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# Predisposed and learned preferences for multipoint visual statistics in visually naive newly hatched chicks

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Recent studies have revealed that human and non-human animals (rats) can detect luminance distribution and correlations between pixels in an image (ranging from 2-point to 4-point). This sensitivity is believed to stem from optimization processes in the visual system operating through efficient coding mechanisms that retain the most informative and significant features (here identified as the most variable correlations), thereby reducing costs to extract biologically relevant information from the environment. However, it is yet to be determined whether this optimization is evolutionarily given by inborn mechanisms or shaped by visual experience. Here we report that newly hatched visually naive domestic chicks (*Gallus gallus*) spontaneously prefer to approach luminance, 2-point and 4-point correlation patterns (respectively, horizontal lines and rectangular patterns), while showing no preference for 3-point correlation over noise controls. This parallels the ranking observed in adult humans and rats, thus suggesting that evolutionarily given biological predispositions largely drive efficient coding of natural images. We also found that learning by exposure to visual stimuli, as occurs naturally during visual imprinting, induced a preference for noise over point correlation patterns in chicks exposed to 3- and 4-point patterns. We hypothesize that this behaviour could reflect chicks' preference for stimuli of lower statistical (correlation-based) complexity.

## 1. Introduction

A prominent theory in the field of systems neuroscience is that sensory systems have evolved to efficiently encode the structure of the natural world. According to the hypothesis of efficient coding, neuronal tuning is shaped by the need to optimally encode the statistical structure of input signals [1–6]. In vision, this implies that perception should be tuned to the statistical features that are both the most informative and biologically significant (here identified as the most variable correlation features), while discarding less relevant ones to reduce costs. This idea raises a fundamental question: how do basic image properties shape visual perception in animals?

Natural images can, for example, be described by their pixel correlations (e.g. up to fourth-order correlations among two to four adjacent pixels; figure 1a; [7,9]). These correlations define regions, patterns and objects. Single-pixel averages capture overall luminance; 2-point correlations generate oriented patterns; 3-point form L-shapes; 4-point create rectangles and squares. Higher-order correlations would encode more complex textures. In contrast, images with no pixel correlations -'white noise'- have pixels assigned independently, minimizing all multi-point correlations.

Analyses of natural scenes show that 2-point correlations vary most (bigger variance in the frequency of appearance) across image patches, followed by 4-point and then 3-point correlations [7,9]. Under efficient coding, sensory systems should be most sensitive to the most variable, and thus most informative, statistics. Here, the 2–4–3 ranking reflects how much each correlation type changes across image locations, not pattern complexity. If efficient coding holds, behavioural preferences should mirror this variability-based ranking rather than any ordinal ordering.

Hermundstad *et al.* [9] tested this idea with psychophysical discrimination tasks using the same texture classes. Human sensitivity was then compared with predictions from natural-image statistics. Participants were most sensitive to the most variable correlations: performance was highest for 2-point, followed by 4-point, and lowest for 3-point patterns. This enhanced sensitivity to the most informative features supports the view that the visual system encodes information efficiently by prioritizing less predictable statistics.

These findings were recently replicated in rats [10]. After learning to distinguish white noise from structured textures, rats performed a discrimination task in which stimuli varied in correlation strength, and performance was quantified with psychometric fits. Rats showed the same sensitivity hierarchy as humans (stronger sensitivity to 1- and 2-point than to 4- and 3-point correlations), indicating that visual perception aligns with efficient coding principles.

Whether this ranking holds in non-mammalian vertebrates remains unknown. Efficient coding predicts that it should, as any visual system should allocate resources to the most informative natural-image features. This expectation is further supported by broad vertebrate similarities in visual circuitry [11–13].

The origins of efficient coding remain unclear: they may arise from ontogenetic learning through exposure to natural image statistics [2,14–16], from evolutionarily inherited predispositions shaped by natural history [17,18], or from both.

To investigate this, we examined perception of multipoint correlation patterns in newly hatched domestic chicks, a precocial species well suited for studying biological predispositions and early learning [18–24]. Chicks hatch with several visual biases that support early behaviours, including food selection [25,26], animacy detection [20] and recognition of social partners [27–29], prey [30,31] and predators [32].

We focus on spontaneous preferences for textures defined by multipoint correlations and on how exposure to these stimuli shapes choices through filial imprinting, a form of exposure non-associative learning. Here, 'learning' refers specifically to this imprinting phase, restricted to a critical period during which chicks acquire features of a stimulus through passive exposure rather than associative mechanisms.

In Experiment 1, chicks were hatched in darkness to avoid prior exposure to visual statistics and then tested in free-choice tasks comparing 1-point (luminance), 2-point (horizontal lines), 3-point (L-shapes with a bottom-right corner) and 4-point (rectangles) correlations against white noise (Experiment 1a; figure 1a). We also tested additional 2-point patterns (horizontal, vertical and oblique lines) not used in earlier animal work (Experiment 1b; figure 1a), both to assess possible orientation biases in asymmetric, non-rotationally invariant textures [33] and to align more closely with human studies [9].

In Experiment 2, we asked whether exposure influences learning through filial imprinting. Newly hatched naive chicks were exposed for 1 day to each texture type from Experiment 1a and then tested for preferences between the familiar (imprinted) pattern and white noise (and the reverse, with imprinting on noise).

## 2. Experiment 1: Spontaneous choice

We assessed chicks' spontaneous preferences for different texture statistics over white noise using free dual-choice tests. A preference indicates discriminability, whereas lack of preference does not rule it out. Sex ratios were balanced across groups (see figures 2 and 3).

In Experiment 1a, we tested the four texture classes previously used in rats: 1-point, 2-point horizontal, 3-point and 4-point correlations.

In Experiment 1b, we tested additional 2-point patterns (horizontal, vertical, oblique) to probe possible orientation biases in asymmetric, non-rotationally invariant textures [33]. Horizontal patterns align with stimulus motion, while vertical ones are orthogonal, potentially inducing Barber-Pole-like illusions [34,35]. Chicks also prefer objects moving along their elongation axis, a cue for animacy [36]. Testing multiple orientations also enabled closer comparison with humans, who show higher sensitivity to cardinal than oblique orientations [9,37].

### (a) Results

#### (i) Experiment 1a

Chicks' preference over time (figure 2a) shows comparable male and female trends for 1-, 3- and 4-point patterns. Both sexes preferred the 1-point luminance pattern over noise (females: min 5 preference index (PI) = 0.56 ± 0.17, 95% confidence interval

