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SHORT COMMUNICATION

Drivers of the dive response in trained harbour porpoises (*Phocoena phocoena*)

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ABSTRACT

Pronounced dive responses through peripheral vasoconstriction and bradycardia enable prolonged apnoea in marine mammals. For most vertebrates, the dive response is initiated upon face immersion, but little is known about the physical drivers of diving and surfacing heart rate in cetaceans whose faces are always mostly submerged. Using two trained harbour porpoises instrumented with an ECG-measuring sound-and-movement tag (DTAG-3), we investigated the initiation and progression of bradycardia and tachycardia during apnoea and eupnoea for varying levels of immersion. We show that paranasal wetting drives bradycardia initiation and progression, whereas apnoea leads to dive-level bradycardia eventually, but not instantly. At the end of dives, heart rate accelerates independently of lung expansion, perhaps in anticipation of surfacing; however, full tachycardia is only engaged upon inhalation. We conclude that breathing drives surface tachycardia, whereas blowhole wetting is an important driver of bradycardia; however, anticipatory/volitional modulation can overrule such responses to sensory inputs.

KEY WORDS: Heart rate, Bradycardia, Tachycardia, Cetacean, Submersion, Anticipation

INTRODUCTION

The dive response is a critical enabler of extended underwater foraging in marine mammals by prolonging both aerobic and anaerobic dive times. It is, to some degree, found in all air-breathing vertebrates as a response to submersion and apnoea. The peripheral vasoconstriction and concurrent bradycardia conserve blood oxygen for the hypoxia-sensitive brain and heart (Dykes, 1974a; Irving et al., 1942; Scholander, 1940; Zapol et al., 1979), making myoglobin-bound oxygen stores available for local use (Kooyman, 1985).

Although the dive response in marine mammals has been broadly considered a strict reflex (Scholander, 1940, 1963), studies from the past half-century have demonstrated that the response is highly dynamic (Harrison et al., 1972; Jones et al., 1973; Kooyman and Campbell, 1972), depending on dive depth, duration, exercise (Andrews et al., 1997; Boyd et al., 1999; Hill et al., 1987; McDonald and Ponganis, 2014; McDonald et al., 2018; Noren et al., 2012; Williams et al., 2015) and volitional control (Elmegaard et al., 2016; Elsner et al., 1966; Noren et al., 2012). For most vertebrates, the dive response is triggered by apnoea and stimulation of

thermoreceptors and mechanoreceptors in the paranasal area (Dykes, 1974a,b; Panneton, 2013), but pinnipeds can initiate a strong dive response-like bradycardia in air, during trained breath holding (Kaczmarek et al., 2018; Ridgway et al., 1975) as well as naturally occurring sleep apnoea (Andrews et al., 1997; Castellini et al., 1994). A facial bradycardia trigger has never been tested for in cetaceans, for which the trait might be unfavourable given that most of their face is submerged, even when breathing.

Marine mammals maximize the time they spend submerged by efficient respiratory gas exchange at the surface, resulting from a greatly accelerated heart rate (f_H) during the inspiratory phase of respiratory sinus arrhythmia (RSA) (Hayano et al., 1996). The gas exchange is further augmented by a pre-surfacing tachycardia to facilitate the use of remaining lung and blood oxygen stores at the end of a dive, while re-perfused tissues release carbon dioxide and nitrogen into the blood and lungs (Irving et al., 1941; Kooyman and Campbell, 1972; McDonald and Ponganis, 2014; Noren et al., 2012; Thompson and Fedak, 1993). Pre-surfacing tachycardia is often ascribed to the anticipation of surfacing or breathing (Kooyman and Campbell, 1972; McDonald and Ponganis, 2014), and has been shown to be initiated during depressurisation in seals (Kooyman and Campbell, 1972).

Here, we investigated the physical stimulators of diving bradycardia and surfacing tachycardia, whether through autonomic or volitional routes, to better understand the drivers of the cetacean diving physiology. By comparing (1) how the onset of bradycardia relates temporally to breaths and submergence, (2) the progression of bradycardia between trained tasks and (3) the f_H acceleration when ending these tasks with or without lung ventilation, we tested the hypotheses that submersion is a primary driver of diving bradycardia, as predicted from other vertebrates, or alternatively that RSA alone drives diving bradycardia and surfacing tachycardia, as predicted from convergently evolved pinnipeds.

