

1 Article

2 Spontaneous learning of visual structures in domestic 3 chicks

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11 **Simple Summary:** Our aim is to investigate the recognition of the structure of multi-element
12 configurations, one mechanism that supports communicative functions in different species.
13 Cognitive mechanisms involved in this ability might not have evolved specifically for
14 communicative use, but derive from other functions. Thus, it is crucial to study these abilities in
15 species that are not vocal learners and with stimuli from other modalities. We know already that
16 domestic chicks can learn the temporal statistical structure of sequences of visual shapes, however
17 their abilities to encode the spatial structure of visual patterns (configurations composed of multiple
18 visual elements presented simultaneously side-by-side) is much less known. Using filial imprinting
19 learning, we showed that chicks spontaneously recognize the structure of their imprinting stimulus,
20 preferring it to one composed of the same elements in different configurations. Moreover, we found
21 that in their affiliative responses chicks give priority to information located at the stimulus edges, a
22 phenomenon that was so far observed only with temporal sequences. This first evidence of a
23 spontaneous edge bias with spatial stimuli further stresses the importance of studying similarities
24 and differences between the processing of linguistic and non-linguistic stimuli and of stimuli
25 presented in various sensory modalities.

26 **Abstract:** Effective communication crucially depends on the ability to produce and recognise
27 structured signals, as apparent in language and birdsong. Although it is not clear to what extent
28 similar syntactic-like abilities can be identified in other animals, recently we reported that domestic
29 chicks can learn abstract visual patterns and the statistical structure defined by a temporal sequence
30 of visual shapes. However, little is known about chicks' ability to process spatial/positional
31 information from visual configurations. Here, we used filial imprinting as an unsupervised learning
32 mechanism to study spontaneous encoding of the structure of a configuration of different shapes.
33 After being exposed to a triplet of shapes (ABC or CAB), chicks could discriminate those triplets
34 from a permutation of the same shapes in different order (CAB or ABC), revealing a sensitivity to
35 the spatial arrangement of the elements. When tested with a fragment taken from the imprinting
36 triplet that followed the familiar adjacency-relationships (AB or BC) vs. one in which the shapes
37 maintained their position with respect to the stimulus edges (AC), chicks revealed a preference for
38 the configuration with familiar edge elements, showing an edge bias previously found only with
39 temporal sequences.

40 **Keywords:** domestic chicks; *Gallus gallus*; imprinting; implicit learning; statistical learning; sequence
41 learning; spatial/visual configurations; positional information

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44 1. Introduction

45 The ability to detect regularities in the sensory input is crucial for communication. For instance,
46 human language and birdsong require the processing of complex structures of auditory stimuli [1–
47 3]. However, some cognitive abilities underlying these communicative adaptations might not have
48 evolved *de novo* to support them. Rather, they might have been co-opted from other cognitive
49 mechanisms used for visual processing or for learning action sequences, including “statistical
50 learning” (general mechanisms that enable the acquisition of structured information and the
51 detection of regularities in the sensory input [1–3], reviewed in [4–6]).

52 To understand the origins of communicative systems, we must investigate these mechanisms
53 from a comparative perspective in non-vocal learning animals and non-linguistic tasks (e.g., with
54 visual stimuli structured in space; see [4]). This allows to identify mechanisms that are common to
55 various sensory modalities and species and others that are not (e.g. [7]; see also [6]). Here we follow
56 this approach and study implicit learning of spatially defined visual sequences in young domestic
57 chicks.

58 Statistical learning of temporal sequences has been implicated in birdsong and in human
59 language (reviewed in [6]). The first step to process linguistic input is to parse the continuous speech
60 stream into words [8]. This can be done by recognizing the frequency with which groups of sounds
61 occur in a given order, an ability shown by human infants and adults [9–12]. However, this ability is
62 not restricted to linguistic or even auditory input [13–15] and is shown also by non-human animals
63 [3,16–20]. Likewise, other abilities necessary to the evolution and acquisition of linguistic syntax,
64 investigated by studies that test humans’ and animals’ capability to recognize various kinds of
65 regularities in the temporal order of a sequence of elements [21–27], are not restricted to language
66 [28–30] or to humans [23,25,31–43]. However, the use of linguistic inputs and communicative signals
67 facilitates some of these tasks for human infants [44,45].

68 These abilities seem to be supported by general mechanisms that can process different types of
69 stimuli, such as auditory linguistic stimuli, visual patterns or touches (even though they are
70 modulated and constrained differently in the way they operate across modalities and domains
71 [4,6,46]). For example, visual statistical learning has also been investigated for the processing of
72 spatial information (i.e. the spatial relationship between multiple visual elements simultaneously
73 presented in different spatial positions). These studies showed that both human adults and infants
74 spontaneously learn the properties of spatially defined visual patterns [15,47,48], which helps infants
75 with the initial structuring of the visual environment [49]. Similar evidence has been reported also in
76 adult animals, using conditioning procedures [50]. Spatial configurations of visual elements have also
77 been used also to study the capacity to create abstract representations that can be applied to new
78 exemplars, both in human infants [51] and in non-human animals [52–57].

79 Infants’ ability to recognize spatially defined series (linear arrangements) of visual elements was
80 studied with a method similar to that used in the present work. Sequences of three audio-visual
81 elements (conventionally labelled as A, B and C) were organized both by their temporal and spatial
82 order, according to the sequence ABC or CAB. Sensitivity to the spatiotemporal order of the elements
83 has been demonstrated by showing, for example that infants habituated to the stimulus ABC and
84 discriminated it from CAB [58,59].

85 To understand the development of linguistic and visual processing, it is important to study
86 which kind of learning can develop in an unsupervised way, encoding the structure of complex
87 inputs without direct feedback or reinforcement [60]. Chicks of precocial species [61,62] are
88 particularly advantageous on this regard, thanks to the learning phenomenon of filial imprinting [63]:
89 they learn, by mere exposure and without reinforcement, the features of the conspicuous objects they
90 are exposed to, and they restrict their approach and affiliative responses to those objects (reviewed
91 in [64–66]). Although, in the chicks’ natural setting the imprinting stimulus will be a single object (the
92 mother hen), there is increasing evidence that imprinting might apply also to a grouped configuration
93 of elements (e.g. [18,42,53,57]).

94 In the current study, we used domestic chicks to take advantage of this powerful form of
95 spontaneous learning. Domestic chicks present also other advantages to investigate the fundamental

96 mechanisms at the basis of communicative functions, since they are the precocial offspring of non-
97 vocal learners: the encoding of environmental regularities may show some differences between vocal
98 learners and non-vocal learners and precocial and altricial species [6].

99 Based on these advantages, in a recent paper using filial imprinting we investigated chicks'
100 spontaneous capability to recognize the structure underlying a stream of visual stimuli, revealing a
101 remarkable capacity to recognize the temporal order of pairs of shapes [18]. In contrast, little is known
102 about chicks' capacity to spontaneously encode the spatial relationship between multiple visual
103 elements all simultaneously present in the visual scene, although this ability has been extensively
104 investigated in human infants and adults [15,47,58].

