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ORIGINAL PAPER

Generalization of visual regularities in newly hatched chicks (*Gallus gallus*)

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Abstract Evidence of learning and generalization of visual regularities in a newborn organism is provided in the present research. Domestic chicks have been trained to discriminate visual triplets of simultaneously presented shapes, implementing AAB versus ABA (Experiment 1), AAB versus ABB and AAB versus BAA (Experiment 2). Chicks distinguished pattern-following and pattern-violating novel test triplets in all comparisons, showing no preference for repetition-based patterns. The animals generalized to novel instances even when the patterns compared were not discriminable by the presence or absence of reduplicated elements or by symmetry (e.g., AAB vs. ABB). These findings represent the first evidence of learning and generalization of regularities at the onset of life in an animal model, revealing intriguing differences with respect to human newborns and infants. Extensive prior experience seems to be unnecessary to drive the process, suggesting that chicks are predisposed to detect patterns characterizing the visual world.

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Introduction

Learning regularities from the sensory input enable many living creatures to discover the structure of their environment. The sensory world is indeed composed of objects, events and sounds related to each other and combined into patterns. Despite being one of the core mechanisms of language acquisition (e.g., Brown 1973), learning regularities displayed as strings of multiple elements can be broadly conceived as a general process that operates across domains, modalities and species (see ten Cate and Okanoya 2012 for a review). Once relevant patterns are acquired, learners are sometimes required to generalize to novel situations, extending the learned structure beyond the perceptual features of the input (Frost et al. 2015). Marcus et al. (1999) familiarized 7-month-old infants with a set of syllable triplets following two patterns: ABB and ABA, where A and B could be implemented by any given syllable, i.e., *ga-ti-ti* and *ga-ti-ga*. Infants were then able to recognize the familiar regularity by discriminating novel triplets that followed the pattern from those that did not, i.e., *wo-fe-fe* and *wo-fe-wo*. Crucially, new exemplars did not share perceptual information with the familiar input; thus, infants could not have simply memorized syllable strings to succeed in the task. They were required to detect the same/different relation underlying string elements, independently of syllable identity; for instance, the pattern defined as ABB can be described as one syllable followed by two identical syllables, but different from the former.

Human learning of regularities instantiated by acoustical and visual sequences seems to be constrained by perceptual

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aspects of the input. When elements implementing a pattern are salient for the learner, the pattern is better acquired. For instance, visual regularities displayed as triplets of dog/cat images representing different breeds (Saffran et al. 2007) and sequences of spoken syllables (Marcus et al. 1999) were more efficient in driving infants' attention to the pattern than non-linguistic sounds (e.g., piano notes and animal calls; Marcus et al. 2007) and geometrical shapes (Johnson et al. 2009), implementing the same type of patterns (see Thiessen 2012; Dawson and Gerken 2009 for further discussion).

Another perceptual aspect of the input that may influence learning and generalization of regularities is the presence/absence of adjacent reduplicated elements that confer also an asymmetrical structure to the pattern. For example, in AAB two identical As are adjacent to one another (asymmetrical structure), as opposed to ABA where the same item is repeated in non-adjacent positions within the triplet (symmetrical structure). Research focused on the generalization of acoustic regularities revealed that repetitions matter. Gervain et al. (2008) showed learning differences when ABB syllable sequences (e.g., *mu-ba-ba*) were presented to neonates with respect to ABA sequences (e.g., *mu-ba-mu*), both contrasted with random (ABC) stimuli (e.g., *mu-ba-ge*). This study showed greater activation of temporal and left frontal brain regions only when ABB strings were presented, demonstrating that neonates could discriminate those patterns from random stimuli. A perceptual mechanism that privileges adjacent repetitions in acoustic stimuli had been previously proposed in the literature. Endress et al. (2007) showed that human adults could generalize familiar tone sequences to novel ones, only when adjacent repetitions characterized the structure of the sequence. Moreover, participants proved to be sensitive to different positions of the repetition within the sequence, showing successful generalization only when repetitions were located at the final edge of the string (e.g., ABCDE*FF* vs. ABCDE*EE*F; Endress et al. 2005). Even though the role of repetitions has been mostly investigated in the auditory domain, learning and generalization of visual structures appear to be similarly constrained. Regularities comprising adjacent reduplications of shapes (AAB and ABB) are better acquired than those with non-adjacent identical items (ABA), (e.g., Johnson et al. 2009). In sum, although humans can easily track regularities from different domains, the nature of the input affects the learning outputs. Perceptual constraints seem to be: (1) learners' familiarity with the input (saliency), (2) input symmetrical versus asymmetrical structure, (3) presence or absence of adjacent repetitions and (4) modality–specificity (see also, Saffran and Thiessen 2007).

In order to further investigate the phylogenetic origins of regularity learning, a handful of studies have explored this process in several non-human species. Rats (*Rattus norvegicus*) showed generalization to novel instances of patterns defining strings of tones (Murphy et al. 2008) and sequences of consonants and vowels (de La Mora and Toro 2013). Similar evidence has been found in the rhesus monkey (*Macaca mulatta*; Hauser and Glynn 2009) who can discriminate short strings of species-specific vocalizations displayed as ABB or AAB, and generalize to perceptually new strings. As regards to avian species, among the songbirds, European starlings (*Sturnus vulgaris*) and Zebra finches (*Taeniopygia guttata*) have been extensively studied in this field because of their rich repertoire of vocalizations (see ten Cate and Okanoya 2012 for a review), revealing strong learning of elaborate patterns defining their own songs. In spite of that, songbirds' generalization capacities seem to be controversial. It has been showed that starlings generalized regularities instantiated by song motifs such as rattles and warbles (e.g., rattle–warble–rattle–warble representing ABAB) to stimuli composed of novel rattles and warbles. As generalization sequences were formed by elements belonging to the same category, it was unclear whether starlings generalized based on phonetic similarity or whether they really detected the structures (Gentner et al. 2006). A subsequent study by Comins and Gentner (2013) demonstrated that starlings' generalization might be perceptually constrained. The birds could learn sequences of song motifs organized as XXYY or XYXY, but they could not generalize to new exemplars if the novel sounds did not follow natural acoustic categories. Zebra finches also revealed a limited degree of generalization. In a recent study, Chen et al. (2015) trained the finches to differentiate sequences of song elements arranged according to ABA or AAB. All birds recognized the reinforced pattern, whereas none of them could identify it when implemented by novel song items.

