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Evidence of dominant parasympathetic nervous activity of great cormorants (*Phalacrocorax carbo*)

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Abstract The characteristics of autonomic nervous activity were examined on captive great cormorants *Phalacrocorax carbo hanedae*, using a power spectral analysis of heart rate variability. Heart rates were calculated from recordings of the electrocardiograms of the birds via embarked data loggers. We investigated the effects of blockades of the sympathetic or parasympathetic nervous systems using the indices of autonomic nervous activity such as high frequency (0.061–1.5 Hz) component, low frequency (0.02–0.060 Hz) component and the low frequency power component to high frequency power component ratio. Resting heart rate (85.5 ± 6.1 bpm) was lower than the intrinsic heart rate (259.2 ± 15.3 bpm). The heart rate drastically increased after the injection of the parasympathetic nervous blocker, on the other hand it slightly decreased after the injection of the sympathetic nervous blocker. The sympathetic, parasympathetic and net autonomic nervous tones calculated from heart rate with and without blockades were 40.9 ± 27.6, -44.5 ± 7.4 and $-29.5 \pm 9.0\%$, respectively. The effect of the parasympathetic nervous blockade on low frequency and high frequency power was greater than that of the sympathetic nervous blockade. Those data suggested that the parasympathetic nervous activity was dominant for great cormorants.

Keywords Heart rate variability · Great cormorant · Power spectral analysis · Autonomic nervous activity · Electrocardiogram

Abbreviations

bpm	Beat per minute
IHR	Intrinsic heart rate
HF	High frequency
LF	Low frequency
S-tone	Sympathetic tone
P-tone	Parasympathetic tone
N-tone	Net autonomic tone

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Introduction

Heart rate [heart rate in beat per minute (bpm)] is an excellent parameter to investigate autonomic nervous function, which is regulated by the balance between sympathetic and parasympathetic nervous activity (Pagani et al. 1986; von Borell et al. 2007). The autonomic nervous system plays a role in the maintenance of homeostasis under circulatory control. Since heart rate is increased by sympathetic nervous activity and decreased by parasympathetic

nervous activity, a common way of investigating the autonomic nervous system is to analyze the power spectrum of the heart rate variability (Kitney and Rompelman 1980; Akselrod et al. 1981; Pagani et al. 1986; Kuwahara et al. 1994, 1996). Such approaches applied to mammalian species have revealed that the power spectrum of the heart rate variability consists of two essential spectral components: the high frequency (HF 0.15–0.4 Hz) component is thought to reflect primarily parasympathetic nervous function, under the control of respiratory functions and the low frequency (LF 0.04–0.15 Hz) component, which corresponds to the balance between vasomotor and baroreceptor control. These power spectra are now widely recognized as reflecting the sympathetic and parasympathetic nervous activities (Akselrod et al. 1981; Pagani et al. 1986; Kuwahara et al. 1996, 1999; von Borell et al. 2007).

In contrast to mammals, power spectral analysis of heart rate variability in birds is not a common practice because of a difficulty for obtaining fine quality data for analysis heart rate variability from poultry, particularly when using non-invasive equipment and a lack of fundamental research evaluating the physiological meaning of heart rate variability indices in avian species (reviewed by von Borell et al. 2007). There are some studies conducted on embryos and hatchlings of chicken (Tazawa et al. 1991; Tazawa et al. 2002; Aubert et al. 2004), gulls (*Larus schistisagus* and *L. crassirostris*; Pearson et al. 2000), and emus (*Dromaius novaehollandiae*; Dzialowski et al. 2007).

Yet, birds, especially seabirds and among them Phalacrocoracidae (cormorants and shags), represent ideal models for investigations on the autonomic nervous system as they display impressive physiological performances in the field, whether this relate to their extraordinary diving ability (an illustration of this can be found in the online database *The penguiness book*, which compiles the diving performances of a large range of air-breathing species, Ropert-Coudert et al. 2006a) or their use of a flight mode that requires almost uninterrupted flapping activity (Pennycuick 1989). Their adaptation to underwater locomotion is such that the heart rate of double-crested cormorants (Phalacrocorax auritus) has been shown to change dramatically during and after submergence, progressing from a bradycardia during the dive itself (reaching as low as 88.4 bpm) to a tachycardia during the period at the sea surface immediately following a dive (raising to a maximum of 397 bpm) (Enstipp et al. 2001). With such drastic changes over limited periods, cormorants are regarded as species with especially high heart rate regulation capacity. Previous study on horses, which also show remarkable heart rate change during exercise (from 20 to 275 bpm (Marasland 1968), reported that these animals display a parasympathetic dominant autonomic nervous function during resting but shows a remarkable elevation in

their heart rate following an injection of a parasympathetic nervous blocker (Kuwahara et al. 1996). In this context, understanding the mechanisms that regulate the balance between sympathetic and parasympathetic nervous activity in these species would bring important information about the characteristics of autonomic nervous function of animals with high heart rate regulation capacity.

