

Face Recognition in Newly Hatched Chicks at the Onset of Vision

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How does face recognition emerge in the newborn brain? To address this question, we used an automated controlled-rearing method with a newborn animal model: the domestic chick (*Gallus gallus*). This automated method allowed us to examine chicks' face recognition abilities at the onset of both face experience and object experience. In the first week of life, newly hatched chicks were raised in controlled-rearing chambers that contained no objects other than a single virtual human face. In the second week of life, we used an automated forced-choice testing procedure to examine whether chicks could distinguish that familiar face from a variety of unfamiliar faces. Chicks successfully distinguished the familiar face from most of the unfamiliar faces—for example, chicks were sensitive to changes in the face's age, gender, and orientation (upright vs. inverted). Thus, chicks can build an accurate representation of the first face they see in their life. These results show that the initial state of face recognition is surprisingly powerful: Newborn visual systems can begin encoding and recognizing faces at the onset of vision.

Keywords: controlled rearing, chick, face recognition, newborn, automation, *Gallus gallus*

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Social animals depend heavily on their ability to recognize faces. For instance, face recognition (i.e., the ability to encode and recognize specific faces) allows animals to form and maintain social relationships and identify key competitors in their group. Previous studies have examined face recognition abilities days, months, and years after birth (e.g., Carey & Diamond, 1977; de Haan, Johnson, Maurer, & Perrett, 2001; Frank, Vul, & Johnson, 2009; Kelly et al., 2007; Pascalis, Deschonen, Morton, Deruelle, & Fabregrenet, 1995; Sugita, 2008). To date, however, little is known about the “initial state” of face recognition (i.e., the state of face recognition at the onset of vision). Can newborn¹ animals encode and recognize faces at the onset of both face experience and object experience? Or does face recognition have a protracted development, requiring extensive exposure to faces and/or objects in order to develop?

In the present study, we used an automated controlled-rearing method to address three questions: (a) Can newborn animals build an accurate representation of the first face they see in their life?; (b) What types of face changes can newborn animals detect at the onset of vision?; and (c) Are there individual differences in newborn animals' face recognition abilities?

To be clear at the outset, this study was not designed to test whether face recognition depends on the same mechanisms or

different mechanisms than object recognition. Rather, our goal was to examine whether newborn animals are capable of encoding and recognizing faces at the onset of vision. In the discussion, we return to the issue of whether face recognition and object recognition depend on shared versus unique mechanisms at the onset of vision.

Chickens as an Animal Model for Studying the Initial State of Face Recognition

Face recognition is a form of visual learning. According to a growing body of work in the neurosciences, visual learning occurs rapidly within the visual system (e.g., Espinosa & Stryker, 2012; Gavornik & Bear, 2014; DiCarlo, Zoccolan, & Rust, 2012). For instance, the visual cortex uses statistical redundancies present in the natural environment to fine-tune the response properties of neurons (Edelman & Intrator, 2003; Olshausen & Field, 1996). Further, studies of monkeys show that category-selective regions emerge in the cortex on the basis of early visual experience (Srihasam, Mandeville, Morocz, Sullivan, & Livingstone, 2012), with significant changes in the response patterns of neural populations occurring as little as 1 hr after exposure to an altered visual world (Li & DiCarlo, 2008). Because the visual system is rapidly shaped by visual experience, studying the origins of a visual learning ability like face recognition requires a controlled-rearing approach with a newborn animal model. With controlled-rearing methods, it is possible to systematically manipulate an animal's visual experiences, and thus assess the impact of specific experiences on the development of perceptual and cognitive abilities.

In the current study, we used a controlled-rearing method with domestic chicks (*Gallus gallus*). Five characteristics make chicks

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¹ The term “newborn” is used to refer to an animal at the beginning of the postembryonic phase of its life cycle.

an ideal animal model for studying the initial state of face recognition. First, chicks can be raised in environments devoid of both faces and objects. Unlike newborn primates, newly hatched chicks do not require parental care and, because of precocial motor development, are immediately able to explore their environment. Second, chicks imprint to conspicuous objects seen in the first few days of life (e.g., Bateson, 1966; Horn, 2004). Chicks develop a strong attachment to their imprinted objects, treating them as social partners. Thus, this imprinting behavior can be used to test chicks' visual recognition abilities without training. Third, adult birds can discriminate between human faces, and rely on similar facial features for face recognition as human adults (Bogale, Aoyama, & Sugita, 2011; Gibson, Wasserman, Gosselin, & Schyns, 2005). These findings provide evidence that human and avian visual systems build similar face representations as one another. Fourth, chicks show a preference for face-like stimuli at the onset of face experience (Rosa-Salva, Farroni, Regolin, Vallortigara, & Johnson, 2011; Rosa-Salva, Regolin, & Vallortigara, 2010, 2012), akin to newborn humans. The current study builds on these findings by examining whether chicks can encode and recognize *specific* faces at the onset of vision. Fifth, chickens and humans use similar neural circuits to process sensory information (Karten, 2013). Although mammalian and avian brains differ in their macroarchitecture (i.e., layered vs. nuclear organization, respectively), they are nearly identical from the perspective of the cells and circuits that process sensory information (reviewed by Karten, 2013). Together, these five characteristics make chicks an ideal and unique animal model for studying the emergence of face recognition in a biological visual system.

