Effects of early social experience on sexual behavior in Japanese quail (*Coturnix Japonica*)

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Abstract

Experiences during immature phases of development, especially social experiences with individuals of the opposite sex, have implications for adult sexual behavior. Nevertheless, whether and how early experience can affect sexual learning in adulthood is still unclear. We present two experiments exploring how early experience impacts adult sexual Pavlovian conditioning in male Japanese quail. In Experiment 1, 25 male Japanese quail divided into three groups received different stimuli presentations at an early age, namely paired presentations of a conditioned stimulus (CS; a terry cloth model) and an unconditioned stimulus (US; an adult female quail), unpaired presentations of CS and US, and no exposure to stimuli. When they reached sexual maturity, we performed a sexual Pavlovian conditioning procedure with all groups using the same stimuli and tested their conditional response. In Experiment 2, we replicated the first experiment but with younger subjects and additional control variables. In the first experiment, we observed shorter approaching latencies to the CS and longer times near the CS in subjects with paired CS-US presentations compared to unpaired stimuli presentations. This was not replicated in Experiment 2. In both experiments, we found shorter approaching latencies and longer times near the CS in the groups with early exposure to the stimuli (paired or unpaired) compared to the group without this experience. Our findings indicate that the early presentations of stimuli at early stages of life can influence males' (speed of) sexual Pavlovian conditioning during adulthood.

Keywords Sexual behavior · Early experience · Sexual conditioning · Quail

Introduction

Michael Domjan and colleagues' research on sexual learning (see Domjan & Gutiérrez, 2019) has provided evidence that the sexual behavior system is more flexible than previously proposed (Lorenz, 1981; Mayr, 1974). Their studies have shown that Pavlovian conditioning is a crucial source of sexual behavioral variation in all stages of the sexual behavior repertoire of a species that impacts reproductive fitness. For example, male Japanese quail exposed to a Pavlovian conditioning procedure in which visual or copulatory access to a female is predicted by arbitrary (e.g., Domjan et al., 1986) or species-typical cues (e.g., Köksal et al., 1994) acquire conditional responses such as a faster approach to those cues.

The potential impact of sexual learning on reproductive fitness is made evident by studies showing that male quail's copulatory efficacy increases behaviorally and physiologically after sexual conditioning. Males show a decrement in their latency to copulate under non-competitive (Domjan et al., 1986) and competitive situations (Gutiérrez & Domjan, 1996), and an increment in the volume of sperm (Domjan et al., 1998), the number of fertilized eggs (Mahometa & Domjan, 2005), and the number of hatchlings (Matthews et al., 2007).

Since behavior is more plastic during immature phases of development (West-Eberhard, 1989, 2003), early-life experiences should significantly impact adult sexual behavior. Many aspects of the sexual behavior system and its physiological

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correlates are affected by early social experiences. First, studies with different bird species have shown that mate preference can be influenced by early exposure to social companions (e.g., *Anas platyrhynchos*, Krujit et al., 1982; *Taeniopygia guttata*, ten Cate, 1987). Pérez and Gutiérrez (2006) found a similar effect in female quail who grew up in the company of males. When these females reached sexual maturity, they spent more time close to non-familiar than familiar males. In contrast, females in social isolation at an early age did not show such preference. Furthermore, Gallagher (1977) suggested that male quails' sexual preference for albino females may result from early exposure to them (i.e., albino female exposure for 10–15 days from the first day of age).

Second, early social experience can affect the physiological aspects of reproduction. Immature male quail exposed to adult females have a faster development of their sexual organs and hormones than males with no early exposure to adult females (Delville et al., 1984). Previous studies have also shown that the development of sexual organs in female quail can be stimulated by male songs (Guyomarc'h et al., 1984).

Third, early social experience can also affect sexual performance. For instance, adult CD-1 mice, socially isolated after weaning, showed shorter copulations, longer mounting latencies, and longer intromission latencies than males reared with conspecifics (Liu et al., 2019). Also, male guppies (*Poecilia reticulata*; Guevara-Fiore, 2012) raised with visual exposure to adult females showed a higher rate of forced copulation attempts and lower duration of courtship than males raised with visual exposure to adult males or conspecifics of both sexes.

The previous findings suggest that early social experiences (or their absence) with conspecifics have clear implications for sexual behavior and its physiological correlates. Nevertheless, whether and how early experience can affect sexual learning in adulthood is still unclear. Here we present two experiments that explore how early social experiences affect sexual Pavlovian conditioning in male Japanese quail, and seek to extend Domjan's research on sexual learning from a developmental perspective. We tested the effect of early anticipated and not anticipated visual exposure to sexually mature females on the later sexual conditioning of male quail. Afterward, this procedure was replicated with younger subjects and additional control variables.

Experiment 1

Method

Subjects

Twenty-five 22-day-old male Japanese quail (*Coturnix japonica*), purchased from a commercial supplier, were used as subjects. To track their health and sexual maturity, we took inter-daily measures of body weight and proctodeal gland (frontal length × side length of the gland in mm from its beginning to the outermost point). All birds had a 16:8-h light-dark cycle with lights on at 06:00 h, and full access to food and water during the whole experiment. Lighting and feeding conditions were the same in all the experiments of this study. Sexually mature females were used as unconditioned stimuli (US). Males were not exposed to females when housed in their home cages.

Apparatus

The experimental arenas were eight wooden cages (110 cm wide × 70 cm deep × 70 cm high). Each experimental arena was connected to a smaller lateral cage (50 cm wide × 30 cm deep × 30 cm high) where females were placed. The experimental arena and the lateral cage were separated by a plastic grid allowing visibility side to side and an opaque wooden screen lifted by a pulley. The floor of the experimental arena had a squared mark called the CS zone next to the lateral cage (Fig. 1).

We used a quail-shaped model of terry cloth as a CS (Fig. 2). This quail-shaped model has been frequently used as CS in sexual conditioning studies with Japanese quail because males of this species show clear sexual responses directed at them, including approaches and mounts, once they are conditioned (Köksal et al., 2004). The CS glued on a small rectangular wooden base was tied to a pulley system that allowed us to lower or raise it at the CS zone mark on the floor of the experimental arena.

Two video cameras were used to record the experimental sessions. The videos were analyzed using the software X-Plo-Rat 2005 version 1.1.0, developed in the Laboratory of Exploratory Behavior of the University of Sao Paulo, Brazil.

Procedure

Subjects were randomly assigned to one of three groups called the paired group (P, *n*=8), the unpaired group (U, *n* = 9), and the no-exposure group (N, *n* = 8). The experiment was divided into three phases: habituation, early exposure, and test.