In the present study, we give the first description of the power spectral curve of the heart rate of captive great cormorants *P. carbo hanedae*, so as to examine autonomic nervous activity in this species. In addition, we examined how heart rate variability and power spectrum components, such as LF and HF power modes, are influenced by the autonomic nervous activity. For this, we injected into the birds blockers of the sympathetic or parasympathetic nervous systems. We finally discuss the significance and characteristics of autonomic nervous activity in cormorants in the light of what is know in mammals and birds.

Materials and methods

Animals

Four pre-fledging, wild great cormorants were captured at Gyotoku colony (35°40′N, 139°15′E), Chiba, Japan and were kept in a cage (2 m long × 2 m wide × 4 m high) in a room at the Nippon Veterinary and Life Science University, Tokyo between May 1999 and September 2000. The birds were fed ad libitum with saurels *Trachurus japonicus*, and supplied with fresh water. Sunlight and fresh air came into the room through a window. The hearts of the cormorants were collected after birds were killed by pentobarbital venous injection under complete anesthesia.

Experimental protocol

During the experiments, birds were transferred and maintained into a 25°C room. In order to eliminate the influence of post-feeding heat increment on the autonomic nervous system, birds were not fed for 24 h before the measurements, although they were given water.

While most studies recording the electrocardiogram of Phalacrocoracidae used devices implanted into the abdominal cavity (Woakes et al. 1995) or external devices with electrodes implanted close to the heart (Andrews 1998), here, we were able to record clear electrocardiogram peaks using an entirely externally-attached apparatus, without the need for surgery. Cormorants were equipped with miniaturized, cylindrical electrocardiogram data logger (UWE-200ECG, 12-bit resolution, 105 × 20 mm, 52 g, Little Leonardo, Japan, cf. Kuroki et al. 1999;

Ropert-Coudert et al. 2006b). Three cables (1 mm diameter) emerged from the logger and ended with disposable, round plate electrodes (electrode N for newborn, Advance, Japan), which were cut to 12-mm diameter and soldered to the cable. The logger recorded the electric potential difference between two electrodes at a range of −5.9 to +5.9 mV, with 2.88×10^{-3} mV resolution in an 8 MB flash memory. The last electrode was an earth wire, used to reduce the electric noise. This logger records electrocardiogram for 2.5 h at 1-ms sampling interval. A piece of plastic grid (2 cm long × 10 cm wide) was first glued onto the feathers of the lower back of the birds with cyanoacrylate adhesive (Loctite 401) and the electrocardiogram logger was then attached to the grid with plastic cable ties.

In order to detect the QRS peaks (so as to calculate R–R intervals) we placed the electrodes above and below the central part of the sternum as the heart of cormorants is located below the middle part of the sternum, along the longitudinal axis of the birds (Fig. 1). The earth wire was placed on the back of the bird near the body of the electrocardiogram logger (Fig. 1). A few feathers were removed to delimitate a patch of bare skin onto which the electrodes were glued with collodion glue (A. EEG, NEC Medical System, Japan). The three lead wires connecting the electrodes to the body of logger were glued to the feathers in several points.

Before deployment, we verified the correctness of the signal using an analogue electrocardiogram monitor (electrocardiogram automatic analysis device α6000AX-D, Fukuda ME Kogyo, Japan) onto which the electrodes were plugged. This verification lasted 5 min and was performed while birds were not moving.

To avoid having human proximity influencing the cormorant heart rate, birds were left alone for 1 h following the equipment with electrocardiogram loggers. The heart rates measured during the first 5 min after 1 h had passed were taken as the closest approximation of the resting heart rate of the birds.

The cormorants used in this study were dissected after the experiment and the average heart mass was measured.