Previous controlled-rearing studies have also demonstrated that chicks are a promising animal model for studying the origins of object recognition and visual learning more generally. For instance, chicks begin binding color and shape features into integrated object representations at the onset of vision (Wood, 2014), and can build a viewpoint-invariant representation of the first object they see in their life (Wood, 2013, 2015; Wood & Wood, 2015). Chicks also begin encoding and recognizing movements and movement sequences within the first few days of life (Goldman & Wood, 2015). The present study builds on this previous work by examining whether newly hatched chicks can build accurate representations of faces at the onset of vision. Face recognition is a prototypical example of subordinate-level object recognition because all faces share a general configuration (Carey, Schonen, & Ellis, 1992). Thus, face recognition requires more fine-grained discrimination than basic-level object recognition.

An Automated Controlled-Rearing Method for Studying Face Recognition

In the past, newborn animals' behavior has been quantified through direct observation by trained researchers. Although direct observation has revealed many important insights about newborn cognition, there are limitations to this approach (Dell et al., 2014). Direct observation produces a limited amount of data with relatively low spatial and temporal resolution. Further, the resulting data are a subjective description of the subject's behavior, rather than an exact record of events. Direct observation therefore allows for the possibility of experimenter bias, a well-recognized problem in both comparative and de-

velopmental psychology. In contrast to direct observation, automated experimental methods allow researchers to collect large amounts of data from each subject and quantify behavior at scales not previously possible. Further, because the observations are not made by a researcher, automated methods remove the possibility of experimenter bias.

Here, we describe an automated "complete data" controlled-rearing method for studying the initial state of face recognition. This automated approach has previously been used to study the initial state of object recognition (Wood, 2013, 2014, 2015) and action recognition (Goldman & Wood, 2015); here, we extend the method to the domain of face recognition. We use the term "complete data" because the method involves recording *all* of the newborn subjects' behavior (24 hours/day, 7 days/week) with high precision (9 samples/second). This approach produces a complete digital record of each subject's behavior across their life span.

The goal of the current study was to examine the initial state of face recognition by testing newly hatched chicks' face recognition abilities across a wide range of face-change conditions. In their first week of life (the input phase), chicks were raised in controlled-rearing chambers that contained no objects other than a single virtual human face. In their second week of life (the test phase), we tested whether chicks could distinguish that virtual face from a variety of unfamiliar faces. Because we recorded all of the chicks' behavior, it was possible to present each subject with a large number of test trials (~140 test trials per chick) across 10 face-change conditions. As a result, we were able to determine the general features used by each chick to recognize faces and compare the face recognition strategies employed by different subjects.

Method

Subjects

Thirteen domestic chicks of unknown sex were tested. No subjects were excluded from the analyses. Fertilized eggs were obtained from a local distributor and incubated in darkness in an OVA-Easy (Brinsea Products Inc., Titusville, FL) incubator. The temperature and humidity were maintained at 99.6 °F and 45%, respectively, for the first 19 days of incubation. On Day 19, we increased the humidity to 60%. The incubation room was kept in darkness. On Day 1 of life, the chicks were moved from the incubator room to the controlled-rearing chambers in darkness with the aid of night vision goggles.

Controlled-Rearing Chambers

The chicks were raised for 2 weeks within controlled-rearing chambers (66 cm length × 42 cm width × 69 cm height). The chambers were constructed from white, high-density plastic. Face stimuli were presented to the chicks by projecting animated videos onto two display walls (19-in. liquid crystal display monitors with 1440 × 900 pixel resolution) situated on opposite sides of the chamber (Figure 1A).

The chambers contained no rigid, bounded objects other than the virtual face presented on the display walls. All care of the chicks was performed in darkness with the aid of night vision

