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RESEARCH ARTICLE

Impact of natural and artificial prenatal stimulation on the behavioural profile of Japanese quail

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ABSTRACT

As the sensory systems of vertebrates develop prenatally, embryos perceive many environmental stimuli that can influence the ontogeny of their behaviour. Whether the nature and intensity of prenatal stimuli affect this ontogeny differently remains to be investigated. In this context, this study aimed to analyse the effects of prenatal auditory stimulation (natural stimulation, NS; predator vocalisations or artificial stimulation, AS; metallic sounds) on the subsequent behaviour of young Japanese quail (*Coturnix coturnix japonica*). For this, behavioural variables recorded during ethological tests evaluating emotional and social reactivity were analysed using a principal component analysis. This analysis revealed significant differences between the behavioural profile of stimulated chicks and that of non-exposed chicks. Indeed, chicks exposed to NS expressed more intense emotional responses in fearful situations, but less neophobia when exposed to a novel environment or object, whereas chicks exposed to AS appeared more sensitive to social isolation. Our results show that the acoustic environment of embryos can influence the way young birds subsequently interact with their social and physical environment after hatching, and face challenges in changing living conditions.

KEY WORDS: Auditory stimulation, Behavioural development, Emotivity, Social behaviour, Prenatal stress

INTRODUCTION

Sensory systems begin to develop during the prenatal period. In vertebrate and some invertebrate species, this follows a chronological and invariant sequence: the somatosensory system (tactile and vestibular) develops first, followed by the chemosensory system (olfactory and gustatory), the auditory system and finally the visual system (Carlsen and Lickliter, 1999; Gottlieb, 1976; Hepper, 2015; Lickliter, 2000; Romagny et al., 2012; Spreen et al., 1995). Nevertheless, this chronological development of sensory systems has not yet been consistently described for every species (e.g. cuttlefish: Mezrai et al., 2019). Embryos/fetuses can perceive and possibly react to different environmental stimuli. Thus, these prenatal stimuli can influence the behaviour of individuals and their effects can persist after birth/hatching. For example, tactile and vestibular stimulation can modulate the rate of activity of young birds after hatching (domestic hens: Guyomarc'h et al., 1973). Visual stimuli, such as light, can influence the visual laterality of the young (domestic chick: Riedstra and Groothuis, 2004; Rogers, 1989, 2012; bobwhite quail: Casey and Lickliter, 1998). Many behavioural traits are modulated by the prenatal environment, such as food preference (mammals: Coureaud et al., 2002; Hepper and Wells, 2006; Hepper, 1996; Mennella et al., 2001; birds: Bertin et al., 2010, 2012; Sneddon et al., 1998; cuttlefish: Darmaillacq et al., 2006, 2008), maternal and social recognition (mammals: DeCasper and Fifer, 1980; DeCasper and Spence, 1986; Graven and Browne, 2008; Hepper, 2015, 1996; Lecanuet et al., 1987; birds: Gottlieb, 1991; Sleigh et al., 1996) and also predator recognition (extensively studied in amphibians: Ferrari et al., 2010, 2016; Ferrari and Chivers, 2009a,b, 2010; Golub, 2013; Mathis et al., 2008; Saglio and Mandrillon, 2006).

Most of the time, the effects of prenatal stimulation are beneficial for the postnatal survival of the young as perception of the environment by embryos can prepare them for their postnatal life. Nevertheless, prenatal stimulation can also have deleterious effects on behavioural profile. As sensory systems develop with some degree of overlap, inadequate stimulation of one sensory system can reorganize the development of the others. Gottlieb and then Lickliter and colleagues frequently demonstrated this phenomenon using environmental over-stimulation (Gottlieb et al., 1989; Carlsen and Lickliter, 1999; Honeycutt and Lickliter, 2001; Jaime and Lickliter, 2006; Lickliter, 1994, 2000, 2011; Lickliter and Lewkowicz, 1995; Sleigh and Lickliter, 1996, 1998). For example, chronic light stimulation can have an impact on maternal recognition ability. Chicks of bobwhite quail have a preference for the maternal vocalisations they perceived in their egg. However, when prenatal exposure to maternal calls is coupled with light stimulation, chicks do not develop this auditory preference (Honeycutt and Lickliter, 2001).

The impacts of environmental stimuli on individual postnatal phenotypes can be related to embryonic stress processes. For example, chronic prenatal exposure of rainbow trout, *Oncorhynchus mykiss*, to conspecific alarm pheromones reduces postnatal fear-related behaviour, increases activity and induces cognitive deficits (Poisson et al., 2017). These behavioural effects are similar to those reported for mammals and birds following prenatal maternal stress (Braastad, 1998; Groothuis et al., 2005; McGowan and Matthews, 2018; Sarkar et al., 2007; Weinstock, 2008). Although the effects of prenatal maternal stress are well documented in the literature, the effects on the young of stress applied to the embryo (embryonic stress) have been explored less. Indeed, stress can be experienced by non-mammalian species by both mothers and embryos when they develop in their egg and then outside their mother.