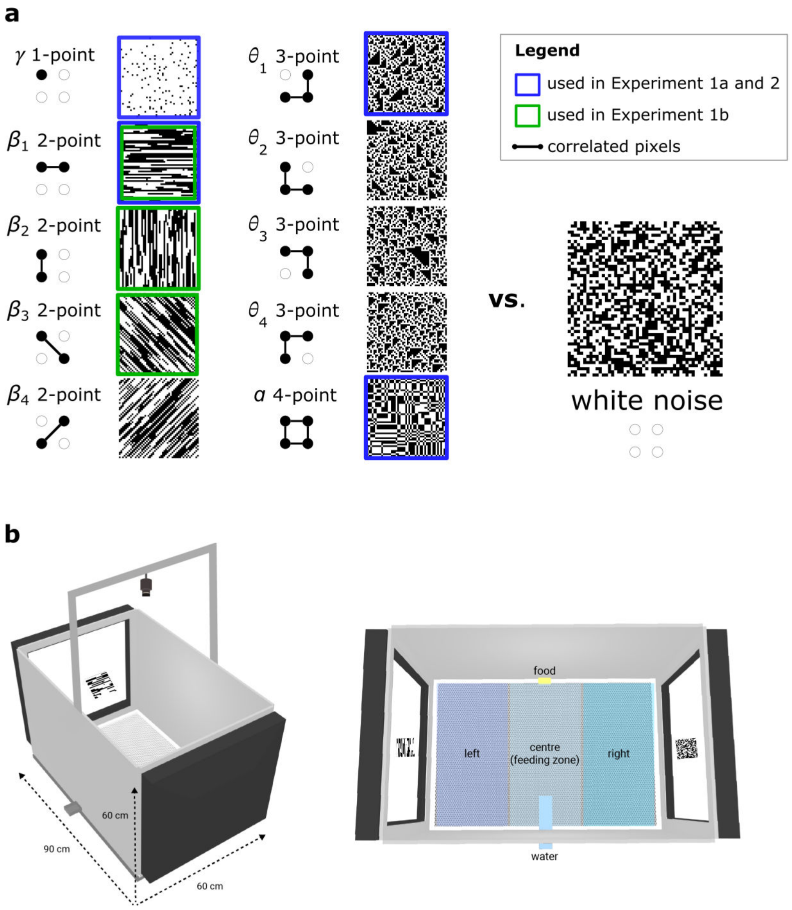

**Figure 1.** *Stimuli and apparatus*. (a) Example textures defined by pixel statistics (correlations among up to four pixels in a 2 × 2 arrangement, illustrated by the gliders). Each coordinate (Greek letters, following Victor and Conte [7]) corresponds to a specific correlation type: 1-point; 2-point horizontal, vertical, oblique–left, oblique–right; 3-point corners (bottom/right, bottom/left, top/right, top/left); and 4-point correlations. White-noise images have all correlations up to fourth order set to zero. Textures outlined in green were used in Experiments 1a and 2; those in blue in Experiment 1b. (b) Experimental setup schematic [8]: lateral cage view and dimensions (left); top view showing the distinct choice areas (right).

(CI) [0.20, 0.93]; min 10 = 0.65 ± 0.15, CI [0.32, 0.97]; males: min 5 = 0.66 ± 0.14, CI [0.38, 0.95]; min 10 = 0.71 ± 0.11, CI [0.47, 0.94]). For 3-point patterns, performance remained at chance (females: min 5 = −0.06 ± 0.16, CI [−0.40, 0.28]; min 10 = −0.08 ± 0.17, CI [−0.43, 0.28]; males: min 5 = −0.23 ± 0.17, CI [−0.59, 0.13]; min 10 = −0.08 ± 0.19, CI [−0.47, 0.30]). For 4-point patterns, preference for the structured texture increased over time (females: min 1 = 0.07 ± 0.19, CI [−0.33, 0.47]; min 15 = 0.39 ± 0.18, CI [0.02, 0.75]; males: min 1 = 0.00 ± 0.23, CI [−0.47, 0.48]; min 15 = 0.13 ± 0.21, CI [−0.31, 0.57]).

For 2-point patterns, the sexes diverged: females initially preferred the pattern but later shifted toward noise, whereas males consistently preferred noise (females: min 1 = 0.26 ± 0.19, CI [−0.13, 0.66]; min 15 = −0.39 ± 0.18, CI [−0.76, −0.02]; males: min 1 = −0.44 ± 0.20, CI [−0.85, −0.03]; min 15 = −0.39 ± 0.18, CI [−0.76, −0.02]). This early divergence between the sexes was also evident in the first-choice analysis (electronic supplementary material, figure S1). Minute-by-minute values are provided in electronic supplementary material, table S1.

Percent choice (strength of choice, independent of its direction; figure 2b) aligned across sexes for all conditions, with no male–female differences in permutation tests (1-point: $p = 0.47$; 2-point: $p = 0.30$; 3-point: $p = 0.97$; 4-point: $p = 0.48$). Combined-sex data appear in figure 2c.

Averaging in 5 min bins (figure 2d) showed stable discrimination for 1-point patterns across all intervals (mins 1–5 $p < 0.01$; 6–10 $p < 0.01$; 11–15 $p < 0.01$) and likewise for 2-point patterns (all intervals $p < 0.01$). Discrimination of the 4-point pattern emerged from min 6 onward (mins 1–5 $p > 0.05$; 6–10 $p < 0.01$; 11–15 $p < 0.01$). The 3-point pattern was never discriminated (all intervals $p > 0.05$).

Comparisons among the multipoint patterns (2-, 3- and 4-point) showed: mins 1–5: 2- versus 3-point (Holm-corrected $p = 0.04$), 2- versus 4-point ($p = 0.02$); mins 6–10: 4- versus 3-point ($p = 0.03$); mins 11–15: 2- versus 3-point ($p = 0.04$), 4- versus 3-point ($p = 0.02$).

### (ii) Experiment 1b

Looking at chicks' preferences over time (figure 3a), males and females show similar trends for 2-point vertical and oblique patterns. In the vertical group, both sexes show slight preference (females, min 5: PI = 0.07 ± 0.14, 95% CI [−0.21, 0.35]; min 10: PI = 0.17 ± 0.13, 95% CI [−0.10, 0.44]; males, min 5: PI = 0.15 ± 0.15, 95% CI [−0.16, 0.45]; min 10: PI = 0.20 ± 0.15, 95% CI [−0.11, 0.50]). For oblique patterns, there is no preference (females, min 3: PI = 0.02 ± 0.15, 95% CI [−0.28, 0.31]; min 12: PI = 0.01 ± 0.15, 95%

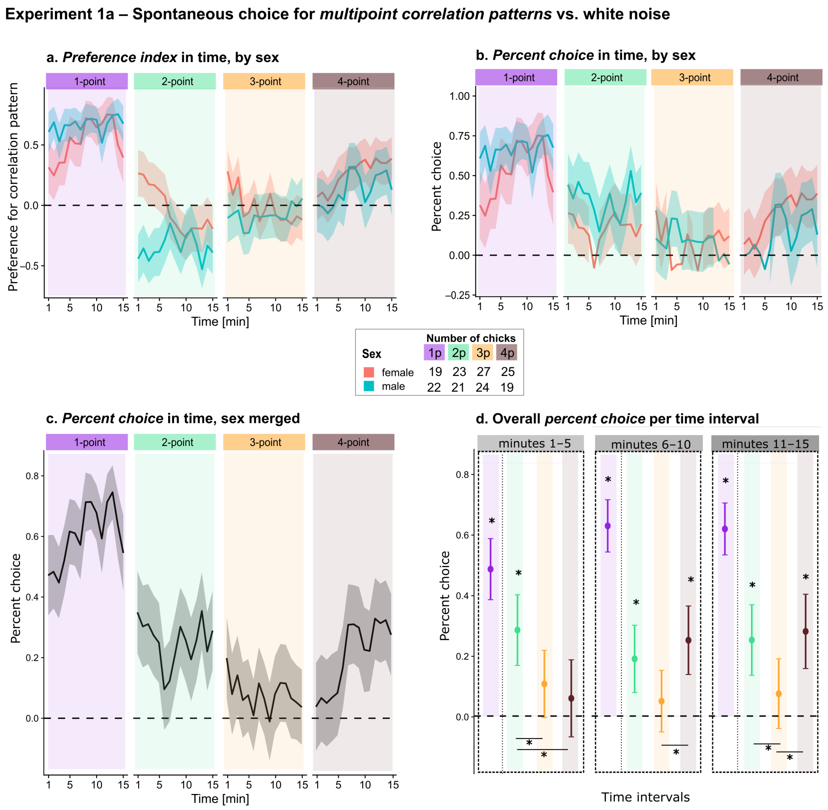

**Figure 2.** *Results for Experiment 1a*. (a) Preference index (PI > 0 indicates preference for the correlation pattern) over the first 15 min after the first choice, shown by condition and sex. (b) Percent choice (>0 indicates selection of pattern or noise) over the same period, by condition and sex. (c) Percent choice with sexes merged, by condition. (d) Average percent choice in 5 min intervals (mins 1–5, 6–10, 11–15). Dotted lines show chance level; asterisks (*) indicate significance versus chance ($p <$ 0.05).

CI [–0.29, 0.31]; males, min 3: PI = 0.07 ± 0.15, 95% CI [–0.23, 0.37]; min 12: PI = 0.06 ± 0.15, 95% CI [–0.23, 0.35]). For horizontal patterns, sexes initially show opposite preferences: males prefer white noise, while females prefer the pattern early in the test (females, min 1: PI = 0.27 ± 0.13, 95% CI [0.02, 0.53]; min 15: PI = 0.01 ± 0.13, 95% CI [–0.25, 0.27]; males, min 1: PI = −0.37 ± 0.14, 95% CI [–0.66, –0.08]; min 15: PI = −0.30 ± 0.14, 95% CI [–0.58, –0.01]). This initial sex difference is also visible from the first choice (electronic supplementary material, figure S2). Minute-by-minute data are in electronic supplementary material, table S2.

