Does parental heart rate affect embryonic heart rate during incubation? An experiment in Common Terns *Sterna hirundo*

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Abstract

Embryonic heart rate is a strong determinant of metabolic rate and the rate of embryonic development in oviparous species. In humans, embryonic heart rate is positively correlated with the heart rate of the mother. However, human embryos do not develop autonomously from the maternal circulatory system, making it impossible to separate maternal control from an independent embryonic adjustment of its heart rate to that of its mother. In birds, embryonic development does occur autonomously from the mother, while the embryo can audiotively perceive the heart rate of the incubating parent. In this study, we used Common Terns (*Sterna hirundo*) to experimentally test whether the embryonic heart rate is affected by parental heart rate during incubation. We artificially incubated freshly laid eggs under standardized conditions and continuously exposed them to the sound of either a slow or fast parental heart rate throughout the first 18 days of embryonic development. At day 18 of embryonic development (a few days before hatching) there was no significant difference in the embryonic heart rate between both treatments. There was also no effect of treatment on either total duration of embryonic development or hatching success. We suggest that embryonic heart rate and development rate may not be affected by the heart rate of the parent because natural parental heart rates are very sensitive to external conditions that may fluctuate drastically, while embryos may need a relatively stable heart rate for optimal development.

Keywords Acoustic stimulation · Maternal effect · Parent-offspring coadaptation · Parent-offspring communication · Prenatal development

Zusammenfassung

Beeinflusst die elterliche Herzfrequenz die embryonale Herzfrequenz während der Inkubation? Ein Experiment an Flussseseschwalben

Die embryonale Herzfrequenz ist ein bestimmender Faktor für die Stoffwechselrate und die embryonale Entwicklungsgeschwindigkeit bei oviparen Arten. Bei Menschen korreliert die embryonale Herzfrequenz positiv mit der Herzfrequenz der Mutter. Dennoch entwickeln sich menschliche Embryos nicht autonom vom mütterlichen Kreislaufsystem, was es unmöglich macht die mütterliche Kontrolle von der unabhängigen embryonalen Anpassung ihrer Herzfrequenz an die ihrer Mutter zu trennen. Bei Vögeln hingegen findet die embryonale Entwicklung unabhängig von der Mutter statt, obwohl der Embryo die Herzfrequenz des inkubierenden Elternteils akustisch wahrnehmen kann. In der vorliegenden Studie untersuchten wir an Flussseseschwalben (*Sterna hirundo*), ob die embryonale Herzfrequenz von der ihrer Eltern während der Inkubation beeinflusst wird. Dazu inkubierten wir frisch gelegte Eier künstlich unter standardisierten Bedingungen, und

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setzten diese kontinuierlich entweder dem Sound einer langsamen oder schnellen Herzfrequenz während der ersten 18 Tage der embryonalen Entwicklung aus. Am 18. Tag der embryonalen Entwicklung (ein paar Tage vor dem Schlupf) war kein signifikanter Unterschied zwischen den beiden Verfahren festzustellen. Zudem gab es weder einen Effekt der beiden Verfahren auf die Gesamtinkubationszeit noch auf den Schlupferfolg. Wir nehmen daher an, dass die embryonale Herzfrequenz und die embryonale Entwicklungsgeschwindigkeit nicht von der Herzfrequenz der Eltern beeinflusst werden, weil die natürlichen elterlichen Herzfrequenzen sensibel gegenüber äußeren Einflüssen sind, welche drastisch schwanken können, während Embryos eine relativ stabile Herzfrequenz für ihre optimale Entwicklung benötigen.

Introduction

An individual's heart rate is the speed of the heartbeat measured by the number of contractions (beats) of the heart muscle per minute (bpm). With a heartbeat, blood is pumped through the circulatory system to supply all regions of the body with nutrients and oxygen. As such, an individual's metabolic rate is a direct function of its heart rate, as well as the stroke volume and the oxygen content of the blood (Butler et al. 2004). In oviparous species, embryos with faster heart rates also develop faster, confirming that heart rate is a major component of the response of the embryo to an increase in the demand for oxygen and nutrients that comes with faster embryonic development (Du et al. 2009; Vedder et al. 2017).

Interestingly, despite the human embryo having a much faster heart rate than the mother, there is a strong positive correlation between embryonic and maternal heart rate in humans (Patrick et al. 1982). Focusing on short phases of embryonic-maternal heart rate synchronization, a study in humans suggests that the embryonic circulatory system might be able to react to the maternal heart rate (Van Leeuwen et al. 2009). This phenomenon also appears to be present in rats (*Rattus norvegicus*; Timofeeva et al. 2015). In placental mammals, however, the embryo is provided with maternal hormones, nutrients, and oxygen via the placenta (Knipp et al. 1999), providing the opportunity for the mother to directly tune embryonic heart rate, instead of the embryo reacting autonomously to the mother.

