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ORIGINAL PAPER

Spontaneous generalization of abstract multimodal patterns in young domestic chicks

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Abstract From the early stages of life, learning the regularities associated with specific objects is crucial for making sense of experiences. Through filial imprinting, young precocial birds quickly learn the features of their social partners by mere exposure. It is not clear though to what extent chicks can extract abstract patterns of the visual and acoustic stimuli present in the imprinting object, and how they combine them. To investigate this issue, we exposed chicks (*Gallus gallus*) to three days of visual and acoustic imprinting, using either patterns with two identical items or patterns with two different items, presented visually, acoustically or in both modalities. Next, chicks were given a choice between the familiar and the unfamiliar pattern, present in either the multimodal, visual or acoustic modality. The responses to the novel stimuli were affected by their imprinting experience, and the effect was stronger for chicks imprinted with multimodal patterns than for the other groups. Interestingly, males and females adopted a different strategy, with males more attracted by unfamiliar patterns and females more attracted by familiar patterns. Our data show that chicks can generalize abstract patterns by mere exposure through filial imprinting and that multimodal stimulation is more effective than unimodal stimulation for pattern learning.

Keywords Pattern learning · Filial imprinting · Abstract rule · Generalization · Chicks · Rule learning

Introduction

Making sense of visual and auditory stimuli requires a grasp of the structure of the environment. Many studies have revealed a range of specialized perceptual and learning mechanisms than can help human adults, infants and non-human animals to detect patterns from structured visual and auditory input (Endress et al. 2009; Fitch and Friederici 2012; reviewed in Dehaene et al. 2015), ranging from identification of repetitions (Marcus et al. 1999) and use of predictors (Versace et al. 2008; Meyer and Olson 2011) to extraction of positional regularities (Endress et al. 2010; Chen et al. 2014), statistical regularities (Saffran et al. 1996; Fiser and Aslin 2001, 2002; Kirkham et al. 2002; Gentner et al. 2006; Sonnweber et al. 2015) and abstract patterns (Marcus et al. 1999; Stobbe et al. 2012; Wang et al. 2015; Spierings and ten Cate 2016). Although regularities can be defined in abstract terms (e.g. A^nB^n, or XYX, see, for instance, Fitch and Friederici 2012), with no explicit reference to the modality used to extract or produce specific stimuli, it has been shown that stimuli in one modality can affect the processing in another modality (e.g. Shimojo and Shams 2001; Ernst and Bulthoff 2004; Seitz et al. 2007; Robinson and Sloutsky 2013). Little is known, though, on the effects on pattern learning when stimuli combine different modalities.

Elisabetta Versace and Michelle J. Spierings have contributed equally to this work.

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The investigation of rule learning capacities in non-human species is often based on the use of operant conditioning paradigms (ten Cate and Okanoya 2012). Although these paradigms can provide insight in what animals might be able to learn about various patterned strings of stimuli, about their learning strategies and what aspects of the stimuli are important, spontaneous behaviours can reveal which capacities are available in naturalistic conditions (ten Cate and Okanoya 2012). Newly hatched birds of precocial species learn by mere exposure the features of the conspicuous objects they are exposed to, a phenomenon called "filial imprinting", that occurs without explicit reinforcement (reviewed in Bateson 1966; Bolhuis 1991; Horn 2004; McCabe 2013). After a few minutes spent with the imprinting stimulus, chicks show affiliative responses, such as approach, towards it (Bateson and Jaeckel 1976; van Kampen and Bolhuis 1991). In the wild, filial imprinting enables chicks to keep proximity with close kin, thus increasing survival prospects of the youngsters. In the laboratory, chicks imprint on visual (Horn and McCabe 1984; Wood 2013) and acoustic stimuli (van Kampen and Bolhuis 1991; Miklósi et al. 1996), showing approach responses even to artificial imprinting objects presented on computer screens (Mascalzoni et al. 2010; Wood 2013, 2014). This means that they are sensitive to both the visual and the acoustic stimulation in their environment during imprinting.