As regards to the visual domain, the most important evidence of regularity learning comes from pigeons, Clark's nutcrackers and honeybees. Although the investigations conducted on these models were guided by slightly different research questions than those addressed in previous studies, these works provide evidence supporting the domain generality of these mechanisms. Pigeons (*Columba livia*) are well known for their impressive capacities of visual object recognition, being able to track invariant properties across groups of objects depicted as pictures and to employ these features to form relatively abstract object categories (see Soto and Wasserman 2014, for a review). Recently, same/different abstract concept learning has been demonstrated in the Clark's nutcracker (*Nucifraga columbiana*) (Magnotti et al. 2015; Wright et al. 2016). In addition, also an invertebrate organism such as the honeybee (*Apis mellifera*) is capable of forming a similar same/different concept involving visual stimuli. Through a

matching-to-sample task, the bees learned to match a test stimulus to a training one, on the basis of some visual properties (e.g., vertical and horizontal configurations). The bees then succeeded at transferring the learning to unseen visual stimuli and to different sensory modalities (Giurfa et al. 2001).

Cross-species evidence showed that learning and generalization of regularities are quite strong mechanisms that operate in different domains and organisms. However, little is known about the earliest stages of these processes in the animal kingdom. The vast majority of the above-mentioned studies focused on non-human adult learners, leaving open the question of how the learning of regularities operates at the onset of life. Do newborn organisms, with very limited experience with the sensory world, show similar learning and generalization of patterns to what found in adult learners? In a comparative perspective, this knowledge would shed light on the ontogeny of these cognitive traits and would allow researchers to compare young human and non-human learners, providing new information on cross-species differences in the development of generalization abilities. The first aim of the present study (Exp. 1) is thus to investigate discrimination and generalization of visual regularities in a newborn animal model, the domestic chick (*Gallus gallus*). Newly hatched chicks were reared in a controlled environment in order to restrict their visual experience prior to the experimental sessions, which were run through an operant conditioning procedure. The second aim of this research (Exp. 2) is investigating whether perceptual mechanisms such as the symmetrical versus asymmetrical structure of the pattern, associated with the presence of adjacent repetitions, constrain generalization in non-human species. This research interest arose from the evidence reported earlier, suggesting that a repetition detector mechanism appears to positively affect these mechanisms in humans from the earliest stages of development. We were thus interested in whether the presence/absence of adjacent repetitions plays such a predominant role in the processing of visual patterns in this model and whether this is the case for regularities presented over the spatial domain (stimuli composed of simultaneously presented items) rather than in the temporal domain (sequences of items, as in Gervain et al. 2008; Endress et al. 2005; 2007; Johnson et al. 2009). To this purpose, we fashioned a second experiment aimed at testing comparisons where all patterns were characterized by adjacent repetitions. We hypothesized that if chicks use the presence/absence of repetitions as a strategy to differentiate the stimuli, they will succeed in Exp. 1 but fail in Exp. 2. The domestic chick represents an ideal animal model to answer our research questions for the following reasons. Being a precocial species, chicks display a full behavioral repertoire (Lorenz 1937) and complete maturation of the visual

pathways at birth (Deng and Rogers 1998). For these reasons, chicks can be tested soon after hatching, controlling for the role of experience prior to training and test procedures. As other avian species, chicks are also characterized by a good visual acuity from the very first days of life. All these aspects make vision in chicks the predominant sensory modality (Schmid and Wildsoet 1998). As a consequence, newborn and juvenile chicks have been extensively used in visual perception (e.g., Rosa-Salva et al. 2013) and in cognitive studies (e.g., Rugani et al. 2010; see also Santolin et al. 2015, Versace et al. 2006 for preliminary evidence on regularity learning).

We predicted that newborn chicks should be able to (1) learn simple regularities involving spatially organized strings of items such as AAB versus ABA and (2) recognize the same patterns implemented by novel items (Exp. 1). However, we did not have clear predictions about whether or not spatial configurations containing adjacent repetitions (AAB vs. ABB; AAB vs. BAA) would be better learned than others (Exp. 2). These predictions are also supported by the fact that, belonging to a precocial species, chicks do not extensively rely on parental care as other species do. They must, thus, interact autonomously and appropriately with their environment within a very short time window after hatching. This makes it essential to learn quickly about predictable features of the environment. It is therefore plausible that newly hatched chicks take advantage of regularities and contingencies characterizing relevant objects of the sensory world (e.g., familiar group of hen and siblings, edible items such as food) in order to correctly represent the environment in the most time-efficient manner.

Methods

Experiment 1

In the present experiment, the comparison tested was AAB versus ABA, implemented by spatially organized triplets of simultaneously presented items. A and B do not have specific identities and can be implemented by any given element. AAB displays an asymmetrical structure, being formed by an adjacent repetition of the same token, whereas ABA possesses a non-adjacent repetition that confers a symmetrical structure to the pattern. Two-day-old domestic chicks were trained to find a food reward hidden behind one of two plastic screens, placed in a triangular arena. The rewarded screen displayed a triplet of geometric shapes following, for instance, the AAB pattern, whereas the neutral screen (no food behind it) displayed the same shapes organized in a different pattern (i.e., ABA). Once completed the training, chicks performed a generalization

test with triplets composed of novel shapes, never seen by the animals, but following the training patterns.