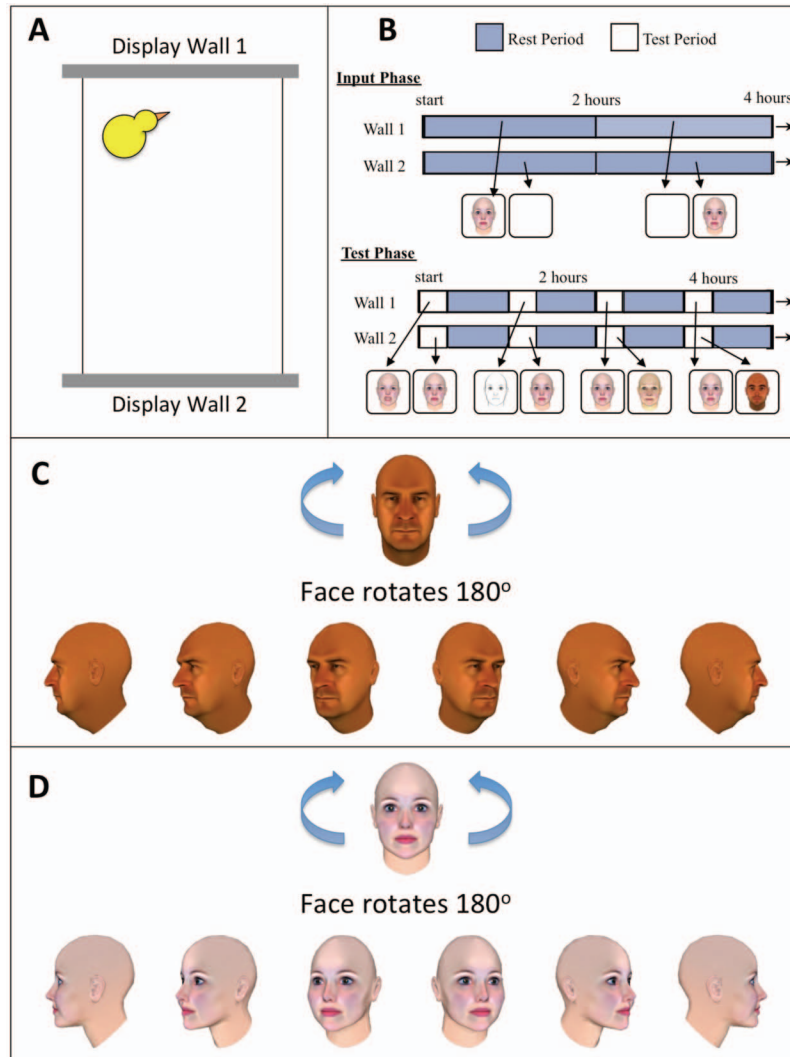


Figure 1. (A) An illustration of the controlled-rearing chambers from a bird's eye perspective (not shown to scale). (B) A schematic of the presentation schedule of the virtual faces on the two display walls during the input phase (top) and the test phase (bottom). (C) Images from the male face animation shown during the input phase. (D) Images from the female face animation shown during the input phase. Each chick was shown either the male face or the female face. See the online article for the color version of this figure.

goggles. Food and water were provided ad libitum in transparent, rectangular troughs in the ground (66 cm length \times 2.5 cm width \times 2.7 cm height). We used grain as food because grain does not behave like an object (i.e., grain does not maintain a rigid, bounded shape). When building these chambers, we attempted to minimize the existence of patterned surfaces as much as possible. All of the walls and ceilings were homogeneous white extended surfaces. We also minimized the saliency of the floor by using black wire mesh supported over a black surface by thin, transparent beams.

Chicks' behavior was tracked by microcameras (1.5 cm diameter) embedded in the ceilings of the chambers and automated image-based animal tracking software (EthoVision XT, Noldus Information Technology, Leesburg, VA). This software calculated the amount of time each chick spent within zones (22 cm \times 42 cm

next to the left and right display walls. Chicks were considered to be in proximity to the face on the left versus right display wall when the chick occupied the zone next to the left versus right display wall, respectively.

Input Phase

During the input phase (the first week of life), chicks were raised in an environment that contained a single virtual face. Imprinting in chicks is subject to a critical period, which ends approximately three days after hatching. Thus, to ensure that the chicks had fully imprinted to the virtual face, we exposed the chicks to the virtual face for the first 7 days of life. Six chicks were shown an older male face (ear-to-ear width = 6.2 cm, height = 10 cm) and seven chicks were shown a younger female face (ear-to-ear width = 6.5 cm; height =

10 cm; Figure 1C and 1D). The virtual face moved continuously, rotating smoothly through a 180° viewpoint range about a frontoparallel vertical axis passing through its centroid. The animations contained 24 frames per second. The individual face frames were created using FaceGen software (Singular Inversions Inc., Toronto, ON). The faces were displayed on a uniform white background and positioned 1 cm off the ground in the middle of the display walls. The imprinted face appeared for an equal amount of time on the left and right display wall and switched walls every 2 hr, following a 1-min period of darkness (Figure 1B).

We used human faces (rather than chicken faces) because the face images could be precisely manipulated along a variety of dimensions using the FaceGen software. More importantly, using human faces allows for a more direct comparison with studies of face recognition in humans and other avian species (Bogale et al., 2011; Gibson et al., 2005; Troje, Huber, Loidolt, Aust, & Fieder, 1999).

Test Phase

During the test phase (the second week of life), we probed the informational content of the face representation built by each chick by using an automated two-alternative forced choice testing procedure. On each test trial, the imprinted face was projected onto one display wall and an unfamiliar face was projected onto the other display wall (see Figure 1B). If chicks recognized their imprinted face, then they should have spent a greater proportion of time in proximity to the imprinted face compared with the unfamiliar face during these test trials. The unfamiliar faces had the same size, motion speed, and viewpoint range as the imprinted

face. The test trials lasted 24 min and were separated from one another by 46-min rest periods. There was one minute of darkness between the test trials and the rest periods. During the rest periods, the imprinted face appeared on one display wall and a white screen appeared on the other display wall. Each chick received 20 test trials per day (two test trials for each of the 10 face-change conditions). The conditions were presented in randomized blocks throughout the test phase.

Because this was the first study to examine chicks' face recognition abilities at the onset of vision, we presented subjects with a wide range of face change conditions to obtain a general sense of their recognition abilities (see Figure 2). In the "edges only" condition, the unfamiliar face was a line drawing of the imprinted face. In the "no color" condition, the unfamiliar face was created by removing all color information from the imprinted face. We included these two conditions to test whether chicks encode only the edge/shape features of a face or whether they also encode the color features of a face. In the "features only" condition, the unfamiliar face had the eyes and mouth of the imprinted face but without any of the surrounding facial context. In the "repositioned features" condition, the unfamiliar face was created by moving the facial features of the imprinted face to new positions. We included these two conditions to test whether chicks encode only the eye and mouth features of a face or whether they encode the surrounding facial context, and also to examine whether chicks encode the positions of the eyes and mouth within the face. In the "inverted" condition, the unfamiliar face was identical to the imprinted face, but in an inverted position. We tested chicks in this condition to



Figure 2. Results from the 10 face-change conditions. Each bar shows the average percent of correct trials in each condition for the male (blue bars on the left) and female (green bars on the right) imprinted face. Chance performance was 50%. Error bars denote standard error. See the online article for the color version of this figure.