105 Importantly, temporal and spatial information require somewhat different types of learning.
106 While spatial configurations of visual elements reduce constraints due to working memory
107 limitations, they also allow for the encoding of different structural properties than temporal
108 sequences. For example, in the study of Santolin et al. [18], the only predictable features were those
109 defining the ordered pairs ("shape A will always be followed by shape B"). In contrast, when
110 simultaneously visible elements maintain fixed reciprocal spatial positions (such as in [58]), subjects
111 can potentially encode a higher variety of properties. For example, given the ABC sequence, an
112 organism could potentially encode the stimulus structure in a multitude of ways. For example, one
113 could represent which shapes are adjacent to each other (A and B are adjacent, A and C are not), the
114 distance dependencies between them (A will be followed by C, with an interleaving element
115 separating them), the left-right order of the elements (A is the first element from the left, B the second
116 etc.), the position of the elements in relation to reference points such as the stimulus edges (A and C
117 are next to the stimulus outer edges, B is not), and so on. Thus, it is unclear if and how learning
118 abilities observed for temporal sequences will translate in this context that offers richer structural
119 information to encode. Previous studies showed the ability of chicks to learn the color configurations
120 of their imprinting stimuli, abstracting the general pattern characterising them [42], but the positional
121 components of these abilities, and the role of shape configurations is unknown. The aim of the present
122 paper is to make a first step in this direction, by investigating young chicks' spontaneous learning of
123 the structural properties of a configuration of visual shapes simultaneously presented in a fixed
124 spatial order [58]. Although we used moving stimuli to attract the animals' attention (imprinting is
125 more effective with moving stimuli), all the elements of each stimulus were always simultaneously
126 visible on the screen, therefore the structure of each stimulus was defined by the relative spatial
127 positions of the elements and not by their temporal order of appearance.

128 2. General Materials and methods

129 2.1. Subjects and rearing conditions

130 Only female chicks (*Gallus gallus domesticus*) of the Aviagen ROSS 308 breed were used, since a
131 pilot experiment showed that females but not males exhibit consistent preferences with these stimuli.
132 It has been previously shown that the imprinting preference can be a sexually dimorphic trait in
133 chicks, potentially masking recognition effects in one of the two genders [57,67]. Hence, to simplify
134 the experimental design and reduce the number of tested subjects we decided to focus only on
135 females. In this strain, sex can be determined using the wing feathers dimorphism.

136 Eggs were obtained by a local commercial hatchery (Agricola Berica, Montegalda, VI, Italy) and
137 were kept in the darkness, inside a MG 140/200 Rural LCD EVO incubator until day 18 of embryonic
138 development. During this incubation stage the temperature was of 37.7° C and humidity was 40-45%.
139 On the 18th day of incubation, the eggs were moved to an MG 316H EVO hatchery, where they were
140 still kept in darkness and at the same temperature, but with 60-70% humidity. Chicks hatched at the
141 21st day of incubation were individually moved from the dark incubator to the housing facilities.
142 Females were immediately housed in individual cages according to the experimental conditions.
143 Males and all individuals after the test were housed in groups. Water and food were available *ad*
144 *libitum* until chicks were donated to local farmers. All the animals were maintained at 29° C, 68%
145 humidity, under a natural 14:10 light:dark cycle.

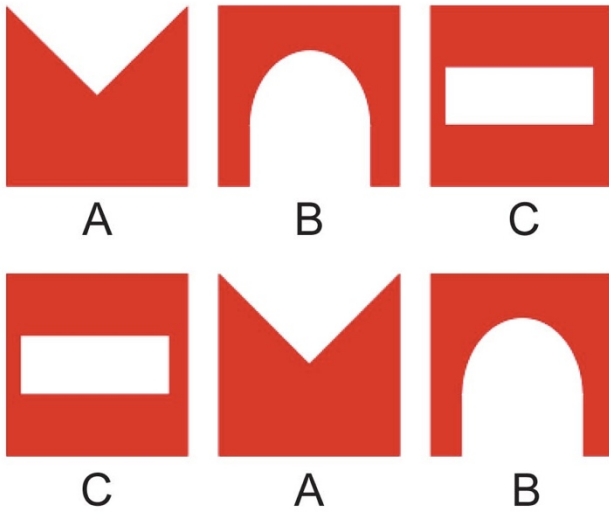
146 Female chicks were housed individually with food and water available *ad libitum* in the
147 imprinting cages, made of black plastic (30 x 38 x 33 cm, *w x l x h*) with a monitor (17", 60 Hz) mounted
148 on the front wall (protected by a thin layer of plexiglass), that was used to play the imprinting
149 stimulus (see below). During the imprinting phase, chicks could not see each other, since they were
150 housed individually in black plastic cages that separated them visually from the other animals (this
151 was done in order to prevent visual imprinting on conspecifics, which could have impaired learning
152 about the artificial imprinting object).

153 2.2. *Imprinting and test stimuli*

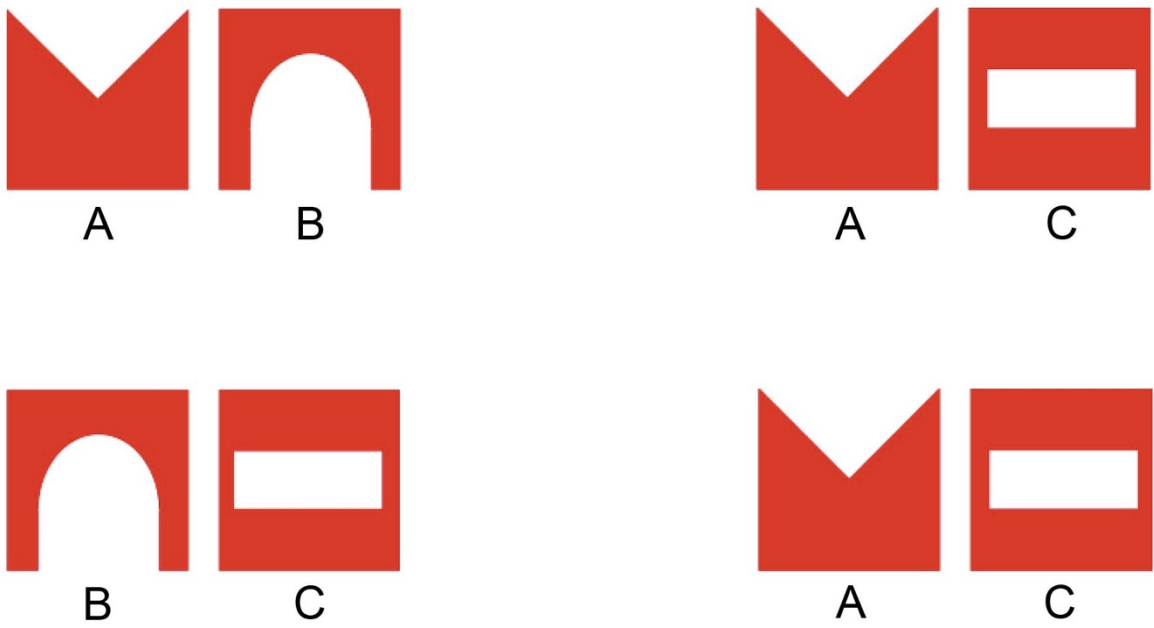
154 During the imprinting phase, the monitor present in each cage played the imprinting stimulus
155 continuously for 14 h each day (during the night, when the lights of the animal house were off, a
156 black screen substituted the imprinting stimulus).

157 The imprinting stimulus was a configuration of three different red shapes, over a white
158 background (see Fig. 1). Each shape used to create the imprinting stimulus fitted in a 3.5 cm square
159 (inter elements distances were of 0.65 cm). The stimulus was presented at a height of 3.2 cm from the
160 lower margin of the screen.

a



b



c



162

Figure 1.

163 The triplets used as imprinting and test stimuli in Exp. 1, ABC and CAB (a); the two pairs of
 164 fragments used as test stimuli in Exp. 2, AB vs. AC, and BC vs. AC (b); the two fragments used as test
 165 stimuli in Exp. 3, AC vs. CA (c).

166 For the entire imprinting phase, each animal was exposed to the same shapes presented in the
 167 same configuration (e.g. only “ABC” or only “CAB”).

168 Since movement elicits imprinting responses [68], the stimulus moved horizontally on the screen
 169 (covering approx. 24 cm), taking 10 s to run an entire cycle from right to left and back, in line with
 170 the procedure used in [57]. Thus, the absolute spatial position of each element on the screen varied.