MATERIALS AND METHODS

Animals and equipment

ECG data were collected from June to October 2015 from two captive female harbour porpoises, *Phocoena phocoena* (Linnaeus 1758), Freja and Sif, at the Fjord & Belt Centre in Kerteminde, Denmark. At the time of data collection, Freja and Sif had been in captivity for 18 and 11 years, respectively, and weighed 54 and 50 kg in August 2015. Both porpoises were by-caught as yearlings in pound nets in Danish waters, and were subsequently housed and trained at the Fjord & Belt Centre under permits SN 343/FY-0014 and 1996-3446-0021 from the Ministry of Environment and Food of Denmark, with approval from the IACUC committee of Aarhus University, and in accordance with recommendations of the Danish Council for Experiments on Animals.

f_H was measured with an animal-borne sound-and-movement tag, ECG-DTAG-3, with two external chlorinated silver electrodes

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embedded in silicone suction cups for easy non-invasive attachment to the animals. Electrodes were attached on each side of the animal, rostral and caudal to the heart, approximately along the axis of the ventricle contraction for an optimal QRS-complex signal (Fig. 1A). The potential difference between the two electrodes was sampled at 10 kHz with 16-bit resolution, and a 4 kHz, 2-pole anti-alias filter. A small amount of conductive paste (Ten20, Weaver and Company, CO, USA) was applied on the silver electrodes to improve skin contact. The tag also recorded sound and pressure, which were used to identify breaths and dive times. Stereo sound was sampled at 500 kHz with 16-bit resolution and a 0.5–150 kHz bandwidth; pressure was sampled at 2 kHz with 16-bit resolution (see McDonald et al., 2018, for details).

Breath-holding tasks

To investigate the initiation and progress of bradycardia, the two porpoises were trained to wear the ECG-DTAG-3 during a suite of trained behaviours of similar low-activity exercise levels and of approximately 20 s duration, during which they would breath hold (Fig. 1B–G). The task duration was defined from the last breath before the task until the first breath when task was completed. One task was performed with the blowhole mostly in air (dorsal swimming, DSw); three were performed with the blowhole right below the surface (ventral swimming, VSw; dorsal station, DSt; ventral station, VSt); one was performed at 1 m depth (station at 1 m depth, ST); and one was performed on land (beaching, B). This allowed examination of the influence of submergence level on f_H. When the animals completed a task correctly, the trainer used a bridge signal (i.e. blew a whistle, ~6 kHz) to get them to return for a fish reward. In between tasks, the

animals spent a minimum of 1 min in low activity at the surface with respiratory frequencies of 6.7 breaths min^{-1} (Sif) and 9.7 breaths min^{-1} (Freja). This ensured CO_2 elimination and full recovery from the preceding task, which is expected after 6–8 breaths for these short dive times (Boutilier et al., 2001).

Dorsal swimming (DSw)

The porpoises swam calmly at the surface with the blowhole mostly in air (Fig. 1B). When breath-hold time reached 15–20 s, the bridge signal was sounded and the animals returned to the trainer, which usually was at a depth of a few metres. Sometimes, they took a breath when they heard the bridge signal, and sometimes they waited until they were back with the trainer; therefore, the duration of this task was defined from the last breath until the bridge signal. By closely inspecting video recordings of tasks, we found average lag times of 2 s (Freja) and close to 0 s (Sif) from the last breath until initiating the dorsal swim.

Ventral swimming (VSw)

This task proceeded as for DSw above, except the porpoises swam with the ventral-side up (Fig. 1C). While the ventral orientation is mostly known from foraging or mating manoeuvres in freely swimming porpoises (Akamatsu et al., 2010; Keener et al., 2018), it here serves to compare f_H in a task with the blowhole submerged with that in a task where the blowhole is in air, while the same approximate proportion of the body is in the water for comparable swimming resistances and body submergence sensory input. The average lag time from the last breath until submergence of the blowhole was 2 s for both animals.
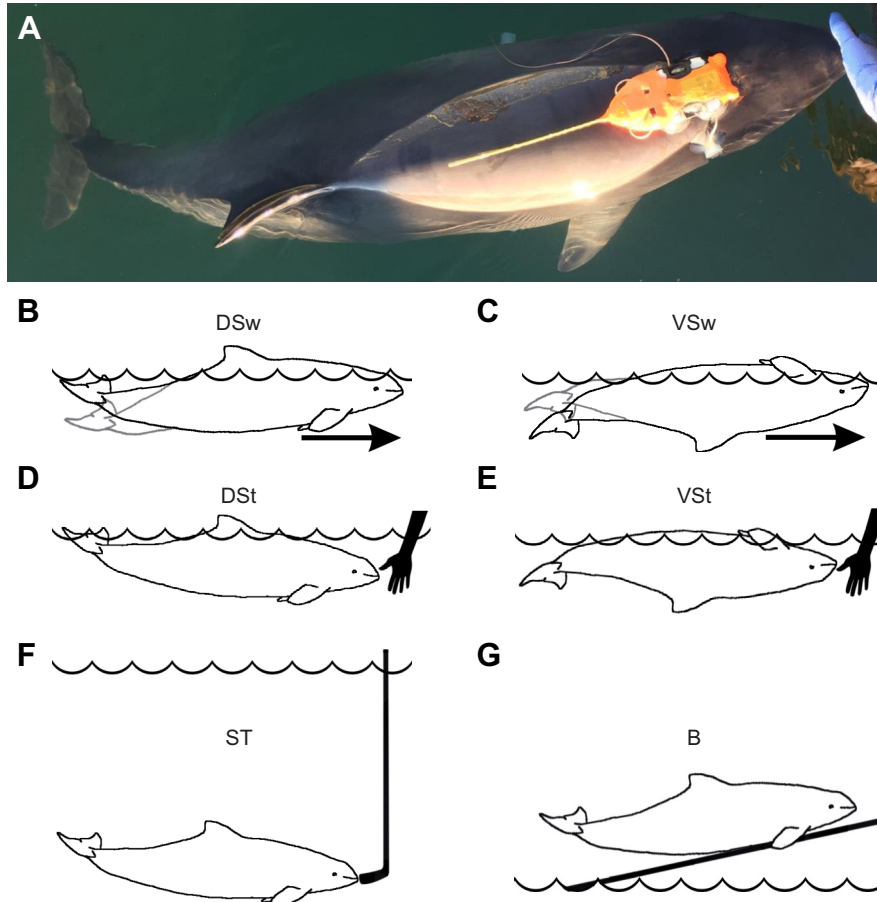