examine whether they encode the spatial orientation of a face. In the “different age” condition, we changed the age of the imprinted face (i.e., for the young woman imprinted face, the unfamiliar face was an older woman; and for the older man imprinted face, the unfamiliar face was a younger man). We modified the gender of the imprinted face in two conditions. In the “different gender coloring” condition, the unfamiliar face had the same shape as the imprinted face, but with color features that were more characteristic of the opposite gender. In the “different gender shape” condition, the unfamiliar face had the same color as the imprinted face, but with shape features that were more characteristic of the opposite gender. We tested chicks in these conditions to examine whether they can distinguish between faces of different identities based on gender and age information. Finally, we tested chicks’ sensitivity to facial expressions: The unfamiliar face was identical to the imprinted face except that it had either an angry (“angry expression” condition) or fearful (“fearful expression” condition) expression. We tested chicks in these conditions to examine whether they build representations of faces that are tolerant to changes in expression. All of the face stimuli used in this study can be viewed in Supplementary Movies 1 and 2 of the online supplemental materials.

Results

A test trial was scored as “correct” when the chick spent a greater proportion of time with the imprinted face compared with the unfamiliar face, and “incorrect” when the chick spent a greater proportion of time with the unfamiliar face compared with the imprinted face. Figure 2 shows the percent of correct trials for each of the 10 conditions.

Bayesian Analyses

To examine whether performance in each condition exceeded chance levels, we used hierarchical Bayesian methods (Kruschke, 2011) that provided detailed probabilistic estimates of recognition ability for both the individual subjects and the overall group. Thus, we report the actual probability that chicks’ mean face recognition performance was above chance, rather than traditional p values.

Bayesian analyses are less common than null hypothesis tests, but they offer several advantages. First, Bayesian analyses do not require the same assumptions as null hypothesis tests (Kruschke, 2011). For most null hypothesis tests, two groups should have normal distributions, similar variance, and similar numbers of samples per condition and subject. In contrast, Bayesian analyses are not subject to these constraints, and the assumptions that do exist are described explicitly in the prior distribution. Second, the output of Bayesian analyses are more intuitive than the output of null hypothesis testing: Rather than reporting p values (i.e., the probability of obtaining data as extreme as the data actually obtained assuming that the null hypothesis is true), Bayesian analyses estimate the actual probability that performance was higher than chance levels (a more intuitive statistic to interpret). Third, unlike traditional null hypothesis testing, Bayesian analyses yield the same result regardless of whether the researcher follows a preplanned “stopping rule” in terms of the number of subjects tested in the study. This is not the case for null hypothesis testing² (for a detailed discussion, see Kruschke, 2010). Finally, Bayesian

models can readily account for dependencies in the structure of the data (Kruschke, 2010). For instance, the Bayesian models used here contained three hierarchically dependent levels (see Figure 3). The top level estimated the overall mean performance across all chicks for the condition. The middle level estimated the mean performance for the chicks imprinted to the male face and the female face. The lower level estimated the performance of each individual chick.

The Bayesian models used here contained two assumptions. First, the models assumed that there were hierarchical dependencies in the data. Second, the models contained a prior distribution of performance. To be conservative, we used an “uninformative” prior consisting of one correct trial and one incorrect trial. The prior distribution also included a parameter, kappa, which represents the consistency in performance across subjects. We used a uniform density prior for kappa (Gelman, 2006) that ranged from 0.000001 to the maximum reasonable kappa. The maximum reasonable kappa was estimated from subjects’ performance during the rest periods in the test phase. The rest periods were expected to produce the greatest consistency across subjects because they presented the easiest choice: Subjects chose whether to spend time with their imprinted face versus a white screen.

We used Markov Chain Monte Carlo sampling to approximate the posterior distribution of the overall performance in each condition and the ability of each subject. The analysis used five chains with a burn-in of 10,000 steps, with 100,000 steps after burn-in. All analyses were performed using R version 2.15.0 (<http://www.r-project.org/>), JAGS (<http://mcmc-jags.sourceforge.net/>), and adaptation of program code from John Kruschke (Kruschke, 2011).

The probability that group performance was above chance was greater than 99% in six of the 10 conditions: edges only, no color, features only, different gender coloring, inverted, and different age conditions. The probability that group performance was above chance was 81% in the gender shape condition, 77% in the fearful expression condition, 67% in the angry expression condition, and 48% in the repositioned features condition. Figures 1 through 10 of the online supplemental materials show the probability density graphs for chicks’ performance in each condition.

Analysis of Effect Sizes

To quantify the magnitude of the chicks’ performance, we computed a one-sample Cohen’s d for each condition. We found large effect sizes (i.e., greater than 0.8) for six of the 10 conditions: edges only ($d = 6.7$), no color ($d = 4.7$), features only ($d = 2.6$), different gender coloring ($d = 1.1$), inverted ($d = 1.2$), and different age ($d = 1.5$). We also found a medium effect size for the different gender shape condition ($d = 0.5$). The remaining conditions had small effect sizes: fearful expression ($d = 0.3$), angry expression ($d = 0.2$), and repositioned features ($d = -0.04$).

² For example, if a researcher performs a null hypothesis test after collecting 20 trials and that analysis is not significant, and then the researcher decides to collect 10 more trials, the second null hypothesis test no longer provides the true false alarm rate.