Habituation phase

For each group, males were put together in a housing cage from day 22 until day 26 after hatching to prevent health problems due to isolation or lack of heat. On day
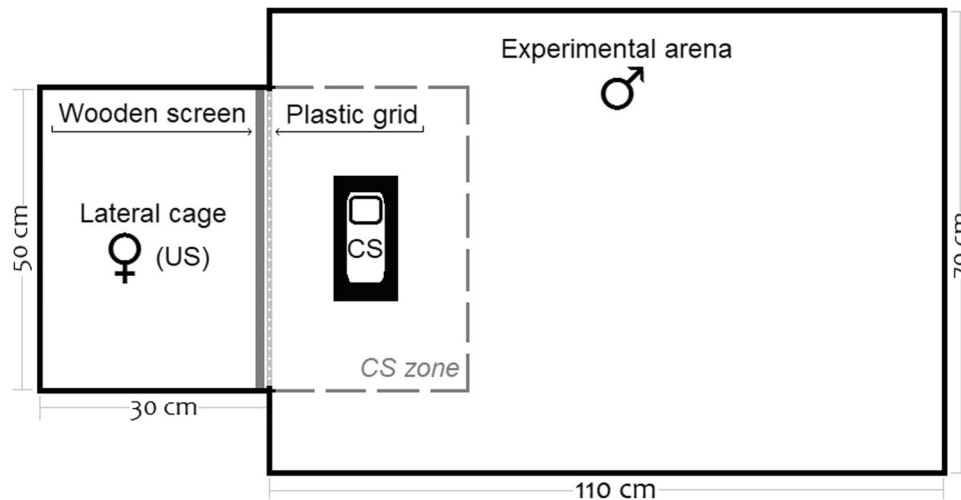
Fig. 1 Apparatus diagram

Fig. 2 Quail model made with terry cloth, used as the conditioned stimulus (taken from Cusato & Domjan, 1998). *Note:* Illustration by Stewart Hilliard

26, subjects from groups P and U were introduced individually in each experimental arena. From that moment until the end of the experiment, we rotated the subjects' location between the experimental arena and their home cages. Each subject of groups P and U were placed in the experimental arena on a rotating basis, remaining there for 24 h starting at 12:00 h and then switching to their housing cage. Subjects of group N were exposed to the experimental arena during the first 5 days of the habituation phase. They then remained in their home cages, receiving no behavioral treatment until the test phase.

Early exposure phase

Immediately after habituation, when males were 29 days old, subjects of group P received 24 paired CS-US trials. The CS was presented for 30 s, after which it was removed, and the US was presented for 300 s by lifting the opaque wooden screen, which allowed the male to have visual access to a sexually mature female located in the lateral cage. The 24 trials were distributed in daily sessions of three trials with 10-min inter-trial intervals. This length of time for the CS and US presentations was proven to be effective to provoke sexual conditioned responses in male adult quail (see Cusato & Domjan, 1998). The number of trials was chosen from pilot studies in our lab that have been shown to ensure that social stimuli are already relevant enough in adults. Also, we did not want to exceed the number of trials to guarantee that the early social pairing occurred before maturation.

Subjects of group U received 24 unpaired trials of CS and US. We used a backward conditioning procedure (US-CS) with a 5-min interval between US and CS. The distribution of the trials was the same as with group P, but the inter-trial interval was 5 min. We used this procedure to control the possibility that the mere early exposure of the stimuli with no explicit pairing would affect behavior during the test phase. In order to avoid conditioning or habituation to a specific female partner, stimulus females were rotated.

The early exposure phase ended when subjects were 36 days old. The development of sexual maturity among male quail starts at approximately 26 days after hatching when sperm begins to be present in the testes (Mather & Wilson, 1964; Ottinger & Brinkley, 1979b). Male quail perform the first copulations attempts at around 35 days and show successful copulations at around 37 days (Ottinger & Brinkley, 1979a). Thus, subjects were in the critical periods of sexual maturity during the early exposure phase.

Test phase

The test phase started when subjects were 60 days old, given that the maximum frequency of copulatory attempts occurs around 52 days (Ottinger & Brinkley, 1978). Although full copulations reach an asymptotic level at approximately 81 days and thus most sexual conditioning studies in Japanese quail use subjects of at least 3 months old, we tried to decrease the time interval between the early exposure and the test phase as much as possible. Cornil and Ball (2010) also used subjects of 8 weeks of age and found that they already showed evidence of sexual motivation and performed full copulations in their first encounter with adult females.

Between the end of the early exposure and test phase, the alternation between experimental arenas and home cages in groups P and U remained unaltered. All three groups received the same procedure, which consisted of nine trials of visual access to a female and nine trials of copulatory access. The procedure was the same as group P during the early exposure phase (30 s CS + 300 s US). The plastic grid was removed for the copulatory test trials, so there was no separation between females and males.

Behavioral measurements

We measured (a) the time subjects remained in the CS zone when the CS was presented and (b) the latency to approach the CS zone since the presentation of the CS. Male sexual responses during the presentation of the US (e.g., copulatory index, number of copulations, the latency of copulation) were also scored and measured. However, none of these showed significant differences between groups.

Data analysis

We run statistical analysis in R (version 4.1.2; R Core Team, 2021). Data distribution was not normal, so we used non-parametric tests. To compare the latency to approach and the time remaining in the CS zone between pairs of groups during the early exposure phase and each session of test phase, we performed Mann-Whitney U tests using the Wilcox test function of the package Conditional Inference Procedures in a Permutation Test Framework (coin, version 1.4-2; Hothorn et al., 2008). Effect sizes were calculated dividing the resulted z value by the squared root of the number of observations considered (r; Tomczak & Tomczak, 2014). A few missing values resulted from technical problems and were excluded from the analyses. We also ran Kruskal-Wallis tests to see if there were significant differences between all groups during each test

phase, for which epsilon squared values (E_R^2) were calculated to account for effect sizes (Tomczak & Tomczak, 2014). A p-value of .05 was considered to reject the null hypotheses in both statistical tests.

Results and discussion

When the CS was presented during the early exposure phase, both group P and group U spent little time in the CS zone (P: $M = 0.63$ s, $SD = 3.01$ s, $Mdn = 0$; U: $M = 0.98$ s, $SD = 0.83$ s, $Mdn = 0$ s). They also showed long latencies to approach that area (P: $M = 28.25$ s, $SD = 1.85$ s, $Mdn = 28.51$ s; U: $M = 27.62$ s, $SD = 3.05$ s, $Mdn = 28.15$ s). No differences between groups were found ($p > .05$). During the CS presentation, subjects of both groups remained more than 50% of the time on the half side opposite the US location. These results suggest that subjects of group P did not acquire any conditional response in this phase. Even though some studies with different species have shown evidence of early conditioning (humans: Crowell et al., 1976; domestic chicken: Davis et al., 2007; Long Evans rats: Sevelinges et al., 2007), the absence of conditional responses in this experiment may be due to the low salience of mature females for sexually developing subjects. As Holloway and Domjan (1993a, 1993b) have pointed out, sexual motivation is critical to acquiring sexually conditioned responses.