To investigate the effects of direct embryonic stressful stimulations, it seems relevant to study oviparous species (Lickliter, 2005). The interest of studying them is twofold. First, as they represent the majority of species (Blackburn, 1999), it is important to understand

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these effects in order to protect and preserve these species. Second, because their embryos develop outside a maternal organism, their prenatal environment can be better controlled. Bird models are particularly ideal to address this question as they have been studied extensively. Bird embryos are able to perceive a wide range of environmental stimuli (Gottlieb, 1971; Höchel et al., 2002; Lalloue et al., 2003; Reynolds and Lickliter, 2002; Vince et al., 1976) and learn from them (Aigueperse et al., 2013; Bertin et al., 2010, 2012; Colombelli-Négrel et al., 2014; Gottlieb, 1991; Harshaw and Lickliter, 2011; Sleigh and Lickliter, 1996; Sneddon et al., 1998). For example, they rely on the auditory sensory modality to learn their mother's vocalisations (Gottlieb, 1991; Harshaw and Lickliter, 2011; Sleigh et al., 1996). In addition, a recent study showed that mothers' vocalisations perceived prenatally can affect long-term behaviour of young zebra finches (chicks exposed to their mother's heat calls were less food neophobic; Katsis et al., 2021). Bird populations can be impacted by stressful environmental changes (e.g. suboptimal temperature influences bird behaviour and neurobiological development; Bertin et al., 2018), as well as by stressful auditory stimulations (urban sounds, human activity; reviewed in Ortega, 2012) which can influence the development and the survival of young. The effects of these stressful auditory stimuli, either natural (linked to predation) or artificial (linked to human activity) on birds remain little explored (Henriksen et al., 2011). However, authors have demonstrated that natural and artificial stress (chronic olfactory and light stimulation) do not have the same effects on some invertebrate species, such as cuttlefish (O'Brien et al., 2017). To overcome this lack of knowledge, the present study aimed to analyse the effects of repeated auditory stimulation during the prenatal period on the behavioural profile of young Japanese quail (*Coturnix coturnix japonica* Temminck and Schlegel 1849). After exposing quail embryos to either natural or artificial auditory stimuli, we evaluated the impact of these stimuli on the subsequent emotional reactivity (response to experimental fear-eliciting situations) and on the social behaviour of stimulated and non-stimulated control chicks.

MATERIALS AND METHODS

Ethics statement

This experiment was performed in accordance with the European Communities Council Directive of 22 September 2010 (Directive 2010/63/EU) as certified by the regional ethics committee.

Egg treatment

General conditions of incubation

The quail eggs for the current study were from a broiler line and originated from an industrial farm (Les Cailles de Chanteloup, Corps-Nuds, France). Eggs were artificially incubated in the laboratory, placed in three identical incubators (Incubator Ducat Version© TU models 140, N=61±1 eggs per incubator; the mass of the eggs was balanced between incubators). Each incubator was placed in a soundproof room to control the auditory environment [mean±s.d. sound level in the rooms: 52.1±1.3 dB(A) and in incubators: 74.7±1.1 dB(A)]. Egg incubation in quail typically lasts 17 days (Orcutt and Orcutt, 1976). The eggs were placed for 14 days at 37.7°C with 45% humidity and one 45 deg rotation every 30 min. Then, for 3 days, rotation was interrupted and humidity was increased to 70% in order to induce hatching.

Auditory stimulation during incubation

We divided the eggs into three groups to evaluate the impact of prenatal auditory stimulation on behavioural profile: a non-stimulated control group, a group exposed to natural stimulation (NS) and a group exposed to artificial stimulation (AS). So that the test juveniles had a similar prenatal experience, we chose to test only chicks that hatched on the 16th, 17th and 18th days of incubation. There were N=13 chicks for the control group, N=11 for the NS group and N=23 for the AS group.

AS and NS embryos were exposed to prenatal stimulation from embryonic day 8 (ED8) to ED14, early during the development of their auditory sensory system (Höchel et al., 2002). NS embryos were subjected to vocalisations of the predatory sparrowhawk *Accipiter nisus* (Del Hoyo et al., 1996; fundamental frequency F_0=1673 Hz; duration: 4.51 s). AS embryos were subjected to a recording of a metal dish falling onto the floor (F_0=997 Hz; 3.73 s). Jones et al. (2006), studying the auditory sensory system of chickens, revealed that selectivity of responses to sound and frequency emerged around ED15 (170–4478 Hz). Given that the incubation period of chickens lasts 21 days, we therefore assumed that the moment of auditory exposure and the stimulus frequencies used in our study would present a strong prenatal stimulation. No auditory stimulation was applied after ED14 to reduce the risk of premature hatching.