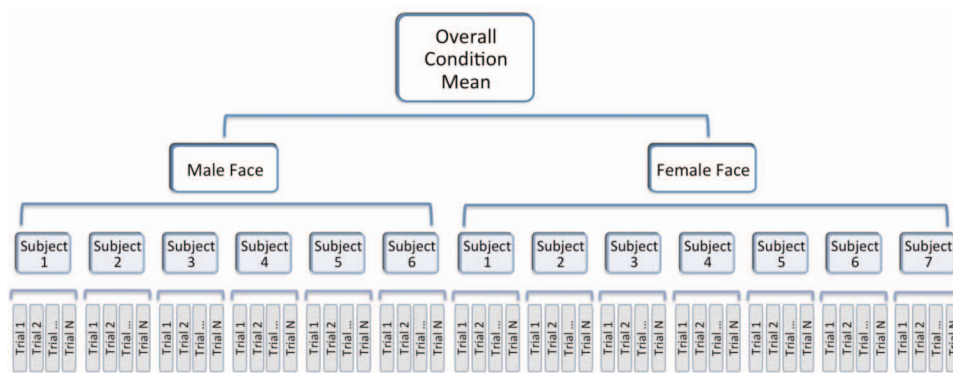


Figure 3. Structure of the Bayesian models. The top level of the model estimated the overall mean performance across all chicks for the condition. The middle level estimated the mean performance for the chicks imprinted to the male face and the female face. The lower level estimated the performance of each individual chick. See the online article for the color version of this figure.

Analysis of Change in Performance Over Time

To examine whether performance changed over the test phase, we calculated the proportion of time that chicks spent in proximity to the imprinted face versus the unfamiliar face as a function of trial number (e.g., first presentation of face stimuli, second presentation, etc.). As shown in Figure 4, there was a significant positive correlation between trial number and performance, $r = .56, p = .04$. However, this positive correlation was largely driven by poor performance during the first trial (i.e., the first presentation of the face stimuli). When the first trial was removed from the analysis, the correlation between trial number and performance was no longer significant, $r = .38, p = .20$.

Thus, additional research is necessary to determine the extent to which chicks' face recognition abilities improve over time in these impoverished visual environments.

Analysis of Individual Subject Performance

With this controlled-rearing method, we were able to collect a large number of test trials from each chick. This made it possible to measure each chick's face recognition abilities with high precision. First, we examined whether all of the chicks were able to build an accurate representation of their imprinted face, by computing whether each chick's performance across the test trials exceeded chance level.

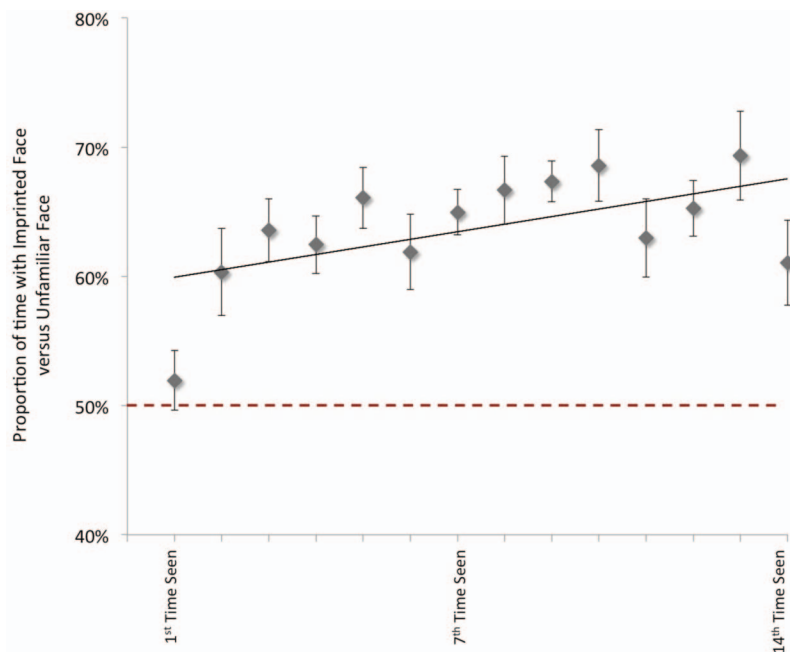


Figure 4. Change over time results. The graph illustrates group mean performance over the full set of face change conditions shown during the test phase, computed for the first, second, third, and so forth, presentation of the conditions. Chance performance was 50%. Error bars denote standard error. See the online article for the color version of this figure.

As shown in Figure 5A, all 13 of the chicks spent more time with the imprinted face compared with the unfamiliar face on the test trials (one-tailed binomial test, all $p_s \leq .05$). This result indicates that all of the chicks were able to build an accurate representation of the virtual face.

Second, we examined whether the chicks used the same general strategy as one another to distinguish the imprinted face from the unfamiliar faces. Figure 5B shows each chick's sensitivity to each of the face changes. Visual inspection of Figure 5B shows that the majority of the chicks were sensitive to the same face changes. To examine whether the chicks' face recognition abilities were correlated with one another, we created a correlation matrix (Figure 5C). This matrix shows the correlation in face recognition performance for each pair of chicks across the conditions (i.e., each box shows the correlation between two chicks' percent of correct trials in each condition).

Chicks' face recognition abilities were highly correlated across the conditions, with an average between-subjects correlation of $r = .58$ ($SEM = 0.02$).