171 During the test, chicks were faced with the choice between a familiar stimulus and a novel one
 172 (in Exp. 1), or between two stimuli that resembled the imprinting stimulus in different respects or to
 173 a different degree (Exp. 2 and 3). In all cases, both stimuli were composed of shapes taken from the
 174 familiar imprinting stimulus, but differed in the spatial arrangement of the shapes. For example, in
 175 Exp. 1 (Fig. 1a), in the familiar stimulus the spatial ordering of the inner elements respected that of
 176 the imprinting object, whereas in the novel stimulus the familiar elements were presented in an
 177 unfamiliar spatial configuration. In Exp. 2 (Fig. 1 b), chicks were presented with fragments of the
 178 imprinting stimulus that either respected the between-elements adjacency-relationships of the
 179 imprinting stimulus (shapes that were close to each other in the imprinting stimulus were close to
 180 each other also in the fragment), or in which the elements maintain their position with respect to the
 181 stimulus edges (shapes that were at the edge of the imprinting stimulus were at the edge also in the
 182 fragment). Finally, in Exp. 3 (Fig. 1c) chicks were faced with two test fragments, one of which
 183 respected the left-right orientation of the shapes in the imprinting stimulus, while the other violated
 184 it.

185 2.3. Test procedure

186 On day 7 after hatching (after 6 days of imprinting), chicks were tested for their preference to
 187 walk towards each of the test stimuli. Before the test, chicks were food deprived for about 2 h to
 188 increase their arousal. Moreover, 20 mins before the beginning of the test, an opaque black partition
 189 was used to occlude the screen in the rearing cage, preventing visual contact with the imprinting
 190 object until the moment of the test. This was done to increase motivation to approach stimuli
 191 resembling the imprinting object during the test, following the procedure used in [18,69].

192 For the test a running wheel (33 cm diameter, 12 cm wide) was used. The running wheel was
 193 suspended 2 cm above the floor at the center of a longitudinal runway (46 x 150 x 45 cm, $w \times l \times h$)
 194 whose interior surface was uniformly lined with black plastic. At the two ends of the runway, two
 195 video screens identical to those used for imprinting showed the test stimuli. The side of presentation
 196 of the two test stimuli was counterbalanced between subjects to rule out the effect of potential
 197 environmental asymmetries.

198 At the beginning of the test, chicks were individually placed in the center of the running wheel,
 199 facing one of the lateral walls, so that they could see both stimuli on the opposite sides of the
 200 apparatus. During the test, that lasted 20 mins, the chick could walk towards either of the two stimuli.
 201 An automated counter measured the distance run (in cm) by the chick in each direction for the whole
 202 test duration. The test session was recorded by a videocamera placed above the apparatus.

203 2.4. Data Analysis

204 For each chick, we analysed the preference for the familiar stimulus (or for the stimulus with the
 205 familiar adjacency relationships in Exp. 2, and with the familiar left-right orientation in Exp. 3). This
 206 was expressed as a proportion of the distance walked towards the two kinds of stimuli, computed
 207 according to the formula:

$$208 \frac{\text{Distance walked towards the familiar stimulus}}{\text{Overall distance walked in both directions}}$$

209 Values of the proportion range from 0 (walking only towards the unfamiliar stimulus) to 1
210 (walking only towards the familiar stimulus). A value of 0.5 corresponds to the chance level. To verify
211 if chicks discriminated between the two stimuli, values of the proportion of preference were
212 compared to chance level by a one-sample two-tailed t-test. Wherever required, in order to compare
213 experimental groups we ran independent samples t-tests. To further interpret non-significant results,
214 in Exp. 3 we ran non-overlapping hypotheses (NOH) Bayes factor (BF) analysis for the one-sample t-
215 test case (scale r on the effect size = 0.707 [70]).

216 2.5. Ethical statement

217 All applicable European and Italian guidelines for the care and use of animals were followed.
218 All procedures performed were in accordance with the ethical standards of the University of Trento,
219 where the study was conducted. The study has been approved by the research ethics committee of
220 the University of Trento (OPBA) and by the Italian Ministry of Health (permit number 1138/2015 PR,
221 987/2017 PR).

222 3. Experiment 1

223 The aim of this experiment was to verify if chicks imprinted on a series of three shapes would
224 spontaneously encode the spatial relationships between these elements, or whether this form of
225 implicit learning by exposure, would result only in encoding of other less subtle properties of the
226 imprinting stimulus (such as, for example, its colour or the shapes of the individual elements).

227 In order to verify whether chicks can recognise the internal spatial relationships characterising
228 the familiar imprinting stimulus, we tested if chicks would show a preference for the familiar
229 stimulus over an unfamiliar permutation of the same elements. This stimulus was composed of
230 identical shapes as the familiar imprinting object, arranged in a different order.

231 3.1. Subjects

232 The sample of this experiment consisted of 64 female chicks.

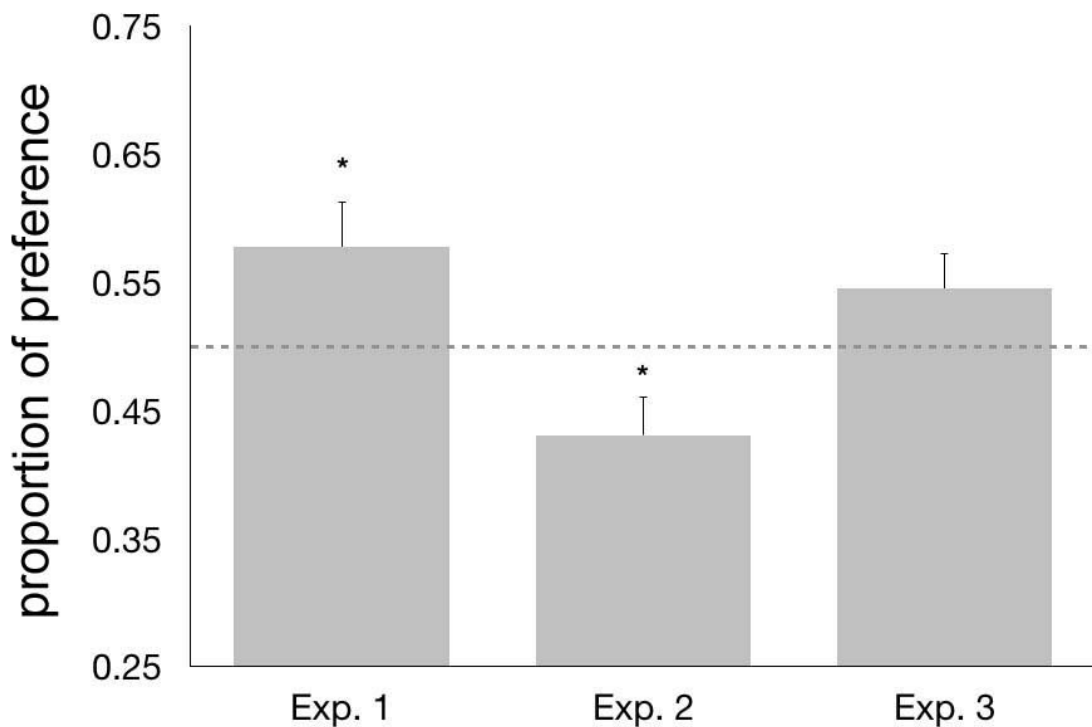
233 3.2. Imprinting and test stimuli

234 Chicks were imprinted on either one of two series of three shapes (designated here by the letters
235 A, B and C, respectively). Both imprinting triplets were composed of the same three shapes and
236 differed only by the order in which the shapes were arranged: ABC and CAB. Half of the chicks were
237 imprinted on ABC, while the remaining subjects were imprinted on the triplet CAB (Fig. 1a).

238 At test, all chicks were presented with the choice between these two triplets, one of which was
239 the familiar imprinting object and the other could be differentiated from it only by the spatial
240 arrangement of the elements (in this design, for part of the chicks, ABC is the familiar triplet and CAB
241 represents the unfamiliar permutation of shapes, and viceversa for the rest of the chicks).