Two loudspeakers, placed directly into each incubator, glued to the centre of the right and left walls (10 cm from the eggs) diffused the auditory stimuli. The loudspeakers were connected to a computer that automatically triggered the broadcast of the stimuli. The two stimuli were broadcast at a maximum intensity of 65 dB(A) (measured on the surface of the eggs; following Alladi et al., 2002). Between ED8 and ED11, the stimuli (AS or NS depending on the group) were repeated randomly 100 times during the day (around 6 h per day for the AS and 7 h per day for the NS). To avoid habituation to these stimuli, the stimuli (AS or NS) were repeated randomly 200 times during the day (12 h per day for the AS and 14 h per day for the NS) from ED11 to ED14. For the same reason, each sequence included breaks of random intervals of 1–5 s.

Chick housing conditions

At hatching, chicks were identified individually by using coloured leg rings. Then, they were placed in experimental groups (101×65×35 cm) in collective cages of approximately 10 individuals each (control cage: N=13 chicks; NS cage: N=11 chicks; and AS cage 1: N=11 chicks and AS cage 2: N=12 chicks). Chicks were reared on wood shavings and provided with water and food *ad libitum*. A warming bulb was placed in each cage to ensure proper thermoregulation until the chicks were 10 days old (38±1°C in each cage). When chicks became able to regulate their own temperature, the warming bulbs were switched off and the temperature in the room was kept at 20±1°C. Chicks were exposed to a 12 h:12 h light:dark cycle.

Somatic development

Body mass, an indicator of somatic growth, was measured twice: at hatching (post-hatching day 0, PHD0) and after the experiment on PHD19 for the three experimental groups.

Behavioural characteristics

Social behaviour and emotional reactivity were evaluated between PHD4 and PHD16 by behavioural tests classically used for *Coturnix japonica* (Forkman et al., 2007) (Fig. 1). As in previous studies done on quail, the tonic immobility test was performed on PHD7 (e.g. Parois et al., 2017). Social behaviour was evaluated before emotional reactivity because the younger the chicks are, the more they are motivated to join conspecifics and the less their social

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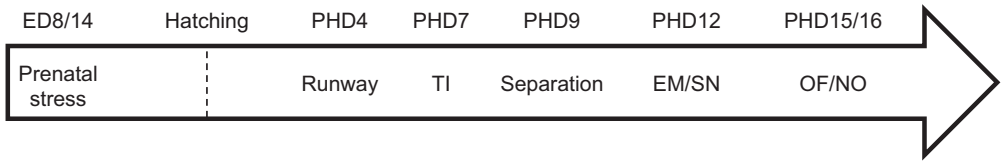

Fig. 1. Timeline of tests on *Coturnix coturnix japonica*. Tests were: runway test, tonic immobility (TI) test, separation test, emergence (EM) test, sudden noise (SN) test, open field (OF) test and novel object (NO) test. ED, embryonic day; PHD, post-hatching day.

behaviour is biased by their emotional reactivity. Behavioural tests were carried out in a soundproof test room during the day from 09:00 h to 18:00 h. The order in which the chicks were tested was randomized between groups. The experimenter was hidden behind a one-way glass during each behavioural test (except tonic immobility). All the chicks in each group were tested. Once the test was over, they were returned to their home cage. The behavioural variables used for analysis are described below.

Runway

The runway test evaluates a quail's social motivation by recording latency to join conspecifics of the same age and spend time near them (Mills et al., 1995; Suarez and Gallup, 1983). The device consisted of an opaque white plastic corridor (90×20×20 cm) with a starting area at one end and a transparent cage with N=4 same-aged unfamiliar chicks at the opposite end (unstressed chicks raised independently of the 3 experimental groups; same chicks for each individual tested). The corridor was divided into four zones: a starting area located in the most distal zone (32 cm long), an intermediate zone (32 cm long), a proximate region (32 cm long) and an area for contact with the social stimulus (4 cm long). To begin this test, a quail was placed in a box (18×18×18 cm) at the entrance of the tunnel for 30 s. The door of the box was then opened, allowing the chick free access to the device. Latency until emergence into the runway was recorded. When a subject did not emerge after 5 min, it was given the maximum score of 5 min.