In contrast, during the early exposure phase, subjects of all groups remained between 25% and 75% of the time in the CS zone when the female was presented. This resembles the social proximity behavior of adult male quail reported by Domjan and Hall (1986), which tends to be stronger with females than with other males, and thus is part of the sexual behavior system (i.e., functioning as mate guarding or surveillance behavior). It remains to be tested if an immature male quail spends less time near an adult male than an adult female.

In the test phase, the latency to approach and the time remained in the CS zone varied between groups, both in the visual test (latency: $\chi^2(2) = 12.513$, $p = .002$, $E_R^2 = .059$, Fig. 3a; duration: $\chi^2(2) = 12.125$, $p = .002$, $E_R^2 = .055$, Fig. 3c) and in the copulatory test (latency: $\chi^2(2) = 43.68$, $p = .000$, $E_R^2 = .196$, Fig. 3b; duration: $\chi^2(2) = 49.259$, $p = .000$ $E_R^2 = .219$, Fig. 3d).

In Session 2 of the visual test, groups P and U showed shorter latency times (P-N: $z = -3.378$, $p = .000$, $r = -.488$, Fig. 4b; U-N: $z = -3.011$, $p = .003$, r = -.422, Fig. 4b) and higher duration times in the CS zone than group N (P-N: $z = 3.111$, $p = .002$, $r = .449$, Fig. 4e; U-N: $z = 2.845$, $p = .004$, $r = .398$, Fig. 4e). This pattern remained in Session 3
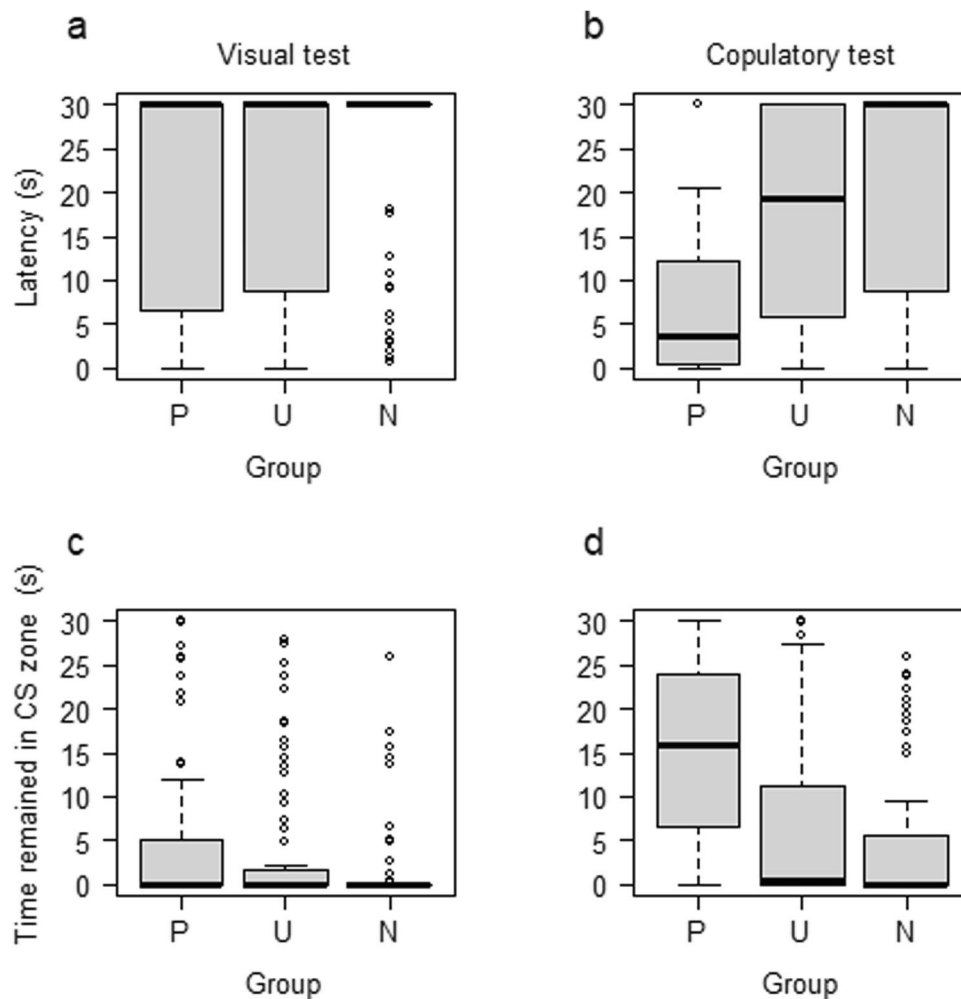
Fig. 3 Boxplot comparing the performance of groups in: (**a**) approximation latency to the conditioned stimulus (CS) zone in the visual test; (**b**) approximation latency to the CS zone in the copulatory test; (**c**) time remained in the CS zone during the visual test; and (**d**) time remained in the CS zone during the copulatory test (Experiment 1)

for group P compared to group N (latency: $z = -2.864$, $p = .004$, $r = -.413$, Fig. 4c; duration: $z = 3.295$, $p = .001$, $r = .476$, Fig. 4f). All other analyses for the visual test revealed non-significant results ($p > .05$).

During the copulatory test, differences between group P and the other two groups increased. Group P showed shorter latencies and higher duration times in the CS zone than group U in Session 2 and Session 3, and when compared to group N during in all sessions (see Table 1 and Fig. 5). The differences found between groups U and N during the visual test disappeared in the copulatory test ($p > .05$; Fig. 5).