In birds, the embryo receives its oxygen from the atmosphere through the porous eggshell (Tazawa 2005), while the nutrients it requires until hatching are provided by the albumen and the yolk in the egg (Lovette and Fitzpatrick 2016). Nevertheless, during embryonic development via natural incubation, the heart rate of the incubating parent represents one of the clearest sounds the embryo can perceive (Arnold et al. 2011; Borneman et al. 2014) and studies suggest that avian embryos can react to auditory cues from their environment (Colombelli-Négrel et al. 2012; Mariette and Buchanan 2016; Noguera and Velando 2019). We, therefore, aimed to test if avian embryos autonomously adjust their heart rate to that of their parents, which, to our knowledge, has *hitherto* never been done. Such heart rate adjustments could act as a mechanism behind family-transmitted stress, which under

certain conditions may be adaptive in birds (Noguera et al. 2017).

To this aim, we artificially incubated freshly laid eggs from wild Common Terns (*Sterna hirundo*), and randomly exposed them to the sound of either a slow or fast parental heart rate, throughout the majority of embryonic development. We subsequently tested whether embryonic heart rate during late embryonic development differed between the parental heart rate treatments and whether this had consequences for the rate of embryonic development. We predicted that, if embryos adjust their heart rate to that of their parents, the fast parental heart rate treatment would lead to a faster embryonic heart rate and a shorter total incubation duration.

Methods

Study species and site

Common terns are socially and genetically monogamous colonially breeding seabirds (Becker and Ludwigs 2004). Incubation starts after the first egg is laid and is shared between the sexes (Becker and Ludwigs 2004). The clutch usually consists of 2–3 eggs laid at intervals of 1–2 days, and the chicks generally hatch after 21–23 days, in the order of laying (Nisbet and Cohen 1975; Becker and Ludwigs 2004).

We studied Common Terns breeding at the Banter See in the city of Wilhelmshaven, at the German North Sea coast (53°30'40" N, 08°06'20" E). This breeding site consists of six concrete islands each measuring 10.7 × 4.6 m with 60 cm high concrete walls protecting against flooding and predation. In recent years, the colony size is ca. 650–700 breeding pairs per year.

Audio recording and processing

To obtain the sound of the heart rate of an incubating adult Common Tern, we placed a microphone (electret capacitor microphone capsule MCE 101; Reichelt Elektronik GmbH & Co. KG, Germany) in a fake egg, which was connected to a digital audio recorder (following Arnold et al. 2011). The egg was placed in the nest for 20–30 min to record the heart

rate of the incubating parent. We made recordings of several individuals, always early in the morning (5–7 am; as the birds incubate most solidly at this time), but only selected the best recording to modify with the audio program Audacity (version 2.3.2, Audacity Team 2019).

We eliminated background noises in the recording by the use of a low pass filter while preserving heartbeats. We chose a sample rate of 11,025 Hz to reduce the maximum noise and normalized the loudest one at -1 dB. To create a new audio track of the bird's heartbeat, we chose one clear clip of a single heartbeat, and attenuated noise of less than 50 Hz and above 800 Hz. By repeating the single heartbeat with a modified inter-beat interval, we created two stable heart rates that varied in inter-beat interval but were otherwise identical. In this way, we created a slow heart rate of 300 beats per minute (bpm) and a faster heart rate of 340 bpm. We chose these values to obtain heart rates within the known heart rate range of Common Tern embryos at 37.5 °C (mean = 301, SD = 23, range = 240–372 bpm; Vedder et al. 2017) and parents (range = 173–525 bpm; Wurm 1996; Wurm and Hüppop 1998). We used two semi-artificially created heart rates, instead of separate recordings of a natural fast and slow heart rate, to ensure that the heart rates only differed in inter-beat interval and not in any other characteristic that may provide information to the embryo.

Data collection and experimental setup

In the breeding season of 2020, we performed twice-daily checks (mornings and afternoons) of the colony site to mark new clutches at the day of first-egg laying. We collected 91 eggs of 35 clutches on the day of laying, which we numbered according to clutch identity and laying order. We replaced the eggs with fake eggs, which were roughly similar in size and colour, and readily accepted by the parents.