Tonic immobility

Tonic immobility is a natural antipredator reaction characterized by a catatonic state of the subject. Its duration is a good indicator of inherent fearfulness as tonic immobility duration is positively correlated to emotional reactivity level (Mills and Faure, 1991). To induce tonic immobility, each subject was placed on its back in a U-shaped device and held in this position for 10 s prior to release. Then, the experimenter, placed out of the subject's sight, recorded the duration of tonic immobility (with a maximum of 5 min). Instances when the subject did not remain in tonic immobility for longer than 10 s were given a score of 0 s.

Separation from siblings

This test evaluated the responsiveness of quail placed in social isolation. To perform this test, a chick was removed from its home cage, separating it from its siblings, and placed in a different room in a similar cage and left alone for 3 min. The number of distress calls and fear behaviour (pacing, jumps against the wall, running, defecation, high observation postures and fear postures) were recorded. This test is known to relate the number of calls and fear-related behaviours to social separation: the greater the number of calls and fear-related behaviours the higher the reactivity to social separation (Launay, 1993).

Emergence test and sudden noise test

The emergence test evaluates the willingness of individuals to leave a small dark environment, considered a safe haven, to explore an unfamiliar environment. We followed a protocol similar to that described by Mills and Faure (1986). The experimental arena was a soundproof cage with one transparent side and a floor covered with wood chips (83×60×35 cm). Quail were placed in a transport opaque box (18×18×18 cm) and positioned at the entrance of the experimental arena. The transport box was kept closed for 1 min and then opened until the chick exited (maximum of 5 min). The experimenter recorded the latency of emergence from the wooden box into the experimental box. When a quail had not emerged after 5 min, a maximum score of 5 min was recorded. Once the subject was in the test cage, the transport box was closed and the chick was left free in the experimental arena for 3 min. Then, a white noise was broadcast for 5 s [60 dB(A) measured in the centre of the box]. At the end of this white noise, the number of distress calls and fear behaviour were recorded for 3 min.

Open-field test and novel object test

In birds, the open-field and the novel object test are more commonly used to measure fearfulness and in particular to assess the fear of the novel: neophobia (Perez et al., 2020; for review, see Crane and Ferrari, 2017; Greggor et al., 2015; Mettke-Hofmann et al., 2017). To perform this test, a quail was placed at the centre of a darkened heptagonal arena marked by white walls (30 cm long and 60 cm high). A test lasted 5 min and began when the light was switched on. Latency of the first step and frequency (number of times) of comfort behaviour (dust bath, preening and scraping the floor) were noted. A long latency to take a first step and a low frequency of comfort behaviours are considered to reflect a high emotional reactivity level (Gallup and Suarez, 1980; Hawkins et al., 2001; Jones et al., 1992; Rushen, 2000; Zimmerman et al., 2011; for review, see Jones, 1996). Indeed, it is traditionally considered that the more a bird is afraid of novelty, the less it will move. A fearful bird will therefore remain motionless and silent (Gallup and Suarez, 1980; Jones et al., 1992; for review, see Jones, 1996).

The novel object test was performed immediately after the open field test and lasted 5 min. The light was switched off and the subject was placed at one extremity of the arena. At the same time, an unknown yellow T-shaped object (20 cm high) was placed at the opposite extremity of the device. Then, the light was switched on and the latency to move close to the novel object was recorded (a maximum of 5 min was noted when a chick did not go near the object).

Statistical analyses

Incubation

Incubation data did not follow a normal distribution; therefore, a non-parametric two-way ANOVA with permutation tests was used to compare incubation times between the three groups (R©3.6.0; Package: lmPerm; formula: p.anova; nperm=9999). Multiple pairwise comparisons were then computed (R©3.6.0; Package: RVAideMemoire; formula: chisq.multcomp; method for P-value correction: 'fdr'). Chi square tests were used to compare numbers of

unfertilized eggs and hatchlings in control, AS and NS groups (R©3.6.0; formula: chisq.test).

Somatic development

A two-way ANOVA was computed to compare morpho-physiological values between the control, NS and AS chicks (R©3.6.0; Package: integrated package; formula: AOV). Tukey tests were then computed as a *post hoc* analysis when the two-way ANOVA showed a significant difference between groups (or tendency).

Behavioural characteristics

In order to test the effect of prenatal stimulation on the behaviour of chicks, first we performed a principal component analysis (PCA) with Spearman correlations on the chicks' behavioural variables (behavioural variables are specified above in the description of each test: latency to take the first step in the open field test; frequency of preening in the open field test; frequency of fear behaviours in the sudden noise test; latency to move close to a novel object in the novel object test; frequency of distress calls during the sudden noise test; latency of emergence of the chick during the emergence test; duration of tonic immobility in the tonic immobility test; frequency of distress calls during the separation test; frequency of fear behaviours in the separation test; latency until emergence in the runway test). We computed a varimax rotation to maximise graphical independence between the components (maximisation to the sum of the variances of the squared loadings and leaving the sub-space invariant), and we chose a criterion of principal component (PC) loading of |0.5| or higher to consider that a variable was relevant to a specific component (Abdi, 2003). This PCA was executed using Excelstat® (2014). Then, in order to compare the behaviour of control, NS and AS chicks, we performed a permutation *t*-test on the PCA values after Varimax rotation (R©3.6.0; Package: RVAideMemoire; formula: perm.t.test; nperm=9999).