The differences between group P and the other groups suggest a latent effect of the CS-US pairing procedure that group P received in the early exposure phase. This latent effect is remarkable given that no differences between

groups were found in the early exposure phase, suggesting no early conditioning. Due to the increased differences between groups P and U during test phases, we may assume that the early exposure to the explicitly paired procedure in group P affected the learning speed, more than a recovery effect or persistence of the conditional response. One possibility is that this effect was mediated by physiological changes related to the Pavlovian procedure to which subjects were exposed. Sevelinges et al.'s (2007) research with Long Evans rats supports this possibility, even though conditioning was already present in the immature phase in that study. New studies with physiological measurements are needed to test this hypothesis. We also should consider that the procedure group U received during the early exposure phase could have promoted a negative contingency between the CS and
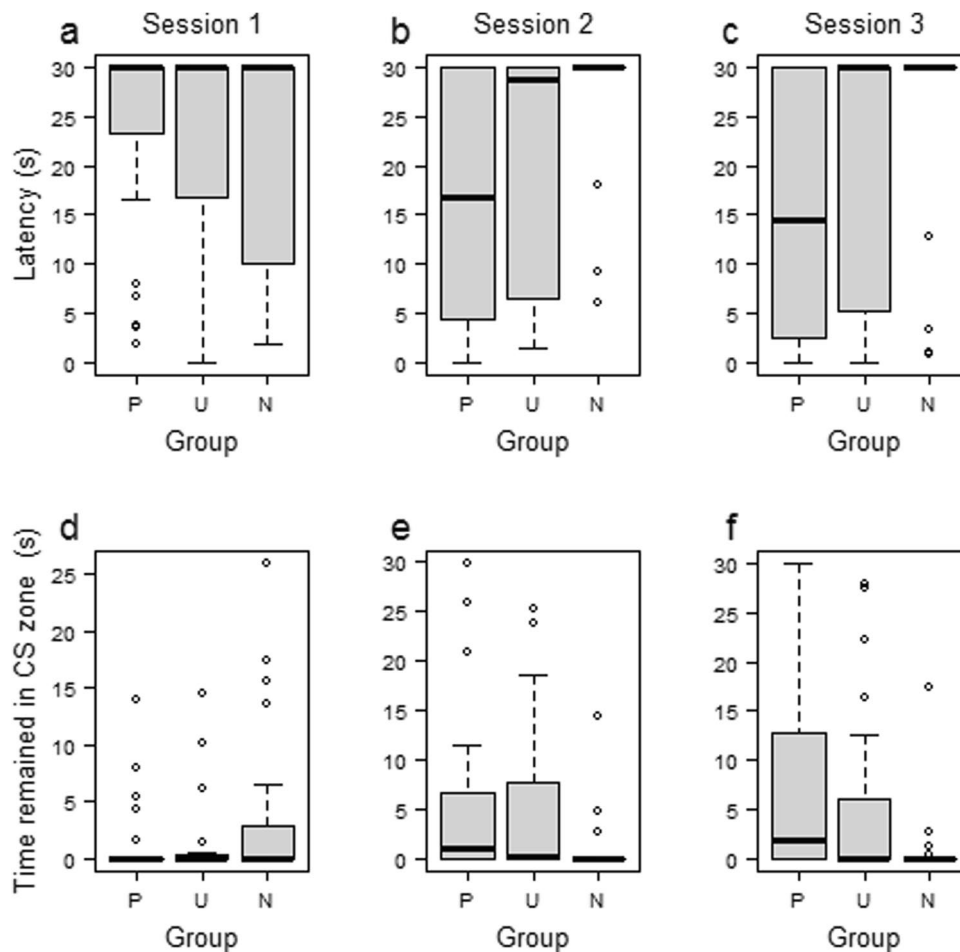
Fig. 4 Boxplot comparing the performance of groups in the visual test by session with respect to approximation latency to the conditioned stimulus (CS) zone (a: Session 1; b: Session 2; c: Session 3) and time remained in the CS zone (d: Session 1; e: Session 2; f: Session 3; Experiment 1)

Table 1 Z scores, p values and effect sizes (r) resulted from Mann-Whitney U tests performed to analyze differences in the latency to approach and the time remained in the conditioned stimulus (CS) zone between pairs of groups during the copulatory test (Experiment 1)

	Latency						Time remained in CS zone					
	P-U			P-N			P-U			P-N		
Session	z	p	r	z	p	r	z	p	r	z	p	r
1	-1.705	p>.05	-	−3.390	.001	−.489	2.013	.044	0.282	3.274	.001	.472
2	−2.714	.006	−.380	−3.321	.001	−.479	2.513	.011	.351	4.055	.000	.585
3	−3.608	.000	−.505	−4.528	.000	−.653	4.565	.000	.639	4.415	.000	.637

Note: values for the comparison between U and N groups are not included because they were not significant ($p > .05$). A p-value of .05 was considered to reject the null hypotheses in both statistical tests

US because the US-CS interval and the inter-trial interval were the same (300 s).

Our results also suggest that early exposure to stimuli can influence later sexual conditioning involving the same stimuli. The differences between group P and group N subjects were more significant than those of group P and group U. Also, subjects of group U showed significantly higher duration times in the CS zone than subjects of group N during the second session of the visual test. This agrees with previous studies done with young animals showing that the
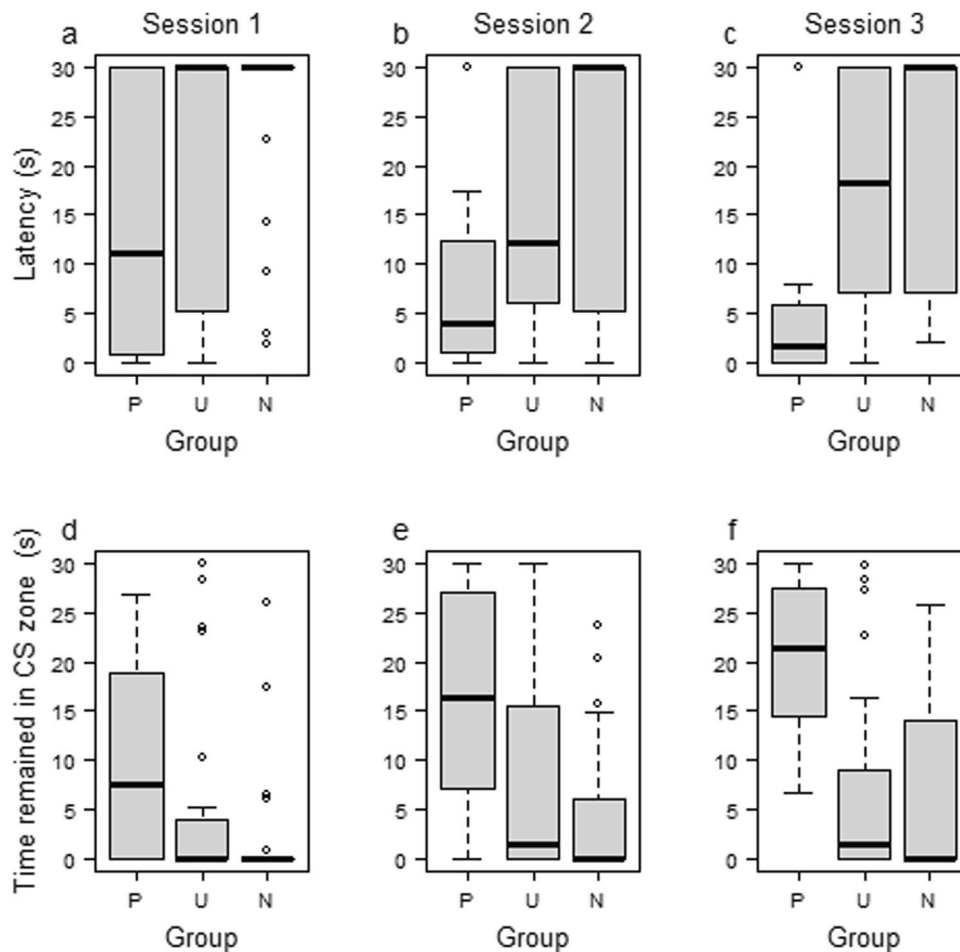
Fig. 5 Boxplot comparing the performance of groups in the copulatory test by session with respect to approximation latency to the conditioned stimulus (CS) zone (a: Session 1; b: Session 2; c: Session 3) and time remained in the CS zone (d: Session 1; e: Session 2; f: Session 3; Experiment 1)