Percent choice curves align between sexes across all conditions (figure 3b; permutation tests: horizontal $p$ = 0.1, vertical $p$ = 0.3, oblique $p$ = 0.7). Merged data are shown in figure 3c.

Averaging scores in 5 min bins (figure 3d) shows stable discrimination for horizontal patterns across all intervals (min 1–5, 6–10, 11–15: $p$ < 0.01). Vertical patterns are discriminated mid-to-late (min 1–5: $p$ > 0.05; 6–10, 11–15: $p$ < 0.01), while oblique patterns are never discriminated (all intervals $p$ > 0.05).

Comparisons between 2-point patterns reveal differences between horizontal versus oblique ($p$ < 0.01) and horizontal versus vertical ($p$ = 0.01) in the first interval (mins 1–5).

## (b) Discussion

### (i) Experiment 1a

Chicks spontaneously preferred 1-point luminance and 2-point correlation textures. Preference for 4-point textures emerged later (mins 6–15). Overall, choices were consistent across sexes, but in the first minutes 2-point patterns showed sex differences: females initially preferred the 2-point pattern, whereas males consistently preferred white noise (see figure 2a and first choice, electronic supplementary material, figure S1). No preference was observed for 3-point patterns.

1-point patterns reflect changes in image luminance, a cue that chicks can readily discriminate [38]. Consistent with previous studies [39,40], chicks showed a spontaneous preference for brighter stimuli (although perceptual salience was not controlled in those studies). For 2-point horizontal patterns, males initially preferred white noise, while females preferred the correlation pattern. The reason for this sex difference is unclear, though it may involve early visual processing mechanisms, from biological motion to face responses [17,19,21,41,42].

Still, irrespective of its direction, spontaneous discrimination of image statistics follows a ranking similar to that seen in humans and rats [9,10]. In rats, 1- and 2-point patterns are most discriminable from white noise, followed by 4- and then 3-point patterns [10]. Likewise, chicks discriminate 1-point patterns, 2-point horizontal patterns and 4-point textures, but not 3-point patterns. This ranking partially matches humans [9], although chicks show no preference for oblique 2-point textures.

When interpreting these findings, it is important to note that a significant preference for a texture over white noise indicates discriminability, but lack of preference does not necessarily mean the texture is not perceived. Chicks could discriminate

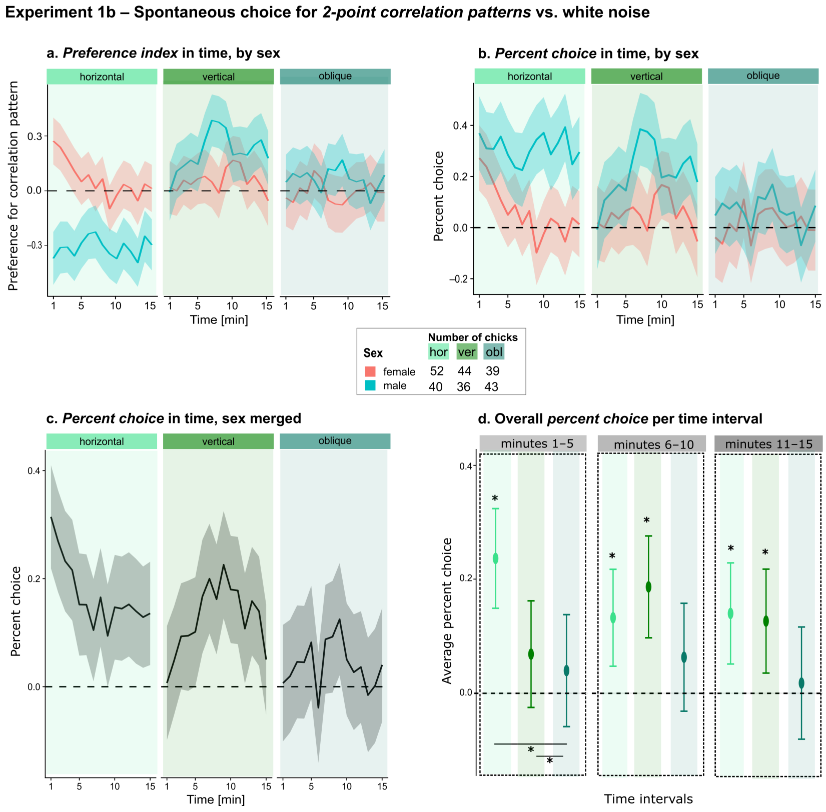

**Figure 3.** *Results for Experiment 1b*. (a) Preference index (PI > 0 indicates preference for the correlation pattern) over the first 15 min after the first choice, by condition and sex. (b) Percent choice (>0 indicates selection of pattern or noise) over the same period, by condition and sex. (c) Percent choice with sexes merged, by condition. (d) Average percent choice in 5 min intervals (min 1–5, 6–10, 11–15). Horizontal dashed lines show chance level; asterisks (*) indicate significance versus chance ($p < 0.05$).

without showing a directional bias, and preference strength may reflect both discriminability and innate attractiveness. Despite these caveats, the results align with efficient coding mechanisms: the observed ranking mirrors the variability of natural image statistics. Moreover, these mechanisms appear to be present at birth, based on spontaneous preferences in visually naive chicks, though evolutionarily driven predispositions could still be shaped by environmental exposure [9,10].

### (ii) Experiment 1b

In this experiment, results for the horizontal group replicated those of Experiment 1a: males and females initially showed opposite spontaneous preferences for horizontal 2-point correlation patterns versus white noise. Interestingly, these preferences and sex differences disappeared when line orientations changed (vertical and oblique; figure 3). Still, vertical patterns were discriminated later (min 6–15), whereas oblique patterns were never preferred. This suggests that chicks do not rely solely on 2-point correlations but they also integrate other cues. In our setup, images moved horizontally to increase their attractiveness because moving stimuli are more engaging [27,43–45]. Horizontal 2-point lines align with motion, while vertical lines are perpendicular, potentially creating illusions such as the Barber-Pole effect [34,35]. Additionally, chicks prefer objects moving along their main elongation axis, which is a cue for animacy [36,44]. Another possible explanation is that cardinal biases, which reflect a predisposition of the visual system to process vertical and horizontal orientations more robustly than oblique ones, may enhance the salience or behavioural relevance of cardinally oriented correlations and thereby overshadow sensitivity to oblique correlations in the observed choices; this interpretation aligns with ongoing debates on the development and functional impact of cardinal orientation biases across species [46]. These factors may explain orientation effects, although why motion perception interacts with sex remains unclear.

## 3. Experiment 2: Discrimination after imprinting

In this experiment, we tested learned preferences of chicks imprinted on different correlation statistics or on white noise. Four groups were imprinted on textures with 1-, horizontal 2-, 3- or 4-point correlations and later tested in a free-dual-choice task against white noise. Four additional groups were imprinted on white noise and tested against one of the four texture statistics (using equivalent white noise stimuli across groups).

## (a) Results

Chicks imprinted above chance on all four patterns and white noise, spending most of the 14 h exposure near the imprinting stimulus (electronic supplementary material, figure S4; average 65%, 95% CI [62%,69%], Cohen's $d = 0.77$).