RESULTS

Incubation duration and hatching ratio

The average incubation duration and hatching rate did not differ significantly between the three groups (Table 1; two-way ANOVA with permutation test: group effect: d.f.=2; mean square=7.48; P=0.73; embryonic time effect: d.f.=6; mean square=39.52; P<0.001; group×embryonic time effect: d.f.=12; mean square=6.48; P=0.99). The ANOVA results showed a hatching peak at ED16 for chicks in the three groups.

Somatic development

At hatching (PHD0), body mass differed significantly between the three groups (Table 2: two-way ANOVA: sex effect: F=0.005; P=0.94; group×sex effect: F=2.18; P=0.12; group effect: F=3.55 P=0.038). *Post hoc* tests revealed that AS chicks tended to weigh less than control chicks (*post hoc* Tukey HSD test: control–AS: upper end point upr=1.50; P=0.06; NS–AS: upr=1.43; P=0.15; NS–control: upr=0.78; P=0.95). On PHD19, body mass no longer differed significantly between the three groups (Table 2: two-way ANOVA: sex effect: F=0.41; P=0.53; group×sex effect: F=0.67; P=0.52; group effect: F=0.47; P=0.63).

Impact on emotivity and social behaviour

The PCA identified three factors that explain 55.9% of the total variance between variables. Fig. 2 presents the contributions of the behavioural variables to each PCA axis (Fig. 2A) and the PCA values of the control, NS and AS groups for the three PCA axes (Fig. 2B).

The first axis (19.5%) was explained, on one side, by long latencies to take the first step in the open field test and long latencies to approach a novel object and, on the other side, by high frequencies of preening in the open field test. This first axis reflects the level of an individual's neophobia in the presence of a novel environment or object and was named the 'neophobia' axis. On this axis, the PCA values of control and AS chicks did not differ significantly (permutation *t*: t=−0.27; P=0.79). However, the PCA values of NS chicks were significantly lower than those of control chicks (t=−2.08; P=0.048) and tended to be lower than those of AS chicks (t=1.98; P=0.055). Consequently, this indicates that NS chicks started to explore quicker in novel situations than did control chicks, and are therefore considered to be less neophobic.

The second axis (20.8%) was characterized by high frequencies of distress calls of chicks when separated from their conspecifics or after hearing a sudden noise and long latencies to go towards unfamiliar conspecifics in the runway test. Thus, this axis reflects the social motivation of isolated chicks to re-establish social contact and was named the 'sociality' axis. On this axis, no significant differences were evidenced between the PCA values of control and NS chicks (t=1.22; P=0.22). However, the PCA values of AS chicks were significantly higher than those of control chicks (t=3.37; P=0.0014) and tended to be higher than those of NS chicks (t=1.93; P=0.057). This indicates that AS chicks appear to be more socially motivated than are the control chicks.

The third axis (15.6%) was characterized by long emergence latencies in the emergence test, long durations of tonic immobility and high frequencies of fear behaviours in the sudden noise test. This last axis reflects the emotional reactivity of subjects and was named the 'emotivity' axis. On this axis, no significant differences were evidenced between the PCA values of NS and of AS chicks (t=−0.22; P=0.82). However, the PCA values of control chicks were significantly lower than those of NS chicks (t=2.22; P=0.038) and tended to be lower than those of AS chicks (t=1.91; P=0.053). This indicates that NS chicks express a stronger emotivity than control chicks in a fearful context.

Table 1. Number of hatchlings in relation to incubation day

	ED14	ED15	ED16	ED17	ED18	ED19	ED20
Control	4	1	8	2	3	0	0
AS	0	7	17	4	3	0	0
NS	0	5	7	3	3	0	1
Total no. of hatchings	4	13	32	9	9	0	1

No significant differences were observed between the three groups concerning the number of fertilized eggs (control chicks: N=53; artificial stimulation AS chicks: N=58; natural stimulation NS chicks: N=55; χ^2 test: χ^2=0.23, d.f.=2, P=0.89); live hatchlings (not malformed) (control chicks: N=18; AS chicks: N=31; NS chicks: N=19; χ^2 test: χ^2=4.62, d.f.=2, P=0.99); and hatchlings hatched between embryonic day 16 (ED16) and ED18 (control chicks: N=13; AS chicks: N=24; NS chicks: N=13; χ^2 test: χ^2=4.84, d.f.=2, P=0.09). We had to exclude N=3 chicks born with a malformed leg and a limp: 1 chick in the AS group and 2 chicks in the NS group.