Fig. 1. Breath-holding behaviours. The two porpoises performed a variety of behaviours that enabled us to uncover drivers of diving bradycardia. (A) The two electrodes of the ECG-DTAG-3 are placed on the sides of the porpoise, rostral and caudal to the heart, close to the ventricle contraction axis to maximise ECG amplitude. (B–G) All breath-hold tasks were of approximately 20 s in duration: DSw, dorsal swim at surface; VSw, ventral swim at surface; DSt, dorsal station at surface; VSt, ventral station at surface; ST, station at 1 m depth; B, beaching. See Materials and Methods for detailed descriptions. The blowhole was submerged in all behaviours except B and G.

Dorsal station (DSt)

The porpoises stationed at the trainer's hand, approximately 10 cm below the surface (Fig. 1D). The average lag time from the last breath until blowhole submergence was 2 s (Freja) and close to 0 s (Sif).

Ventral station (VSt)

The porpoises stationed at the trainer's hand in a belly-up position (Fig. 1E). Comparing the f_H between this task and DSt informed us about the potential cost of the ventral position. In both tasks, the porpoise was at the surface with the blowhole submerged. The average lag time from the last breath until blowhole submergence was 2 s (Freja) and 3 s (Sif).

Station at 1 m depth (ST)

The porpoises swam to a biteplate station at 1 m depth (Fig. 1F) where they remained for approximately 10 s before the bridge signal was sounded, resulting in a 15–20 s breath hold. Both porpoises took their last breath just as they dived, meaning no lag time from the last breath until blowhole submergence.

Beaching (B)

To investigate the effect of apnoea alone on breath-holding bradycardia, f_H was measured when Freja beached herself on a platform for 15 s (Fig. 1G). After the last breath, approximately 6 s were spent swimming for momentum to jump onto the platform. After 15 s on the platform, the bridge signal was sounded and Freja slid back into the water to swim to the trainer for a reward, resulting in a total breath hold of ∼40 s. f_H parameters were calculated for the beaching period only so, unlike the other tasks, the breath hold had already been ongoing for ∼6 s. This behaviour was only repeated 5 times to prevent loss of motivation to perform an important behaviour for health monitoring that is normally just a few seconds long. Therefore, we used it for qualitative comparison only.

Data processing and analysis

Data were processed and prepared using custom-written scripts in MatLab (The MathWorks, Natick, MA, USA). R-peaks of the ECG data were identified with a peak detector and corrected by visual inspection. The instantaneous f_H (beats min^{-1}) for each heartbeat was then calculated from inter-peak intervals (f_H=60/inter-peak interval). Respirations were detected by aural and visual audit of sound files and spectrograms.

Does bradycardia initiate with apnoea or submergence?

In order to test whether blowhole submergence and bradycardia initiation were tightly linked, as predicted from the classical dive reflex, we examined f_H specifically at the points of blowhole submergence, identified by synchronised video recordings. Thus, we could determine whether the initiation related temporally to the respiration or to the time of submergence. For graphical presentation of data, f_H was binned in 1 s bins for each trial. Then, for each task, mean and s.e.m. were calculated for each bin. For this question, we focused solely on the breaking point of when the f_H started to decline after task initiation.

Is f_H influenced by task and submergence level?

To examine the impact of task and submergence level on f_H, we compared the initial 15 s of the tasks as the exact duration varied. Residuals were normally distributed, but heteroscedastic, so we performed Welch's ANOVA and Games–Howell *post hoc* analyses of the lower quartiles (LQ) of the instantaneous f_H (i.e. 25th

percentile, the median of the lower half of instantaneous f_H) between the tasks described (DSw, VSw, DSt, VSt, ST) using the R package *userfriendlyscience* (https://CRAN.R-project.org/package= userfriendlyscience; R v.3.5.2, R Foundation for Statistical Computing, http://www.R-project.org/). In the analysis of variance between tasks, the null hypotheses were rejected at $P<0.05$. The effect of exercise (using acceleration data as an index for activity) on LQ f_H was examined with a generalised least squares model using the R package *nlme* (https://CRAN.R-project.org/package=nlme) and found to be insignificant between the tasks performed, which were all of low activity. In Table S1, a table of f_H parameters can be found.