Subjects and rearing conditions

Subjects were 8 chicks (*Gallus gallus*), 4 males and 4 females, obtained from a local commercial hatchery (Agricola Berica, Montegalda, Vicenza, Italy) few hours after hatching or as fertilized eggs to be hatched in the laboratory. On arrival, eggs were placed in an MG 70/100 incubator (45 × 58 × 43 cm; width × length × height; 100-egg capacity) until Day 19 of incubation. Temperature was maintained at 37.5 °C and humidity was maintained at 55–60 %, providing standard conditions for optimal incubation. From Day 19, the eggs were placed in a hatchery (60 × 65 × 66 cm; width × length × height) with the same temperature as the incubator, but at a higher humidity, ideal conditions for hatching. The incubator, the hatchery and the hatching room were maintained in complete darkness. After hatching, all the chicks were housed in pairs in standard metal cages (28 × 32 × 40 cm; width × length × height). The rearing room was kept under control for temperature (28–31 °C) and humidity (68 %), and it was constantly illuminated by fluorescent lamps (36 W) located 45 cm above each cage. Food and water were available ad libitum in transparent glass jars (5 cm in diameter, 5 cm in height), placed in the center of the each cage. During the first day of life, chicks were reared in pairs, while familiarizing to the housing environment. In order to get used to visual separations from conspecifics, the animals were divided and housed individually from Day 2 (individual training and testing would be distressful to pair-reared chicks). They were also allowed to eat a few mealworms (*Tenebrio molitor* larvae) in their home cage as this will be used as reinforcement during training. Training lasted from Day 3 to Day 5, when testing took place. At the end of the test phase (no later than Day 6), all chicks were caged in pairs with food and water available ad libitum, and after a few hours they were donated to local farmers.

Stimuli

Training stimuli were 10 triplet pairs, composed by shapes similar to those used in Fiser and Aslin (2002) and arranged according to AAB and ABA. One shape was repeated twice (A element), and the other one was presented only once (B element). Within a pair, the two triplets represented different regularities: one triplet implemented AAB (e.g., circle–circle–cross) and the other triplet implemented ABA (e.g., circle–cross–circle; Fig. 1). All stimuli were spatially arranged in a horizontal row and circumscribed in a black frame (5.15 × 2.18 cm; length × height); thus, the three

elements were simultaneously visible. Each stimulus was printed on a cardboard support and attached on the plastic screen (14 × 18 cm; length × height). The cardboard was approximately aligned with the chick's central visual field to guarantee an appropriate view of the entire stimulus.

The animals were individually trained with only 5 triplet pairs; half of the sample was trained with pairs 1–5 (Supplementary Information—SI, Training Pairs 1), and the other half was trained with pairs 6–10 (SI, Training Pairs 2). Several exemplars of the training patterns were used to minimize the learning of some idiosyncratic regularity based on the perceptual aspects of training triplets (for a discussion, see ten Cate and Okanoya 2012). For 4 chicks (2 males), AAB was the rewarded regularity (S+), whereas ABA represented the neutral pattern (Sn, not associated with food nor punished). For the other 4 animals (2 males), ABA represented S+, whereas AAB was Sn, so that the same stimuli were reinforced for one group of animals, and were neutral for the other group. During the generalization test all chicks were presented with 10 novel triplet pairs, implementing the same structures AAB versus ABA. Crucially, the generalization pairs differed from training pairs in terms of perceptual information (new shape and color of the elements) but not in terms of the underlying structure (Fig. 1, see also SI, Test Pairs).

Apparatus

Training and test were carried out in a quiet experimental room, with temperature and humidity maintained at 25 °C and 70 %, respectively. The apparatus showed in Fig. 1 was used for both experimental sessions, and it consisted of a triangular arena whose walls (100 × 25 cm; length × height) and floor were uniformly lined with white plastic sheets. One of the three vertexes of the arena was the chick's starting point, delimited by a removable clear glass partition (10 × 20 cm; length × height), allowing it to see the inside of the arena. The experimental setting (stimuli position and food reward) was positioned before placing the animal in its starting point. During training, two identical plastic screens depicting the stimuli were positioned symmetrically in front of the starting point (35 cm away from it and 20 cm apart from one another). Behind each screen, a small circular dish (*d* = 3 cm) was located but only that behind the screen representing S+ was baited with food. By placing the dishes behind both screens, the animals could not tell which one was hiding the food until they detoured the correct screen, and looked behind it. The only way to discriminate the screens was thus to recognize the pattern depicted on them. The experimental setting was identical for both training and test, except that during test no food reward was provided to the animals (the dishes behind the screens were both empty).

Fig. 1 The *upper part* of the picture represents the screens depicting two examples of training (*left side*) and generalization (*right side*) pairs. The *lower part* of the picture shows a schematic representation of the apparatus used for training and test (bird's eye view). *Oblique lines* indicate the position of the two screens within the apparatus. Food reinforcement is represented by a schematic illustration of a mealworm inserted in the plastic dish (*the orange dot*). The *blue line* represents the clear glass partition behind which the chick is placed at the beginning of each trial (*starting point*) (color figure online)