242 3.3. Results and discussion

243 No difference was apparent ($t_{55.547} = -0.708$, $p = 0.482$; based on the Levene's test, equal variances
244 could not be assumed and the appropriate correction was applied) in the preference for the familiar
245 triplet over its permutation between chicks imprinted on ABC (mean = 0.553, s.e.m. = 0.057) and those
246 imprinted on the CAB triplet (mean = 0.603, s.e.m. = 0.040). The two groups were thus joined and the
247 data from all the subjects were treated together for further analyses. In the overall sample, we
248 observed a significant preference for approaching the familiar triplet over the unfamiliar permutation
249 (mean = 0.578, s.e.m. = 0.035, $t_{63} = 2.247$, $p = 0.028$, Fig. 2).



250
251

Figure 2.

252 From left to right, the columns represent the average values of the preference (proportion of
253 distance walked) for the familiar imprinting triplet (Exp. 1), for the bigram (AB or BC) that respects
254 the between-elements adjacency-relationships (Exp. 2) and for the AC bigram (Exp. 3). Error bars
255 represent the standard error of the mean (s.e.m.). The dotted line indicates the chance level (0.5), and
256 asterisks represent significant departures from chance ($p < 0.05$).

257 This indicates that, after imprinting on a series of three shapes that maintain their reciprocal
258 spatial positions, chicks can discriminate two triplets that differ only in the spatial arrangement of
259 their composing elements. An identical preference for the familiar configuration was observed for
260 chicks imprinted on ABC and on CAB. Thus, we can say that chicks not only can discriminate patterns
261 based on the element order, but more specifically that they encoded this property during the
262 exposure phase and used it to recognise and preferentially approach the familiar imprinting stimulus
263 at test.

264 This result sets the base for the subsequent experiments described in this paper, among other
265 things, by providing us with clear expectations about the direction of the preference that chicks will
266 reveal in this context, which is in this case a preference for familiarity, the most frequent result in
267 female chicks (e.g., [57,67], but see [18,42] see also [71–73] for a theoretical discussion).

268 Overall, it is clear that in order to succeed in this test, chicks must have developed a mental
269 representation of the spatial arrangement of the elements composing the familiar imprinting
270 sequence. However, what is still unclear is which aspects of the familiar stimulus are encoded by this
271 representation, since the two triplets, ABC and CAB, differ in many potentially relevant properties.
272 The following experiments were thus devoted to verify which of these properties are spontaneously
273 encoded by chicks during imprinting.

274 4. Experiment 2

275 With this experiment we wanted to further investigate chicks' capability to encode the spatial
276 arrangement of the elements composing their imprinting stimulus. The discrimination between ABC
277 and CAB, revealed by Exp. 1, could, in fact, be based on a number of different properties that allow
278 the discrimination of the two triplets, any (or any combination) of which could have been used by
279 chicks. For example, chicks imprinted on the ABC triplet could have encoded the adjacency-
280 relationships between the triplet elements (A is adjacent to B, B is adjacent to C, A and C are not
281 adjacent). Alternatively, chicks could have encoded the position of the elements in relation to
282 reference points such as the stimulus margins, rather than relative to each other (e.g., A and C are
283 located at the triplet edges, B is not). In this second experiment we thus tested if chicks would
284 recognise as more familiar a fragment taken from the imprinting triplet, that follows the between-
285 elements adjacency-relationships of the familiar stimulus (e.g. AB), over a fragment that violates
286 those adjacency-relationships, but in which the elements maintain their position with respect to the
287 stimulus edges (e.g. AC).

288 4.1. Subjects

289 The sample of this experiment consisted of 60 female chicks.

290 4.2. Imprinting and test stimuli

291 Chicks were imprinted on the stimulus ABC, identical to the one used in the previous
292 experiment. During the test, chicks were presented with the choice between two stimuli, each
293 containing two of the elements of the imprinting triplet. One of those bigrams was a fragment taken
294 either from the left or from the right side the imprinting triplet (AB or BC, respectively). The other
295 bigram was always AC, composed of the two edge elements of the imprinting stimulus. Half of the
296 chicks were tested for their preference between AB (taken from the left side of the imprinting triplet)
297 and AC, while the remaining chicks were tested with BC (right side of the imprinting stimulus) and
298 AC (Fig. 1c).

299 While AC violates the between-elements adjacency-relationships that define the imprinting
300 stimulus, it resembles the imprinting stimulus in other ways. For example, as it is the case also for
301 ABC, its left and right edges are marked by the elements A and C, respectively. On the contrary, the
302 other two test bigrams, AB and BC, do not resemble the imprinting stimulus in this respect, since
303 they both present B at one of their edges (the right and left edge respectively).

304 Differently from the previous experiment, here none of the test stimuli was perfectly identical to
305 the imprinting triplet. In this case the preference of the chicks was represented as the proportion of
306 distance run towards the bigram that respects the between-elements adjacency-relationships (AB or
307 BC), computed according to the same general formula described above.

308 4.3. Results and discussion

309 No significant difference ($t_{58}=-1.478$, $p=0.145$) appeared between the behaviour of chicks tested
310 with the AB vs. AC pair (mean=0.386; s.e.m.=0.048) and those tested for their preference between BC
311 and AC (mean= 0.475; s.e.m.= 0.034). We thus joined these two groups for further analyses. Overall,
312 chicks showed a significant preference for approaching the AC stimulus, as revealed by the fact that
313 the average preference (proportion of the distance run) for the adjacency-relationships bigrams was
314 below chance level ($t_{59}=-2.281$, $p=0.026$; mean=0.431, s.e.m.=0.03, Fig. 2).

315 This indicates discrimination of the two different kinds of bigrams by the chicks, revealing the
316 presence of a flexible representation of the imprinting stimulus, which allows chicks to recognise
317 some of its properties also when presented in fragments of a different length than the original
318 imprinting object. More specifically, in this case, chicks favoured the bigram that was consistent with
319 the structure of the imprinting object with regards to the position of the elements in relation to the
320 stimulus edges, over fragments that respected the between-elements adjacency-relationships present
321 in the original imprinting pattern. In fact, only the stimulus AC contains at its own edges the two

322 elements that are located at the edges of the imprinting triplet ABC. We can thus conclude that, when
323 presented with a spatial configuration of simultaneously presented visual elements, chicks
324 spontaneously encode the position of its elements in relation to the stimulus edges, rather than in
325 relation to each other.

326 A tendency to prioritise encoding of the sequence edges over information embedded within it
327 has already been reported in the literature for humans and other animals, although only for
328 temporally defined sequences ([7,35,43,74–76] see also the General Discussion). Here, for the first
329 time, we found a similar effect with spatially defined series of simultaneously presented elements.

330 However, it is still unclear to which level of detail chicks encode the information on elements
331 located at the edges of the stimulus. The next experiment was aimed to answering this question.

332 5. Experiment 3

333 Exp. 2 revealed that chicks spontaneously prioritise information about the items located at the
334 stimulus edges over information about adjacency relationships between the elements. The aim of the
335 current experiment was to further investigate the kind of information that is encoded by chicks
336 concerning the elements that are located at the sequence edges. In particular, we wanted to verify
337 whether chicks would encode only the identity of the elements that mark the two sequence edges or
338 whether they could also differentiate between the left and the right sequence edge. To do so, we
339 tested chicks' choice between a bigram that resembled the imprinting triplet (ABC) in the left-right
340 orientation of the two edge elements (AC) and another one in which the two elements exchanged
341 their respective left-right position (CA).

342 5.1 Subjects

343 The sample of this experiment consisted of 76 female chicks.

344 5.2. Imprinting and test stimuli

345 As in the previous experiment, chicks were imprinted on the pattern ABC. During the test, chicks
346 had to choose between approaching the bigram AC or the bigram CA (Fig. 1c). Both the test stimuli
347 contained, at their edges, the two elements that marked the edges of the familiar imprinting stimulus.
348 The two stimuli differed only in the left-right ordering of the edge elements, which respected the
349 orientation of the imprinting stimulus for AC, but not for CA.