Analysis of Differences in Performance Between the Male and Female Imprinted Faces

The Bayesian analyses did not reveal any differences in performance between the chicks imprinted to the male face versus the female face in any condition (see online supplemental material for details). Similarly, a repeated measures ANOVA with the between-subjects factor of Imprinted Face and within-subjects factor of Test Condition revealed a significant main effect of Test Condition, $F(9, 99) = 17.31, p < .001$. However, the main effect

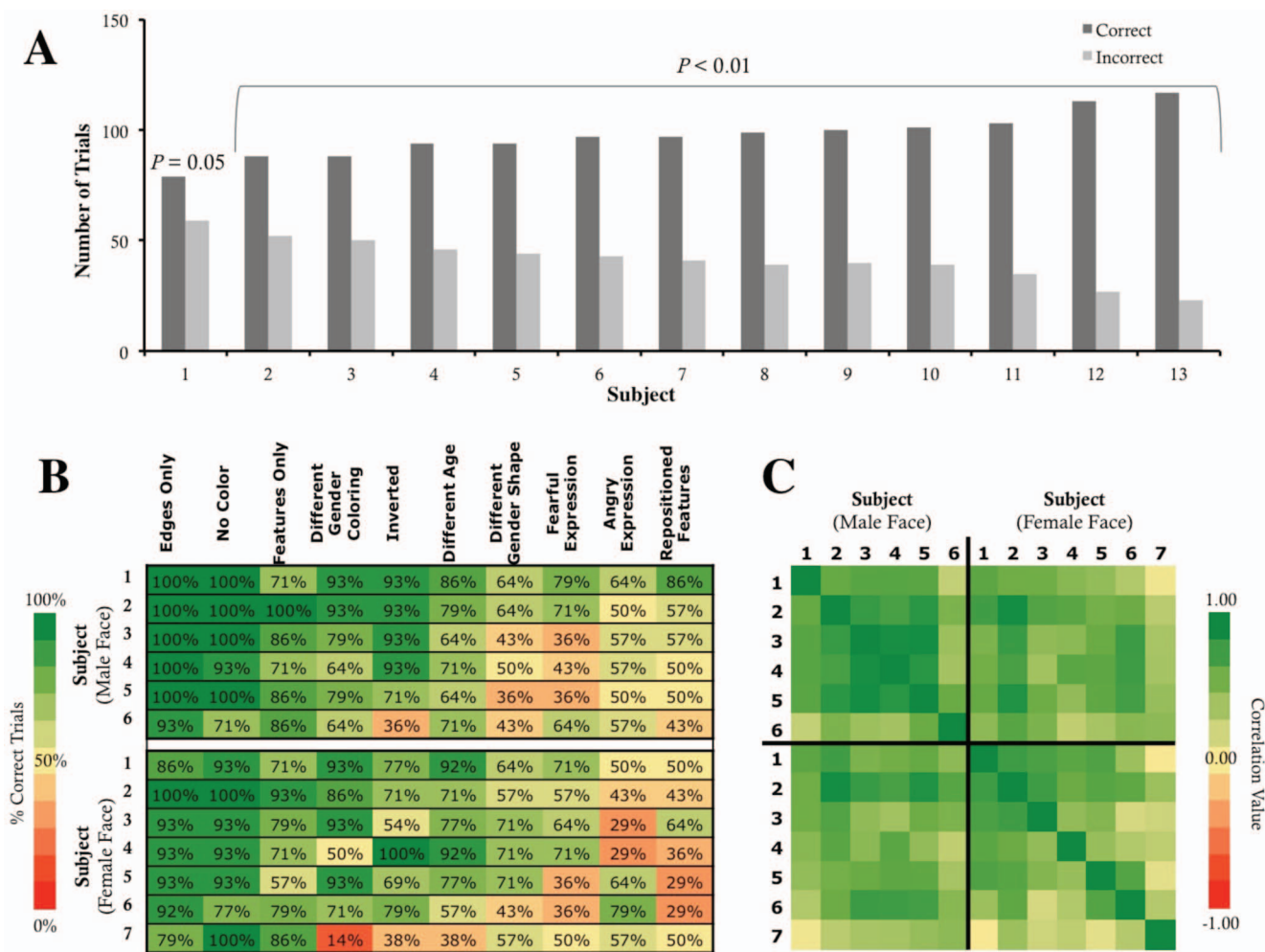


Figure 5. (A) Performance of each individual subject (ordered by performance). The graph shows the total number of correct and incorrect test trials for each chick across the test phase. P values denote the statistical difference between the number of correct and incorrect test trials (computed through one-tailed binomial tests). (B) The percentage of correct trials for each chick in each condition. Chance performance was 50%. Subjects are ordered by overall performance for each imprinted face. (C) A correlation matrix showing the correlation in face recognition performance for each pair of chicks. Each box shows the correlation between two chicks' percent of successful trials in each condition. The subjects are ordered by overall performance for each imprinted face. The cells are color-coded by correlation value. The color scale reflects the full range of possible correlation values. See the online article for the color version of this figure.

of Imprinted Face was not significant, $F(1, 11) = 1.13, p = .31$, nor was the interaction, $F(9, 99) = 0.86, p = .56$.³ In general, chicks' face recognition performance was similar when imprinted to the male face and the female face.

Discussion

This study examined whether newly hatched chicks can encode and recognize faces at the onset of vision. Specifically, chicks were raised in automated controlled-rearing chambers that recorded all of their behavior with high precision. In their first week of life, chicks' visual experience with faces and objects was limited to a single virtual face rotating around a single axis. In their second week of life, we tested whether chicks could distinguish that virtual face from a variety of unfamiliar faces. Three main findings emerged.