early exposure to stimuli facilitates the formation of the later conditional responses (Brasser, 2004; Chotro & Alonso, 1999; Hoffmann & Spear, 1989; Mellon et al., 1991; Yap & Richardson, 2007). However, it contradicts pre-exposure studies in which the previous presentation of CS, US, or both (with non-paired presentations) decreases the future speed of learning in adults (e.g., Baker & Mackintosh, 1979; Lubow, 1965) and immature subjects (e.g., Revillo et al., 2013).

Factors such as the similarity of the context used in the pre-exposure and conditioning phases (Yap & Richardson, 2005) and the number of stimulus presentations (Chotro & Alonso, 1999; Revillo, Gaztañaga, et al., 2014) may produce differences in the latent effect of early pre-exposure. More importantly, the effect of stimulus pre-exposure in early ontogenetic phases varies depending on the behavioral paradigm, which can be related to the maturation of the biological mechanisms involved (Revillo, Castello, et al., 2014; Revillo et al., 2013). Studies with adult quail suggest that

pre-exposure to the CS might not inhibit sexual conditioning (Cusato & Domjan, 1998). Additionally, repeated visual exposure to mature females is associated with shorter copulation latencies in inexperienced subjects (Cornil & Ball, 2010). Thus, the effect of pre-exposure to stimuli in sexual conditioning seems to be the opposite of that observed in other behavioral paradigms like fear conditioning.

A possible shortcoming was the avoidance effect generated by the vertical movement of the CS when it was presented and the opening of the wooden screen when subjects had visual access to the female. During the first trials of the early exposure phase, subjects took distance from the place where both the CS and the wooden screen were located, and, in consequence, this could have altered the time subjects spent in the CS zone. Also, early experience with objects reduced the avoidance response to those objects at a later age (Rubel, 1970; Schaller & Emlen, 1962). Therefore, the differences between group N and the

other two groups during the first sessions of the test phase could be explained by the reduced avoidance effect that groups P and U had after being exposed to those stimuli during the early exposure phase.

Finally, the abovementioned difference between group N and the other groups could also be explained by the different exposure times to the experimental arena; groups P and U remained for more time in the arena than group N during the early exposure phase. Crawford et al. (1994) found that sexually inexperienced male quail were more likely to copulate in familiar contexts.

To better explore some of the previous alternative explanations, we designed a second experiment with the following changes: First, we used subjects 6 days younger than those in Experiment 1 to reduce the likelihood of having sexually mature subjects during the early exposure phase. Second, to prevent a negative contingency between the CS and the US and better interpret the effect of stimulus pre-exposure during the early ontogenetic phase, group U received a random presentation of stimuli during the early exposure phase (see the procedure of Experiment 2 for details). Third, to control the avoidance response possibly generated by the presentation of the CS, a base similar to the one attached to the CS was presented to the subjects of group N during the early exposure phase. Finally, to eliminate the differential effect of context in the test phase, group N remained the same time in the experimental arena as groups P and U during the early exposure phase.

Experiment 2

Method

Subjects

For Experiment 2, we used 25 16-day-old male Japanese quail (*Coturnix japonica*) as subjects. Housing, feeding, and care conditions were the same as in Experiment 1. Nine subjects were assigned to group P, nine to group U, and seven to group N.

Instruments

Same as in Experiment 1.

Procedure

Same as in Experiment 1, with four exceptions:

1) At the start of the experiment, subjects were 16 days old; therefore, individuals started each phase six days earlier than subjects of Experiment 1. This was done to control the possible sexual maturity reached by some of the subjects in the last part of the early exposure phase of Experiment 1.

2) Subjects of group U received either the CS or the US alone six times per session with an inter-stimulus interval of 3 or 7 min. The CS and US were switched between sessions. Inter-stimulus intervals were assigned randomly and varied between subjects and trials. As in Experiment 1, subjects received eight sessions in total, so subjects received 24 presentations of each stimulus (same number as subjects of group P). This was done to avoid a contingency between stimuli in group U and test the effect of the early exposure to CS and US.

3) Subjects of group N remained in the experimental arena for the same amount of time as groups P and U. This procedure was followed to verify that differences observed between the N group and the other groups were not the result of context novelty or any different effect caused by differences in exposure to the experimental arena during the early exposure phase. The recording procedure was also performed to promote habituation.

4) Finally, to reduce the avoidance response of all subjects to the CS, we presented a wood base similar to that supporting the CS, three times a day, at 20-min intervals, during the habituation phase.

For a comparative summary of the experiments, see Table 2.

Results and discussion

Subjects of groups P and U almost did not enter the CS zone during the presentation of CS in the early exposure phase (P: $M = 0.09$ s; $SD = 0.24$ s, $Mdn = 0$ s; U: $M = 0.04$, $SD = 0.07$ s, $Mdn = 0$). Correspondingly, latencies were also very long (P: $M = 29.57$ s; $SD = 1.07$ s, $Mdn = 30$ s; U: $M = 28.85$ s, $SD = 1.54$ s, $Mdn = 30$ s). In fact, the average percentage time subjects remained in the half part of the experimental arena near the lateral cage was less than 16%. We found no statistical differences between groups P and U in this phase, neither in time spent in the CS zone nor in latency to approach ($p > .05$). These data replicate the results of Experiment 1 in the early exposure phase. There was no evidence of learning in group P. In fact, subjects of both groups spent no time in the CS zone. It seems that prior exposure to the wooden base did not reduce the avoidance effect, which, based on our observations, appears to be stronger in younger chicks.