During the dual-choice test, chicks imprinted on patterns or noise showed similar time-varying preferences (figure 4a–b). For 1-point textures, both groups slightly preferred the luminance pattern (imprinted on noise, min 1: PI = 0.20 ± 0.24, 95% CI [−0.31, 0.71]; imprinted on pattern, min 1: PI = 0.17 ± 0.23, 95% CI [−0.31, 0.65]). For 2-point patterns, preferences were near chance (imprinted on noise, min 1: PI = 0.10 ± 0.24, 95% CI [−0.41, 0.61]; imprinted on pattern, min 1: PI = −0.17 ± 0.23, 95% CI [−0.65, 0.31]). For 3- and 4-point patterns, chicks consistently preferred white noise (3-point imprinted on noise, min 2: PI = −0.51 ± 0.20, 95% CI [−0.93, −0.08]; min 14: PI = −0.30 ± 0.22, 95% CI [−0.76, 0.16]; 3-point imprinted on pattern, min 2: PI = −0.19 ± 0.23, 95% CI [−0.67, 0.28]; min 14: PI = −0.27 ± 0.22, 95% CI [−0.74, 0.19]; 4-point imprinted on noise, min 2: PI = −0.44 ± 0.20, 95% CI [−0.86, -0.01]; min 14: PI = −0.54 ± 0.20, 95% CI [−0.97, −0.12]; 4-point imprinted on pattern, min 2: PI = −0.33 ± 0.23, 95% CI [−0.82, 0.17]; min 14: PI = −0.38 ± 0.24, 95% CI [−0.89, 0.12]). Full minute-by-minute choices can be viewed in electronic supplementary material, table S3.

Similarity between groups is also evident in first choices (electronic supplementary material, figure S5) and confirmed by permutation tests on percent choice (1-point: $p = 0.6$; 2-point: $p = 0.7$; 3-point: $p = 0.6$; 4-point: $p = 0.7$). Merged data are shown in figure 4c.

Averaging in 5 min bins (figure 4d) shows stable discrimination for 3-point (mins 1–5, 6–10, 11–15: $p < 0.01$) and 4-point patterns (mins 1–5, 6–10, 11–15: $p < 0.01$). The 1-point pattern was discriminated only late (mins 11–15: $p = 0.03$; mins 1–5 and 6–10: $p > 0.05$), while 2-point patterns were never discriminated (all intervals $p > 0.05$).

Comparisons among multipoint patterns (excluding 1-point) show differences between 2- versus 3-point and 2- versus 4-point in mins 1–5 ($p < 0.01$), 4- versus 2-point in mins 6–10 ($p < 0.01$) and 2- versus 4-point in mins 11–15 ($p < 0.01$).

## (b) Discussion

Previous studies examined sensitivity to different correlation statistics using operant conditioning, requiring subjects to discriminate structured textures from white noise explicitly [9,10]. In rats, this involved associating stimulus identity with reward. In Experiment 2, we tested whether pixel correlations affect a non-associative form of learning—filial imprinting—which aligns more with declarative-like than procedural learning [47].

Chicks imprinted equally well on all patterns and white noise, spending 65% of their time above chance near the displayed object. By contrast, in [28], chicks spent 96% of their time near imprinting objects, suggesting that our correlation patterns are less optimal stimuli, possibly owing to the absence of colour [48–50].

At test, 2-point groups showed no preference and 1-point luminance was preferred only late in the test (mins 11–15), despite Experiment 1 showing that chicks can discriminate these patterns. This suggests that after imprinting, differences in 2-point (and to some extent 1-point) patterns from white noise were not sufficiently salient to elicit strong approach behaviour. Stronger preferences appeared for 3- and 4-point pattern discriminations: chicks preferred white noise whether they were imprinted on it or on the correlation patterns (in the last case, indicating a tendency to explore novel stimuli). Overall, white noise appeared more visually attractive than 3- and 4-point patterns.

Imprinting produces outcomes that are mirror-reversed relative to spontaneous preference tests (Experiment 1). Young chicks seem to modulate their behaviour based on stimulus novelty: completely unfamiliar stimuli tend to be avoided, whereas slight novelty is explored [51–53]. Imprinting ensures recognition of familiar stimuli, which is essential for following conspecifics, while it is well known how a complementary drive toward slight novelty could facilitate exploration and generalization [27,47,54]. In our results, 3- and 4-point patterns elicited clear choices, whereas 1- and 2-point patterns did not.

The correlation patterns increase in complexity in the pixels' correlation structure, from single-pixel luminance to multi-pixel correlations, while white noise has no correlations (figure 1a). If chicks detect this correlation-based complexity, white noise would stand closer, e.g. to 2-point than 4-point patterns. Consistent with this, imprinting led to clear preferences when white noise was compared with 3- or 4-point patterns, but not with 1- or 2-point patterns. Therefore, we can interpret the strong general preference for white noise as reflecting its lower correlation-based complexity, making it visually simpler than higher-order patterns.

Note that data from Experiment 2 come exclusively from female chicks, chosen because they showed clearer responses in Experiment 1a. Future studies including both sexes are needed to examine potential sex differences in imprinting responses to visual statistics.

Moreover, innate preferences (Experiment 1) were measured immediately after hatching and compared with learned preferences after one day of imprinting, ensuring that all chicks were tested at similar developmental stages. This short interval minimizes the likelihood that maturational changes explain the observed differences, indicating that preference shifts primarily reflect the impact of imprinting rather than age-related effects.

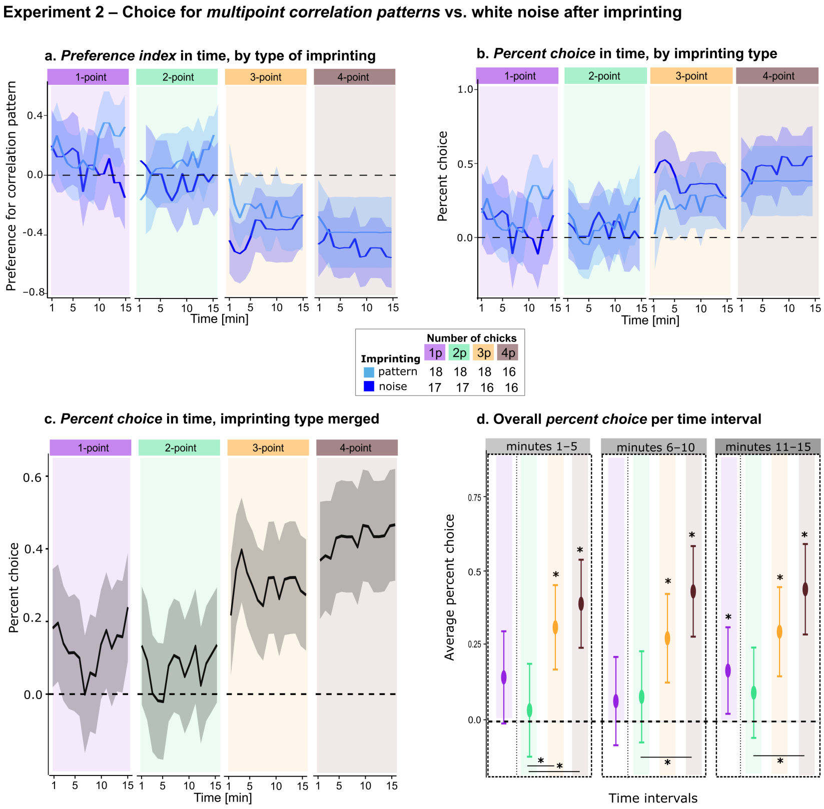

**Figure 4.** Results for Experiment 2. (a) Preference index (PI > 0 indicates preference for the correlation pattern) over the first 15 min after the first choice, by condition and type of imprinting. (b) Percent choice (>0 indicates selection of pattern or noise) over the same period, by condition and type of imprinting. (c) Percent choice with types of imprinting merged, by condition. (d) Average percent choice in 5 min intervals (mins 1–5, 6–10, 11–15). Horizontal dashed lines indicate chance level; asterisks (*) denote significance versus chance ($p < 0.05$).

## 4. Conclusions

We found that newly hatched visually naive domestic chicks show a spontaneous preference to approach 1-point, 2-point and 4-point correlation patterns (respectively, luminance, horizontal lines and rectangular patterns), but no preference at all for 3-point correlation patterns versus white noise. This ranking resembles the one observed in adult humans and rats and it could suggest that evolutionarily set biological predispositions underlie efficient coding of natural images. Interestingly, we also found that imprinting to visual patterns (both multipoint correlation or noise) induces a stronger preference (and thus a discrimination) for white noise over point correlation patterns in animals exposed to 3- and 4-point stimuli, while the preference for 2- and 1-point patterns is no longer present at the beginning of the test. This behaviour could reflect an attraction to stimuli of lower statistical (correlation-based) complexity and an avoidance of strongly novel patterns, with a modulation provided by innate preferences.