Blockers of the sympathetic or parasympathetic nervous systems

We injected into the brachial vein of cormorants 0.3 mg/kg of atropine, 0.4 mg/kg of propranolol, and both blockers (0.3 mg/kg of atropine, 0.4 mg/kg of propranolol) simultaneously, at a minimum interval of 24 h between injections, in order to inhibit the parasympathetic, sympathetic and both the para- and sympathetic activity of the birds, respectively. Electrocardiogram of the hand-held cormorants was then recorded for 18 min, 3 to 15 min

Fig. 1 Schematic location of electrodes and electrocardiogram logger on a captive great cormorant (**a**) and a scheme of the front view of its chest (**b**)
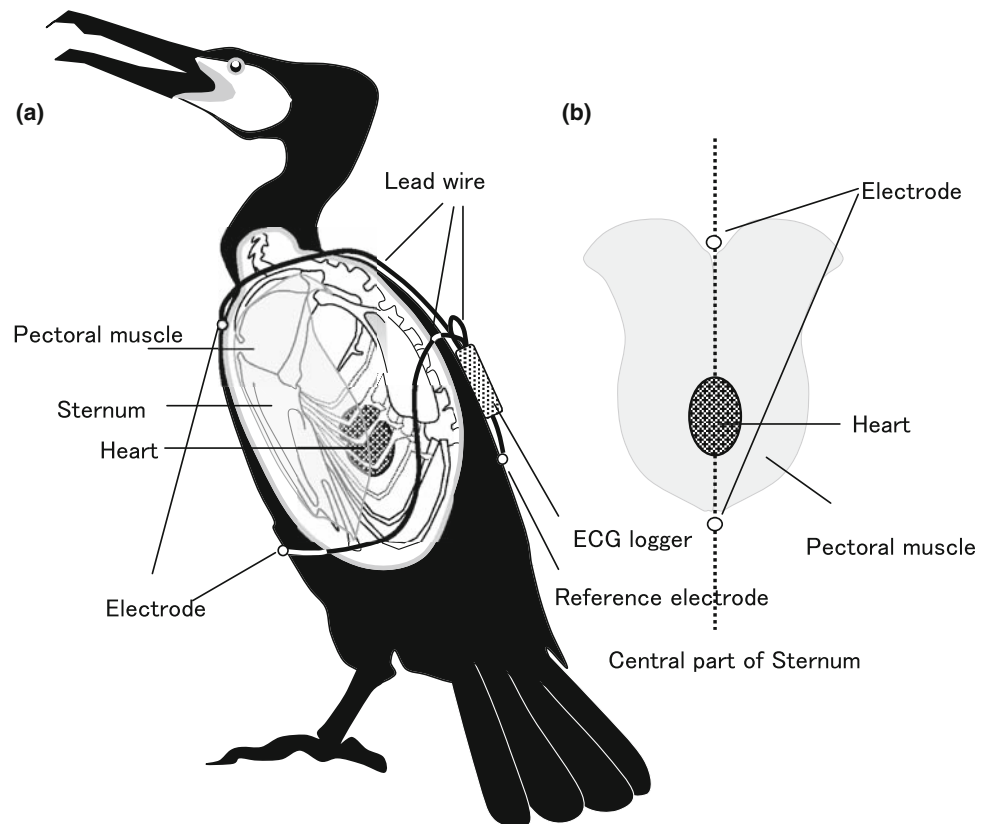
following the injection. Doses were chosen following the method developed by Matsui and Sugano (1987) on chickens (*Gallus gallus*). In a preliminary study, we injected atropine or propanolol in increasing doses, starting at a lower value than that selected by Matsui and Sugano (1987) and finishing at a higher one, so as to determine the dose that correspond to a stabilization of the heart rate of our cormorants. Stabilization was achieved for the same values than those of Matsui and Sugano (1987).