After collection, we assigned eggs to one of two incubation treatments. The first egg of a clutch was randomly assigned to a treatment, while the second egg of a clutch (if present) was always assigned to the opposite treatment of the first egg, and the third egg (if present) assigned to the same treatment as the first egg of the clutch. In this way, we assured that eggs of the same clutch were distributed across the two treatments. Both treatments consisted of artificial incubation (starting within 1 h of egg collection) in a digital air-filled incubator (Rcom max 50; Autoalex Cp., Ltd., South Korea) that was set at 37.5 °C with a relative humidity of 50% (following Vedder et al. 2017). For the different treatments, we used two identical incubators with identical settings, in which we either played a continuous soundtrack of the 300 bpm parental heart rate, or that of the 340 bpm parental heart rate. The soundtracks were played with identical sound stations (MusicMan Mini Soundstation; Technaxx Deutschland GmbH & Co. KG; Germany) mounted inside

the incubators. Once per hour both incubators automatically turned the eggs ca. 90°. To avoid potential temperature gradients in the incubator affecting the eggs, egg positions were manually and randomly changed once per day. The overall hatching success was 84.6%, and not significantly different between the treatments (300 bpm: 80.4% vs. 340 bpm: 88.9%, $\chi^2 = 1.22$, $\Delta df = 1$, $P = 0.269$).

We measured the embryonic heart rate of each viable egg 18 days after the onset of incubation (before pipping of the inner shell membrane by the embryo) with a digital egg monitoring system (Buddy; Avitronics, Truro, United Kingdom), which uses infrared sensors to detect the pulse of a blood vessel. We conducted the heart rate measurements outside of the incubator at room temperature. We recorded the first stable heart rate (in bpm) and the time it took before the heart rate was stable (in s). The latter measure was taken because the embryonic heart rate decreases when an egg cools off (Sheldon et al. 2018). If the heart rate did not stabilize within 3 min, the egg was returned to the incubator and the process repeated after a minimum interval of one hour. The mean time it took before the heart rate was stable was 69 s (SD = 49, range = 6–174 s). We previously showed that embryonic heart rate at 18 days was positively correlated with embryonic heart rate at 19 days, and predictive of total embryonic development time in Common Terns (Vedder et al. 2017). After the measurement, all eggs were transferred to a hatching incubator (Rcom max 50; Autoalex Cp., Ltd., South Korea) with a temperature of 37.0 °C and relative humidity of 60%, with no egg turning.

In the hatching incubator, the eggs were placed in separate compartments divided by wire mesh to allow linking each hatchling to its egg. A digital camera was programmed to take a picture of the content of the hatching incubator every half hour. These pictures were manually scored for the hatching of chicks, defined as the head being completely out of the egg, and the total incubation duration of each chick was calculated by subtracting the time of onset of artificial incubation from the time a chick was first recorded as hatched (in days, with a resolution of 30 min). After hatching, chicks were ringed and returned to their nest of origin within half a day. All parents readily accepted their chicks upon return. The fake eggs were removed from the nest when chicks were returned, or 1–2 days after the last chick was returned in case not all eggs from a clutch hatched.

Statistical analyses

The effect of the parental heart rate treatment (as a categorical fixed effect) on embryonic heart rate on day 18 and the total incubation duration was analyzed at the level of the individual embryo using linear mixed models with normal error distributions that included clutch identity as a random effect, to account for the non-independence of embryos

within clutches (Vedder et al. 2017). The effect of embryonic heart rate, and its interaction with treatment, on total incubation duration, was analyzed in the same way. For the test of a treatment effect on embryonic heart rate, we included the time until a stable heart rate was recorded in the model as a covariate, to correct for the cooling of the embryo at room temperature.

The effect of the treatment (as a categorical fixed effect) on hatching success, reported above, was analyzed using a generalized linear mixed model with a binomial error distribution and a logit link function. Clutch identity was included as a random effect.

All models were run in MLwiN (version 2.22; Rasbash et al. 2004) and significance ($P < 0.05$) was assessed using the Wald statistic.

Results

Exposure to the sound of a faster parental heart rate did not lead to a faster embryonic heart rate, as the embryonic heart rate on day 18 of incubation did not differ significantly between the two treatments (Fig. 1; Table 1a).

A faster parental heart rate also did not lead to faster embryonic development, as the total incubation duration of successfully hatched chicks did not differ significantly between the two treatments (Fig. 2; Table 1b).