Our results provide evidence that efficient coding mechanisms are phylogenetically grounded because they emerge very early in development and thus appear to be predisposed rather than solely acquired through experience. In this sense, we use the term ‘evolutionary grounding’ to indicate that efficient coding represents a conserved principle across species, opening the way to further investigation of its underlying neural and genetic mechanisms. The sex differences observed in our study are more plausibly explained by well-documented variations in exploratory behaviour and social motivation, rather than by sex-specific evolutionary adaptations in efficient coding, which cannot be inferred at this stage.

Given that our data support the predictions of efficient coding, it is natural to ask what other computational frameworks or hypotheses generate distinct predictions that do not agree with the empirical evidence. Efficient coding belongs to a broader class of theories, including predictive coding and various Bayesian accounts of sensory perception that share the common assumption that information processing in the brain is optimally adapted to the statistical structure of the natural environment.

Distinguishing among some of these theories is not possible in a task where spontaneous choices of naive animals are recorded. For instance, predictive coding models suggest that perception minimizes prediction errors, but our tasks involved spontaneous, unrewarded choices without feedback, meaning that this is unlikely to drive the observed preferences. On the other hand, while the efficient coding hypothesis is most naturally and commonly operationalized using the tools of Bayesian modelling, the most important aspect that distinguishes efficient coding models from more general Bayesian approaches is the emphasis on the role of resource limitations, which force the system to behave efficiently and give the theory its name. By contrast, it is possible to develop Bayesian models of perception or behaviour that assume infinite resources. These models, although useful as normative reference points in certain tasks (see for instance [55]), cannot by construction make any predictions about the relative sensitivity of an observer to distinct input features, because an infinitely powerful observer could simply have infinite sensitivity to all of them. Therefore, what appears to be critical in considering alternative theoretical accounts of the sensitivity ranking measured in our study is whether a possible explanation exists that is not based on adaptation to natural image statistics, under a limited resource budget—which is, again, the core tenet of efficient coding.

If we forget this core hypothesis, we can ask what would follow from assuming that the discriminability of texture patterns is only a function of their intrinsic statistical properties, without reference to the patterns' abundance or variability in the natural visual world. This would be the case for a Bayesian observer with unlimited resources, which can use all available information so that its sensitivity is limited only by the stimulus itself. It would also apply to a limited 'efficient coding' observer, which has no prior knowledge of natural stimulus statistics and therefore assumes, in the absence of information, that all patterns are equally likely. Even such an observer can show different sensitivities to different patterns; for example, higher-order patterns may be more or less distinguishable from white noise simply because they involve interactions among many pixels that can only be detected by observing several pixels at once.

We tested this idea using a computational model of texture discrimination. In this model, a statistical learning algorithm (a linear support vector classifier (SVC)) was trained to distinguish textures from white noise at varying intensity levels, using only the intrinsic statistical structure of the images (encoded as frequency counts of all 2 × 2 pixel patterns). This allowed us to evaluate how pattern complexity affects discriminability without assuming any prior knowledge of natural images.

This analysis revealed that the discriminability of texture stimuli from noise depended only on the intensity of the statistic and not on the texture type (electronic supplementary material, figure S6; see §5 for details on the decoder). We can therefore conclude that the difference in discriminability between texture patterns is not a simple consequence of their intrinsic statistical properties.

Moving from the computational to the algorithmic level of analysis [56], a different type of explanation for the behavioural phenomena we observe is that they may be driven by perceptual salience mechanisms. However, because low-level features such as luminance are carefully controlled in our experiment, any salience arising from the patterns themselves (like e.g. in [33]) must be intrinsically tied to the correlation structures defining each condition, which is again fully consistent with efficient coding predictions. Finally, motivational or ecological relevance of the stimuli is unlikely to explain the results, as the correlation-based patterns are artificial and lack functional value. Taken together, while alternative explanations cannot be entirely ruled out, the constraints of the experimental design and the nature of the stimuli strongly suggest that the observed preferences are most consistently interpreted within an efficient coding framework.

To date, there is no direct evidence for neural substrates specifically dedicated to efficient coding of statistical patterns. However, a large body of work demonstrates the existence of neurons tuned to simple geometric features such as lines and bars, beginning with the seminal discovery of orientation-selective cells in mammalian V1 [57,58]. Such line sensitivity may be related, e.g. to the processing of simple two-point configurations. In our study, the correlation patterns are actually defining simple structures, suggesting that their elaboration could plausibly occur already at the earliest stages of visual elaboration. In mammals, this corresponds to V1, while in birds, a functionally analogous region is the visual Wulst (dorsomedial telencephalon). We therefore propose that the visual Wulst may serve as the likely neural substrate for efficient coding mechanisms in chicks, with higher-order regions integrating these early feature-based representations.

# 5. Material and methods

## (a) Subjects

Group sizes were determined *a priori* via power analysis. For the spontaneous preference test (Experiment 1a), we assumed a two-tailed dependent-samples *t*-test (to compare time spent near white noise versus texture) with $\alpha = 0.05$ and power = 0.8. Based on an expected effect size of Cohen's $d = 0.55$ (from Caramellino *et al.* [10]), this analysis indicated that 28 chicks were required for each group. For the imprinting test (Experiment 2), using an expected effect size of $d = 0.75$ (from Lemaire *et al.* [28]) under the same assumptions, 16 chicks per group were sufficient. Experiment 1b, testing different 2-point orientations, was performed a posteriori: using the observed effect size from Experiment 1a ($d = 0.37$ for the horizontal 2-point group), a sample size of 47 chicks per group was needed toa power of 0.8. These effect sizes were chosen based on prior literature and preliminary data to detect biologically meaningful differences while minimizing animal use.

Overall, 671 Ross 308 chicks (*Gallus gallus*) (263 males) were tested; 529 (184 males) were included in analyses after excluding non-moving animals (see §5e). Eggs were obtained from Azienda Agricola Crescenti (Brescia) and incubated in darkness at 37.7 °C and 40% humidity. Three days pre-hatching, eggs were moved to opaque boxes within a hatching chamber at 37.7 °C and 60% humidity. Chicks were briefly sexed under dim light (wing feather dimorphism) and singly housed in central positions in testing cages. All procedures were approved by the University of Trento Ethical Committee and Italian Ministry of Health (permit 53/2020-PR, 21/01/2020).

## (b) Apparatus

All experiments were conducted in $90 \times 60 \times 60$ cm testing cages with ad libitum food and water. Two opposite sides of each cage had high-frame-rate (120 Hz) screens displaying stimuli. Stimulus presentation was automated via a custom Matlab script, controlling timing and randomizing screen positions to avoid positional bias [8]. Each chick's behaviour was continuously recorded with an overhead camera. Experimental setup and methods are detailed in Zanon *et al.* [8]; a schematic is shown in figure 1b.

## (c) Stimuli

Textures with different multipoint correlations and white noise were generated using Metex [59], which systematically controls the probability of specific correlations while minimizing contributions from others by sampling from the maximum-entropy distribution compatible with the requested correlation [7]. White noise contains no correlations. All multi-point stimuli (2-, 3-, 4-point) had equal black/white pixel ratios (50 : 50), while the 1-point condition varied in luminance (not controlled for perceptual salience). Preferences thus cannot be attributed to brightness differences.

Texture intensity, ranging from –1 to +1, parameterizes structure: intensity 0 corresponds to white noise, while extreme values (+0.9 used here) yield highly discriminable patterns with characteristic features (figure 1a; [7]). These features (lines, rectangles, corners) arise intrinsically from correlations, so behavioural preferences reflect sensitivity to correlations rather than to shapes *per se*.

Experiments 1a and 2 used 1-point, 2-point horizontal, 3-point bottom-right corner and 4-point patterns; Experiment 1b used 2-point horizontal, vertical and oblique left patterns (figure 1a). Remaining patterns were not tested owing to time and presumed low biological relevance. Ten images per statistic were created. During dual-choice tests, each chick saw a pattern versus novel white noise; in Experiment 2 imprinting, patterns were randomly varied across the 10 images to prevent imprinting on a specific stimulus.

