. After this initial decline, the heart rate fell much more slowly, reaching 150 beats min^{-1} after

9 s of submergence. Although the cardiac responses to voluntary submergence were variable, in the majority of chicks, initial heart rates during first ever head submergence and first ever voluntary, shallow, dives were similar to the adult birds. For the cormorant chicks, which were ~ 10 weeks old, this was their first exposure to water. Consequently, there can be no doubt that cardiac adjustments to submergence are reflex in nature and this reflex is fully developed by the first submergence event. In both cormorant chicks and adults, the heart rate established early in the dive was around 225 beats min^{-1} and much of the variability in the cardiac responses of cormorant chicks was due to the heart rate immediately before diving. If pre-dive heart rate was low, then the initial cardiac response to diving was not obvious. In fact, similar arguments can be advanced to explain much of the variability in initial cardiac responses to diving in tufted ducklings [16].

The nature of the reflex pathway initiating the decline in heart rate in the first few seconds of the dive is unknown. This decline is present from the first head submergence or dive, although only markedly, when the pre-dive heart rate is at least double the resting rate. An initial rapid decline in heart rate is seen in many birds, in both voluntary dives and forced submergence, when the pre-dive heart rate is markedly elevated above resting [11,14,15,21]. Anaesthetisation of the narial region has only minor effects on the initial cardiac retardation in diving ducks [6]. In fact, ducks can display the whole gamut of cardiac adjustments to diving (pre-dive tachycardia followed by a rapid fall in heart rate)

without actually submerging [21] or before submersion occurs [5], which has led to the suggestion that, in adults, the initial cardiac response can be conditioned [10,20]. The fact that cardiac responses in double-crested cormorant chicks are similar to adults, adds no weight to the conditioning argument. The initial decline in heart rate represents a reflex pathway, stimulated by events associated with the physical act of diving.

Although the nature of this reflex pathway is obscure, especially in view of the results obtained after narial anaesthetisation in ducks [6], the importance of cessation of respiration to the initiation of cardiac events in diving has been seen in Humboldt penguins (*Spheniscus humboldti*) [3] as well as in some of our birds. In Humboldt penguins there is often a prominent sinus arrhythmia when the bird is on the surface, which terminates, at the heart rate during expiration, on head submersion. A similar picture was seen in some of the whole body forced submergences of our chicks. In animals displaying prominent sinus arrhythmia (Fig. 3(d)), the submergence heart rate was established before submersion at the pre-submergence exhalation. Volitional control of breathing in birds is undisputed. Claims of volitional control of heart rate per se, on the other hand, are a red herring. The close linkage between breathing and heart rate provides a plausible mechanism for the initial cardiac adjustments to diving.

In adult cormorants, after the initial cardiac adjustment to submergence, the heart rate continued to decline throughout shallow dives of up to 22 s in duration. In contrast, in adult diving ducks the initial cardiac response is typically the lowest heart rate of the dive. The heart rate then increases to a more or less stable level before rising markedly prior to surfacing [4]. The cardiac response observed during the later (longer) dives of double-crested cormorant chicks more closely resembled the response of adult diving ducks than adult cormorants. In these dives, the heart rate was maintained more or less at the initial level before rising in anticipation of surfacing. The secondary decline in heart rate during shallow diving in adult cormorants has been attributed to chemoreceptor stimulation (Enstipp et al., in preparation). Chemoreceptor driven declines in heart rate can be habituated in forcibly submerged diving and dabbling ducks [8,9]. This is, however, unlikely to be the explanation for the stable diving heart rate during the later (longer) dives of cormorant chicks, since habituation was not detectable in adult birds with a much longer 'dive history'. Furthermore, the possibility that chemoreceptors are not fully developed in our chicks seems improbable, given the strong decline in heart rate during the longer forced submergence trials (30 s), which most likely is facilitated by chemoreceptors [13]. On the other hand, adult cormorants making deep dives show a similar cardiac response as chicks in their later (longer) shallow dives

(Enstipp et al., in preparation). As the depth of submergence increases, so will the arterial oxygen tension (at least initially), unloading the arterial chemoreceptors. Consequently, in the absence of habituation, one could speculate that stable heart rates in diving chicks are a consequence of higher arterial oxygen tensions throughout the dive. Given the present evidence, it is difficult to conceive how this might be accomplished.

4.2. Forced submergence

The extremely low heart rates before the first ever forced submergence are largely accounted for by the strong sinus arrhythmia displayed by the chicks. Over the following submergences, sinus arrhythmia gradually disappeared and the heart rate was kept at an elevated level before submergence. The cardiac response of chicks during early forced submergence, lasting up to 10 s, was comparable to the forced submergence response of immature double-crested cormorants (~ 5 months old) which had breathed 100% oxygen before forced submergence [13]. Heart rate decline was less dramatic in these immature cormorants after breathing oxygen before submergence when compared to breathing air beforehand, with heart rate decreasing from ~ 190 to ~ 130 beats min^{-1} within the first 5 s of submergence. Again, it is tempting to argue that chemoreceptor reflex sensitivity may have not been fully matured in our chicks. On the other hand, forcibly submerging our chicks for 30 s caused the heart rate to fall within the same range (~ 50 beats min^{-1}) as in forcibly submerged adults [18], suggesting a well developed chemoreceptor mechanism. Sinus arrhythmia, as observed during the forced submergence trials, was less obvious in voluntarily submerging chicks. The heart rate before voluntary submergence was double the rate before forced submergence and never fell below ~ 190 beats min^{-1} even during the later (longer) dives. Hence, cardiac responses of double-crested cormorants to forced submergence are more extreme than responses during voluntary submergence, as shown previously [15]. Our results show that this difference is apparent in chicks from their very first exposure to water, although much of the difference might be dependant on pre-submergence heart rate, as has been shown for diving ducks [7].

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