Is surface tachycardia driven by anticipation or breathing?

To investigate whether surface tachycardia depends on lung expansion, we examined f_H in the 3 s before and after the breath ending each breath-hold task. In most cases, the porpoises took a full breath after completing a task, but sometimes they only exhaled (probably a training artefact). These differing breaths allowed us to examine whether, and to what extent, surface tachycardia was due to anticipation of surfacing or lung ventilation. Some tasks (B, DSw, VSw – see above description) were excluded because the task-ending breath did not directly follow the shift in behaviour from performing the task to surfacing. In these tasks, porpoises swam back to the trainer in a variety of activity levels, which was reflected in their presumably exercise-modulated f_H, potentially masking the initial surface tachycardia. The instantaneous f_H around the breaths was plotted for respiration types and animals, and smooth trend lines were added using a local polynomial regression fitting algorithm using the *ggplot2* R package (Wickham, 2016).

RESULTS AND DISCUSSION

Like many marine mammals, harbour porpoises have a bimodal f_H, with low f_H during dives, ensuring conservation of oxygen, and high f_H at the surface, for fast and efficient gas exchange (Eskesen et al., 2009; Kastelein and Meijler, 1989; McDonald et al., 2018; Reed et al., 2000). Accordingly, the porpoises in this study displayed a breath-holding (apnoeic) submergence mode of 76 beats min^{-1} (Freja) and 77 beats min^{-1} (Sif) and a breathing (eupnoeic) mode of 143 beats min^{-1} (Freja) and 162 beats min^{-1} (Sif) during surface intervals (Fig. S1). Here, we investigated the drivers of these modes, which are ascribed to both the dive response and RSA (Fahlman et al., 2019).

Does bradycardia initiate with apnoea or submergence?

We hypothesized that apnoea is the primary driver of diving bradycardia in harbour porpoises, as found for pinnipeds (Kaczmarek et al., 2018), as the facial triggers of the classic dive response might be counterproductive, given their constant facial submersion, where only the blowhole area is exposed during ventilations (Dykes, 1974b; Kaczmarek et al., 2018; Panneton, 2013). From the first seconds of f_H during the tasks (Fig. 2A,B), it was apparent that breath holding is not the primary trigger of bradycardia; rather, bradycardia is initiated at the time of blowhole submergence. Without blowhole submersion, bradycardia developed more gradually during a breath hold (Fig. 2A,B: DSw). Thus, for harbour porpoises, apnoea is not an instant trigger, in contrast to recent findings in some pinnipeds (Kaczmarek et al., 2018). Instead, the correlation with submergence indicates that the nasal sensory mechanism responsible for initiating the dive response migrated with the nares from the tip of the snout to the top of the cranium during the protocetid evolution, although we cannot account for the conservation or loss of additional contributing facial sensory
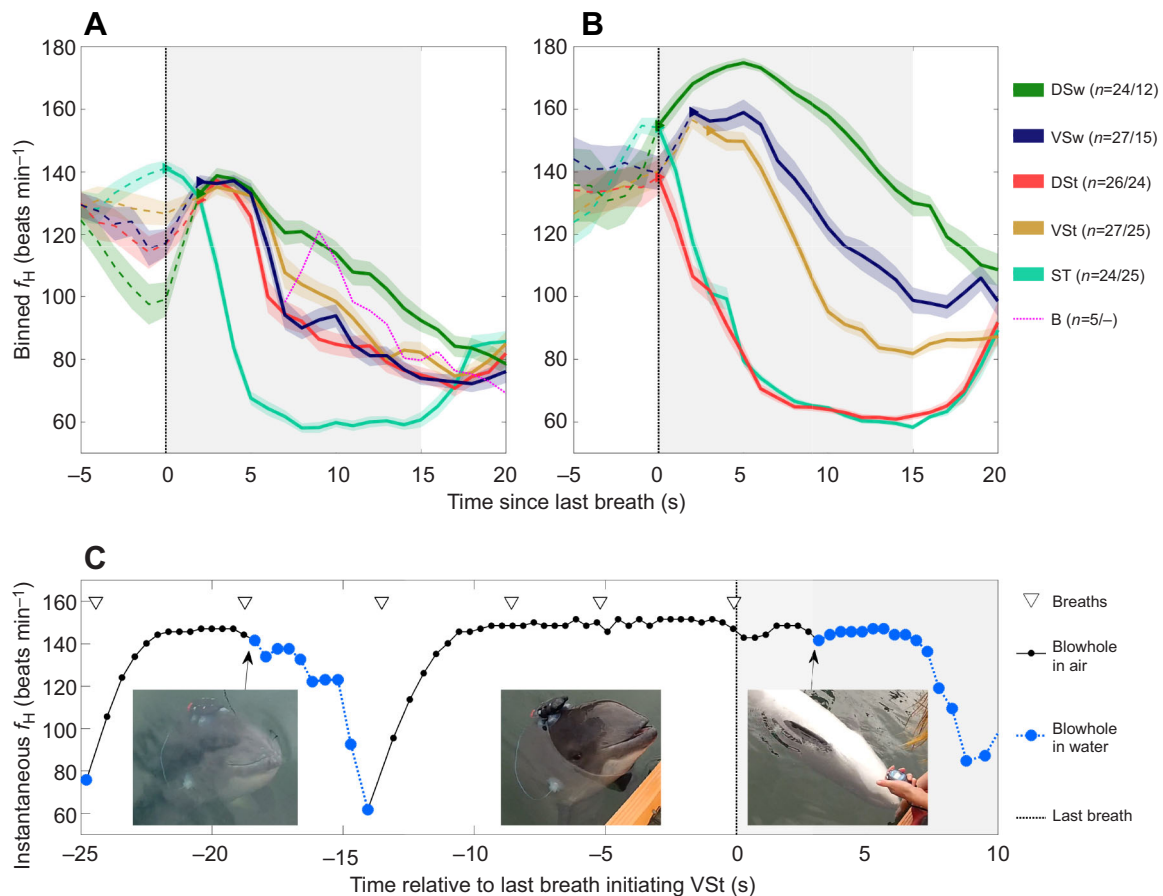
Fig. 2. Modulation of bradycardia in relation to submersion. (A,B) Heart rate (f_H) of porpoises (A: Freja, B: Sif) during breath-holding tasks. f_H was binned in 1 s bins, so lines represent mean and shading represents s.e.m. The dotted vertical line signifies the last breath, marking the onset of the breath hold. The f_H lines are dashed before the moment of blowhole submergence (onset of swimming for DSw), at which point the lines turn solid. The grey shaded background shows the period of time included in the analyses. n values refer to first Freja then Sif. (C) Plasticity of bradycardia initiation. Example of Freja's instantaneous f_H during a surface interval and beginning a VSt breath-holding task. Arrows indicate the onset of blowhole submergence, and blue dotted f_H lines mark the entire interval of submergence. Black f_H lines indicate that the blowhole is free of the water. In the first submergence period, bradycardia is initiated instantly upon blowhole submersion. In the second submergence period, as Freja initiates a VSt, the bradycardia onset is delayed 7 s into the breath hold and 4 s into the blowhole submersion, suggesting anticipatory control. Such a delay was observed in 52–74% of the ventrally oriented tasks (VSt and VSw).