Power spectrum analysis

The electrocardiogram of birds is generally rS type or QS type (Kisch 1957; Szabuniewicz and McCrady 1967; Amend and Eroschenko 1976; Sawazaki et al. 1976; Boulianne et al. 1992; Nap et al. 1992; Machida 2001). Our study revealed that the electrocardiogram of cormorants is QS type (see result; Fig. 2) so that by detecting Q
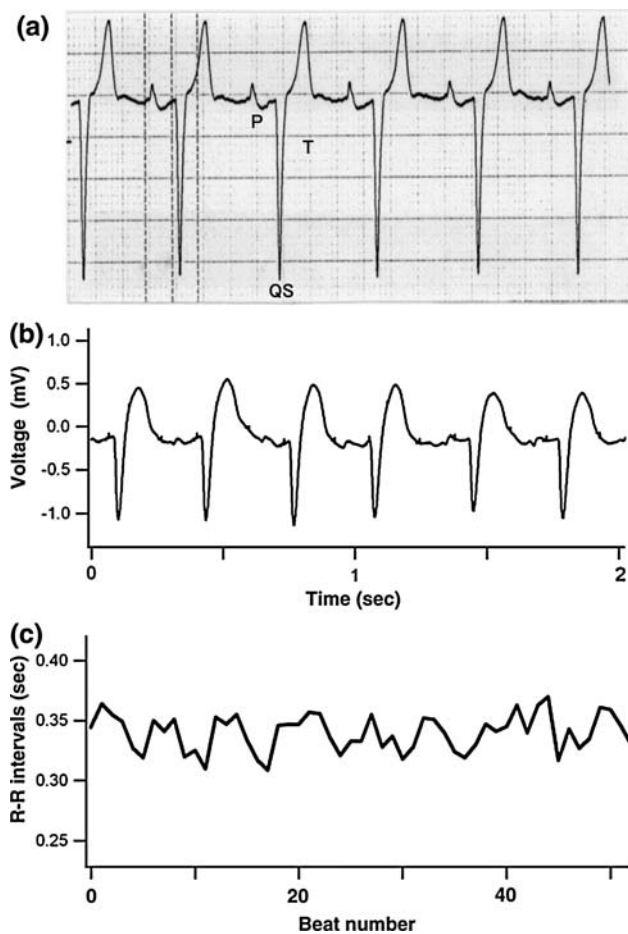

Fig. 2 Electrocardiogram of a captive great cormorant measured by an analogue electrocardiogram monitor (**a**) and by an electrocardiogram logger (**b**). The speed of sheet was 50 minor tics/s for (**a**). *Alphabets* in the figure show P, QS and T waves. Sequential data of R–R intervals (**c**) of a captive great cormorant

peaks we were able to calculate the intervals between R peaks (R–R intervals) using a purpose-written software (Igor, Japanese version 3.1.6, Wavemetrics, USA).

Power spectral analysis of heart rate variability was performed using an electrocardiogram processor (Softron, Japan), as described in Kuwahara et al. (1994). Briefly, R–R intervals data were interpolated at 1-ms sampling interval to form a R–R tachogram, in which 512 points long (following Pagani et al. 1986) datasets were resampled at 100-ms interval. A Hamming window and fast Fourier transformation were applied to each dataset to obtain the power spectrum of the fluctuation in heart rate. Squared magnitudes and the products of the computed discrete Fourier transformations were averaged to obtain spectral estimates.

Heart rate is expected to be maximum under sympathetic nervous activity and when the action of parasympathetic nervous activity is absent and conversely, it will be minimum under parasympathetic nervous activity and when sympathetic nervous activity is inhibited. Sympathetic and parasympathetic tones are used as indices of sympathetic and parasympathetic nervous activity, respectively. Net autonomic tone is an index that shows the valance of autonomic nervous activity. These indexes can be calculated by using the following equations (Walsh 1969; Yayou et al. 1993).

Sympathetic tone (S-tone) $= 100 \times HR_a - IHR/IHR$

Parasympathetic tone (P-tone) $= 100 \times HR_p - IHR/IHR$

Net autonomic tone (N-tone) $= 100 \times (HR_{cont} - IHR)/IHR$,

where HR_a, HR_p, and intrinsic HR (IHR) are the mean heart rates after injections of atropine, propanolol, and under total autonomic blocking (both atropine and propanolol, *sensu* Jose 1966), respectively. HR_{cont} is the heart rate before injection.

Results are shown as grand mean ± SD. Statistical comparisons were conducted using Wilcoxon matched-pair signed-rank test.