Images measured 300 × 300 pixels (8.3 × 8.3 cm), providing a minimum visual angle of 2.9° at 90 cm and 0.11° per pixel at 45 cm [60], ensuring detectability from cage centre. Stimuli moved horizontally to attract attention, with translation amplitude 0.32 (42.5 cm spanned) and frequency 0.11 (275 cm $\text{min}^{-1}$), controlled via Matlab [8].

## (d) Experimental pipeline

### (i) Experiment 1

Experiments 1a and 1b were spontaneous dual-choice tests. Chicks, placed at the cage centre, were presented with one multipoint pattern versus white noise (each chick was assigned to a specific texture; figure 1a). Tests lasted for 30 min, but only the first 15 min were analysed. Chicks that did not approach either stimulus within 15 min were excluded. The experimental texture appeared on a random side, with white noise on the opposite screen; both stimuli moved horizontally to enhance attractiveness [27,39,43–45].

### (ii) Experiment 2

This experiment involved a 1-day imprinting exposure followed by a dual-choice test. Chicks, placed at the cage centre, underwent 24 h of imprinting (seven 2 h sessions: 14 h active imprinting plus 10 h overnight resting with black screens; see [28,61]). The stimulus appeared on a single screen, with the active screen randomized in each session, and a new instance of the same pattern (or white noise) was shown each time to prevent learning of a specific stimulus or location.

After imprinting, chicks were repositioned at the centre to avoid positional bias for the dual-choice test (pattern versus white noise), which mirrored Experiment 1, with horizontally translating stimuli randomly assigned to screens. Only female chicks were tested, as they are typically more socially attached [62–65] and showed stronger texture preferences in Experiment 1 (figures 2a and 3a).

## (e) Data analysis

### (i) Behavioural analysis

For all of the experiments, the location of the subjects within the arena was analysed with DeepLabCut [66,67]. The animal was considered close to a screen (stimulus) when it was less than 30 cm from it.

We analysed the first 15 min following the subject's first choice. We discarded from the analyses chicks that stayed in the centre of the apparatus and that did not make a choice between the presented stimuli for more than 15 min (see electronic supplementary material, table S1 for the exact numbers of chicks used and analysed).

With respect to potential side biases (a preference for the right or left screen), the absence of such biases is implicit in the main analysis: because stimuli were randomly alternated between the left and right screens across time, any systematic side bias would result in overall choice indices at chance level. Further data showing time spent closer to the left and right screen depending on stimulus position for each experiment are reported in electronic supplementary material, figure S7.

To take into account that chick preferences or discrimination performance could vary during different epochs of the 15 min, we ran the statistical analysis independently in 5 min intervals ('beginning': mins 1–5; 'middle': mins 6–10; and 'end': mins 11–15; see details below).

As metrics for evaluating chick preferences, we recorded the first stimulus approached by each animal and calculated a time-based *preference index* (at single-minute resolution) using the formula:

$$preference\ index = \frac{t_{pattern} - t_{noise}}{t_{pattern} + t_{noise}},$$

with $t$ being the seconds spent close to a stimulus (respectively, correlation patterns and white noise). This index reflects the preference of the animals for the displayed stimuli. An index value of +1 indicates that the animals spent all their time close to the multipoint texture; an index value of −1 indicates that the animals spent all their time close to the white noise; while a value of 0 indicates chance level.

### (ii) Statistical analysis

We analysed actual choice (pattern versus white noise) over time by plotting the chicks' average preference index (PI) minute by minute, separated by sex. Sex was considered in Experiment 1 because early visual processing mechanisms, ranging from biological motion perception to responses to face-like stimuli, can be sex-dependent in young chicks [17,19,21,41,42].

To compare with prior studies [9,10], we focused on chicks' general ability to discriminate multipoint patterns from white noise, rather than their directional preference for one stimulus. Discrimination was quantified as a percent choice derived from the PI. For each subgroup (defined by sex, statistical condition and time interval), the mean PI was first calculated. If this mean was negative (indicating a consistent preference for white noise), the sign of all individual PIs in that subgroup and interval was inverted; if positive, no transformation was applied. This aligned group-level preferences, allowing assessment of discrimination strength regardless of stimulus identity. Higher percent choice values reflect stronger discrimination. Individual time points may still show negative values, representing temporary divergence from the overall trend. Notably, a percent choice of zero does not imply absence of discrimination, but rather a lack of consistent preference across subjects or across the time interval.

All statistical analyses were performed on percent choice values to determine whether each multipoint pattern was discriminated from noise across time intervals (beginning, middle, end). Analyses were conducted in RStudio (v.1.4.17.17) [68] using R (v.4.1.0, R Core Team, 2017) [69].

We first assessed the influence of sex (Experiment 1) or type of imprinting (Experiment 2) for each pattern using permutation tests (5000 permutations) on male versus female (Experiment 1) or imprinting on noise versus pattern (Experiment 2). If no significant differences were found, data were merged and percent choice differences from chance (zero) were evaluated for each interval using permutation tests. For this, 5000 random datasets were generated by randomly inverting individual PIs to simulate random choice, producing a null distribution of means. The $p$-value was calculated as $p = (b + 1)/(\text{n\_perm} + 1)$, where $b$ is the number of random means more extreme than the observed mean, and n_perm = 5000 [70].

To compare differences between multipoint patterns, Holm-corrected permutation tests were applied. Following previous work [9], comparisons included only 2-, 3- and 4-point patterns (Experiments 1a and 2) or 2-point horizontal, vertical and oblique patterns (Experiment 1b), as the 1-point pattern corresponds to luminance changes and is not a multipoint correlation.

### (iii) Intrinsic discriminability analysis

We measured the intrinsic discriminability of textures with a decoding approach. We considered textures of type $\gamma$, $\beta_1$, $\beta_3$, $\theta_1$, $\alpha$ and a range of 11 values of statistic intensity ($r = 0, 0.1, 0.2, \ldots, 1$); for each texture type and intensity level we generated 10 000 samples of size 12 × 12 pixels (we did not consider $\beta_2$ as for the purpose of this analysis it is equivalent by construction to $\beta_1$). For each texture type and intensity level, we used this data together with a sample of 10 000 white noise images to train and test a decoder that classified images as texture or noise. As a preprocessing step, each image was represented as a 16-dimensional vector that contained the empirical frequency counts for the image of all possible states of a 2 × 2 pixel glider. This representation was designed to maximize the capacity of the decoder to capture the statistics that are relevant for this task (all 1-, 2-, 3- and 4-point statistics of the image) while keeping the dimensionality of the feature space low. These vectors were then fed to a linear SVC. The performance of the decoder was evaluated by 20-fold, nested, stratified cross-validation. In other words, we used two nested 20-fold crossvalidation loops, the outer one to evaluate decoder performance on a validation set and the inner one (performed only using the training data from the outer loop) to select the value of the regularization hyperparameter of the SVC. The results of the analysis are shown in electronic supplementary material, figure S6. Larger image sizes (16 × 16, 20 × 20) were also tested, leading to similar results (decoding performance did not depend on texture type), only with better overall decoding performance (data not shown).

Ethics. All procedures received approval from the Ethical Committee of the University of Trento and the Italian Ministry of Health (permit number 53/2020-PR released on 21/01/2020).

Data accessibility. All the materials and scripts to replicate the analysis are freely available in the Figshare repository [71].

Supplementary material is available online [72].