Example of a training pair   Example of a generalization pair
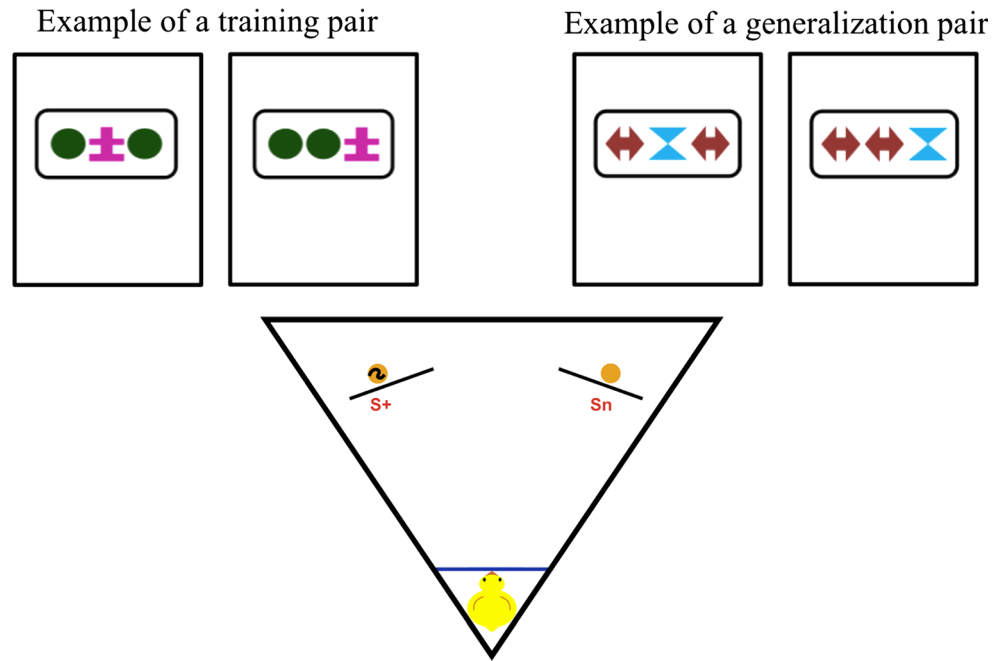
Procedure

To follow, a detailed description of training and test sessions is provided. Each animal was trained and tested individually.

Training On the morning of the Day 3, following 2 h of food deprivation (water was available ad libitum) chicks underwent to a 20 min pre-training session aimed at familiarizing the animals with the experimental environment and learning the detour response. Through a shaping procedure, chicks were trained to go behind a screen to reach the food reinforcement. The screen was blank, without any stimulus depicted in it, and was placed centrally in the arena to reduce the possibility to develop a positional bias, i.e., preference for the left or right side of the apparatus. Training with the first triplet pair (first phase of training) began as soon as the detour response was established. At the beginning of every training trial, the chick was placed behind the glass partition defining the starting point, and it could see both stimuli for ∼10 s. The partition was then removed, and the subject could express a choice for one of the screens. If the chick went behind the S+ screen, it could eat from the baited feeder, and a correct response was scored. In contrast, if the chick chose the Sn screen, the response was scored as incorrect. Importantly, in this latter case the chick was not allowed to reach the food behind S+: The animal was immediately placed back in the starting point. The detour response was considered valid whenever the chick's head was aligned with one of the horizontal margins of the screen or when that point was surpassed (as visible through the camera). Left–right

position of the stimuli in the apparatus followed a semi-random order so that the rewarded triplet never appeared more than two consecutively times in the same position. The learning criterion was established at 17 correct choices out of 20 consecutive trials; once it was reached for the first pair, training of the second pair immediately started (second phase of training). As soon as the subject reached the criterion for the fifth pair, an additional training phase was carried out (shuffle phase). The shuffle phase consisted of a series of trials in which all five training pairs were semi-randomly presented (no consecutive repetitions of a same pair were allowed). This session was aimed at familiarizing chicks with a rapid exposure to several instances of the patterns, similarly to what shall occur in the subsequent generalization test. The shuffle phase ended once the animals reached again the learning criterion (17 correct choices/20 consecutive trials). After this session, chicks spent a 2-h resting period in their home cage before the generalization test started. The number of training trials conducted each day flexibly varied based on the animals' motivation to perform the task. Whenever the chick did not exhibit a detour response within 2 min after being released from the starting point, we assumed that the animal was no longer motivated to continue. The training was then suspended, and the chick was placed back in its home cage without food in order to regain motivation (water was instead available ad libitum). On average chicks completed the training between Day 3 and Day 5.

Generalization test This session included 20 probe trials featuring perceptually new triplet pairs implementing the familiar AAB versus ABA comparison. Probe trials were

not associated with food reward. Over the 20 probe trials, each test pair was presented twice and in a semi-random order so that the same pair never appeared twice in a row. The order of presentation of test pairs was counterbalanced between subjects. The 20 probe trials were alternated with 30 training trials, in which familiar pairs were presented in semi-random order. To avoid response extinction, training trials were reinforced as during training. Chicks' responses in the probe trials were coded online by recording the first screen detoured. The entire sample was also scored off-line by a different coder blind to experimental hypotheses and conditions in order to confirm on-line coding accuracy (for subject #8, only the first 10 test trials were scored off-line because of technical failure related to the video of the last 10 test trials). Results showed high consistency of the two codings (intraclass correlation coefficient, average measure = 0.98; $p < 0.001$).

Data analysis

As regards the training, we calculated the mean number of trials needed to reach the criterion for each proper training phase, i.e., for each triplet pair and for the additional shuffle phase. For the generalization test, the dependent measure analyzed was the number of trials during which chicks chose the triplet resembling the trained pattern (regarded as the correct choice) over 20 probe trials. The number of correct choices has been compared to the chance level (10), using a one-sample two-tailed t test. Individual performances have been also measured using a nonparametric (one tail) Binomial test; a cutoff of 15 correct trials out of 20 has been set, establishing the significance of the test.

Results and discussion

Training On average, chicks needed 204.25 (SD = 49.11) trials to complete the entire training: 181.38 (SD = 48.7) trials to complete the five proper training phases and 24.63 (SD = 6.86) trials to complete the shuffle phase. As noticeable from the graph reported in Fig. 2, the animals needed a lower number of trials to reach the criterion as the training progressed (see SI for further details). This suggests that the learning speed grew within the first three proper training phases, during which trials to criterion decreased importantly from an average of 62 to 23. Afterward, chicks' performance flattened, and the criterion for the fifth triplet pair was reached on average in 24 trials. Clearly, the representation of the pattern started to be generated at the beginning of the training; otherwise, there would not have been such a reduction in the trials to criterion starting from the second triplet pair.