Results

The reliability of the electrocardiogram data monitored on the cormorants was confirmed by the synchronicity and similarity in shape of the signals recorded by the logger and that recorded by the analogue electrocardiogram monitor (Fig. 2a, b). The analysis of the electrocardiogram signal revealed that the electrocardiogram of cormorants is predominantly QS type, with clear QS peaks separated by 46–48 ms. Following the automatic identification of the QS peaks (cf. methods) we calculated the R–R intervals

(Fig. 2c), onto which we applied a power spectral analysis. As a result, we highlighted the two major spectral components with the HF component being at 0.068–0.117 Hz in resting birds and 0.2–0.6 Hz in hand-held birds, and the LF component being at 0.02–0.05 Hz in both resting and hand-held birds (Fig. 3). To examine that HF spectrum corresponded to respiratory frequency, we measured the respiration rate by palpation of the belly of the birds, while the data-logger were monitoring the electrocardiogram. The HF peak of hand-held birds corresponded to the frequency of respiration (Fig. 3). We, therefore, defined the frequency range of LF and HF as 0.02–0.06 and 0.061–1.5 Hz, respectively, and proceeded onto calculating the coefficient of variance of the heart rate (coefficient of variance = $100 \times$ SD/mean, in %), the power of LF and HF (ms^2) and total power spectrum (ms^2), and the ratio of LF to HF powers (LF/HF) of resting great cormorants (Table 1).

Heart rate rapidly increased after the injection of atropine, but only slightly decreased after the injection of propranolol. When both blockers were injected together, the IHR was higher than that before injection (Table 1). The coefficient of variance substantially decreased after the injection of atropine or both blockers, and the total power spectrum, the LF and the HF components also significantly decreased, but the LF/HF increased (Table 1). When 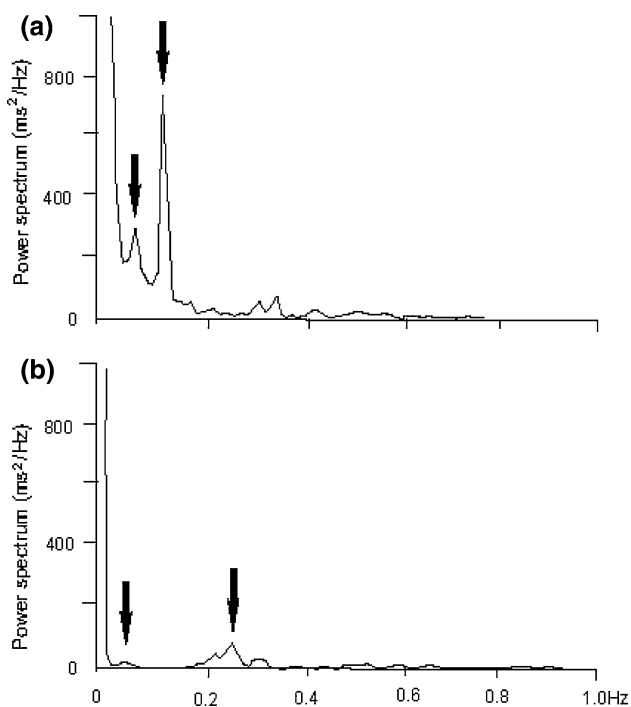only propanolol was injected, the LF and the LF/HF decreased but the HF increased (Table 1). To summarize, LF/HF was high with parasympathetic nervous blockade and low with sympathetic nervous blockade. Conversely, the coefficient of variance was high with sympathetic nervous blockade and low with parasympathetic nervous blockade.

The S-tone, P-tone and N-tone were 40.9 ± 27.6, -44.5 ± 7.4 and $-29.5 \pm 9.0\%$ ($n = 4$), respectively. A negative N-tone suggests that the parasympathetic nervous activity of great cormorant was dominant before the injection of blockers of the sympathetic or parasympathetic nervous systems.

Discussion

As in mammals or chicken embryo (Akselrod et al. 1981; Pagani et al. 1986; Kuwahara et al. 1994; Ishii et al. 1996; Kuwahara et al. 1999; Aubert et al. 2004), HF peaks (0.068–0.6 Hz) measured in adult great cormorants are likely to reflect the parasympathetic nervous activity since we showed that HF peaks were within the respiratory range of the cormorants (Akselrod et al. 1981; Pagani et al. 1986). Equally, we can assume that the LF component of our great cormorants relates to fluctuations in both the vasomotor and baroreceptor [once identified as a mid-frequency peak by Akselrod et al. (1981)] controls, respectively regulated by sympathetic and parasympathetic nervous activities (Pagani et al. 1986; Kuwahara et al. 1996, 1999, cf. introduction). Though the numbers and locations of baroreceptors of members of the aves genera are different from those of mammals, they are expected to share similar characteristics and to be governed by similar feedback control systems of blood pressure regulations (Smith 1994). The link between the modes of the power spectrum and the autonomic nervous activity was confirmed by the substantial decrease in the LF and HF components when parasympathetic nervous activity of the cormorant was blocked with atropine injection and by the attenuation of LF components when the sympathetic nervous activity of the cormorant was blocked with propanolol injection. Our results offer pharmacological evidence that the LF/HF can be used as a reliable index of the balance between sympathetic and parasympathetic nervous activities, while the coefficient of variance is a good index of parasympathetic nervous activity. Further experiments using physiological parameters, such as respiratory and/or blood pressure controls, could confirm our observation.