afferents. Blowhole submersion was associated with immediate bradycardia in dorsally oriented tasks (Fig. 2A,B: DSt, ST) and during the time intervals between tasks (Fig. 2C). In contrast, bradycardia onset was delayed several seconds into submergence during 52–74% of ventrally oriented tasks (example in Fig. 2C). This indicates that higher level anticipatory control can modify the onset of bradycardia, consistent with the anticipatory control of diving f_H that was recently demonstrated in porpoises (Elmegaard et al., 2016). It could be that cetaceans can override or evoke bradycardia and peripheral vasoconstriction by volition, akin to their completely voluntary breathing (Lilly, 1958).

Is bradycardia influenced by task and submergence level?
We hypothesised that the progression and severity of diving bradycardia, once initiated, depends on the level of submergence, within the limit of 1 m depth. A relationship between dive depth and degree of diving bradycardia has been documented in several marine mammal species (McDonald and Ponganis, 2014; Williams et al., 2015). In support of this hypothesis, both porpoises exhibited the lowest LQ f_H at 1 m depth (Freja: 58.8±1.5 beats min^{-1}; Sif: 63.5±0.7 beats min^{-1}) and the highest LQ f_H with the blowhole in air (Freja: 108.8±3.3 beats min^{-1}; Sif: 151.8±3.5 beats min^{-1})

(Fig. 2A,B; Table S1). However, when investigating the relationship between submergence level and f_H for all of the behaviours, we found it was not consistent between the two porpoises. For Freja, there was a statistically significant difference of LQ f_H between some of the tasks (Welch's one-way ANOVA: $F_{4,59.7}$=68.5, $P<0.0001$), where LQ f_H grouped according to a gradual response to submergence (see Games–Howell *post hoc* analysis results in Table S2). The lowest breath-hold f_H was at 1 m depth (ST), there was an intermediate breath-hold f_H category just below the surface (DSt, VSt, VSw) and the highest breath-hold f_H was found when the blowhole was out of the water (DSw). This is similar to what was observed in trained bottlenose dolphins and killer whales, which displayed a more profound bradycardia at 2 and 5 m depth, respectively, compared with that at the surface (Bickett et al., 2019; Elsner et al., 1966). In contrast, Sif did not display as clear a relationship between submergence level and f_H; rather, each task had a distinctive bradycardia progression (Welch's one-way ANOVA: $F_{4,36.6}$=265.3, $P<0.0001$) in spite of similar levels and durations of exercise and submergence (Fig. 2A,B; Table S2). The only LQ f_H that did not differ from each other were for DSt and ST (Games–Howell *post hoc* analysis: $P=0.999$), showing that the level of bradycardia observed at 1 m depth can also be obtained just