As in Experiment 1, the latency to approach and the time remained in the CS zone varied between groups, both in the visual test (latency: $\chi^2(2) = 17.764$, $p = .000$, $E_R^2 = 0.081$, Fig. 6a; duration: $\chi^2(2) = 15.932$, $p = .000$, $E_R^2 = 0.072$, Fig. 6c) and in the copulatory test (latency: $\chi^2(2) = 44.908$, $p = .000$, $E_R^2 = .201$, Fig. 6b; duration: $\chi^2(2) = 49.132$, $p = .000$, $E_R^2 = .220$, Fig. 6d). In the test phases, no differences were found between groups P and U in any measure ($p \geq .05$),

Table 2 Methodological differences between Experiments 1 and 2

Experiment	Group	Sample size	Habituation phase		Early exposure phase		Test phase	
			Age	Type of procedure	Age	Type of procedure	Age	Type of procedure
1	P	8	From 22–29 days old.	Housed in group from 22–25 days old and individually from 26–29 days old on a rotating basis, remaining in the arena for 24 h	From 29–36 days old	24 paired CS-US trials with visual access to a female.	From 60–65 days old	9 paired CS-US trials with visual access to a female (visual test) and 9 paired CS-US trials with copulatory access to a female (copulatory test)
	U	9				24 unpaired (backward conditioning) US-CS trials with visual access to a female		
	N	8		No exposure		No exposure		
2	P	9	From 16 to 23 days old.	Housed in group from 16–19 days old and individually from 20–23 days old on a rotating basis, remaining in the arena for 24 h	From 23–30 days old	24 paired CS-US trials with visual access to a female		
	U	9				24 presentations of CS and 24 presentations of US alone		
	N	7				Exposure to the experimental arena only		

but both groups showed higher times in the CS zone and shorter latencies than group N (Fig. 6). These differences were higher in copulatory than visual tests (see Fig. 6).

No differences between groups P and U were found during the test phase in Experiment 2 (see Fig. 7 and Fig. 8). During the visual test, groups P and U showed shorter approaching latencies than group N in Session 2 (P-N: $z = -2.345$, $p = .019$, $r = -.338$, Fig. 7b; U-N: $z = -2.013$, $p = .044$, $r = -.290$, Fig. 7b) and Session 3 (P-N: $z = -3.829$, $p = .000$, $r = -.552$, Fig. 7c; U-N: $z = -3.478$, $p = .000$, $r = -.502$, Fig. 7c). Also, both groups spent more time in the CS zone in Session 3 compared to group N (P-N: $z = 3.950$, $p = .000$, $r = .570$, Fig. 7f; U-N: $z = 3.553$, $p = .000$, $r = .512$, Fig. 7f). These differences were replicated in all sessions of copulatory test for both approaching latencies and times remained in the CS zone (see Table 3 and Fig. 8). All other analyses for the test phases revealed non-significant results ($p > .05$).

The differences we found in Experiment 1 between groups P and U were not observed in Experiment 2. The early exposure to an explicitly paired procedure in group P's subjects had no differential effect on their performance in adulthood compared to group U's subjects. This might be explained by amnesia associated either with the early age of the subjects or with the long time interval between the early exposure phase and test phase (Campbell & Spear, 1972; Spear, 1979). Thus, the faster conditioning of groups P and U than group N during the test phase could be caused by non-learning mechanisms. It is also possible that the avoidance response to the early presentations of the CS would have altered the effect of the early exposure phase on group P. Pavlovian conditioning requires the CS to be less biologically relevant than the US (Domjan, 2005). Therefore, how we presented the CS to young chicks could have generated a more robust unconditioned fear response than the response generated by introducing an adult quail of the opposite sex. The results of Experiment 1 should be further replicated given the increased learning speed of subjects early exposed to paired stimuli, despite them being juveniles during the early exposure phase and the time window between phases being long. This type of research question remained highly unexplored (but see Sevelinges et al., 2007) and might be very relevant in understanding intraspecific behavioral differences.

The results of Experiment 2 strongly support a latent effect of the early exposure to stimuli on the future performance of subjects in a conditioning procedure involving those stimuli. Given that subjects of group N remained the same time in the experimental arena as the subjects of the other groups, we can conclude that this effect is not a product of the context, as considered based on Crawford et al.'s (1994) findings. Instead, it suggests that stimuli pre-exposure during early ontogenetic stages can facilitate
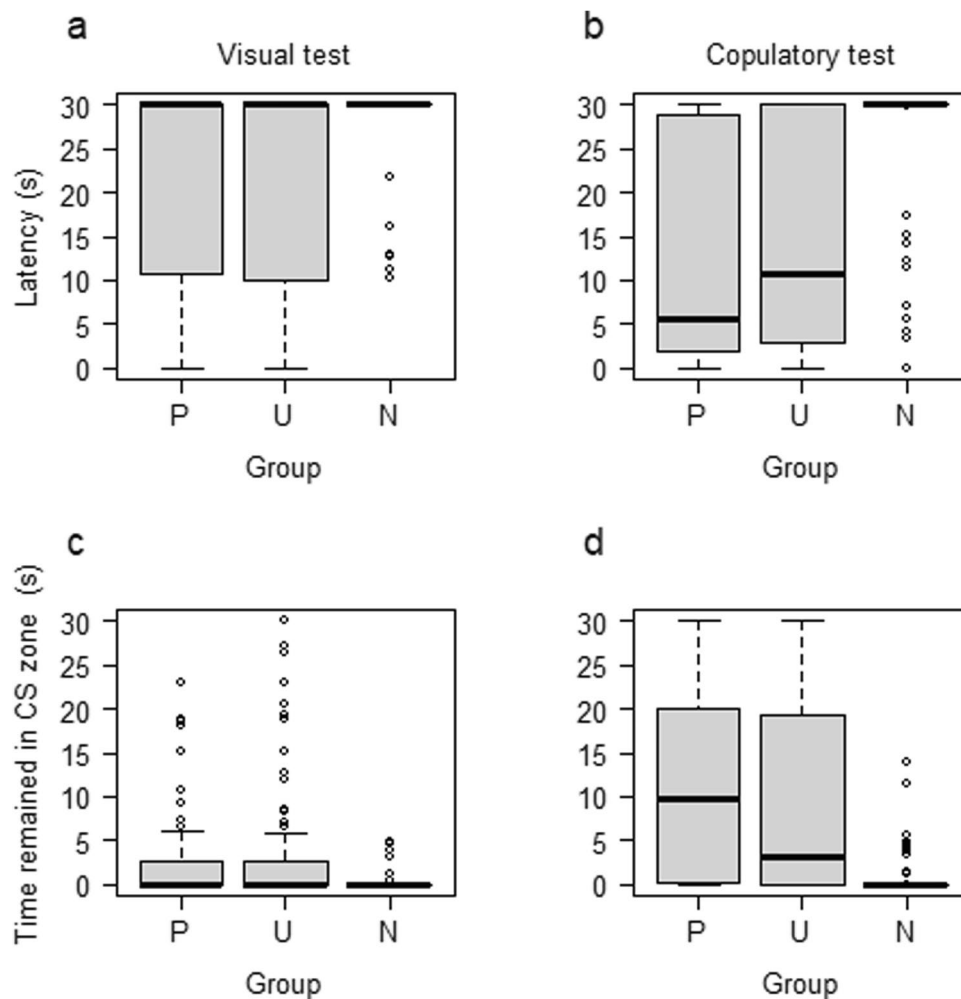
Fig. 6 Boxplot comparing the performance of groups in: (**a**) approximation latency to the conditioned stimulus (CS) zone in the visual test; (**b**) approximation latency to the CS zone in the copulatory test; (**c**) time remained in the CS zone during the visual test; and (**d**) time remained in the CS zone during the copulatory test (Experiment 2)