The characteristics of autonomic nervous function of great cormorants

Several cues, such as a IHR > resting heart rate, a negative N-tone and greater effects of parasympathetic nervous

Fig. 3 Representative power spectrum for heart rate variability of a resting (**a**) and a hand-held great cormorant (**b**). *Arrows* show peak frequency of LF and HF, respectively

Table 1 Heart rate and the indices of autonomic nervous activity at resting and at the injection of autnomic nervous blockers of great cormorants

Treatment	Heart rate (bpm)	Coefficient of variance (%)	Total power spectrum (ms^2)	LF (ms^2)	HF (ms^2)	LF/HF
Resting	85.5 ± 6.1	12.2 ± 1.0	2362.4 ± 477.2	613.6 ± 121.3	1459.7 ± 266.5	0.365 ± 0.058
Control (before injection)	178.8 ± 18.6	9.6 ± 1.6	293.5 ± 136.1	39.6 ± 35.1	240.2 ± 148.0	0.302 ± 0.407
Atropine	359.0 ± 32.6*	2.6 ± 0.5*	1.8 ± 0.8*	0.7 ± 0.6*	0.6 ± 0.4*	1.845 ± 1.461*
Propranolol	142.1 ± 4.8*	9.9 ± 1.2*	468.7 ± 92.2*	24.9 ± 13.5*	432.4 ± 95.0*	0.066 ± 0.054*
Atropine and propranolol	259.2 ± 30.6*	3.9 ± 2.5*	15.7 ± 23.5*	6.2 ± 7.4*	1.9 ± 1.6*	2.361 ± 0.964*

Resulted in each category are mean ± SD. * $P < 0.01$; significantly different from the control

blockade on LF component, HF component and the coefficient of variance than those of sympathetic nervous blockade suggest that parasympathetic nervous activity of great cormorants is dominant over the sympathetic nervous activity, like in horses and Göttingen miniature swines (Kuwahara et al. 1996, 1999). Yet, the response of the autonomic nervous system to different blockers showed some unexpected deviations from what is observed in mammals. Indeed, one would expect LF component to decrease and HF component to remain constant when sympathetic nervous activity is blocked but, while the LF of cormorants decreased, their HF increased under propranolol injection (Table 1). Such an increase has been reported in horses, which show a dominant parasympathetic nervous activity (Kuwahara et al. 1996). In the light of the above (plus the fact that sympathetic and parasympathetic nervous activities are opposing each other) we propose that this increase is due to a partial inhibition of the sympathetic nervous activity under the influence of propranolol. Another fact tends to confirm that

parasympathetic nervous activity was remarkably dominant in our cormorants. A hand-held cormorant should be under acute stress (increase in heart rate under the influence of the corticotropin releasing factor, Fisher et al. 1983; Brown et al. 1986), hence atropine and propranolol injections should lead to higher and lower heart rates than would be the case in a resting bird, respectively. This is what we observed but since our stressed birds still showed a negative net tone (−29.5%), we should expect an even higher net tone in resting conditions. Also note that cormorants displayed a high heart rate following atropine injection (four times higher than resting heart rate).