First, despite lacking any prior face and object experience, chicks were able to build an accurate representation that supported face recognition across a range of conditions. Although previous studies have shown that newborn animals can detect face-like configurations soon after birth (Johnson, Dziurawiec, Ellis, & Morton, 1991; Rosa-Salva et al., 2010, 2011), the current study indicates that newborn animals can also encode and recognize specific faces at the onset of vision. For instance, chicks were sensitive to changes in their imprinted face's age, gender, and orientation (upright vs. inverted). Further, chicks showed little to no sensitivity to changes in facial expression, which suggests that a chick's first face representation can be tolerant to some identity-preserving facial transformations. Together, this pattern of results shows that chicks can build a selective and tolerant representation of a face. This study extends the existing literature concerning chicks' visual learning abilities. Previous controlled-rearing experiments show that chicks can build an integrated and invariant representation of the first object they see in their environment (Wood, 2013, 2014). The present study shows that chicks can also build an accurate representation of the first face they see. Thus, chicks can learn rapidly about a variety of entities at the onset of vision.

Second, these results provide evidence that chicks build similar face representations as one another at the onset of face and object experience. As shown in Figure 5B, most of the chicks were sensitive to the same visual features when recognizing faces, and as shown in Figure 5C, most of the chicks' face recognition abilities were highly correlated with one another. Thus, different chicks use a common strategy to distinguish between faces.

Third, these results begin to reveal the types of face information that can be encoded at the onset of vision. Our results provide evidence that color information is an important cue for chicks' face recognition abilities because subjects reliably distinguished their imprinted face from unfamiliar faces that had different color features, but identical shape features (i.e., edges only, no color, and different gender coloring conditions). Likewise, many studies have shown that color information plays an important role in human adults' face recognition abilities (e.g., Farah, Wilson, Drain, & Tanaka, 1998; Hill, Bruce, & Akamatsu, 1995; Said & Todorov, 2011). Our results also provide suggestive evidence that chicks use shape and/or orientation information to recognize faces, because subjects reliably distinguished the imprinted face from an inverted version of the imprinted face. More generally, these results accord

with previous controlled rearing experiments of object recognition, which show that chicks can encode both the color and shape of objects (Wood, 2014).

Although the current study focused on the initial state of face recognition, previous developmental studies have shown that experience and maturation play an important role in shaping and calibrating face recognition machinery, with significant changes occurring over the first 16 years of life in humans (Bruce et al., 2000; Carey & Diamond, 1977; Mondloch, Le Grand, & Maurer, 2010). Some researchers have suggested that the development of face recognition is protracted because sensitivity to configural effects does not emerge until relatively late in development (Carey & Diamond, 1977). Our findings are consistent with this suggestion because chicks were not able to distinguish their imprinted face from an unfamiliar face in which the features of the imprinted face were located at different positions (i.e., repositioned features condition).

It is important to emphasize two potential limitations of the current study. First, these chicks observed the imprinted face for an extended period of time throughout the input phase. Thus, additional studies are needed to determine whether chicks can build an accurate face representation after seeing a face briefly, akin to human adults, or whether they need to see a face for an extended period of time.

Second, this experiment was not designed to test whether chicks' face recognition abilities depend on domain-specific versus domain-general recognition mechanisms. Some researchers have proposed that face recognition and object recognition depend on separate, domain-specific systems from birth (Carey, 2009; Spelke & Kinzler, 2007; Vallortigara, 2012). Conversely, other researchers have proposed that face recognition and object recognition initially depend on common domain-general computations, with domain-specific neural populations emerging in the cortex on the basis of visual experience. According to this second proposal, domain-specific face recognition should emerge relatively late in development, only after the animal has been exposed to different classes of objects and faces (reviewed by Wallis, 2013). Support for this domain-general position comes from studies showing that face memory undergoes domain-specific development during the first 10 years of human life (Weigelt et al., 2014), that newborns' early emerging face preferences can be explained by domain-general computations operating over binocular input (Wilkinson, Paikan, Gredebäck, Rea, & Metta, 2014), and that category-selective regions (e.g., regions selective for faces or letter symbols) emerge in the cortex on the basis of early visual experiences (Röder, Ley, Shenoy, Kekunnaya, & Bottari, 2013; Srihasam et al., 2012). It would be interesting for future studies to use this automated controlled-rearing method to examine whether face recognition and object recognition depend on shared versus unique computations at the onset of vision, by examining whether newly hatched chicks use similar computations when building their first face and object representations.

³In addition, independent samples *t* tests did not reveal significant differences between any of the 10 conditions after Bonferroni correction. Prior to Bonferroni correction, only one condition (the edges only condition) had a significant ($p < .05$) difference between the chicks imprinted to the male face versus the female face.

Future studies could also use this controlled-rearing approach to explore a range of other questions about the initial state of face recognition. For example, what specific facial features do newborn animals use to recognize faces at the onset of vision? How do these features change as the animal acquires experiences with faces and/or objects? Are some face changes easier to detect on male faces versus female faces? And how do more abstract facial categories (e.g., categories for race, gender, and age) emerge in the visual system as a function of specific face and object experiences?

In sum, our study provides systematic evidence that newly hatched chicks are capable of recognizing faces. Impressively, chicks are able to distinguish different faces from one another soon after hatching, which shows that experience with a rich visual world is not necessary for developing face recognition.