Declaration of AI use. During the preparation of this work, the authors used ChatGPT exclusively to improve English and the readability in some sentences. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Authors' contributions. M.Z.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; B.S.L.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; E.P.: formal analysis, investigation, validation, visualization, writing—review and editing; R.C.: investigation, validation, writing—review and editing; C.N.: validation, writing—review and editing; V.B.: validation, writing—review and editing; J.G.: conceptualization, funding acquisition, investigation, supervision, validation, visualization, writing—review and editing; D.Z.: conceptualization, funding acquisition, investigation, supervision, validation, visualization, writing—review and

editing; G.V.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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## References

1. Barlow H. 2001 Redundancy reduction revisited. *Netw. Comput. Neural. Syst.* **12**, 241–253. (doi:10.1088/0954-898X/12/3/301)
2. Matteucci G, Piasini E, Zoccolan D. 2024 Unsupervised learning of mid-level visual representations. *Curr. Opin. Neurobiol*. **84**, 102834. (doi:10.1016/j.conb.2023.102834)
3. Ratliff CP, Borghuis BG, Kao YH, Sterling P, Balasubramanian V. 2010 Retina is structured to process an excess of darkness in natural scenes. *Proc. Natl Acad. Sci. USA* **107**, 17368–17373. (doi:10.1073/pnas.1005846107)
4. Simoncelli EP. 2003 Vision and the statistics of the visual environment. *Curr. Opin. Neurobiol*. **13**, 144–149. (doi:10.1016/s0959-4388(03)00047-3)
5. Tesileanu T, Piasini E, Balasubramanian V. 2022 Efficient processing of natural scenes in visual cortex. *Front. Cell. Neurosci*. **16**, 1006703. (doi:10.3389/fncel.2022.1006703)
6. Tkacik G, Prentice JS, Victor JD, Balasubramanian V. 2010 Local statistics in natural scenes predict the saliency of synthetic textures. *Proc. Natl Acad. Sci. USA* **107**, 18149–18154. (doi:10.1073/pnas.0914916107)
7. Victor JD, Conte MM. 2012 Local image statistics: maximum-entropy constructions and perceptual salience. *J. Opt. Soc. Am. A* **29**, 1313–1345. (doi:10.1364/JOSAA.29.001313)
8. Zanon M, Lemaire BS, Vallortigara G. 2021 Steps towards a computational ethology: an automatized, interactive setup to investigate filial imprinting and biological predispositions. *Biol. Cybern*. **115**, 575–584. (doi:10.1007/s00422-021-00886-6)
9. Hermundstad AM, Briguglio JJ, Conte MM, Victor JD, Balasubramanian V, Tkačik G. 2014 Variance predicts salience in central sensory processing. *eLife* **3**, e03722. (doi:10.7554/eLife.03722)
10. Caramellino R, Piasini E, Buccellato A, Carboncino A, Balasubramanian V, Zoccolan D. 2021 Rat sensitivity to multipoint statistics is predicted by efficient coding of natural scenes. *eLife* **10**, e72081. (doi:10.7554/eLife.72081)
11. Vallortigara G. 2012 The cognitive chicken: visual and spatial cognition in a non-mammalian brain. In *The Oxford handbook of comparative cognition* (eds EA Wasserman, TR Zentall), pp. 48–66. Oxford, UK: Oxford University Press.
12. Knudsen EI. 2020 Evolution of neural processing for visual perception in vertebrates. *J. Comp. Neurol*. **528**, 2888–2901. (doi:10.1002/cne.24871)
13. Vallortigara G. 2004 Visual cognition and representation in birds and primates. In *Vertebrate comparative cognition: are primates superior to non-primates?* (eds LJ Rogers, G Kaplan), pp. 57–94. New York, NY: Kluwer Academic/Plenum Publishers. (doi:10.1007/978-1-4419-8913-0_2)
14. Berardi N, Pizzorusso T, Maffei L. 2000 Critical periods during sensory development. *Curr. Opin. Neurobiol*. **10**, 138–145. (doi:10.1016/s0959-4388(99)00047-1)
15. Espinosa JS, Stryker MP. 2012 Development and plasticity of the primary visual cortex. *Neuron* **75**, 230–249. (doi:10.1016/j.neuron.2012.06.009)
16. Matteucci G, Zoccolan D. 2020 Unsupervised experience with temporal continuity of the visual environment is causally involved in the development of V1 complex cells. *Sci. Adv.* **6**, eaba3742. (doi:10.1126/sciadv.aba3742)
17. Rosa-Salva O, Grassi M, Lorenzi E, Regolin L, Vallortigara G. 2016 Spontaneous preference for visual cues of animacy in naïve domestic chicks: the case of speed changes. *Cognition* **157**, 49–60. (doi:10.1016/j.cognition.2016.08.014)
18. Vallortigara G. 2021 *Born knowing: imprinting and the origins of knowledge*. Cambridge, MA: MIT Press.
19. Di Giorgio E, Loveland JL, Mayer U, Rosa-Salva O, Versace E, Vallortigara G. 2017 Filial responses as predisposed and learned preferences: early attachment in chicks and babies. *Behav. Brain Res*. **325**, 90–104. (doi:10.1016/j.bbr.2016.09.018)
20. Lorenzi E, Vallortigara G. 2021 Evolutionary and neural bases of the sense of animacy. In *The Cambridge handbook of animal cognition* (eds AB Kaufman, J Call, JC Kaufman), pp. 295–321. Cambridge, UK: Cambridge University Press. (doi:10.1017/9781108564113.017)
21. Rosa Salva O, Mayer U, Vallortigara G. 2015 Roots of a social brain: developmental models of emerging animacy-detection mechanisms. *Neurosci. Biobehav. Rev*. **50**, 150–168. (doi:10.1016/j.neubiorev.2014.12.015)
22. Rosa-Salva O, Mayer U, Versace E, Hébert M, Lemaire BS, Vallortigara G. 2021 Sensitive periods for social development: Interactions between predisposed and learned mechanisms. *Cognition* **213**, 104552. (doi:10.1016/j.cognition.2020.104552)
23. Versace E, Martinho-Truswell A, Kacelnik A, Vallortigara G. 2018 Priors in animal and artificial intelligence: where does learning begin? *Trends Cogn. Sci*. **22**, 963–965. (doi:10.1016/j.tics.2018.07.005)
24. Versace E, Vallortigara G. 2015 Origins of knowledge: insights from precocial species. *Front. Behav. Neurosci.* **9**, 338. (doi:10.3389/fnbeh.2015.00338)
25. Gamberale-Stille G, Tullberg B. 2001 Fruit or aposematic insect? Context-dependent colour preferences in domestic chicks. *Proc. R. Soc. B* **268**, 2479–2484. (doi:10.1098/rspb.2001.1814)
26. Roper TJ, Marples NM. 1997 Colour preferences of domestic chicks in relation to food and water presentation. *Appl. Anim. Behav. Sci*. **54**, 207–213. (doi:10.1016/s0168-1591(96)01178-1)
27. Bolhuis JJ. 1991 Mechanisms of avian imprinting: a review. *Biol. Rev*. **66**, 303–345. (doi:10.1111/j.1469-185x.1991.tb01145.x)
28. Lemaire BS, Rucco D, Josserand M, Vallortigara G, Versace E. 2021 Stability and individual variability of social attachment in imprinting. *Sci. Rep.* **11**, 7914. (doi:10.1038/s41598-021-86989-3)
29. McCabe BJ. 2019 Visual imprinting in birds: behavior, models, and neural mechanisms. *Front. Physiol.* **10**, 658. (doi:10.3389/fphys.2019.00658)
30. Vasconcelos RO, Bolgan M, Matos AB, Van-Dunem SP, Penim J, Amorim MCP. 2024 Characterization of the vocal behavior of the miniature and transparent fish model, *Danionella cerebrum*. *J. Acoust. Soc. Am*. **155**, 781–789. (doi:10.1121/10.0024346)
31. Mascalzoni E, Osorio D, Regolin L, Vallortigara G. 2012 Symmetry perception by poultry chicks and its implications for three-dimensional object recognition. *Proc. R. Soc. B* **279**, 841–846. (doi:10.1098/rspb.2011.1486)