350 In this experiment, we thus computed the preference of the chicks for AC (again calculated as
351 the proportion of distance run towards this stimulus), which was used as a dependent variable.

352 5.3. Results and discussion

353 No significant preference was found for the fragment AC, characterised by the familiar left-right
354 orientation, over CA ($t_{75}=-1.592$, $p=0.116$, $\text{mean}=0.545$, $\text{s.e.m.}=0.028$, Fig. 2). Even though the average
355 level of preference seemed to suggest a trend in this direction, variability of the sample was too high,
356 preventing this result from reaching statistical significance. We are thus unable to confirm that chicks
357 spontaneously encode and/or recognise the left-right ordering of the edge elements of the imprinting
358 triplet. Based on this result, we thus suggest that chicks could be sensitive to the fact that these
359 elements should be specifically located at the edges of the sequence, without however discriminating
360 between the left and the right edge. Non-significant results are notoriously of difficult interpretation
361 and should be treated with caution. In order to strengthen our interpretation of these data, we tested
362 this null result by Non-overlapping Hypotheses (NOH) Bayes factors, obtaining a scaled JZS Bayes
363 Factor = 2.374, which favors the null hypothesis indicating a more than two-fold higher chance that
364 the null hypothesis is correct. Therefore, the data support the hypothesis that there is no difference
365 between chicks' observed performance in this experiment and the value of 0.5, expected in the
366 absence of any preference between the two test stimuli. This could be in line with other evidence
367 suggesting that the discrimination of stimuli which have been mirrored across the left-right axis is a

368 particularly difficult task for animals, more so than the discrimination of stimuli which have been
369 mirrored across the vertical axis [77–82].

370 6. General Discussion

371 The aim of this work was to investigate implicit learning of visual configurations, using filial
372 imprinting to verify if domestic chicks spontaneously recognize structural properties of spatial multi-
373 element arrays. Previous studies showed the ability of precocial bird species to learn structural
374 features of imprinting objects, such as the presence of identical/different components [53,57]. Moreover
375 sophisticated abilities had already been found in chicks for temporal visual sequences, revealing
376 recognition of the order of appearance of shape pairs [18].

377 Similar to what had already been done with human infants [58], here we used patterns
378 composed of three visual elements simultaneously presented in a fixed spatial configuration to
379 investigate whether chicks recognized the structure of the imprinting stimulus. The stimuli used in
380 the current study contain different structural properties, most of which were not available in the
381 continuous temporal stream of shapes used by Santolin et al. [18]. Here we provide the first evidence
382 of spontaneous encoding of spatial relationships between multiple elements all simultaneously
383 present in the visual scene in this animal model. These results can open the way to further
384 investigations of sensitivity to the structures of visuo-spatial displays in chicks, bridging the gap to
385 the literature on human adults and infants [15,47,58]. The current paper confirms that imprinting
386 learning can go beyond the perceptual features of a single object to those of a grouped configuration
387 of elements [18,53,57], a necessary prerequisite for this kind of investigation. In addition, our results
388 show that, although differences in shapes are less salient than color differences in imprinting [83], the
389 shape can be taken into account to discriminate between stimuli (discrimination based on positional
390 properties had been previously observed by [42] with manipulations of the color of imprinting
391 stimuli).

392 More specifically, we showed, for the first time, that chicks spontaneously learn at least some
393 information on the reciprocal positions of the visual elements since they discriminated stimuli such
394 as ABC and CAB (Exp. 1). As the stimuli were constantly moving along the screen, chicks could not
395 rely on the absolute position of items on the screen, but must have encoded relational spatial
396 information to succeed in the task. Chicks were also capable of recognizing familiar properties of the
397 imprinting stimulus from smaller fragments of it. In fact, after imprinting on ABC they discriminated
398 AC from AB or BC (Exp. 2), indicating some degree of generalization. In this context, chicks'
399 preference for AC suggests that they prioritise information regarding the elements placed at the edges
400 of the imprinting stimulus. However, chicks failed to discriminate between AC and CA, which
401 differed only in the left-right orientation of edge elements (Exp. 3). Thus, chicks seemed not to
402 distinguish between the left and the right margin of the stimulus. This could be due to the intrinsic
403 difficulty of discriminating stimuli mirrored across the vertical axis [77–82], or to the specific
404 bidirectional motion pattern that we employed in the present study. Our stimuli, in fact, constantly
405 alternated rightward and leftward movements. This way, in the ABC triplet, the leading end was
406 represented equally often by its rightmost or its leftmost element (A and C). Since young organisms
407 seem to be predisposed to map moving agents identifying their leading and trailing ends in relation
408 to their motion direction (i.e. to represent stimuli in terms of “head” and “tail”) [84], the motion
409 pattern we employed might have impaired the differentiation of the left-right extremities of the
410 stimuli. Another explanation for the lack of preference observed between AC and CA could be that
411 chicks might have interpreted them as representing the same object when viewed from the two
412 different viewpoints. In fact, since A and C are symmetrical shapes, CA is the perfect mirrored image
413 of AC (Fig. 1c). Thus, if one imagines the AC stimulus as if it were painted on a translucent sheet, it
414 should look identical to the CA stimulus to an observer standing behind the sheet (i.e. looking at it
415 from the other side of the sheet). Future studies could test this possibility by using non-symmetrical
416 shapes to compose the stimuli.

417 Based on the results of Exp. 2 and 3, we could hypothesise that chicks learn only the identity of
418 the elements located at the edges, without encoding any positional information (meaning that their

419 representation of the imprinting object could be summarized as “the imprinting stimulus contains
420 both the elements A and C”, which would support the preference for AC over AB and BC). However,
421 the results of Exp. 1 allow us to exclude this possibility, since in this case both test stimuli (ABC and
422 CAB) comprised all the three elements. Thus, the most parsimonious interpretation of the results is
423 that chicks represent at least some positional information about the elements located at the stimulus
424 edges, even though they do not discriminate between left and right margins. Chicks could learn that
425 A and C should be located at the edge of the stimulus (ignoring their left-right orientation). Future
426 studies should investigate whether chicks learn additional information from the imprinting stimulus
427 (e.g. information about the central element, B).

428 Even though in the first two experiments chicks clearly revealed a significant preference for one
429 of the two test stimuli, that preference was not very large (e.g. average proportion of preference of
430 about 0.58 in the first experiment). This is consistent with what often reported in the literature on
431 spontaneous social responses and filial imprinting, e.g. [42,57,85–87], probably due to the
432 spontaneous nature of this learning task. Moreover, in the natural environment a multitude of visual,
433 acoustical and olfactory features can be used to discriminate the familiar imprinting object from an
434 unfamiliar one. On the contrary, here (as in the studies cited above), the two stimuli can be
435 distinguished only by the ordering of their elements, making the difference between them harder to
436 detect.

437 A most interesting result of the current study is chicks’ tendency to privilege information on the
438 elements located at the edges of the imprinting stimulus. To the best of our knowledge, this is the
439 first study to find this effect for spatial configurations of simultaneously presented elements, either
440 in humans or non-human animals. Similar results had been previously reported for non-human
441 primates with temporal acoustical sequences [35,43], in line with the importance of marginal elements
442 in syntax acquisition. This mechanism seemed to be shared at least between primates, suggesting that
443 it did not evolve specifically to support language, but it could rather reflect general functional
444 constraints for the processing of temporal auditory sequences, then co-opted by linguistic and
445 communicative functions. Studies with operant training in pigeons seemed to suggest that similar
446 mechanisms might extend also to avian species and to temporally-organized sequences of visual
447 elements (that have to be selected in a given sequence by the animals) ([74–76], but see [88] for a
448 different interpretation). However, until now, no evidence had ever been reported of an edge-
449 advantage on avian species using unsupervised learning paradigms comparable to those employed
450 with human and non-human primates [35,43]. Moreover, this represents also the first evidence of an
451 edge advantage for purely spatial configurations, without temporal-components defining their
452 structure. This is particularly relevant, because it may indicate a higher level of generality of the
453 underlying mechanism than originally thought, not only in terms of the phylogenetic distance
454 between species, but also extending it beyond the acoustic modality, to the visual processing of
455 patterns articulated over space, rather than over time. However, existing evidence suggests that
456 general learning mechanisms might be modulated by factors like the sensory modality (e.g., [7]), as
457 well as the distribution of regularities over space or over time and the specific learning task (e.g.
458 imprinting vs. associative learning), making it crucial to experimentally verify assumptions on the
459 presence of general underlying mechanisms.