Table 1 Summary of models testing for effects of the parental heart rate treatment on embryonic heart rate (a) and total incubation duration (b)

Model	Coefficient (SE)	χ^2	Δdf	P
(a) Dependent variable: embryonic heart rate (bpm)				
Intercept	317.79 (5.44)			
Clutch ID (random)	213.38 (86.86)	6.04	1	0.014
Time until stable heart rate (s)	− 0.15 (0.05)	9.27	1	0.002
Treatment (300 bpm = ref)	− 6.13 (4.18)	2.16	1	0.142
(b) Dependent variable: total incubation duration (day)				
Intercept	21.48 (0.08)			
Clutch ID (random)	0.06 (0.04)	3.16	1	0.075
Treatment (300 bpm = ref)	0.10 (0.09)	1.17	1	0.279

As found previously (Vedder et al. 2017), total incubation duration was shorter with a faster embryonic heart rate (Fig. 3; coefficient $\pm$ SE = -0.010 ± 0.002 day/bpm, $\chi^2 = 24.10$, $\Delta df = 1$, $P < 0.001$). This effect was not significantly different between treatments (heart rate $\times$ treatment interaction: coefficient $\pm$ SE = -0.003 ± 0.004 day/bpm, $\chi^2 = 0.46$, $\Delta df = 1$, $P = 0.499$).

Fig. 1 Boxplots (showing the median, interquartile range, 10th and 90th percentile, and individual data points outside this range) of embryonic heart rate (bpm) at day 18 of incubation for the two different parental heart rate treatments ($n = 39$ eggs from 30 clutches for 300 bpm, $n = 43$ eggs from 33 clutches for 340 bpm)

Fig. 2 Boxplots (showing the median, interquartile range, 10th and 90th percentile, and individual data points outside this range) of total incubation duration (day) for the two different parental heart rate treatments ($n = 37$ eggs from 29 clutches for 300 bpm, $n = 40$ eggs from 30 clutches for 340 bpm)

Fig. 3 Total incubation duration (day) plotted against embryonic heart rate (bpm) at day 18 for the two different parental heart rate treatments. The trend line represents the overall model prediction

Discussion

By artificial incubation of freshly laid eggs, we were able to measure the embryonic heart rate on day 18 of incubation and the total incubation duration under standardized conditions that only differed in the speed of the parental heart rate the embryos were auditorily exposed to. Although we did not find that Common Terns embryos adjust their heart rate and speed of development to the speed of the experimental parental heart rate in this study, this was, to our knowledge, the first experimental test of whether the heart rate of avian embryos is sensitive to the heart rate of their parents.

Other studies have suggested that embryonic heart rate in birds is sensitive to environmental conditions (Sheldon et al. 2018), in particular to temperature (Vedder et al. 2017; Sheldon et al. 2018; Stier et al. 2020). Indeed, we found a decrease in embryonic heart rate as egg temperature declined during the measurement at room temperature (see Table 1a). Hence, the lack of an effect of parental heart rate in our study does not stem from a general insensitivity of embryonic heart rate to the environment but reflects a specific insensitivity to the parental heart rate.

Mechanistically, the observed lack of a response may be explained by a lack of perception of the parental heart rate. Analysis of the avian embryo sensory system revealed that auditory perception develops at a late stage (Gottlieb 1968). However, in the Chicken (*Gallus domesticus*), which has a similar embryonic development time as Common Terns, it

was found that hearing begins on day 16 of embryonic development (Jones et al. 2006). In semi-precocial species, which include the Common Tern, hearing generally develops in the last third of incubation (Golubeva and Tikhonov 1985). As day 18 is well into the last third of incubation in Common Terns, we do not deem a lack of perception to be the most likely explanation for the lack of an effect. However, we cannot rule out that our semi-artificial parental heart rates do not provide the correct stimulus for the embryo, because they will be more monotonous than natural. In our incubation set-up, there is also no direct contact between the parent and egg shell, which could make it more difficult for the embryo to perceive the vibrations of the parental heart rate.

Alternatively, from a functional perspective, it may not be adaptive for the embryo to adjust its heart rate to that of its parents. In general, the heart rate of incubating birds can be extremely dynamic (Odum 1941). This is also found in Common Terns, in which ambient temperature and disturbance of the parents can have a large effect on parental heart rate during incubation (Wurm 1996; Wurm and Hüppop 1998). Adjusting the embryonic heart rate to such a dynamic cue may disturb embryonic development and reduce embryo viability. As such, it may be adaptive to adjust embryonic heart rate to the external energy the parent supplies during incubation (i.e., to incubation temperature), but not to dynamic environmental cues.

In conclusion, our experimental results do not suggest that embryonic heart rate and development rate are affected by the heart rate of the parent in Common Terns. Although we cannot rule out that our experiment did not provide the right stimulus, we suggest that embryos do not adjust their heart rate to their parent's because it may not be adaptive for them to do so.

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Data availability Data will be available upon request to the corresponding author.

Declarations

Conflicts of interest We declare no conflicts of interest.

Ethics approval All procedures complied with current German law.

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