Like in our cormorants, resting lesser scaup *Aythya affinis* show a high P-tone, a low S-tone and a N-tone with dominant parasympathetic nervous activity (McPhail and Jones 1999, Table 2). In contrast, a low P-tone, a high S-tone and a sympathetic-dominant N-tone have been documented in resting chicken but it should be noted here that the rate of increase from resting heart rate to heart rate with atropine in chicken was less than that in cormorants

Table 2 Heart rate and the indices of autonomic nervous activity of mammals and birds

Species	Body mass (kg)	Resting HR (bpm)	HR with atropine (bpm)	HR with propranolol (bpm)	IHR (bpm)	S-tone (%)	P-tone (%)	N-tone (%)	References
Cattle	411–680	62.1	57.4	73	74	−1.4	−22.4	−16.1	Matsui and Sugano (1987)
Thoroughbred horses	526–655	29.9	33.4	81.4	82	−0.7	−59.3	−63.6	Matsui and Sugano (1987)
Ponny	203–305	44.1	44.6	97.4	95.5	2.0	−53.3	−53.9	Matsui and Sugano (1987)
Pig	160–250	109.5	89.9	158	108.9	45.1	−17.4	0.5	Matsui and Sugano (1987)
Goat	25–33	85.1	74.8	130.8	110.2	18.7	−32.1	−22.8	Matsui and Sugano (1987)
Dog	30	73	75	172	127	35.4	−40.9	−42.5	Palazszolo et al. (1998)
Miniature swine	22.2–30.2	80	67	187	126.3	48.1	−47.0	−36.7	Kuwahara et al. (1999)
Muskrat (*Ondatra zibethicus*)	0.8–1.0	195	190	288	–	–	–	–	Signore and Jones (1995)
Rat	0.3–0.4	337.1	327.9	394.7	372.7	5.9	−12.0	−9.6	Kuwahara et al. (1994)
Mouse	0.046	627.8	499.2	692	543.7	27.3	−8.2	15.5	Ishii et al. (1996)
Vole (*Microtus arvalis*)	0.045	480.7	412	562.9	479.4	17.4	−14.1	0.3	Ishii et al. (1996)
Great cormorant[a]	1.9	88.2	142	359	259	40.9	−44.5	−29.5	This study
Lesser scaup (*Aythya affinis*)	0.6	190	141	373	322	15.8	−56.2	−41.0	McPhail and Jones (1999)
Chicken	0.8–1.0	346.7	246	365	253.4	44.0	−2.9	36.8	Matsui and Sugano (1987)

[a] Data of great cormorants was calculated by using data of this study

(Matsui and Sugano 1987). Despite the limited number of studies, it seems that the predominance of an autonomic nervous activity over another differ between avian species like it does in mammals, some birds being sympathetic-dominant and others being parasympathetic-dominant. In summary, our results indicate that the dominance of para-sympathetic nervous activity in great cormorants allows them to increase their heart rate extensively from their extremely low resting level. The adaptative significance of this is discussed below.

Surprisingly, heart rate, S-tone and P-tone were unex-pectedly high and simultaneously, the total power spectrum, LF and HF components were unexpectedly low before the injection of the blocker than during resting. This high sympathetic activity probably resulted from the han-dling of the birds that stressed them. We can assume that in the absence of stress the parasympathetic and sympathetic nervous activities during resting are higher and lower, respectively, than that before injection.

The balance between the two autonomic nervous activities is species-specific. With the difference between resting heart rate and heart rate with atropine being generally substantial in animals with dominant parasym-pathetic nervous activity (Table 2). Since resting heart rate is lower than IHR in these animals, the decrease of para-sympathetic nervous activity and the increase of sympathetic nervous activity should lead to drastic eleva-tions in their heart rate. For example, the resting heart rate of thoroughbred is about 30 bpm but their heart rate during maximum exercise exceeded 200 bpm, i.e. about 7× rest-ing heart rate (Butler et al. 1993). Butler et al. (1993) explained this drastic raise in heart rate by a reversal of parasympathetic nervous activity and sympathetic nervous activity.

The average resting heart rate of great cormorant in our study, at 85.5 bpm, is within the range reported for win-tering Greenland great cormorants (i.e. 50–100 bpm, Grémillet et al. 2005) but is lower than that reported in other species of similar size, i.e. 137.9 bpm in double-crested cormorants (Enstipp et al. 2001) and 93 bpm in South Georgian shags *P. georgianus* (Bevan et al. 1997). However, it is much lower than the resting heart rate cal-culated from their body mass via

Heart rate = 155.8 body mass$^{-0.23}$

(Lasiewski and Calder 1971).