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Table 2. Body mass of chicks in the three groups at hatching and after the experiment

	Sex	Body mass (g)	
		PHD0	PHD19
Control chicks	6♀ and 7♂	10.23±0.29*	143.85±5.42
AS chicks	13♀ and 10♂	9.49±0.18*	139.28±3.54
NS chicks	2♀ and 9♂	10.09±0.17	144.92±5.15

Data are means±s.d. for chicks in the control, artificial stimulation (AS) and natural stimulation (NS) groups on post-hatching day 0 (PHD0) and PHD19.
*Groups differ at $0.05 \leq P \leq 0.1$ (*post hoc* Tukey HSD).

DISCUSSION

This study assessed and compared the effect of natural and artificial stimulation on post-hatching behaviours of quail. We found that chronic acoustic stimulation during the embryonic period affected quail chicks' postnatal behaviour. Moreover, these effects depended on the type of acoustic stimulation perceived by the embryos.

As shown on the PCA (3rd axis), chicks exposed to NS (predator vocalisations) were more emotive than control chicks, and chicks exposed to AS (metallic sounds) seemed to be more emotive than control chicks. This indicates that exposed chicks may react more strongly to a sudden noise, remain longer in tonic immobility and wait longer before emerging in the emergence test. Others have observed this effect when prenatal stress was applied to a mother during the laying phase (De Haas et al., 2017; Groothuis et al., 2005; Guibert et al., 2010; Henriksen et al., 2011; Houdelier et al., 2011). Indeed, maternal stress (change of diet, noise, manipulation by humans, etc.) has strong effects on bird (quail and domestic hens) reproduction and on the postnatal behaviour of their offspring. It can induce impairment in some behaviours such as an increase of emotional reactivity and activity in domestic hens (De Haas et al., 2017; Groothuis et al., 2005; Guibert et al., 2010; Henriksen et al., 2011; Houdelier et al., 2011). Prenatal maternal stress induces a modulation of hormone levels in the eggs and this in turn can influence the behaviour of chicks (variation in sex steroid levels such as testosterone and androstenedione; Groothuis et al., 2005; Guibert et al., 2010; Henriksen et al., 2011; Houdelier et al., 2011). So, possibly the change in emotional behaviour we observed in this study reflects the fact that quail embryos had been stressed by the prenatal stimulation. However, we did not stress the mothers, but we did stimulate the embryos. In order to know whether stimulations