sexual learning in adult subjects. It remains unclear whether this effect was caused by presenting one or both stimuli and the mechanisms involved. Based on studies showing that sexual motivation increases in inexperienced male quail when exposed to adult females (e.g., Cornil & Ball, 2010), it is likely that pre-exposure to the US is causing the differences between groups P and U, and group N. Also, a maturation effect might be physiologically mediated in both males and females (Delville et al., 1984; Guyomarc'h et al., 1984).

General discussion

Our findings show how early social experiences can impact sexual behavior. In the two experiments, the sexual response of quail exposed to early social experience was affected compared with isolated quail, and early social exposure led

to faster sexual conditioning. The results of Experiment 1 suggest that this effect might be more robust with the paired presentation of the stimuli during the early phase. We suggest possible explanations for each of the effects reported, but many questions remained unsolved.

One of the biggest challenges is to disentangle the physiological and behavioral effects of the early exposure to conspecifics of the opposite sex. According to previous studies, an increased maturation of reproductive structures may cause an increase in sexual motivation of the subjects exposed early to sexually mature conspecifics (Delville et al., 1984; Guyomarc'h et al., 1984). Studies have also shown that early experiences can have temporal and even permanent impacts over neurobiological and epigenetic processes, which contribute to adult behavior and can cause transgenerational effects (Champagne, 2008; Weaver et al., 2004). In terms of sexual conditioning, the amygdala is a sensitive brain structure for associative learning, especially
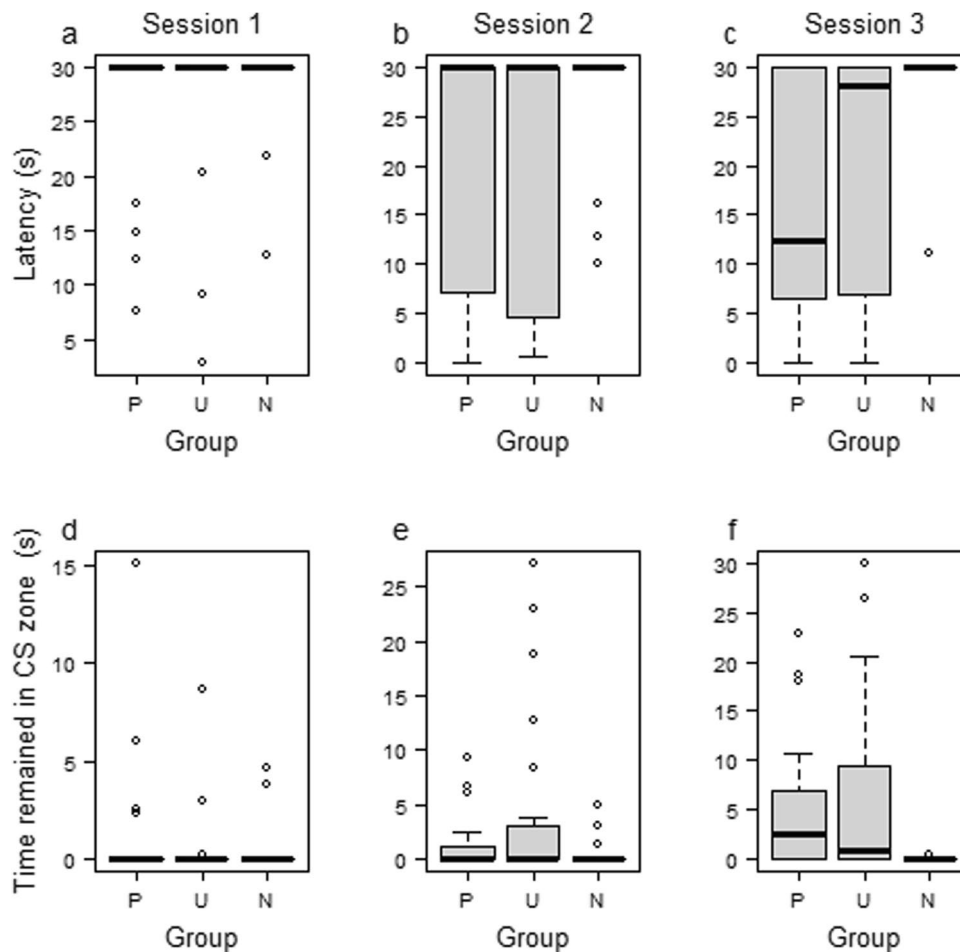
Fig. 7 Boxplot comparing the performance of groups in the visual test by session with respect to approximation latency to the conditioned stimulus (CS) zone (a: Session 1; b: Session 2; c: Session 3) and time remained in the CS zone (d: Session 1; e: Session 2; f: Session 3; Experiment 2)

when the US has a strong biological relevance. Specifically, the expression of the *c-fos* gene in the nucleus taeniae of the amygdala of male Japanese quail (the likely homolog of the medial amygdala in mammals) is strongly related to the exposure to a CS previously paired with a female (Taziaux et al., 2007). The nucleus taeniae controls motivational aspects of social behavior and this structure develops at very early stages of life (Ikebuchi et al., 2013), suggesting that its maturation could be affected by the exposure to conspecifics at an early age. The nucleus taeniae of the amygdala, together with other areas like the medial preoptic nucleus and the bed nucleus of stria terminalis, form a network that controls the sexual behavior of male Japanese quail (Can et al., 2007), and it is likely that neurons of these areas can be also affected by the exposure to sexually relevant stimuli.