Generalization test At the group level, chicks' choice for the correct pattern was significantly above chance ($t_7 = 11.121$, $p < 0.001$, mean = 16.63, SD = 1.68, effect size $r = 0.97$), (Fig. 3, left column), suggesting that they recognized the familiar regularity even when implemented by unfamiliar items. Individual results showed that 7 out of 8 animals performed significantly above chance scoring 15 or more correct responses out of 20 test trials ($p = 0.02$; see Table 1 for individual data), confirming the result obtained at the group level. These findings revealed chicks' capacity to recognize the trained regularity (both AAB and ABA) and, to generalize to novel exemplars following the same pattern. The variety of stimuli used during training and test decreases the chance that chicks' performance

Fig. 2 Training trend of Exp. 1 and 2. Trials to criterion are represented on the *Y* axis, the five training pairs are represented on the *X* axis
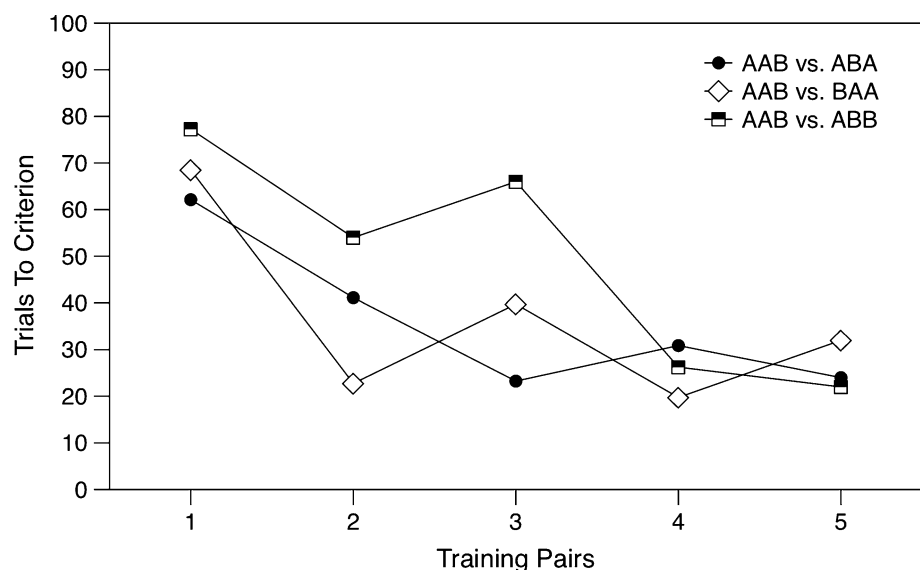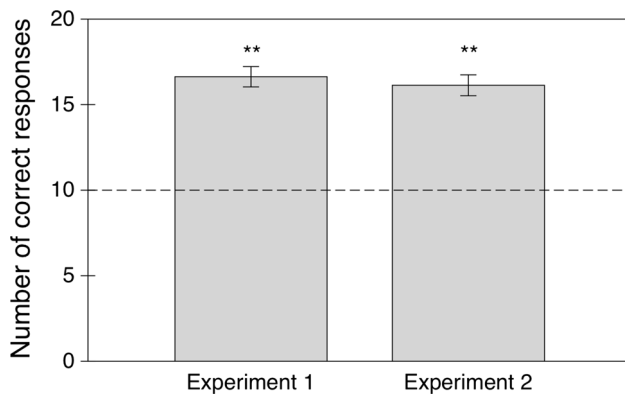
Fig. 3 Number of correct responses over 20 test trials of Exp. 1 (on the *left*) and Exp. 2 (on the *right*). *Error bars* show standard errors of the mean. *Asterisks* indicate significant ($p < 0.001$) departures from chance level (10 correct responses), marked by the *dotted line*

Table 1 Individual performances at the generalization test for Exp. 1 (columns 1 and 2) and Exp. 2 (columns 3 and 4)

Experiment 1 AAB versus ABA	Correct choices/20	Experiment 2	Correct choices/20
Subject 1	18	Subject 1 (AAB vs. ABB)	17
Subject 2	14	Subject 2 (AAB vs. ABB)	16
Subject 3	18	Subject 3 (AAB vs. ABB)	14
Subject 4	17	Subject 4 (AAB vs. ABB)	19
Subject 5	19	Subject 5 (AAB vs. BAA)	14
Subject 6	16	Subject 6 (AAB vs. BAA)	15
Subject 7	15	Subject 7 (AAB vs. BAA)	17
Subject 8	16	Subject 8 (AAB vs. BAA)	17

reflected a response to low-level features of the stimuli (luminance, contrast, color, shape, etc.). Having obtained evidence of chicks' ability to discriminate and generalize AAB and ABA regularities, we wanted to investigate which mechanisms chicks may have used to do so. Chicks could have indeed discriminated the patterns based on the asymmetrical structure of AAB with respect to ABA. As mentioned earlier, this comparison comprises an asymmetrical pattern given by an adjacent repetition of the same token (AAB), and a symmetrical one characterized by a non-adjacent repetition interleaved by a different one (ABA). Therefore, chicks may have easily learned to distinguish the patterns based on this difference. In order to control for this plausible strategy and the role of repetitions, new contrasts were created, in which all patterns included adjacently repeated items.

Experiment 2

All regularities compared in the current experiment comprised adjacent repetitions that gave the triplets an asymmetrical structure. In Condition 1, AAB was compared to ABB; the first pattern was characterized by a repetition placed at the beginning (AA), whereas the second pattern was characterized by a repetition placed at the end (BB). In Condition 2, AAB was instead compared to BAA, again characterized by a reduplicated element located at the final edge of the pattern.

Subjects and rearing conditions

Subjects were a novel group of domestic chicks (4 males and 4 females), obtained from the commercial hatchery Agricola Berica few hours after hatching or as fertilized eggs to be hatched in the laboratory, as specified in Exp. 1. Four animals (2 males) were assigned to Condition 1, and 4 animals were assigned to Condition 2. Rearing conditions were also identical to those illustrated in Exp. 1.