below the surface. The inconsistencies between the porpoises may be partly due to the limited range (1 m) of submergence depth in this study. Although depth, duration and exercise are known to affect diving f_H (Andrews et al., 1997; Boyd et al., 1999; Hill et al., 1987; McDonald et al., 2018; McDonald and Ponganis, 2014; Noren et al., 2012; Williams et al., 2015), so does anticipatory f_H regulation (Elmegaard et al., 2016; Elsner et al., 1966; Noren et al., 2012), which may also offer an explanation for this variation. Such a strong anticipatory influence on f_H entails concerns as to how cetaceans could respond to some anthropogenic noises while at depth. For example, stranding of several cetacean species has been linked to naval sonar exercises (Frantzis, 1998; Wright et al., 2013), and some of these beached animals had severe gas emboli, suggesting problems with gas management (Jepson et al., 2003; Rommel et al., 2006). Altered diving behaviour as well as altered cardiovascular regulation by diversion of attention away from aspects of the diving response that are under volitional control could explain such fatal outcomes (Fahlman et al., 2006).

To investigate whether the dive response would be absent without the sensory input associated with submergence, we recorded f_H when Freja was out of the water (beaching behaviour: B; Fig. 2A). At the end of the beaching behaviour, f_H was strikingly similar to the bradycardia obtained when Freja was submerged near the surface (DSt, VSt and VSw; Fig. 2A). This indicates that bradycardia is not contingent on immersion, although the data suggest that blowhole

wetting and complete submergence are important drivers of the immediate initiation and severity of bradycardia.

Is surface tachycardia driven by anticipation or breathing?

Marine mammals maximise submergence time by exhibiting both a diving bradycardia and a pronounced surface and pre-surface tachycardia. Pre-surfacing f_H acceleration was initiated by depressurisation during a forced dive of an elephant seal in a pressure chamber, suggesting that baroreceptors or lung expansion may trigger the tachycardia (Kooyman and Campbell, 1972). Pre-surfacing acceleration of heart rate has also been noted in trained tursiops when surfacing from 2 to 15 m depth (Elsner et al., 1966; Irving et al., 1941; Noren et al., 2012). We investigated pre- and post-surfacing f_H, independent of substantial pressure changes and pre-surfacing lung expansion (all depths ≤1 m) by comparing f_H changes before and after the first breath at the end of each DSt, VSt and ST task (Fig. 3). We found pre-surfacing f_H acceleration without depressurisation and also without a subsequent lung ventilation, leading us to posit that f_H increases in anticipation of surfacing, rather than in anticipation of breathing per se. The supposed tachycardia-facilitated wash out of carbon dioxide and nitrogen from tissues to the blood and lungs as well as residual oxygen uptake from the blood may be beneficial whether the breath is a few seconds or a few tens of seconds away (Thompson and Fedak, 1993). Following an exhalation only, f_H decreased again, after
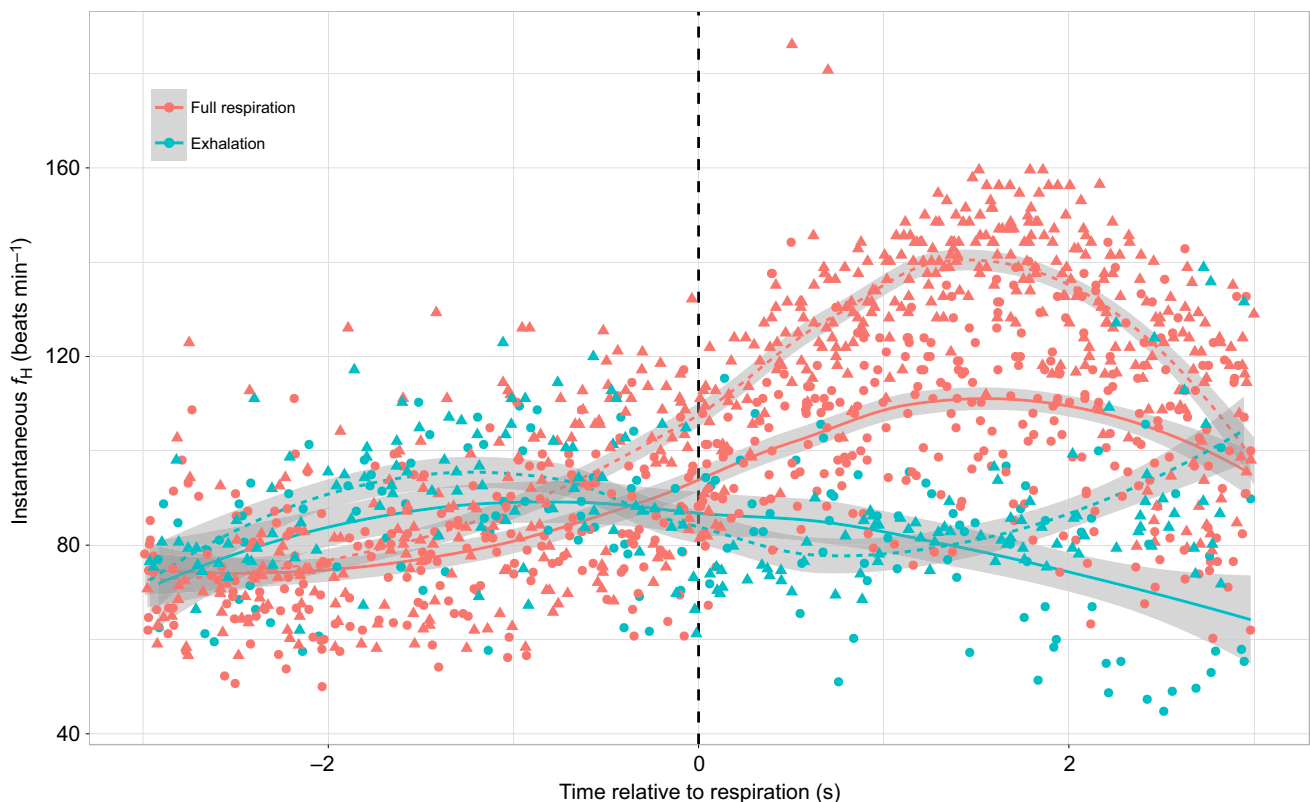