460 7. Conclusions

461 To conclude, this work represents the first step in the investigation of unsupervised learning of
462 spatial configurations of visual elements that differ only in shape, in a non-vocal learning model
463 characterized by precocial development and a wide phylogenetic distance from the human species.
464 These are all features that, in the most recent literature, are considered important to the
465 understanding of the evolutionary history of the mechanisms underlying the development of
466 communicative adaptations, such as human language and birdsong.

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479 REFERENCES

- 480 1. Fehér, O.; Ljubičić, I.; Suzuki, K.; Okanoya, K.; Tchernichovski, O. Statistical learning in songbirds: from
481 self-tutoring to song culture. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **2017**, *372*, 20160053,
482 doi:10.1098/rstb.2016.0053.
- 483 2. Menyhart, O.; Kolodny, O.; Goldstein, M. H.; DeVogd, T. J.; Edelman, S. Juvenile zebra finches learn the
484 underlying structural regularities of their fathers’ song. *Front. Psychol.* **2015**, *6*, 571,
485 doi:10.3389/fpsyg.2015.00571.
- 486 3. Takahasi, M.; Yamada, H.; Okanoya, K. Statistical and prosodic cues for song segmentation learning by
487 bengalese finches (*Lonchura striata var. domestica*). *Ethology* **2010**, *116*, 481–489, doi:10.1111/j.1439-
488 0310.2010.01772.x.
- 489 4. Armstrong, B. C.; Frost, R.; Christiansen, M. H. The long road of statistical learning research: past, present
490 and future. *Philos. Trans. R. Soc. B Biol. Sci.* **2017**, *372*, 20160047, doi:10.1098/rstb.2016.0047.
- 491 5. Dehaene, S.; Meyniel, F.; Wacongne, C.; Wang, L.; Pallier, C. The neural representation of sequences: from
492 transition probabilities to algebraic patterns and linguistic trees. *Neuron* **2015**, *88*, 2–19,
493 doi:10.1016/j.neuron.2015.09.019.
- 494 6. Santolin, C.; Saffran, J. R. Constraints on statistical learning across species. *Trends Cogn. Sci.* **2018**, *22*, 52–
495 63, doi:10.1016/j.tics.2017.10.003.
- 496 7. Conway, C. M.; Christiansen, M. H. Modality-constrained statistical learning of tactile, visual, and auditory
497 sequences. *J. Exp. Psychol. Learn. Mem. Cogn.* **2005**, *31*, 24–39, doi:10.1037/0278-7393.31.1.24.
- 498 8. Cole, R. A.; Jakimik, J.; Cooper, W. E. Segmenting speech into words. *J. Acoust. Soc. Am.* **1980**, *67*, 1323–1332.
- 499 9. Morgan, J. L.; Meier, R. P.; Newport, E. L. Structural packaging in the input to language learning:
500 contributions of prosodic and morphological marking of phrases to the acquisition of language. *Cognit.*
501 *Psychol.* **1987**, *19*, 498–550, doi:10.1016/0010-0285(87)90017-X.
- 502 10. Pelucchi, B.; Hay, J. F.; Saffran, J. R. Statistical learning in a natural language by 8-month-old infants. *Child*
503 *Dev.* **2009**, *80*, 674–685, doi:10.1111/j.1467-8624.2009.01290.x.
- 504 11. Saffran, J. R.; Newport, E. L.; Aslin, R. N.; Tunick, R. A.; Barrueco, S. Incidental language learning: listening
505 (and learning) out of the corner of your ear. *Psychol. Sci.* **1997**, *8*, 101–105, doi:10.1111/j.1467-
506 9280.1997.tb00690.x.
- 507 12. Saffran, J. R.; Aslin, R. N.; Newport, E. L. Statistical learning by 8-month-old infants. *Science* **1996**, *274*, 1926–
508 1928, doi:10.1126/science.274.5294.1926.
- 509 13. Bulf, H.; Johnson, S. P.; Valenza, E. Visual statistical learning in the newborn infant. *Cognition* **2011**, *121*,
510 127–132, doi:10.1016/j.cognition.2011.06.010.
- 511 14. Kirkham, N. Z.; Slemmer, J. A.; Johnson, S. P. Visual statistical learning in infancy: evidence for a domain
512 general learning mechanism. *Cognition* **2002**, *83*, B35–42, doi:10.1016/S0010-0277(02)00004-5.
- 513 15. Fiser, J.; Aslin, R. N. Statistical learning of new visual feature combinations by infants. *Proc. Natl. Acad. Sci.*
514 *U. S. A.* **2002**, *99*, 15822–15826, doi:10.1073/pnas.232472899.