The capacity to generalize imprinting responses enables young precocial birds to recognize social partners in spite of their heterogeneity and changes in appearance (e.g. mother hen and siblings seen from different angles and during development; Bateson 1973): imprinting in fact extends to stimuli presented from novel points of view (Wood 2013), and to objects with the same shape but different colour compared to the imprinting object (Bolhuis and Horn 1992). The preference for slightly novel stimuli has been viewed as a learning strategy that helps youngsters to learn the different features of social partners (e.g. the front and back view of the mother hen are very different indeed; Bateson 1973, 1979). Although the natural imprinting stimulus will be a single object, there is increasing evidence suggesting that the mechanism of imprinting might be able to go beyond the perceptual features of a single object to those of a grouped configuration of elements: Versace et al. (2006) showed that chicks imprinted on coloured cylinders that followed the $(AB)^n$, $(A)^n(B)^n$ and (A(BB)A) patterns could recognize the familiar pattern irrespectively of its colour. In this test, chicks preferentially approached unfamiliar patterns, confirming the preference for novel stimuli that has been documented at specific times after the initial imprinting exposure (see, for instance, Bateson and Jaeckel 1976; Vallortigara and Andrew 1994). The ability of young chicks to generalize from the stimuli used during the exposure to a similar arrangement of novel ones was also demonstrated in a recent conditioning experiment with young chicks (Santolin et al. 2016), suggesting that chicks are able to detect a relationship among a set of items. This was also shown for filial imprinting in another precocial species by Martinho and Kacelnik (2016), who showed that ducklings can recognize the XX (two identical items, with central symmetry) versus XY (two different items) patterns in visual items and generalize the pattern of their imprinting items to novel items following the same pattern. This suggests that these animals learned the abstract relation between two visual items.

In the present study, we used filial imprinting to examine the spontaneous capacity of chicks of the domestic fowl (*Gallus gallus*) to generalize the visual, acoustic and multimodal patterns XX and XY to novel objects. This may indicate an ability to learn an abstract pattern, i.e. a pattern independent of the particular stimuli by which it is instantiated. As the propensity for approaching unfamiliar social stimuli has been shown to be stronger in male than in female chicks in various tasks (reviewed in Vallortigara and Andrew 1991, 1994), we took sex differences into account.

We first exposed newly hatched chicks to stimuli that followed either the XX or XY pattern in the visual, acoustic or visual and acoustic modality. In the test phase, chicks were given a choice between novel stimuli in both patterns and we measured their preference for each of the patterns. Chicks showed significantly different approach responses towards the novel stimuli during the test, showing that they can use the imprinting pattern to evaluate novel items, with females preferring the familiar pattern and males preferring the unfamiliar pattern. Moreover, multimodal visual and acoustic stimuli were more effective than visual-only or acoustic-only stimuli.

Methods

Ethics statement

All experiments complied with the current Italian and European Community laws for the ethical treatment of animals and the experimental procedures were approved by the Ethical Committee of University of Trento and licensed by the Italian Health Ministry (permit number 1138/2015 PR).

Experimental design

To investigate the capacity for generalization of abstract XX (two identical items) and XY (two different items) patterns, we imprinted chicks on either XX or XY stimuli and then tested chicks' approach responses towards novel XX and XY stimuli. Significant differences in the preference for novel XX and XY stimuli between chicks imprinted on different patterns show the capacity to generalize the information gained during imprinting. To understand the role of visual, acoustic and multimodally presented stimuli, the test stimuli were presented to different experimental groups either visually, acoustically or multimodally. Given that male and female chicks had been previously shown to exhibit different preferences for familiar and unfamiliar stimuli, we analysed each sex separately. Each test was replicated with two sets of stimuli that differed only with respect to the items used to instantiate them.

Materials

Subjects

This study was conducted with 388 newly hatched chicks of domestic fowl (*Gallus gallus*) of the Ross 308 strain (Aviagen). Table 1 shows how many males and females were tested in each condition. The eggs were collected from a commercial hatchery (Agricola Berica, Montegalda, Italy) and incubated at the University of Trento under controlled conditions at 37.7 °C and 40% humidity. Three days before hatching they were moved to a hatching chamber (37.7 °C and 60% humidity) in opaque individual boxes, where the chicks hatched in complete darkness. After hatching, food and water were available ad libitum.