From this equation, the resting heart rate is expected to range from 133 to 144 bpm. The cormorants live with lower heart rate than their IHR, because their parasympathetic nervous activity is dominant. How can cormorants maintain their own body with such a low heart rate? A first element of answer lies in the fact that, compared to mammals, avian

heart mass is relatively large (and heart rate are relatively low) with regards to their body mass (Grubb 1983; Schmidt-Nielsen 1984). For instance, birds >1 kg body mass and with a large heart mass/body mass ratio are the great northern diver, *Gavia immer*, with heart mass of 2.5–4.9 kg (1.1–1.3%), great blue herons, *Ardea herodias*, with a heart mass of 2.0 kg (1.0%) and Anhingas (or darters), *Anhinga anhinga*, with a heart mass of 1.25 kg (1.0%, Hartman 1955). By comparison, the heart mass of *P. auritus* has been reported to range 1.5–1.8 kg, i.e. 0.89% of the body mass, while that of *P. Olivaceus* is 1.2 kg, i.e. 0.82% of their body mass (Hartman 1955). In the present study, the heart of the cormorants accounted for 1.4 ± 0.1% of their body mass (Hayama, unpublished data), a value much above that calculated from the equation of Lasiewski and Calder (1971, 0.77–0.79%) that relates heart mass to body mass via

Heart mass = 0.0082 body mass$^{0.91}$.

In other words, the heart mass of great cormorants account for a considerable proportion of the body mass among Phalacrocoracidae and even among other birds of similar sizes. Since stroke volume is directly proportional to body mass and heart mass is directly proportional to body mass (Grubb 1983), it is reasonable to assume that stroke volume is also directly proportional to heart mass. If a relatively large heart mass allows for a larger stroke volume, then great cormorants should be able to distribute efficiently blood throughout their body even with a relatively low heart rate.

Heart rate is positively correlated to oxygen consump-tion rate (Butler 1993) so that a strong increase in heart rate between a resting to an exercising state should generally correspond with a substantial increase in the metabolic rate, although it may not be necessarily linear (e.g. McPhee et al. 2003; Ward et al. 2002). Most aerobic scopes (maximum to minimum metabolic rates ratio) of birds and mammals are comprised between 6 and 35 (reviewed by Bishop 1999), except dominant parasympathetic nervous activity animals, like horses for which the aerobic scope is higher than 60 (Jones et al. 1989), and fast-running animals such as dog and pronghorn (*Antilocapra americana*, Bishop 1999). In contrast, it is generally considered that animals with low aerobic scope, such as mice, do not present large difference in heart rate between resting and exercising and have a sympathetic-driven nervous activity (Bishop 1999). In other words, autonomic nervous activity would be related to the level of activity of an animal, with animals performing exercises that require a high oxygen consumption rate showing dominant parasympathetic ner-vous activity. This can be illustrated by the positive correlation that exists between body mass and the meta-bolic costs of certain energy-demanding activities, such as

flight or fast running locomotion (Schmidt-Nielsen 1984). Large birds, for instance, use either flapping flight or gliding flight (Pennycuick 1989). The mean heart rate of South Georgian shags during flapping flight is 309 bpm, 3× the resting heart rate, i.e. 104 bpm (Bevan et al. 1997). In contrast, heart rate of wandering albatrosses (*Diomedea exulans*) during take off is 130 bpm, 2× the resting heart rate, i.e. 60 bpm and still above the gliding heart rate, i.e. 95 bpm (Weimerskirch et al. 2000).

The large heart mass and extensive heart rate increase ability suggest that cormorants might have high circulatory capacity, an advantage when performing sustainable flapping flight. In this regard, the flight costs of great cormorant might be further exacerbated by the fact that their food load can reach on average 288 and 199 g for males and females, respectively, with maximum load up to 800 g (Grémillet et al. 2000). With such a heavy mass to carry through sustained flapping flight such a circulatory adaptation would bring a significant amount of extra aerobic capacity to the birds.

It would also enhance their diving ability, especially since cormorants are known to increase their heart rate following a dive in order to recover from the accumulated oxygen debt during diving (Bevan et al. 1997).

In summary, our study demonstrates that great cormorant present a dominant parasympathetic nervous activity, which in turn lowers the birds resting heart rate, phenomenon that they compensate by increasing the stroke volume thanks to a relatively large heart mass. This parasympathetic dominancy can be regarded as a helpful feature to assist birds, as well as other parasympathetic dominant animals such as horses, in performing energy-demanding behavior. In this regard, our methodological approach investigating the characteristics of the autonomic nervous function and the morphological feature of heart could enhance our understanding of the physiological adaptations to energy-demanding behavior.

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