Stimuli

New stimuli displaying AAB, ABB and BAA were created. Additionally, new shapes and colors were employed to construct training and test triplets improving the stimuli design (see SI for the whole set of stimuli). Each shape could be inscribed in an invisible square of 2×2 cm, and the colors employed were four complementary shades: red and orange (warm hues), and green and blue (cold hues), (e.g., Jones et al. 2001). Previous findings showed that chicks can differentiate these four colors and categorize them based on perceptual similarities, similar to what humans do (Ham and Osorio 2007). A pilot study with 4 chicks confirmed that the animals were capable of learning and generalizing ABA versus AAB implemented by these new shapes and colors (similarly to what obtained in Exp. 1, chicks' average performance at test was of 15.5/20 correct trials). Triplet pairs were printed on photographic paper and controlled for the absence of UV radiations with a spectrophotometer. In order to avoid generalization based on textural properties of the stimuli, color contingencies between training and generalization stimuli were reversed. One of the warm hues (red or orange) was assigned to the A items implementing the training set, and one of the cold hues (blue or green) to the A items implementing test stimuli. As in Exp. 1, triplets were formed by simultaneously visible shapes, spatially organized in a horizontal row and circumscribed in a black frame.

Apparatus and procedure

Apparatus and procedure used in training and test sessions were identical to Exp. 1. In order to confirm on-line coding accuracy, the entire sample was scored off-line by a second coder, blind to experimental hypotheses and conditions.

Results showed high consistency between coders (Intraclass correlation coefficient, average measure = 0.98; $p < 0.001$).

Data analysis

Dependent measure and statistical analyses were identical to Exp. 1. In addition, a Mann–Whitney U test was performed to compare the two experimental groups (Condition 1 and Condition 2),[1] and an independent samples t test was operated to draw a final comparison between experiments.

Results

Training To complete the entire training, chicks assigned to Condition 1 needed an overall average of 275.25 (SD = 90.26) trials: 245.5 (SD = 85.03) trials to complete the five proper training phases, and 29.75 (SD = 10.43) trials to complete the shuffle phase. Chicks assigned to Condition 2 instead needed an overall average of 196.75 (SD = 48.57) trials: 182.75 (SD = 36.31) trials to complete the five proper training phases and 20.25 (SD = 2.06) trials to complete the shuffle phase. As for Exp. 1, the animals needed a lower number of trials to reach the criterion as the training progressed (see Fig. 2 and SI for further details). Chicks seemed to need a larger number of trials than in Exp. 1 probably because patterns employed here were not discriminable based on the presence of adjacent repetitions and symmetry. This could have influenced the performance especially at the beginning of the learning phase, when chicks had to discover pattern structures for the first time. Anyway, when considered across the five training phases, the number of trials to criterion followed a similar decreasing trend with respect to Exp. 1, since the fifth phase required on average only 27 trials.

Generalization test A Mann–Whitney U performed on the number of correct responses over 20 probe trials revealed a non-significant difference between conditions ($U = 9.500$; $p = 0.686$); thus, data of the two groups were pooled together and considered as a single group for subsequent analyses. The mean of correct choices operated during test phase revealed that chicks chose the triplet resembling the reinforced regularity significantly above chance (16.13 of correct test trials over 20; $t_7 = 10.032$, $p < 0.001$, SD = 1.72, effect size $r = 0.97$), (Fig. 3, right column). The analysis of individual performance also confirmed this result; in both conditions, 3 out of 4 subjects performed significantly above chance level scoring 15 or

more correct responses out of 20 test trials ($p = 0.02$; Table 1).

A comparison between experiments revealed no differences (Exp. 1: mean 16.63, SD = 1.68; Exp. 2: mean = 16.13, SD = 1.72; $t_{(7)} = 0.586$, $p = 0.567$), supporting the idea that chicks can extract visual patterns independently of the presence/absence of adjacent reduplications of tokens in spatially arranged displays of simultaneously presented elements. Further discussion of this evidence will be provided in the next section.

Results of Exp. 2 have some implications for chicks' learning abilities. During training of Condition 1 (AAB vs. ABB), the rewarded regularity could have been learned by detecting the different *identity* of the repeated element within pairs (AA vs. BB). For example, for a given training pair, chicks could have just learned that the reinforced pattern was the stimulus where the red cross was repeated as opposed to that where the repetition involved the green hourglass. However, as our test stimuli were formed by new colors and forms, this strategy would not have been sufficient to support generalization. Thus, in Condition 1, chicks spontaneously encoded the trained discrimination in a way that could support generalization, even though another strategy (*identity*) was available at training. Moreover, in Condition 2 (AAB vs. BAA) we could exclude that, during training, the patterns were distinguished solely based on the *identity* of the repetition. Following the above-mentioned example, subjects could not have learned that the reward was associated with the reduplicated red cross since that shape was repeated in both triplets composing a pair. In fact, results revealed that chicks distinguished AAB when compared to BAA (and vice versa), indicating that they can discriminate structures characterized by identical adjacent repetitions placed in different positions within the stimuli. It is worth noting that this evidence confirms the results obtained in Exp. 1, which showed for the first time that chicks can recognize the training pattern even when instantiated by novel elements. Results of Exp. 2 give further support to this initial evidence, demonstrating that chicks can do that even in the most challenging contrast that comprises identical repetitions in both triplets forming a pair.

General discussion

In two experiments it has been showed that newborn chicks can detect regularities implemented by triplets of simultaneously visible elements. Generalization is revealed by chicks' capacity to respond differentially to pattern-violating and pattern-following test triplets formed by novel elements. This evidence suggests that chicks are able to abstract away from the surface information of the stimuli

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[1] This non-parametric test was applied given the small sample size of the two groups.

(forms and colors of the training stimuli), picking up underlying structures.