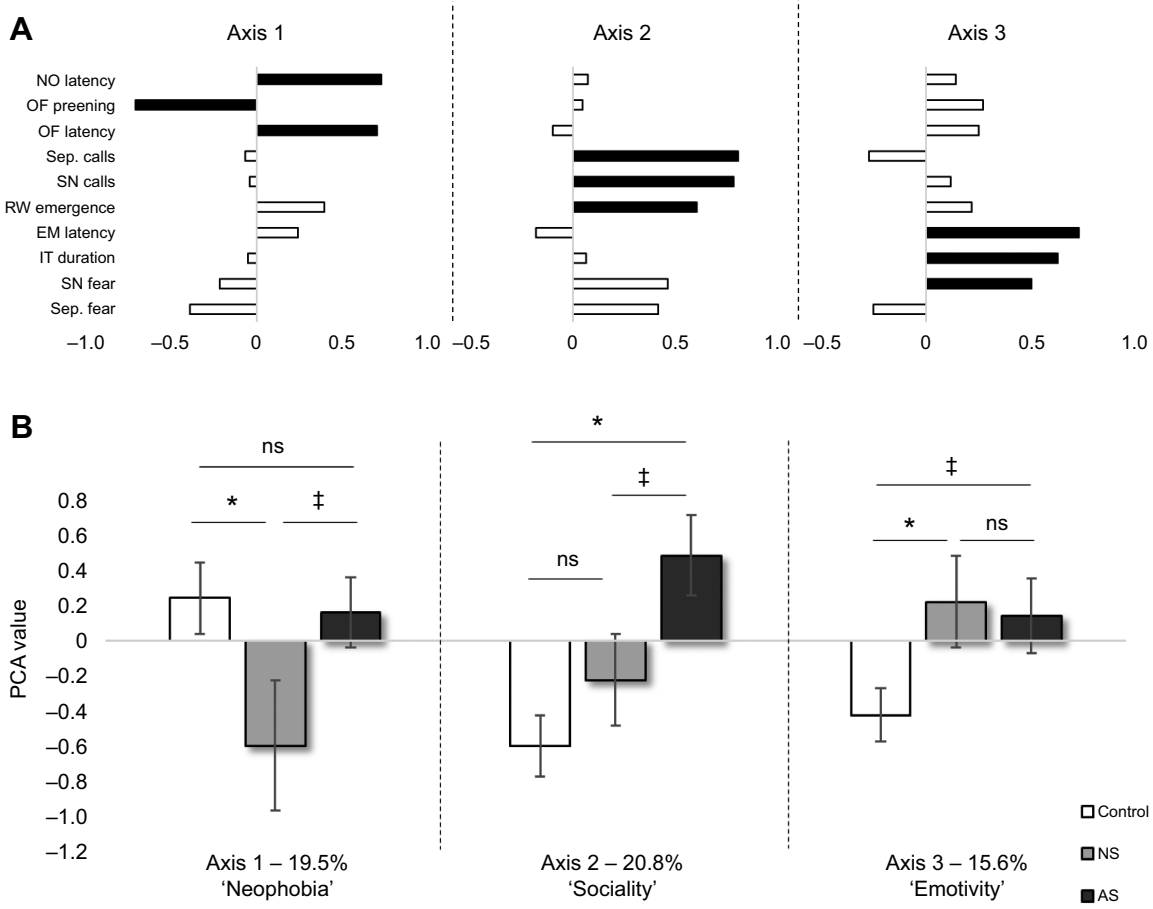

Fig. 2. Impact on neophobia, emotivity and social behaviour. (A) Contributions (black indicates a significant contribution) of the different behavioural variables to the three axes of the principal component analysis (PCA) computed on relevant behavioural data from the emotionality and sociability tests. NO latency, latency to move close to a novel object in the novel object test; OF preening, frequency of preening in the open field test; OF latency, latency to take the first step in the open field test; Sep. calls, frequency of distress calls during the separation test; SN calls, frequency of distress calls during the sudden noise test; RW emergence, latency until emergence in the runway test; EM latency, latency until emergence of the chick in the emergence test; IT duration, duration of tonic immobility; Sep. fear, frequency of fear behaviours in the separation test; SN fear, frequency of fear behaviours in the sudden noise test. (B) PCA values (means±s.d.) of the control, natural stimulation (NS) and artificial stimulation (AS) groups of chicks on axis 1, 2 and 3 of the PCA. Permutation *t*-tests: $^{*}P<0.05$; $^{\ddagger}0.05 \leq P \leq 0.1$; ns: $P>0.1$. For axis 1, the more positive a value is, the more neophobic chicks will be; for axis 2, the more positive a value is, the more social reactivity chicks will have; for axis 3, the more positive a value is, the more emotional reactivity chicks will have.

perceived directly by the embryos could be considered as prenatal embryonic stress, further evidence concerning hatchling endocrine levels is needed (i.e. hormonal dosages in eggs embryos; Henriksen et al., 2011; Quillfeldt et al., 2011; Rettenbacher et al., 2009). Finally, we can also consider the body mass of the individuals in order to know whether the stimuli used in our study could be stressful. Indeed, several studies reported mass loss at birth/hatching of individuals that were stressed during their prenatal period (mammals: Davis et al., 2009; O'Donnell et al., 2009; birds: Awerman and Romero, 2010; Schneider-Kolsky et al., 2009; Shinder et al., 2009). We found that AS chicks tended to weigh less than control chicks. However, body mass at hatching was not affected by the NS treatment, revealing that the type of stressful stimulation could influence embryonic growth differently.