Fig. 3. Tachycardia in relation to surfacing and breathing. Instantaneous f_H around the first breath, ending breath-holding behaviours DSt, VSt and ST. Points represent instantaneous f_H from both animals (Freja: circles, Sif: triangles) during full respirations (red points; n=390 heart beats from 55 recordings for Freja; n=420 heart beats from 53 recordings for Sif) and exhalations (blue points; n=122 heart beats from 18 recordings for Freja; n=146 heart beats from 21 recordings for Sif). Anticipatory f_H acceleration before breaking the surface and breathing (dashed line at t=0) is evident in both animals before a full breath as well as before exhaling. However, true tachycardia only develops after lung ventilation. A porpoise breath is typically <1 s in duration including both the initial exhalation and following inhalation. Polynomial regression lines were fitted for both animals and respiration types to ease visualisation (Freja: solid line, Sif: dashed line). The shaded area depicts the 95% confidence interval.

reaching maximum values of 91.4±3.4 beats min^{-1} (Freja) and 94.9 ±4.1 beats min^{-1} (Sif), whereas full breaths with lung ventilation led to full tachycardia of 115.2±2.1 beats min^{-1} (Freja) and 146.0± 1.5 beats min^{-1} (Sif). It may be noted that these investigations, as well as prior investigations of similar topics, were performed with trained animals. A controlled study with specified behaviours would be very hard to pursue in animals in the wild, and such studies thus emphasise the value of healthy trained captive animals for advancing knowledge of animals in the wild.

Conclusion

We conclude that harbour porpoises exhibit dynamic diving f_H during short breath-hold submergence, and that diving f_H is highly context dependent, highlighting that the cardiovascular adjustments to diving are a regulated response rather than a reflex. We found that blowhole submersion, rather than apnoea alone, drives the initiation and rate of bradycardia; however, breath holding in air also leads to submergence-level bradycardia, albeit with slower progression. We further show that anticipatory f_H acceleration occurs independent of depressurisation and lung expansion, although it only leads to full tachycardia upon lung ventilation. Thus, the pronounced f_H dynamics of harbour porpoises may be categorised as respiration-driven tachycardia and submergence-driven bradycardia, and not just an extreme sinus arrhythmia. We conclude that blowhole wetting is an important sensory input for f_H regulation in cetaceans; however, higher-level control may define both the timing and progression of f_H dynamics.

Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.208637.supplemental

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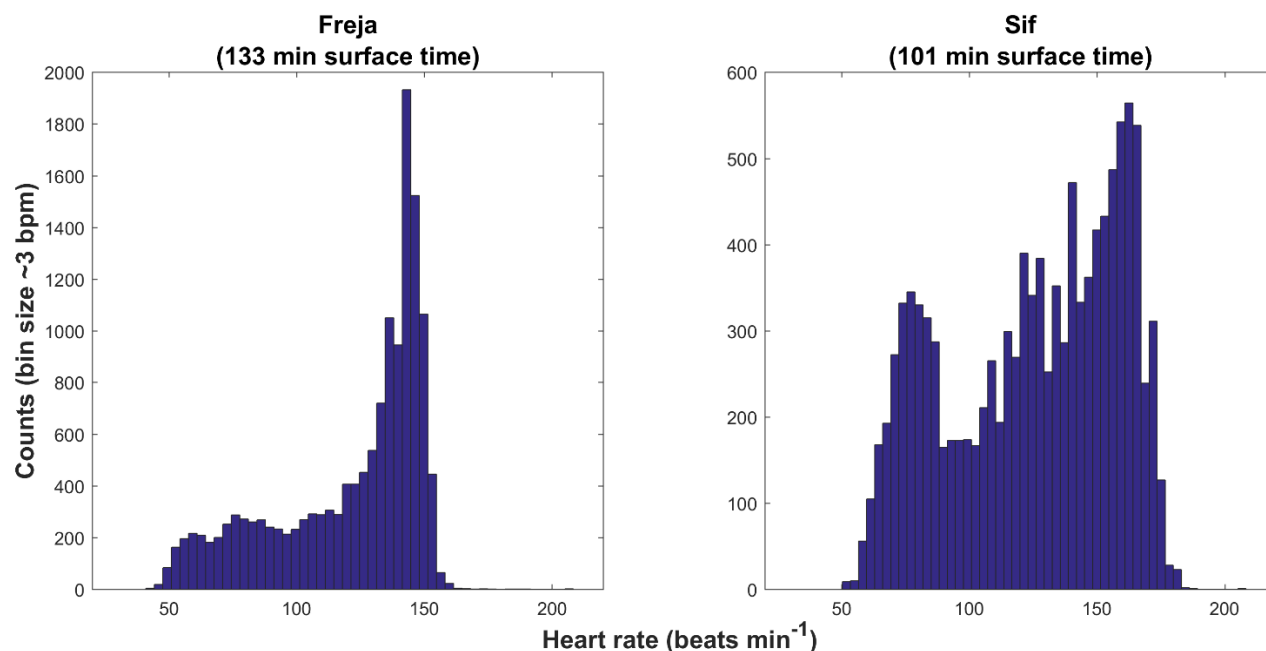
Fig S1. Bimodal f_H of the harbour porpoises. Histograms of f_H during surface intervals (30 seconds preceding and 30 seconds following tasks) for each porpoise. To find the most prevalent f_H of tachycardia and bradycardia, we found the mode of f_H below and above 100 beats min^{-1}. The high f_H mode was 143 (Freja) and 162 (Sif) beats min^{-1}, and the low f_H mode was 76 (Freja) and 77 (Sif) beats min^{-1}. 50 bins and f_H ranges of 41-208 (Freja) and 50-208 (Sif) beats min^{-1} result in bin sizes of ~3 beats min^{-1}.

Table S1. Breath-hold duration and f_H parameters of tasks performed. Calculations of f_H are based on the initial 15 seconds of the tasks, except beaching (B) which are based on the 15 second beaching period.

Animal	Task	n	Duration (seconds) mean	Minimun f_H (beats min^{-1}) mean ±s.e.m.	Mean f_H (beats min^{-1}) mean ±s.e.m.	Median f_H (beats min^{-1}) mean ±s.e.m.	Lower quartile f_H (beats min^{-1}) mean ±s.e.m.
Freja	DSw	24	22.1	87.1 ±3.6	121.7 ±2.4	123.6 ±2.9	108.8 ±3.3
	VSw	27	19.1	66.3 ±1.2	111.4 ±1.9	116.4 ±3.1	84.6 ±2.8
	ST	24	20.1	54.0 ±1.1	85.9 ±2.0	66.7 ±2.0	58.8 ±1.5
	DSt	26	20.0	68.7 ±2.5	106.9 ±2.5	102.0 ±3.5	84.0 ±3.1
	VSt	27	20.3	69.2 ±1.6	114.1 ±2.1	118.8 ±3.3	94.4 ±3.0
	B	5	17.4 (40.4)	59.7 ±1.8	92.3 ±1.1	92.0 ±2.8	78.5 ±2.9
Sif	DSw	12	16.5	127.8 ±4.3	161.0 ±2.4	165.3 ±2.3	151.8 ±3.5
	VSw	15	17.3	97.0 ±3.3	139.4 ±3.0	145.8 ±3.7	121.0 ±3.1
	ST	25	20.6	56.8 ±0.6	87.4 ±1.9	74.1 ±1.2	63.5 ±0.7
	DSt	24	19.8	57.1 ±0.7	83.1 ±2.1	72.1 ±1.8	63.2 ±0.8
	VSt	25	19.4	78.5 ±1.0	127.4 ±1.8	134.1 ±2.8	97.0 ±2.2

Table S2. Results (p-values) from Games-Howell post hoc analysis of lower quartile f_H to examine which task f_H differ and which group. Symbols: ns (not significant), * (p ≤ 0.05), ** (p ≤ 0.01), *** (p ≤ 0.001).

	Freja				Sif			
	DSw	**VSw**	**DSt**	**VSt**	**DSw**	**VSw**	**DSt**	**VSt**
VSw	***				***			
DSt	***	ns			***	***		
VSt	*	ns	ns		***	***	***	
ST	***	***	***	***	***	***	ns	***