- 515 16. Toro, J. M.; Trobalón, J. B. Statistical computations over a speech stream in a rodent. *Percept. Psychophys.*
516 **2005**, *67*, 867–875.
- 517 17. Meyer, T.; Olson, C. R. Statistical learning of visual transitions in monkey inferotemporal cortex. *Proc. Natl.*
518 *Acad. Sci. U. S. A.* **2011**, *108*, 19401–19406, doi:10.1073/pnas.1112895108.
- 519 18. Santolin, C.; Rosa-Salva, O.; Vallortigara, G.; Regolin, L. Unsupervised statistical learning in newly hatched
520 chicks. *Curr. Biol. CB* **2016**, *26*, R1218–R1220, doi:10.1016/j.cub.2016.10.011.
- 521 19. Chen, J.; Ten Cate, C. Zebra finches can use positional and transitional cues to distinguish vocal element
522 strings. *Behav. Processes* **2015**, *117*, 29–34, doi:10.1016/j.beproc.2014.09.004.
- 523 20. Hauser, M. D.; Newport, E. L.; Aslin, R. N. Segmentation of the speech stream in a non-human primate:
524 statistical learning in cotton-top tamarins. *Cognition* **2001**, *78*, B53–64, doi:10.1016/S0010-0277(00)00132-3.
- 525 21. Fitch, W. T.; Friederici, A. D. Artificial grammar learning meets formal language theory: an overview.
526 *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **2012**, *367*, 1933–1955, doi:10.1098/rstb.2012.0103.
- 527 22. Brown, R. *A first language: the early stages*; Harvard University Press.; Cambridge, Massachusetts, 1973; Vol.
528 1.
- 529 23. Gomez, R. L.; Gerken, L. Artificial grammar learning by 1-year-olds leads to specific and abstract
530 knowledge. *Cognition* **1999**, *70*, 109–135, doi:10.1016/S0010-0277(99)00003-7.
- 531 24. Marcus, G. F.; Vijayan, S.; Bandi Rao, S.; Vishton, P. M. Rule learning by seven-month-old infants. *Science*
532 **1999**, *283*, 77–80, doi:10.1126/science.283.5398.77.
- 533 25. Saffran, J.; Hauser, M.; Seibel, R.; Kapfhamer, J.; Tsao, F.; Cushman, F. Grammatical pattern learning by
534 human infants and cotton-top tamarin monkeys. *Cognition* **2008**, *107*, 479–500,
535 doi:10.1016/j.cognition.2007.10.010.
- 536 26. Saffran, J. R. The use of predictive dependencies in language learning. *J. Mem. Lang.* **2001**, *44*, 493–515,
537 doi:10.1006/jmla.2000.2759.
- 538 27. Saffran, J. R. Constraints on statistical language learning. *J. Mem. Lang.* **2002**, *47*, 172–196,
539 doi:10.1006/jmla.2001.2839.
- 540 28. Ferguson, B.; Franconeri, S. L.; Waxman, S. R. Very young infants learn abstract rules in the visual modality.
541 *PloS One* **2018**, *13*, e0190185, doi:10.1371/journal.pone.0190185.
- 542 29. Gebhart, A. L.; Newport, E. L.; Aslin, R. N. Statistical learning of adjacent and nonadjacent dependencies
543 among nonlinguistic sounds. *Psychon. Bull. Rev.* **2009**, *16*, 486–490, doi:10.3758/PBR.16.3.486.
- 544 30. Johnson, S. P.; Fernandes, K. J.; Frank, M. C.; Kirkham, N.; Marcus, G.; Rabagliati, H.; Slemmer, J. A.
545 Abstract rule learning for visual sequences in 8- and 11-month-olds. *Infancy Off. J. Int. Soc. Infant Stud.* **2009**,
546 *14*, 2–18, doi:10.1080/15250000802569611.
- 547 31. Abe, K.; Watanabe, D. Songbirds possess the spontaneous ability to discriminate syntactic rules. *Nat.*
548 *Neurosci.* **2011**, *14*, 1067–1074, doi:10.1038/nn.2869.
- 549 32. Chen, J.; van Rossum, D.; ten Cate, C. Artificial grammar learning in zebra finches and human adults:
550 XYX versus XXY. *Anim. Cogn.* **2015**, *18*, 151–164, doi:10.1007/s10071-014-0786-4.
- 551 33. Comins, J. A.; Gentner, T. Q. Perceptual categories enable pattern generalization in songbirds. *Cognition*
552 **2013**, *128*, 113–118, doi:10.1016/j.cognition.2013.03.014.
- 553 34. de la Mora, D. M.; Toro, J. M. Rule learning over consonants and vowels in a non-human animal. *Cognition*
554 **2013**, *126*, 307–312, doi:10.1016/j.cognition.2012.09.015.
- 555 35. Endress, A. D.; Carden, S.; Versace, E.; Hauser, M. D. The apes' edge: positional learning in chimpanzees
556 and humans. *Anim. Cogn.* **2010**, *13*, 483–495, doi:10.1007/s10071-009-0299-8.
- 557 36. Gentner, T. Q.; Fenn, K. M.; Margoliash, D.; Nusbaum, H. C. Recursive syntactic pattern learning by
558 songbirds. *Nature* **2006**, *440*, 1204–1207, doi:10.1038/nature04675.
- 559 37. Hauser, M. D.; Glynn, D. Can free-ranging rhesus monkeys (*Macaca mulatta*) extract artificially created rules
560 comprised of natural vocalizations? *J. Comp. Psychol.* **2009**, *123*, 161–167, doi:10.1037/a0015584.
- 561 38. Murphy, R. A.; Mondragón, E.; Murphy, V. A. Rule learning by rats. *Science* **2008**, *319*, 1849–1851,
562 doi:10.1126/science.1151564.
- 563 39. Neiworth, J. J.; London, J. M.; Flynn, M. J.; Rupert, D. D.; Alldritt, O.; Hyde, C. Artificial grammar learning
564 in tamarins (*Saguinus oedipus*) in varying stimulus contexts. *J. Comp. Psychol.* **2017**, *131*, 128–138,
565 doi:10.1037/com0000066.
- 566 40. Spierings, M. J.; Ten Cate, C. Budgerigars and zebra finches differ in how they generalize in an artificial
567 grammar learning experiment. *Proc. Natl. Acad. Sci. U. S. A.* **2016**, *113*, E3977–3984,
568 doi:10.1073/pnas.1600483113.

- 569 41. van Heijningen, C. A. A.; Chen, J.; van Laatum, I.; van der Hulst, B.; ten Cate, C. Rule learning by zebra
570 finches in an artificial grammar learning task: which rule? *Anim. Cogn.* **2013**, *16*, 165–175,
571 doi:10.1007/s10071-012-0559-x.
- 572 42. Versace, E.; Regolin, L.; Vallortigara, G. Emergence of grammar as revealed by visual imprinting in newly-
573 hatched chicks. In *The Evolution of Language*; WORLD SCIENTIFIC, 2006; pp. 457–458 ISBN 978-981-256-
574 656-0.
- 575 43. Wilson, B.; Slater, H.; Kikuchi, Y.; Milne, A. E.; Marslen-Wilson, W. D.; Smith, K.; Petkov, C. I. Auditory
576 artificial grammar learning in macaque and marmoset monkeys. *J. Neurosci. Off. J. Soc. Neurosci.* **2013**, *33*,
577 18825–18835, doi:10.1523/JNEUROSCI.2414-13.2013.
- 578 44. Ferguson, B.; Lew-Williams, C. Communicative signals support abstract rule learning by 7-month-old
579 infants. *Sci. Rep.* **2016**, *6*, 25434, doi:10.1038/srep25434.
- 580 45. Marcus, G. F.; Fernandes, K. J.; Johnson, S. P. Infant rule learning facilitated by speech. *Psychol. Sci.* **2007**,
581 *18*, 387–391, doi:10.1111/j.1467-9280.2007.01910.x.
- 582 46. Frost, R.; Armstrong, B. C.; Siegelman, N.; Christiansen, M. H. Domain generality versus modality
583 specificity: the paradox of statistical learning. *Trends Cogn. Sci.* **2015**, *19*, 117–125,
584 doi:10.1016/j.tics.2014.12.010.
- 585 47. Fiser, J.; Aslin, R. N. Unsupervised statistical learning of higher-order spatial structures from visual scenes.
586 *Psychol. Sci.* **2001**, *12*, 499–504, doi:10.1111/1467-9280.00392.
- 587 48. Fiser, J.; Aslin, R. N. Encoding multielement scenes: statistical learning of visual feature hierarchies. *J. Exp.*
588 *Psychol. Gen.* **2005**, *134*, 521–537, doi:10.1037/0096-3445.134.4.521.
- 589 49. Gibson, E. J. *Principles of perceptual learning and development*; Appleton-Century-Crofts: New-York, 1969.
- 590 50. Goujon, A.; Fagot, J. Learning of spatial statistics in nonhuman primates: contextual cueing in baboons
591 (*Papio papio*). *Behav. Brain Res.* **2013**, *247*, 101–109, doi:10.1016/j.bbr.2013.03.004.
- 592 51. Saffran, J. R.; Pollak, S. D.; Seibel, R. L.; Shkolnik, A. Dog is a dog is a dog: Infant rule learning is not specific
593 to language. *Cognition* **2007**, *105*, 669–680, doi:10.1016/j.cognition.2006.11.004.
- 594 52. Grainger, J.; Dufau, S.; Montant, M.; Ziegler, J. C.; Fagot, J. Orthographic processing in baboons (*Papio*
595 *papio*). *Science* **2012**, *336*, 245–248, doi:10.1126/science.1218152.
- 596 53. Martinho, A.; Kacelnik, A. Ducklings imprint on the relational concept of “same or different.” *Science* **2016**,
597 *353*, 286–288, doi:10.1126/science.aaf4247.
- 598 54. Santolin, C.; Rosa-Salva, O.; Regolin, L.; Vallortigara, G. Generalization of visual regularities in newly
599 hatched chicks (*Gallus gallus*). *Anim. Cogn.* **2016**, *19*, 1007–1017, doi:10.1007/s10071-016-1005-2.
- 600 55. Sonnweber, R.; Ravignani, A.; Fitch, W. T. Non-adjacent visual dependency learning in chimpanzees. *Anim.*
601 *Cogn.* **2015**, *18*, 733–745, doi:10.1007/s10071-015-0840-x.
- 602 56. Stobbe, N.; Westphal-Fitch, G.; Aust, U.; Fitch, W. T. Visual artificial grammar learning: comparative
603 research on humans, kea (*Nestor notabilis*) and pigeons (*Columba livia*). *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*
604 **2012**, *367*, 1995–2006, doi:10.1098/rstb.2012.0096.
- 605 57. Versace, E.; Spierings, M. J.; Caffini, M.; Ten Cate, C.; Vallortigara, G. Spontaneous generalization of
606 abstract multimodal patterns in young domestic chicks. *Anim. Cogn.* **2017**, *20*, 521–529, doi:10.1007/s10071-
607 017-1079-5.
- 608 58. Lewkowicz, D. J. Perception of serial order in infants. *Dev. Sci.* **2004**, *7*, 175–184, doi: 10.1111/j.1467-
609 7687.2004.00336.x.
- 610 59. Lewkowicz, D. J. Serial order processing in human infants and the role of multisensory redundancy. *Cogn.*
611 *Process.* **2004**, *5*, 113–122, doi:10.1007/s10339-004-0015-1.
- 612 60. ten Cate, C.; Okanoya, K. Revisiting the syntactic abilities of non-human animals: natural vocalizations and
613 artificial grammar learning. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **2012**, *367*, 1984–1994,
614 doi:10.1098/rstb.2012.0055.
- 615 61. Versace, E. Precocial. In *Encyclopedia of Animal Cognition and Behavior*; Vonk, J., Shackelford, T., Eds.;
616 Springer International Publishing: Cham, 2017; pp. 1–3 ISBN 978-3-319-47829-6.
- 617 62. Versace, E.; Vallortigara, G. Origins of knowledge: insights from precocial species. *Front. Behav. Neurosci.*
618 **2015**, *9*, 338, doi:10.3389/fnbeh.2015.00338.
- 619 63. Vallortigara, G.; Versace, E. Filial Imprinting. In *Encyclopedia of Animal Cognition and Behavior*; Vonk, J.,
620 Shackelford, T., Eds.; Springer International Publishing: Cham, 2018; pp. 1–4 ISBN 978-3-319-47829-6.
- 621 64. Bateson, P. P. G. The characteristics and context of imprinting. *Biol. Rev. Camb. Philos. Soc.* **1966**, *41*, 177–
622 211.