32. Hébert M, Versace E, Vallortigara G. 2019 Inexperienced preys know when to flee or to freeze in front of a threat. *Proc. Natl Acad. Sci. USA* **116**, 22918–22920. (doi:10.1073/pnas.1915504116)
33. Jones CD, Osorio D. 2004 Discrimination of oriented visual textures by poultry chicks. *Vision Res.* **44**, 83–89. (doi:10.1016/j.visres.2003.08.014)
34. Snowden RJ, Freeman TCA. 2004 The visual perception of motion. *Curr. Biol.* **14**, R828–R831. (doi:10.1016/j.cub.2004.09.033)
35. Sun P, Chubb C, Sperling G. 2015 Two mechanisms that determine the Barber-Pole Illusion. *Vision Res.* **111**, 43–54. (doi:10.1016/j.visres.2015.04.002)
36. Rosa-Salva O, Hernik M, Broseghini A, Vallortigara G. 2018 Visually-naïve chicks prefer agents that move as if constrained by a bilateral body-plan. *Cognition* **173**, 106–114. (doi:10.1016/j.cognition.2018.01.004)
37. Girshick AR, Landy MS, Simoncelli EP. 2011 Cardinal rules: visual orientation perception reflects knowledge of environmental statistics. *Nat. Neurosci*. **14**, 926–932. (doi:10.1038/nn.2831)
38. Zolman JF, Lattin WJ. 1972 Development of brightness preferences in young chicks: effects on brightness discrimination learning. *J. Comp. Physiol. Psychol.* **79**, 271–283. (doi:10.1037/h0032565)
39. Clarke CH, Jones BR. 2000 Domestic chicks' attraction to video images: effects of stimulus movement, brightness, colour and complexity. *Int. J. Comp. Psychol*. **13**, T593. (doi:10.46867/c4t593)
40. Delius JD, Thompson G. 1970 Brightness dependence of colour preferences in herring gull chicks. *Z. Für Tierpsychol*. **27**, 842–849. (doi:10.1111/j.1439-0310.1970.tb01905.x)
41. Miura M, Matsushima T. 2012 Preference for biological motion in domestic chicks: sex-dependent effect of early visual experience. *Anim. Cogn*. **15**, 871–879. (doi:10.1007/s10071-012-0514-x)
42. Rosa-Salva O, Regolin L, Vallortigara G. 2010 Faces are special for newly hatched chicks: evidence for inborn domain-specific mechanisms underlying spontaneous preferences for face-like stimuli. *Dev. Sci.* **13**, 565–577. (doi:10.1111/j.1467-7687.2009.00914.x)
43. Hess EH. 1959 Imprinting. *Science* **130**, 133–141. (doi:10.1126/science.130.3368.133)
44. Lemaire BS, Vallortigara G. 2023 Life is in motion (through a chick's eye). *Anim. Cogn*. **26**, 129–140. (doi:10.1007/s10071-022-01703-8)
45. Lorenz KZ. 1937 The companion in the bird's world. *Auk* **54**, 245–273. (doi:10.2307/4078077)
46. Petroff ZJ, Jayaraman S, Smith LB, Candy TR, Bonnen K. 2025 The world through infant eyes: evidence for the early emergence of the cardinal orientation bias. *Proc. Natl Acad. Sci. USA* **122**, e2421277122. (doi:10.1073/pnas.2421277122)
47. Bateson P. 1990 Is imprinting such a special case? *Phil. Trans. R. Soc. Lond. B* **329**, 125–131. (doi:10.1098/rstb.1990.0157)
48. Wang S, Vasas V, Freeland L, Osorio D, Versace E. 2024 Spontaneous biases enhance generalization in the neonate brain. *iScience* **27**, 110195. (doi:10.1016/j.isci.2024.110195)
49. Osorio D, Miklósi A, Gonda Zs. 1999 Visual ecology and perception of coloration patterns by domestic chicks. *Evol. Ecol*. **13**, 673–689. (doi:10.1023/a:1011059715610)
50. Zylinski S, Osorio D. 2013 Visual contrast and color in rapid learning of novel patterns by chicks. *J. Exp. Biol*. 085001. (doi:10.1242/jeb.085001)
51. Bateson P. 1979 Brief exposure to a novel stimulus during imprinting in chicks and its influence on subsequent preferences. *Anim. Learn. Behav*. **7**, 259–262. (doi:10.3758/bf03209281)
52. Jackson PS, Bateson PPG. 1974 Imprinting and exploration of slight novelty in chicks. *Nature* **251**, 609–610. (doi:10.1038/251609a0)
53. Versace E, Spierings MJ, Caffini M, ten Cate C, Vallortigara G. 2017 Spontaneous generalization of abstract multimodal patterns in young domestic chicks. *Anim. Cogn*. **20**, 521–529. (doi:10.1007/s10071-017-1079-5)
54. Bateson PP. 1973 Preferences for familiarity and novelty: a model for the simultaneous development of both. *J. Theor. Biol.* **41**, 249–259. (doi:10.1016/0022-5193(73)90117-3)
55. Tavoni G, Doi T, Pizzica C, Balasubramanian V, Gold JI. 2022 Human inference reflects a normative balance of complexity and accuracy. *Nat. Hum. Behav*. **6**, 1153–1168. (doi:10.1038/s41562-022-01357-z)
56. Marr D. 1982 *Vision: a computational investigation into the human representation and processing of visual information*. Cambridge, MA: MIT Press.
57. Hubel DH, Wiesel TN. 1959 Receptive fields of single neurones in the cat's striate cortex. *J. Physiol.* **148**, 574–591. (doi:10.1113/jphysiol.1959.sp006308)
58. Hubel DH, Wiesel TN. 1962 Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol*. **160**, 106–154. (doi:10.1113/jphysiol.1962.sp006837)
59. Piasini E. 2021 metex - Maximum Entropy TEXtures (v.1.1.0) (doi:10.5281/zenodo.4753198)
60. Wisely CE, Sayed JA, Tamez H, Zelinka C, Abdel-Rahman MH, Fischer AJ, Cebulla CM. 2017 The chick eye in vision research: an excellent model for the study of ocular disease. *Prog. Retin. Eye Res.* **61**, 72–97. (doi:10.1016/j.preteyeres.2017.06.004)
61. Goldman JG, Wood JN. 2015 An automated controlled-rearing method for studying the origins of movement recognition in newly hatched chicks. *Anim. Cogn.* **18**, 723–731. (doi:10.1007/s10071-015-0839-3)
62. Cailotto M, Vallortigara G, Zanforlin M. 1989 Sex differences in the response to social stimuli in young chicks. *Ethol. Ecol. Evol*. **1**, 323–327. (doi:10.1080/08927014.1989.9525502)
63. Vallortigara G. 1992 Affiliation and aggression as related to gender in domestic chicks (*Gallus gallus*). *J. Comp. Psychol.* **29**, 56–57. (doi:10.1016/j.cub.2019.05.039)
64. Vallortigara G, Cailotto M, Zanforlin M. 1990 Sex differences in social reinstatement motivation of the domestic chick (*Gallus gallus*) revealed by runway tests with social and nonsocial reinforcement. *J. Comp. Psychol*. **104**, 361–367. (doi:10.1037//0735-7036.104.4.361)
65. Workman L, Andrew RJ. 1989 Simultaneous changes in behaviour and in lateralization during the development of male and female domestic chicks. *Anim. Behav*. **38**, 596–605. (doi:10.1016/s0003-3472(89)80004-1)
66. Mathis A, Mamidanna P, Cury KM, Abe T, Murthy VN, Mathis MW, Bethge M. 2018 DeepLabCut: markerless pose estimation of user-defined body parts with deep learning. *Nat. Neurosci.* **21**, 1281–1289. (doi:10.1038/s41593-018-0209-y)
67. Nath T, Mathis A, Chen AC, Patel A, Bethge M, Mathis MW. 2019 Using DeepLabCut for 3D markerless pose estimation across species and behaviors. *Nat. Protoc.* **14**, 2152–2176. (doi:10.1038/s41596-019-0176-0)
68. Posit team. 2025 RStudio: Integrated Development Environment for R (Version 1.4.17.17). PBC, Boston, MA: Posit Software. See http://www.posit.co/.
69. R Core Team. 2025 R: A language and environment for statistical computing (Version 4.1.0). Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org/.
70. Davison AC, Hinkley DV. 1997 *Bootstrap methods and their application (reprinted with corrections 2003)*. Cambridge, UK: Cambridge University Press.
71. Zanon M, Lemaire BS, Piasini E, Caramellino R, Nallet C, Balasubramanian V, Gervain J, Zoccolan D, Vallortigara G. 2025 Predisposed and learned preferences for multipoint visual statistics in visually naïve newly hatched chicks. Figshare. (doi:10.6084/m9.figshare.28846787)
72. Zanon M *et al*. 2026 Supplementary material from: Predisposed and learned preferences for multipoint visual statistics in visually naïve newly hatched chicks. Figshare. (doi:10.6084/m9.figshare.c.8287173)