In addition to emotional reactivity, our results show that the chicks' behavioural profile varied in relation to the nature of the acoustic stimulation. The PCA (2nd axis) showed that AS chicks were more social than controls: they seemed to be more responsive to social isolation. In birds, breaking the links between social partners induces distress responses such as distress calls and jumping (Schweitzer et al., 2010). In the present study, AS individuals were more responsive to social separation, emitting more distress calls than control individuals. But the 2nd axis also showed that AS chicks appeared less motivated to go towards unfamiliar chicks: their latency to go towards unknown chicks in the runway test tended to be longer. These two results appear contradictory because individuals more vulnerable to social isolation usually have greater social motivation to go towards congeners (Recoquillay et al., 2013; Richard et al., 2008). Nevertheless, possibly, chicks are more motivated to go towards familiar chicks than towards unknown chicks. We therefore hypothesize that AS quail were more attached to familiar partners than to unfamiliar chicks, suggesting that the artificial prenatal stimulation had influenced the development of their social behaviour. Aigueperse et al.'s (2020) study presented similar results related to maternal prenatal stress. Chicks of mothers stressed during the laying phase (social stress) and thereafter adopted by unstressed mothers, emitted more requests to their mother (more distress calls and fear behaviours when they were isolated from their mother). However, the PCA (1st axis) showed that prenatal stimulation had effects on neophobia: NS chicks seemed to be less neophobic than control chicks in an open-field situation (shorter first step latency and higher rates of preening) and in the presence of a novel object (approached unknown objects much faster). Short latencies to take the first step were considered to reflect high exploration tendency (Rushen, 2000) and high frequencies of preening were believed to reflect low emotional levels (Hawkins et al., 2001; Rushen, 2000; Zimmerman et al., 2011). These results indicate that in anxiety-inducing conditions, NS chicks are less neophobic, and more inclined to explore and approach a novel object. Therefore, natural prenatal stimuli could play a key role in shaping an adaptative response to a stressful environment. Indeed, in the case of chronic stress, most responses are adaptive and benefit the survival of the animal (reviewed in Herman, 2013). For example, predator cues are important for amphibian embryos as they enhance their short-term survival after hatching when predators are present (Ferrari et al., 2010; Ferrari and Chivers, 2010; Mathis et al., 2008).

In the present study, the chicks' behavioural profile differed depending on the type of acoustic stimulation they had perceived. Whereas AS affected social behaviour, NS influenced neophobia. In the literature, artificial sounds such as traffic sounds probably have the most widespread and greatest indirect effect on birds (reviewed in Kociolek et al., 2011; Reijnen et al., 1996). Birds may be particularly affected by anthropogenic sounds because they rely extensively on acoustic communication (reviewed in Kociolek et al., 2011). Conversely, NS as a predator cue is important as it can prepare individuals for their future living conditions. Many oviparous species are able to detect predator cues before hatching (e.g. cephalopods: Mezrai et al., 2020; amphibians: Ferrari et al., 2010; Ferrari and Chivers, 2010; Mathis et al., 2008; birds: Noguera and Velando, 2019). These stimulated embryos presented a developmental plasticity of their defensive phenotypes that enhanced their short-term survival rate after birth when predators were present (Ferrari et al., 2010; Ferrari and Chivers, 2010; Mathis et al., 2008; Noguera and Velando, 2019). These differential effects show that the impacts of prenatal auditory stimulation depend on the characteristics of the stimulus. Two hypotheses could explain this. (1) The structure of the sound could play a role in these prenatal effects. Indeed, although we controlled the sound level of the two stimuli, they still differed in frequency, duration and sequential organization, and these parameters may be perceived at different times during embryonic development (Konishi, 1973). (2) Our two stimuli may also be 'integrated/interpreted' differently by each individual, inducing a distinct behavioural profile. This phenomenon is more difficult to demonstrate. It would however be instructive to find out whether there are other embryonic responses to both stimuli including physiological and behavioural markers. For example, cardiac responses, movements or vocal responses of embryos could be evaluated to determine whether they differ following the AS and NS stimuli. Data concerning these traits would help to decide between these two hypotheses. To sum up, over-stimulation caused by NS and AS could possibly have over-stimulated the embryos' auditory system. The functions of these prenatal stimuli have long been studied by Gottlieb (1981, 1971, 1976, 2003), who identified three potential functions of early prenatal experiences: 'maintenance', 'induction' and 'facilitation'. Stimulations can have a maintenance effect that helps maintain the integrity of an already fully formed neural or behavioural system (Gottlieb, 1976). These stimuli can also have an inducing effect, directing the development in one direction rather than another. Finally, prenatal stimulation can facilitate behavioural development. Gottlieb (1976, 1971) described facilitation as a process leading to accelerated behavioural development. Behavioural capacity appears earlier in stimulated individuals than in non-stimulated individuals. Unlike induction, facilitation experiences regulate maturation, improve performance and increase perceptual differentiation and learning ability (Gottlieb, 1976, 1971). In our study, prenatal stimulation possibly directed the chicks' behavioural profile in one direction rather than another (inductive effect).

To conclude, despite the small number of individuals studied, we identified different behavioural profiles and these profiles varied according to the type of auditory stimulation perceived. On the one hand, AS, linked to an anthropic environment will make individuals more emotional and more social. On the other hand, NS, linked to predation pressure, will make chicks more responsive to emotional events but also more likely to explore more in an unfamiliar environment. Auditory stimuli therefore have a impact on an individual's behaviour profile. They can induce either positive or negative adaptation effects. Study of the effects of these environmental stimuli therefore is essential because organisms (terrestrial and marine) constantly experience changes in their environment to which they must provide appropriate individual responses. These responses can affect their growth, reproduction

and fertility and thus have consequences for the spatiotemporal dynamics of the populations to which they belong.

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