- 623 65. Bolhuis, J. J. Mechanisms of avian imprinting: a review. *Biol. Rev. Camb. Philos. Soc.* **1991**, *66*, 303–345.
- 624 66. McCabe, B. J. Imprinting. *Wiley Interdiscip. Rev. Cogn. Sci.* **2013**, *4*, 375–390, doi:10.1002/wcs.1231.
- 625 67. Vallortigara, G.; Andrew, R. J. Lateralization of response by chicks to change in a model partner. *Anim.*
626 *Behav.* **1991**, *41*, 187–194, doi:10.1016/S0003-3472(05)80470-1.
- 627 68. ten Cate, C. Stimulus movement, hen behaviour and filial imprinting in Japanese quail (*Coturnix coturnix*
628 *japonica*). *Ethology* **1989**, *82*, 287–306, doi:10.1111/j.1439-0310.1989.tb00509.x.
- 629 69. Rosa-Salva, O.; Regolin, L.; Vallortigara, G. Faces are special for newly hatched chicks: evidence for inborn
630 domain-specific mechanisms underlying spontaneous preferences for face-like stimuli. *Dev. Sci.* **2010**, *13*,
631 565–577, doi:10.1111/j.1467-7687.2009.00914.x.
- 632 70. Rouder, J. N.; Speckman, P. L.; Sun, D.; Morey, R. D.; Iverson, G. Bayesian t tests for accepting and rejecting
633 the null hypothesis. *Psychon. Bull. Rev.* **2009**, *16*, 225–237, doi:10.3758/PBR.16.2.225.
- 634 71. Bateson, P. P. G. How do sensitive periods arise and what are they for? *Anim. Behav.* **1979**, *27*, 470–486,
635 doi:10.1016/0003-3472(79)90184-2.
- 636 72. Bateson, P. P. G. Preferences for familiarity and novelty: a model for the simultaneous development of
637 both. *J. Theor. Biol.* **1973**, *41*, 249–259.
- 638 73. Bateson, P. P. G.; Jaeckel, J. B. Chicks' preferences for familiar and novel conspicuous objects after different
639 periods of exposure. *Anim. Behav.* **1976**, *24*, 386–390, doi:10.1016/S0003-3472(76)80048-6.
- 640 74. Scarf, D.; Colombo, M. Representation of serial order: a comparative analysis of humans, monkeys, and
641 pigeons. *Brain Res. Bull.* **2008**, *76*, 307–312, doi:10.1016/j.brainresbull.2008.02.022.
- 642 75. Straub, R. O.; Terrace, H. S. Generalization of serial learning in the pigeon. *Anim. Learn. Behav.* **1981**, *9*, 454–
643 468, doi:10.3758/BF03209775.
- 644 76. Terrace, H. S. Chunking by a pigeon in a serial learning task. *Nature* **1987**, *325*, 149–151,
645 doi:10.1038/325149a0.
- 646 77. Gierszewski, S.; Bleckmann, H.; Schluessel, V. Cognitive abilities in Malawi cichlids (*Pseudotropheus sp.*):
647 matching-to-sample and image/mirror-image discriminations. *PloS One* **2013**, *8*, e57363,
648 doi:10.1371/journal.pone.0057363.
- 649 78. Lohmann, A.; Delius, J. D.; Hollard, V. D.; Friesel, M. F. Discrimination of shape reflections and shape
650 orientations by *Columba livia*. *J. Comp. Psychol.* **1988**, *102*, 3–13, doi:10.1037/0735-7036.102.1.3.
- 651 79. Mackintosh, J.; Sutherland, N. S. Visual discrimination by the goldfish: The orientation of rectangles. *Anim.*
652 *Behav.* **1963**, *11*, 135–141.
- 653 80. Sutherland, N. S. Visual Discrimination of Orientation and Shape by the Octopus. *Nature* **1957**, *179*, 11–13,
654 doi:10.1038/179011a0.
- 655 81. Sutherland, N. S. Visual discrimination of orientation by octopus: mirror images. *Br. J. Psychol.* **1960**, *51*, 9–
656 18, doi:10.1111/j.2044-8295.1960.tb00719.x.
- 657 82. Tee, K. S.; Riesen, A. H. Visual right-left confusions in animal and man. *Adv. Psychobiol.* **1974**, *2*, 241–265.
- 658 83. Maekawa, F.; Komine, O.; Sato, K.; Kanamatsu, T.; Uchimura, M.; Tanaka, K.; Ohki-Hamazaki, H.
659 Imprinting modulates processing of visual information in the visual wulst of chicks. *BMC Neurosci.* **2006**,
660 *7*, 75, doi:10.1186/1471-2202-7-75.
- 661 84. Hernik, M.; Fearon, P.; Csibra, G. Action anticipation in human infants reveals assumptions about
662 anteroposterior body-structure and action. *Proc. Biol. Sci.* **2014**, *281*, 20133205, doi:10.1098/rspb.2013.3205.
- 663 85. Vallortigara, G.; Regolin, L. Gravity bias in the interpretation of biological motion by inexperienced chicks.
664 *Curr. Biol.* **2006**, *16*, R279–280, doi:10.1016/j.cub.2006.03.052.
- 665 86. Vallortigara, G.; Regolin, L.; Marconato, F. Visually inexperienced chicks exhibit spontaneous preference
666 for biological motion patterns. *PLoS Biol.* **2005**, *3*, e208, doi:10.1371/journal.pbio.0030208.
- 667 87. Vallortigara, G.; Andrew, R. J. Differential involvement of right and left hemisphere in individual
668 recognition in the domestic chick. *Behav. Processes* **1994**, *33*, 41–57, doi:10.1016/0376-6357(94)90059-0.
- 669 88. Scarf, D.; Colombo, M. Representation of serial order in pigeons (*Columba livia*). *J. Exp. Psychol. Anim.*
670 *Behav. Process.* **2010**, *36*, 423–429, doi:10.1037/a0020926.