Interestingly, the Boolean map theory of human visual attention, which has been recently put forward, could in principle account for our data. According to the Boolean principles, the visual system forms a spatial representation of the input by selecting one feature *per* dimension among all possible dimensions characterizing a visual scene (color, location, orientation, etc.). In a Boolean map, the selected feature is mapped along the spatial dimension identifying two complementary regions: the one containing the selected feature, and the area covering the rest of the space (Huang and Pashler 2007; Huang et al. 2007; Huang 2010). It can be argued that chicks' performance can be explained on the basis of Boolean maps, one created to cover the two repeated objects (As) and another one formed to cover the non-repeated element (B). This theory appears to represent an alternative explanation for our results, which does not imply the extraction of abstract regularities. Disentangling these two possibilities exceeds the aim of the present work; however, future studies could address this issue by manipulating the spatial arrangement of triplet elements between training and test phases. If chicks' generalization is based on abstract regularities, it should be robust to this manipulation, which should, on the contrary, destroy performance based on the generation of Boolean maps.

Based on the results provided by Exp. 2, chicks seem to equally generalize spatial patterns that are not discriminable on the basis of perceptual symmetry/asymmetry of their structures and presence of adjacent reduplications. This indicates that generalization does not prioritize regularities with a certain spatial structure or with repetitions, in this species. In a comparative perspective, this evidence is particularly interesting since human data revealed that adjacent repetitions do enhance generalization, at least when regularities have to be detected over a temporal dimension. Neonates in fact, prefer repetition-based temporal regularities being able to distinguish ABB but not ABA compared with random (ABC) stimuli (Gervain et al. 2008). This finding has been interpreted as the result of a repetition detector mechanism that might facilitate subsequent speech perception abilities. Gervain et al. (2008) pointed out that neonates are consistently bombarded by linguistic information and that this input is marked by contiguous repetitions of words and sentences (see also, Ferguson 1983). Furthermore, infants' first attempts to speech production are characterized by repeated elements (babbling and first words). According to this view, the neonate brain appears to be tuned to the structure of the sensory information, to guarantee adequate processing and representation. Our findings may be interpreted within a similar framework. Ecologically speaking, there might be no need for chicks to being able to master reduplicated elements in a visual scene. This might be due to the nature of chicks' typical visual environment, which probably does not comprise such a great number of identical objects adjacently repeated. The underlying assumption is that the chick brain is predisposed to detect the structure of the sensory input which may not comprise repetitions. An interesting explanation for the discrepancy between our results and those of human infants could be associated with the ecology of each species, assuming that the functional domain profiting from regularity learning can also influence the role of different features of the stimuli in this process. That is to say that differences between species can be linked to predispositions to learn species-specific behaviors. Learning regularities from spatially arranged visual stimuli might support several natural adaptive behaviors in chicks such as spatial navigation, food localization and identification of relevant social "objects" through filial imprinting. Considering the functional domain profiting from this learning process, cross-species differences can be interpreted in the light of the role played by different features of the stimuli (e.g., adjacent vs. non-adjacent repetitions) in that given functional domain. For instance, infants and juvenile songbirds are vocal learners, identifying and arranging vocal elements in new sequences during a learning phase (babbling, for infants; sub-song, for songbirds). Therefore, one can expect features that are prominent in these kinds of sensorimotor learning contexts (e.g., adjacent repetitions), to have a crucial role in the performance of infants and songbirds. On the contrary, the same features may not be so relevant for other contexts, such as spatial navigation. Thus, species such as chicks, for which regularity learning might have an adaptive role in these other contexts, can be expected to be less influenced in their performance by the presence of adjacent reduplications.

On the other hand, it has to be noted that our task involved the processing of spatial regularities formed by simultaneously presented items. At present, in the human infant literature, there is no evidence that adjacent repetitions provide any advantage when patterns are implemented in the spatial domain (e.g., Saffran et al. 2007). Therefore, the effect of adjacent reduplications could be altered by modality of presentation (temporal vs. spatial, see below for further discussion) as well as by differences in the ecology of diverse species.

The current research provides the first evidence of generalization of regularities presented as strings of visual elements in a newborn animal model. Even though the learning was obtained through a conditioning procedure

(whereas generalization was unreinforced), it is plausible that chicks are predisposed to track relations between objects characterizing the visual environment within the first days of life. Controlled-reared studies indeed imply that abilities exhibited by young animals are likely to be the result of early predispositions (Vallortigara 2012). The present results conform to similar capacities revealed by species whose predominant sensory modality is vision (e.g., pigeons), broadening the ecological value of regularity learning and generalization as mechanisms that allow efficient processing of complex environments, in order to rapidly detect their components.

Future investigations will be devoted to explore whether this process is constrained by other perceptual aspects of the stimuli. As mentioned in Introduction, modality–specificity represents one of the aspects that broadly influence learning and generalization of regularities, at least in humans. It has been suggested that acoustic regularities are preferentially learned when presented as a temporal sequence of sounds, whereas visual patterns are better acquired when elements are simultaneously visible (Saffran 2001, 2002; Gebhart et al. 2009). This is due to the nature of the sensory input, mostly characterized by spatially organized rather than temporally presented visual objects. According to this view, infants tested in previous studies may have failed to generalize some visual patterns when implemented by temporal sequences (Johnson et al. 2009), and succeeded when similar patterns were displayed as strings of simultaneously visible objects (Saffran et al. 2007). By presenting items one at a time, it may be possible to observe interesting differences in the generalization capacity exhibited by our model. Is generalization prevented when visual objects are presented as a temporal sequence? Moreover, differences in sensitivity to repetitions placed in diverse positions within the sequence may be found, as shown by infants in the visual domain (see Johnson et al. 2009 for further information about early vs. late repetitions), and by adults in the linguistic domain (Endress et al. 2005). The use of sequentially presented visual patterns would provide new insights about the role of perceptual constraints on the learning process, investigating whether some regularities would be easier to learn than others in this species. This would have important implications about the extent to which the computational principles serving human learning are similarly constrained across species.