Table 1 Number of subjects tested in each condition, mean preference for the XX pattern and standard error of the mean

Imprinting pattern	Sex	Modality tested	*N*	Mean	SEM
XX	Female	Acoustic	38	0.517	0.034
XX	Female	Multimodal	33	0.644	0.033
XX	Female	Visual	31	0.589	0.046
XY	Female	Acoustic	32	0.489	0.034
XY	Female	Multimodal	37	0.378	0.031
XY	Female	Visual	28	0.460	0.047
XX	Male	Acoustic	35	0.511	0.040
XX	Male	Multimodal	29	0.363	0.037
XX	Male	Visual	33	0.502	0.044
XY	Male	Acoustic	32	0.584	0.046
XY	Male	Multimodal	27	0.482	0.039
XY	Male	Visual	33	0.539	0.048

Stimuli

An overview of the imprinting and test stimuli is presented in Table 2. The chicks were imprinted with an XX (two identical items) or with an XY (two different items) pattern. In the visual condition, chicks were imprinted with two patterns (e.g. V_1V_1 and V_2V_2) presented visually, while a single item (e.g. A_7) was presented acoustically; in the acoustic condition, two patterns were presented acoustically (e.g. A_1A_1 and A_2A_2), while a single visual stimulus (V_7) was presented on the monitor, and in the multimodal condition, two visual patterns (e.g. V_1V_1 and V_2V_2) and two acoustic patterns (A_1A_1 and A_2A_2) were presented simultaneously. In each condition, half of the chicks were imprinted with the XX pattern and half with the XY pattern. To avoid pseudo-replication, we repeated the experiments with two sets of stimuli (e.g. A_1A_1 and A_2A_2, A_3A_3 and A_4A_4).

Acoustic stimuli

Figure 1a shows spectrograms of the acoustic stimuli used. The acoustic stimuli were artificially created in Praat (version 6.0.16). In total, there were seven different acoustic stimuli; six were used to create the imprinting patterns (A_1–A_6) and one as the single imprinting sound for the visual condition (A_7, Table 2). As shown in Fig. 1a, the six sounds for the patterns were created to differ in duration (between 122 and 180 ms), fundamental frequency, pitch contour and formant frequencies in order to make them easily distinguishable, but they were all played with the same amplitude of 75 dB. To create the XX and XY pattern, two sounds were concatenated with a 50-ms pause between them, and this created duplets ranging in duration between 300 and 400 ms. During playback, there were always three duplets presented in 6 s, spaced equally in time. This acoustic playback scheme matched with the visual playback in which the stimulus took 6 s to cross the screen. The A_7 sound used in the visual condition was a natural recording of a chick vocalization with a duration of 104 ms and an amplitude of 75 dB. This sound was also presented three times in 6 s, spaced equally over time. All sounds used in this study were within the hearing range of a newly hatched chick.

Visual stimuli

Figure 1b shows the visual stimuli used. The seven visual stimuli were built in MATLAB and were created to be as distinct as possible. All stimuli fitted in a 4.5-cm square, but they varied in shape, colour, number of corners, amount of area filled and presence/absence of central symmetry, presence of round/sharp edges. The XX and XY

Table 2 Overview of the imprinting and test stimuli used

Modality tested	Imprinting pattern	Set	Imprinting stimuli		Test stimuli	
			Acoustic	Visual	Acoustic	Visual
Multimodal	XX	One	A_1A_1 and A_2A_2	V_1V_1 and V_2V_2	A_5A_5 versus A_5A_6	V_5V_5 versus V_5V_6
		Two	A_3A_3 and A_4A_4	V_3V_3 and V_4V_4	A_1A_1 versus A_1A_2	V_1V_1 versus V_1V_2
	XY	One	A_1A_2 and A_4A_3	V_1V_2 and V_4V_3	A_5A_5 versus A_5A_6	V_5V_5 versus V_5V_6
		Two	A_3A_4 and A_5A_6	V_3V_4 and V_5V_6	A_1A_1 versus A_1A_2	V_1V_1 versus V_1V_2
Visual	XX	One	A_7	V_1V_1 and V_2V_2	A_7	V_5V_5 versus V_5V_6
		Two	A_7	V_3V_3 and V_4V_4	A_7	V_1V_1 versus V_1V_2
	XY	One	A_7	V_1V_2 and V_4V_3	A_7	V_5V_5 versus V_5V_6
		Two	A_7	V_3V_4 and V_5V_6E	A_7	V_1V_1 versus V_1V_2
Acoustic	XX	One	A_1A_1 and A_4A_4	V_7	A_5A_5 versus A_5A_6	V_7
		Two	A_3A_3 and A_4A_4	V_7	A_1A_1 versus A_1A_2	V_7
	XY	One	A_1A_2 and A_4A_3	V_7	A_5A_5 versus A_5A_6	V_7
		Two	A_3A_4 and A_5A_6	V_7	A_1A_1 versus A_1A_2	V_7