Some of our findings suggest that learning mechanisms (e.g., differences between P and U groups in both experiments) might also be involved, although this effect was less clear in the second experiment. Pavlovian conditioning

procedures applied to immature subjects can lead to different effects with a few days of age difference between the subjects. For example, 17-day-old rats exposed to a fear conditioning procedure did not show a renewal effect 2 days later, while 23-day-old rats did (Yap & Richardson, 2007). This and other developmental effects of fear conditioning extinction seem to be explained by differences in the neurobiological processes involved (Kim & Richardson, 2010), which could also apply to the differences between experiments concerning the comparison between groups P and U.

In sum, there is a complex and dynamic relationship between physiological and behavioral processes during development and further studies are needed to unravel the explanations explored above. Whatever the involved mechanisms, our study contributes to a growing body of research showing that there are multiple processes that account for phenotypic variation (Champagne, 2018; Danchin et al., 2011; West-Eberhard, 1989, 2003), and developmental plasticity is critical to understand ontogenetic and phylogenetic
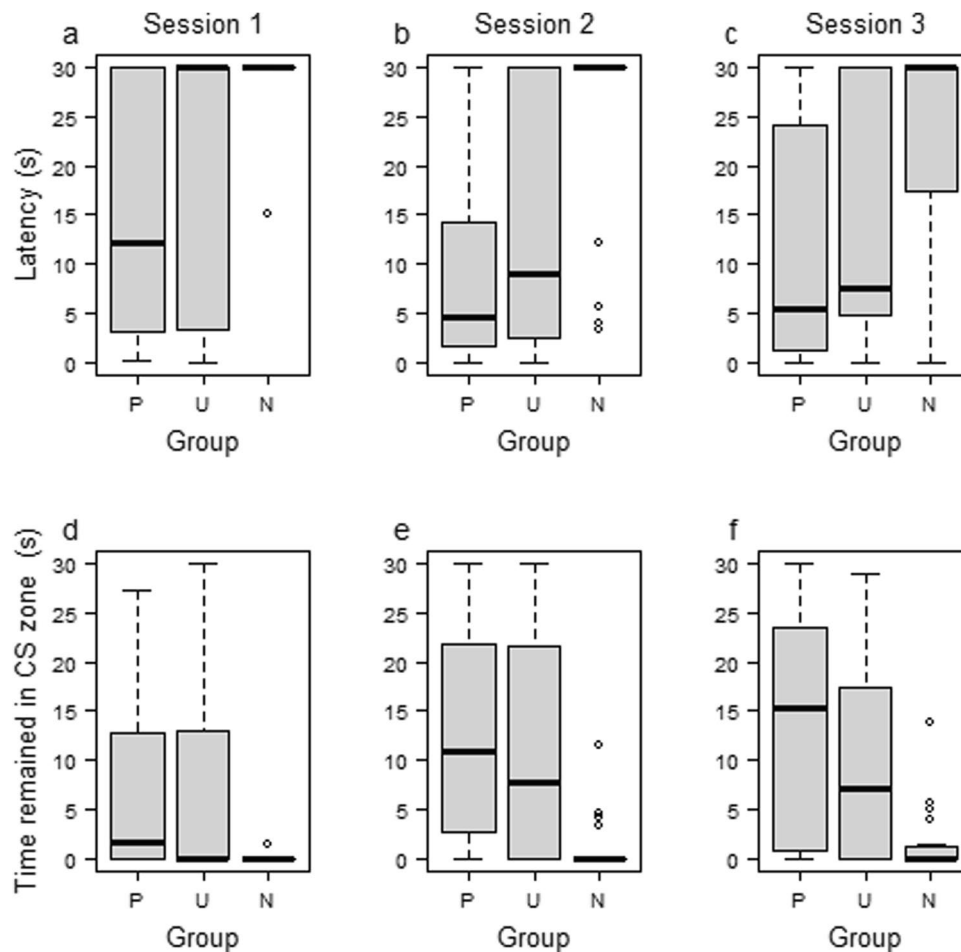
Fig. 8 Boxplot comparing the performance of groups in the copulatory test by session with respect to approximation latency to the conditioned stimulus (CS) zone (a: Session 1; b: Session 2; c: Session 3) and time remained in the CS zone (d: Session 1; e: Session 2; f: Session 3; Experiment 2)

Table 3 Z scores, p values and effect sizes (r) resulted from Mann-Whitney U tests performed to analyzed differences in the latency to approach and the time remained in the CS zone between pairs of groups during the

	Latency						Time remained in CS zone					
	P-N			U-N			P-N			U-N		
Session	z	p	r	z	p	r	z	p	r	z	p	r
1	−3.902	.000	−.563	−3.095	.002	−.447	3.902	.000	.563	3.120	.002	.450
2	−4.421	.000	−.638	−3.264	.001	−.471	4.710	.000	.679	3.512	.000	.507
3	−3.455	.000	−.499	−2.4	.016	−.346	3.895	.000	.562	2.832	.004	.408

Note: Values for the comparison between P and U groups are not included because they were not significant ($p > .05$). A p-value of .05 was considered to reject the null hypotheses in both statistical tests

change (Bateson & Gluckman, 2011; Groothuis & Crews, 2005; Laland et al., 2015; Nettle & Bateson, 2015). There is plenty of theoretical and empirical evidence indicating that the explanation of individual traits must involve an intricate interaction between genetic and environmental factors (Jawaid & Mansuy, 2019; Tariel et al., 2020; Walsh et al., 2015). An integrated framework beyond molecular reductionism and the nature-nurture dichotomy is needed to better understand developmental processes, which are dynamic and should include several levels of analysis, from

molecular (genetic and epigenetic mechanisms) to molar (behavioral, ecosystemic; Crews, 2011; Crews et al., 2014; Lickliter & Witherington, 2017). Our study moves in that direction, since it allows exploring the consequences of environmental factors at the early stages of life on ontogeny (i.e., adulthood). Research questions currently explored by our research group include the effect of early visual exposure to sexually mature males on later sexual receptivity and fertility in female quail (Arteaga-Avendaño et al., in preparation), and transgenerational effects of early exposure to stimuli on sexually conditioned responses (Puentes-Escamilla et al., in preparation).

Kuo (1921) and Tinbergen (2010) eloquently expressed that developmental questions need to be answered to understand behavior fully. However, this type of explanation has been mostly neglected in the study of learning and sexual behavior. Our results suggest that early experiences may impact appetitive and consummatory sequences of the sexual behavioral system in male Japanese quail, which might affect its reproductive fitness. The work of Michael Domjan and his research associates has been a driving force in understanding the relations between learning and evolution using a sexual behavior system. The addition of developmental variables in this explanatory model will offer new insights into understanding the plasticity of sexual behavior.

Declarations

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