Compliance with ethical standards

References

Brown R (1973) A first language: the early stages. Harvard U. Press, Cambridge

Chen J, van Rossum D, ten Cate C (2015) Artificial grammar learning in zebra finches and human adults: XYX versus XXY. Anim Cogn 18:151–164

Comins JA, Gentner TQ (2013) Perceptual categories enable pattern generalization in songbirds. Cognition 128:113–118

de La Mora DM, Toro JM (2013) Rule learning over consonants and vowels in a non-human animal. Cognition 126:307–312

Dawson C, Gerken L (2009) From domain-generality to domain-specificity: 4-month-olds learn an abstract repetition rule in music that 7-month-olds do not. Cognition 111:378–382

Deng C, Rogers LJ (1998) Bilaterally projecting neurons in the two visual pathways of chicks. Brain Res 794:281–290

Endress AD, Scholl BJ, Mehler J (2005) The role of salience in the extraction of algebraic rules. J Exp Psychol Gen 134:406–419

Endress AD, Dehaene-Lambertz G, Mehler J (2007) Perceptual constraints and the learnability of simple grammars. Cognition 105:577–614

Ferguson CA (1983) Reduplication in child phonology. J Child Lang 10:239–243

Fiser J, Aslin RN (2002) Statistical learning of new visual feature combinations by infants. Proc Natl Acad Sci USA 99:15822–15826

Frost R, Armstrong BC, Siegelman N, Christiansen MH (2015) Domain generality versus modality specificity: the paradox of statistical learning. Trends Cogn Sci 19:117–125

Gebhart AL, Newport EL, Aslin RN (2009) Statistical learning of adjacent and nonadjacent dependencies among nonlinguistic sounds. Psychon Bull Rev 16:486–490

Gentner TQ, Fenn KM, Margoliash D, Nusbaum HC (2006) Recursive syntactic pattern learning by songbirds. Nature 440:1204–1207

Gervain J, Macagno F, Cogoi S, Peña M, Mehler J (2008) The neonate brain detects speech structure. Proc Natl Acad Sci USA 105:14222–14227

Giurfa M, Zhang S, Jenett A, Menzel R, Srinivasan MV (2001) The concepts of 'sameness' and 'difference' in an insect. Nature 410:930–933

Ham AD, Osorio D (2007) Colour preferences and colour vision in poultry chicks. Proc R Soc Lond B Biol Sci 274:1941–1948

Hauser MD, Glynn D (2009) Can free-ranging rhesus monkeys (*Macaca mulatta*) extract artificially created rules comprised of natural vocalizations? J Comp Psychol 123:161

Huang L (2010) What is the unit of visual attention? Object for selection, but Boolean map for access. J Exp Psychol Gen 139:162

Huang L, Pashler H (2007) A Boolean map theory of visual attention. Psychol Rev 114:599

Huang L, Treisman A, Pashler H (2007) Characterizing the limits of human visual awareness. Science 317:823–825

Johnson SP, Fernandes KJ, Frank MC, Kirkham N, Marcus GF, Rabagliati H, Slemmer JA (2009) Abstract rule-learning for visual sequences in 8- and 11-month-olds. Infancy 14:2–18

Jones CD, Osorio D, Baddeley RJ (2001) Colour categorization by domestic chicks. Proc R Soc Lond B Biol Sci 268:2077–2084

Lorenz KZ (1937) The companion in the bird's world. The Auk 245-273

Magnotti JF, Katz JS, Wright AA, Kelly DM (2015) Superior abstract-concept learning by Clark's nutcrackers (*Nucifraga columbiana*). Biol Lett 11:20150148

Marcus GF, Vijayan S, Bandi Rao S, Vishton PM (1999) Rule learning in 7-month-old infants. Science 283:77–80

Marcus GF, Fernandes KJ, Johnson SP (2007) Infant rule learning facilitated by speech. Psychol Sci 18:387–391

Murphy RA, Mondragon E, Murphy VA (2008) Rule learning by rats. Science 319:1849–1851

Rosa-Salva O, Rugani R, Cavazzana A, Regolin L, Vallortigara G (2013) Perception of the Ebbinghaus illusion in four-day-old domestic chicks (*Gallus gallus*). Anim Cogn 16:895–906

Rugani R, Kelly DM, Szelest I, Regolin L, Vallortigara G (2010) Is it only humans that count from left to right? Biol Lett 63:290–292

Saffran JR (2001) The use of predictive dependencies in language learning. J Mem Lang 44:493–515

Saffran JR (2002) Constraints on statistical language learning. J Mem Lang 47:172–196

Saffran JR, Thiessen ED (2007) Domain-general learning capacities. In: Hoff E, Shatz M (ed) Handbook of language development, vol 2007. Blackwell, Cambridge, pp 68–86

Saffran JR, Pollak SD, Seibel RL, Shkolnik A (2007) Dog is a dog is a dog: infant rule learning is not specific to language. Cognition 105:669–680

Santolin C, Salva OR, Vallortigara G, Regolin L (2015) Unsupervised visual statistical learning in the newborn chick (*Gallus gallus*). Perception 44:13

Schmid KL, Wildsoet CF (1998) Assessment of visual acuity and contrast sensitivity in the chick using an optokinetic nystagmus paradigm. Vis Res 38:2629–2634

Soto FA, Wasserman EA (2014) Mechanisms of object recognition: what we have learned from pigeons. Front Neural Circuits 8:122

ten Cate C, Okanoya K (2012) Revisiting the syntactic abilities of non-human animals: natural vocalizations and artificial grammar learning. Proc R Soc Lond B Biol Sci 367:1984–1994

Thiessen ED (2012) Effects of inter- and intra-modal redundancy on infants' rule learning. Lang Learn Dev 8:197–214

Vallortigara G (2012) Core knowledge of object, number, and geometry: a comparative and neural approach. Cogn Neuropsychol 29:213–236

Versace E, Regolin L, Vallortigara G (2006) Emergence of grammar as revealed by visual imprinting in newly-hatched chicks. In: The evolution of language. Proceedings of the 6th international conference (EVOLANG6)

Wright AA, Magnotti JF, Katz JS, Leonard K, Kelly DM (2016) Concept learning set-size functions for Clark's nutcrackers. J Exp Anal Behav 105:76–84