There were three conditions that differed in the modality tested: multimodal (both patterns presented in both visual and acoustic modality), visual (patterns presented in the visual modality, a single stimulus presented in acoustic modality) and acoustic (patterns presented in the acoustic modality, a single stimulus presented in visual modality). In each group, the chicks were imprinted with either an XX pattern or an XY pattern, and with set one or set two. The letters (A_1–A_7 for acoustic, V_1–V_7 for visual) indicate the different stimuli used for imprinting and testing in the different sets and groups. Stimuli are shown in Fig. 1

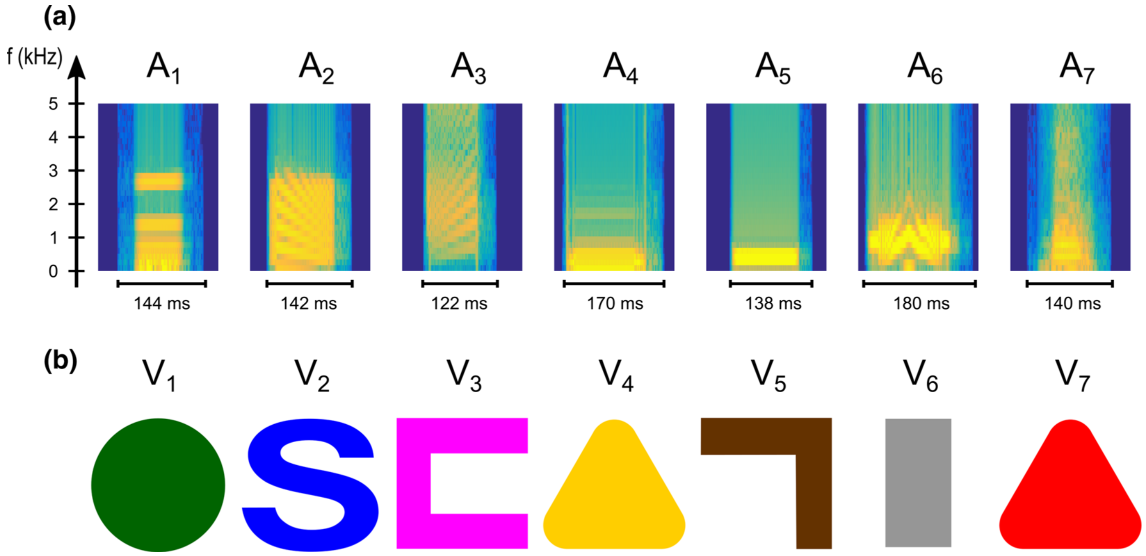

Fig. 1 Overview of the stimuli used for imprinting and test. **a** Acoustic stimuli: A_1–A_7 were used to create duplets with either an XX or an XY pattern. Sound A_7 is a natural chick vocalization and was used as unique acoustic stimulus for imprinting and test in the visual condition. **b** Visual stimuli: V_1–V_7 were used to create duplets with either an XX or an XY pattern. Stimulus V_7 was used as unique visual stimulus for imprinting and test in the acoustic condition

configurations (as well as the V_7 stimulus used in the acoustic condition) moved across the screen horizontally (30 cm), taking 12 s to run an entire cycle from right to left and back.

Imprinting set up

The imprinting procedure started on the day that the chick hatched and lasted three days. The imprinting set up consisted of a black box (30 × 30 × 40 cm, $w \times l \times h$) with a monitor (17″, 60 Hz) mounted on the front wall and a speaker (Logitech, Z150) above the box, both playing the imprinting stimuli.

Test set up

After imprinting, the chicks were tested in the running wheel set up shown in Fig. 2. The apparatus was 150 cm

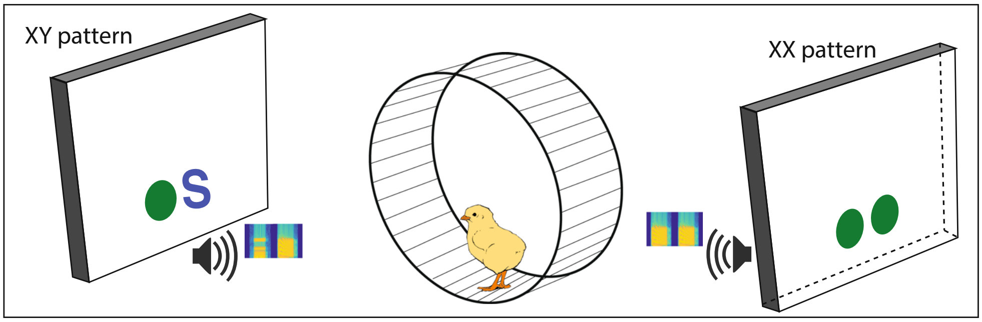

Fig. 2 Schematic illustration of the experimental set up. Monitors and loudspeakers used to present the stimuli were located at the far ends of the apparatus. The chick was placed in a running wheel in the middle of the apparatus, facing the long side. While the chick operated the wheel towards either side to approach the stimuli, an automated system measured the centimetres run in each direction

long, 46 cm wide, 45 cm high, with a running wheel (32 cm diameter, 13 cm large, covered with 1 cm of dark opaque foam on both sides) in the middle of the apparatus. On each side of the wheel was a monitor and speaker identical to those used during imprinting. The speaker was set to 75 dB amplitude. On both sides, monitor and speaker were located 60 cm far from the centre of the apparatus. An automated system recorded the centimetres run on each direction showing this information on a display (see Versace et al. 2017).

Procedure

Imprinting procedure

We individually exposed newly hatched chicks to stimuli that followed the XX or XY pattern. The imprinting lasted three days. In each imprinting cage, the monitor and speaker played the stimuli for 14 h a day continuously for two days and for 8 h a day continuously, followed by 6 h with alternations of 5 min of stimuli playback and 10 min of darkness and silence on the third day. This allowed the chicks to familiarize with the disappearance of the imprinting stimuli. During the remaining 10 h of the day, the screen was black and no sound was played.

Test procedure

At the beginning of the test, each chick was placed in the running wheel facing sideways. The test lasted 20 min. The XX pattern was presented on one side and the XY pattern on the opposite side, and the sides were switched between chicks. Depending on the imprinting modality tested, the test stimuli were novel for the visual pattern, or the acoustic one or both, as summarized in Table 2. The experimenter monitored the distance run in the wheel.

Data analysis

We expected to observe a significant difference in approach towards novel XX and XY patterns between chicks imprinted on XX and XY if chicks could learn the imprinting pattern and generalize it to novel stimuli. To check for this effect, for each chick we computed the XX preference index as

$$\frac{\text{cm run towards XX}}{\text{overall cm run}}$$

We performed an ANOVA on the XX preference index with imprinting pattern (XX, XY), modality (multimodal, visual, acoustic), sex (male, female) and set (one, two) as between-subjects factors. Post hoc two-tailed *t* tests were used to contrast levels of significant effects and interactions. The data set supporting this article has been uploaded as Supplementary material.

Results

Overall preferences

We examined preferences for the XX versus XY pattern in chicks imprinted on XX or XY patterns through a linear model, expecting a difference in XX preference between chicks imprinted on XX versus XY patterns. As independent variables, we used imprinting pattern (XX or XY), modality tested (acoustic, visual, multimodal), sex (male or female) and set of stimuli (one or two). There were no outliers or data points with high leverage, and the model had a good linear fit. Table 3 shows the complete set of results. No significant main effect was present in the analysis, but we observed a trend for modality tested: $F_{2,364} = 2.603$, $P = 0.075$. We observed only two significant interactions: imprinting pattern × sex ($F_{1,364} = 20.497$, $P < 0.001$) and imprinting pattern × modality tested × sex ($F_{2,364} = 3.292$, $P = 0.038$), as shown in

Table 3 Summary of the results of the overall ANOVA for the XX preference

Effect	*df*	*F*	*P*
Imprinting pattern	1	2.467	0.117
Modality tested	2	2.603	0.075
Sex	1	0.372	0.542
Set	1	0.811	0.368
Imprinting pattern × modality tested	2	2.021	0.134
Imprinting pattern × sex	1	20.497	**8.1e–06**
Modality tested × sex	2	2.892	0.057
Imprinting pattern × set	1	0.790	0.375
Modality tested × set	2	0.118	0.889
Sex × set	1	0.371	0.543
Imprinting pattern × modality tested × sex	2	3.292	**0.038**
Imprinting pattern × modality tested × set	2	0.460	0.631
Imprinting pattern × sex × set	1	1.749	0.187
Modality tested × sex × set	2	1.730	0.179
Imprinting pattern × modality tested × sex × set	2	0.504	0.604
Residuals	364		

In this analysis, the independent variables were: imprinting pattern (XX, XY), modality tested (multimodal, visual, acoustic), sex (male, female), set of stimuli (one, two)

Bold values indicate significant results ($P < 0.05$)

Fig. 3. Since the factor set of stimuli was not significant as main effect, nor in any interaction, we can conclude that the observed effects are independent from the stimuli used. Based on the evidence of sex effects in interaction, and on well-documented differences in affiliative responses between male and female chicks (see, for instance, Vallortigara 1992; Vallortigara and Andrew 1994), we ran further separate analyses for males and females.

Female preferences

Females showed a significant main effect of the imprinting pattern ($F_{1,193} = 21.675$, $P < 0.001$), no significant main effect of modality tested ($F_{2,193} = 0.242$, $P = 0.785$) and a significant interaction imprinting pattern × modality tested ($F_{2,193} = 5.390$, $P = 0.005$).

In all tested modalities, females imprinted on XX had a higher tendency to approach the XX (familiar) stimulus compared to females imprinted on XY. Using post hoc two-tailed *t* tests for independent samples, we found a significant effect only in the multimodal test and a trend for the visual modality (multimodal: $t_{67} = 5.865$, $P < 0.001$; visual: $t_{56.75=}1.954, P = 0.055$; acoustic: $t_{67.63} = 0.580, P = 0.563$).

These results show that, after multimodal imprinting on XX versus on XY, females have significantly stronger preference for the familiar pattern, whereas when testing females with unimodally presented patterns, the preferences for familiar patterns are much weaker. These findings suggest a combined effect between modalities in the representation of the imprinting object.

Male preferences

Males showed a significant main effect of the imprinting pattern ($F_{1,183} = 4.51$, $P = 0.035$), a significant main effect of modality tested ($F_{2,183} = 4.511$, $P = 0.012$) and no significant interaction imprinting pattern × modality tested ($F_{2,183} = 0.441$, $P = 0.644$).

In all tested modalities, males imprinted on XX had a higher tendency to approach the XY (unfamiliar) stimulus compared to males imprinted on XY. Using post hoc two-tailed *t* tests for independent samples, we found a significant effect only in the multimodal test (multimodal: $t_{53.34} = -2.211$, $P = 0.031$; visual: $t_{63.64=}-0.565$, $P = 0.574$; acoustic: $t_{62.55} = -1.216$, $P = 0.229$). These results show that, after multimodal imprinting on XX versus imprinting on XY, males have significantly stronger preference for the unfamiliar pattern, whereas when testing males with patterns that differ only in one modality (either acoustic or visual), the preferences for the unfamiliar pattern are much weaker. Similarly to what observed in females, these results suggest an effect between modalities in the representation of the imprinting object.

Discussion

From the early stages of life, learning the regularities associated with specific objects is crucial for building an effective representation of the environment. Through the mechanism of filial imprinting, mere exposure is sufficient

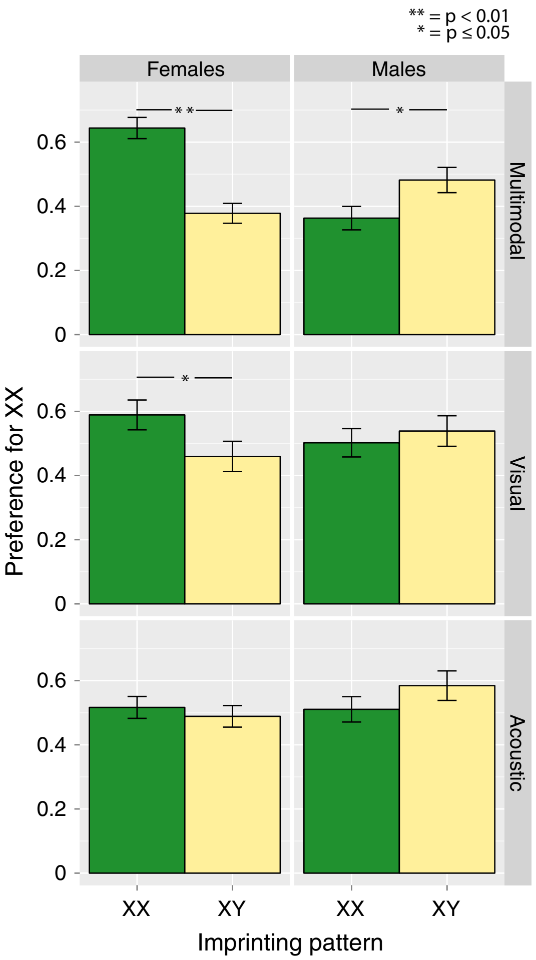

Fig. 3 Mean preference (±1 standard error of the mean) for XX (cm run towards XX/overall cm run) by imprinting pattern (XX or XY), sex and modality tested (multimodal, visual, acoustic)

for newly hatched precocial birds to learn the features of their social partners and use this information to recognize them. For this reason, filial imprinting has been widely used as a system to investigate memory of familiar objects (Bateson 1966; Bolhuis 1991; Horn 2004; reviewed in McCabe 2013). Mounting evidence, though, suggests that the imprinting mechanisms might be powerful enough to extract abstract features of conspicuous objects, such as their visual configurations: Versace et al. (2006) showed that chicks imprinted on coloured cylinders arranged according to the $(AB)^n$, $(A)^n(B)^n$ and (A(BB)A) patterns could discriminate familiar/unfamiliar patterns irrespectively of the hue of stimuli, and Martinho and Kacelnik (2016) showed that imprinted ducklings can discriminate between the XX versus XY configurations of objects that differ in colour or shape from the imprinting objects—a task that could be solved both based on the presence of identical/different items and on the presence/absence of symmetry. In our study, we extend this line of research to auditory and multimodal information, investigating the capacity of chicks imprinted on either XX or XY patterns to discriminate between familiar and unfamiliar patterns in a generalization context. Both increased and reduced preference for familiar patterns show the ability to process and discriminate the patterns.

Our findings confirm chicks' capacity for extracting the abstract XX/XY relation presented in the imprinting stimuli to novel objects, in the absence of explicit training.

Moreover, we observe that consistent visual and acoustic stimuli presented multimodally might have a synergistic effect, since multimodal patterns elicited a stronger differentiation between XX and XY stimuli than unimodal patterns. To better understand the representation of the pattern arising from imprinting, further research should clarify the way in which conflicting and conforming multimodal information contribute to determining approach responses. Rather than overloading the cognitive system or producing interference, presenting novel stimuli in both visual and acoustic modality enhanced the capacity of chicks to discriminate between patterns. This result extends the findings on recognition of imprinting objects in avian species (ten Cate 1989; van Kampen and Bolhuis 1991, 1993 and references therein).

Interestingly, while both male and female chicks could discriminate between familiar and unfamiliar stimuli, they showed opposite preferences with respect to the familiarity of the objects. Both preferences for familiar and unfamiliar stimuli indicate the capacity to discriminate between the patterns. Consistent with the well-known effect of preference for slightly novel stimuli observed in chicks (Jackson and Bateson 1974; Bateson 1979; Versace et al. 2006) especially in males (Vallortigara and Andrew 1994), male chicks consistently approached unfamiliar patterns more than familiar patterns, while females had the opposite preference. Early differences in affiliative responses between male and female chicks have been previously documented in field and laboratory conditions (e.g. Workman and Andrew 1989; Vallortigara et al. 1990; Vallortigara 1992; Vallortigara and Andrew 1994), as differences in social and aggressive motivation between the sexes.

Chicks' spontaneous capacities to abstract pattern generalization suggest that this method might be suitable for investigating the computational capacities used to process abstract and statistical regularities, complementing conditioning paradigms. The comparative investigation of spontaneous responses can shed light on the computational abilities used in the wild to process and extract regularities.

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Authors' contributions EV conceived and designed the study, participated in data collection, analysed the data and drafted the manuscript; MS designed the study, prepared the stimuli, participated in data collection and helped drafting the manuscript; MC prepared the stimuli and helped drafting the manuscript; CTC conceived and designed the study and helped in drafting the manuscript; GV conceived and designed the study and helped in drafting the manuscript. All authors gave final approval for publication.

Compliance with ethical standards

Conflict of interest We have no competing interests.

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