References

- Bateson, P. P. G. (1966). The characteristics and context of imprinting. *Biological Reviews of the Cambridge Philosophical Society*, *41*, 177–217. <http://dx.doi.org/10.1111/j.1469-185X.1966.tb01489.x>
- Bogale, B. A., Aoyama, M., & Sugita, S. (2011). Categorical learning between “male” and “female” photographic human faces in jungle crows (*Corvus macrorhynchos*). *Behavioural Processes*, *86*, 109–118. <http://dx.doi.org/10.1016/j.beproc.2010.10.002>
- Bruce, V., Campbell, R. N., Doherty-Sneddon, G., Langton, S., McAuley, S., & Wright, R. (2000). Testing face processing skills in children. *British Journal of Developmental Psychology*, *18*, 319–333. <http://dx.doi.org/10.1348/026151000165715>
- Carey, S. (2009). *The origin of concepts*. New York, NY: Oxford University Press. <http://dx.doi.org/10.1093/acprof:oso/9780195367638.001.0001>
- Carey, S., & Diamond, R. (1977). From piecemeal to configurational representation of faces. *Science*, *195*, 312–314. <http://dx.doi.org/10.1126/science.831281>
- Carey, S., Schonen, S. D., & Ellis, H. D. (1992). Becoming a face expert. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, *335*, 95–103. <http://dx.doi.org/10.1098/rstb.1992.0012>
- de Haan, M., Johnson, M. H., Maurer, D., & Perrett, D. I. (2001). Recognition of individual faces and average face prototypes by 1- and 3-month-old infants. *Cognitive Development*, *16*, 659–678. [http://dx.doi.org/10.1016/S0885-2014\(01\)00051-X](http://dx.doi.org/10.1016/S0885-2014(01)00051-X)
- Dell, A. I., Bender, J. A., Branson, K., Couzin, I. D., de Polavieja, G. G., Noldus, L. P., . . . Brose, U. (2014). Automated image-based tracking and its application in ecology. *Trends in Ecology & Evolution*, *29*, 417–428. <http://dx.doi.org/10.1016/j.tree.2014.05.004>
- DiCarlo, J. J., Zoccolan, D., & Rust, N. C. (2012). How does the brain solve visual object recognition? *Neuron*, *73*, 415–434. <http://dx.doi.org/10.1016/j.neuron.2012.01.010>
- Edelman, S., & Intrator, N. (2003). Towards structural systematicity in distributed, statically bound visual representations. *Cognitive Science*, *27*, 73–109. http://dx.doi.org/10.1207/s15516709cog2701_3
- Espinosa, J. S., & Stryker, M. P. (2012). Development and plasticity of the primary visual cortex. *Neuron*, *75*, 230–249. <http://dx.doi.org/10.1016/j.neuron.2012.06.009>
- Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. N. (1998). What is “special” about face perception? *Psychological Review*, *105*, 482–498. <http://dx.doi.org/10.1037/0033-295X.105.3.482>
- Frank, M. C., Vul, E., & Johnson, S. P. (2009). Development of infants’ attention to faces during the first year. *Cognition*, *110*, 160–170. <http://dx.doi.org/10.1016/j.cognition.2008.11.010>
- Gavornik, J. P., & Bear, M. F. (2014). Learned spatiotemporal sequence recognition and prediction in primary visual cortex. *Nature Neuroscience*, *17*, 732–737. <http://dx.doi.org/10.1038/nn.3683>
- Gelman, A. (2006). Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis*, *1*, 515–533.
- Gibson, B. M., Wasserman, E. A., Gosselin, F., & Schyns, P. G. (2005). Applying bubbles to localize features that control pigeons’ visual discrimination behavior. *Journal of Experimental Psychology: Animal Behavior Processes*, *31*, 376–382. <http://dx.doi.org/10.1037/0097-7403.31.3.376>
- Goldman, J. G., & Wood, J. N. (2015). An automated controlled-rearing method for studying the origins of movement recognition in newly hatched chicks. *Animal Cognition*. Advance online publication. <http://dx.doi.org/10.1007/s10071-015-0839-3>
- Hill, H., Bruce, V., & Akamatsu, S. (1995). Perceiving the sex and race of faces: The role of shape and colour. *Proceedings. Biological Science / The Royal Society*, *261*, 367–373. <http://dx.doi.org/10.1098/rspb.1995.0161>
- Horn, G. (2004). Pathways of the past: The imprint of memory. *Nature Reviews Neuroscience*, *5*, 108–120. <http://dx.doi.org/10.1038/nrn1324>
- Johnson, M. H., Dziurawiec, S., Ellis, H., & Morton, J. (1991). Newborns’ preferential tracking of face-like stimuli and its subsequent decline. *Cognition*, *40*, 1–19. [http://dx.doi.org/10.1016/0010-0277\(91\)90045-6](http://dx.doi.org/10.1016/0010-0277(91)90045-6)
- Karten, H. J. (2013). Neocortical evolution: Neuronal circuits arise independently of lamination. *Current Biology*, *23*, R12–R15. <http://dx.doi.org/10.1016/j.cub.2012.11.013>
- Kelly, D. J., Quinn, P. C., Slater, A. M., Lee, K., Ge, L., & Pascalis, O. (2007). The other-race effect develops during infancy: Evidence of perceptual narrowing. *Psychological Science*, *18*, 1084–1089. <http://dx.doi.org/10.1111/j.1467-9280.2007.02029.x>
- Kruschke, J. K. (2010). What to believe: Bayesian methods for data analysis. *Trends in Cognitive Sciences*, *14*, 293–300. <http://dx.doi.org/10.1016/j.tics.2010.05.001>
- Kruschke, J. K. (2011). *Doing Bayesian data analysis: A tutorial with R and BUGS*. Burlington, MA: Academic Press.
- Li, N., & DiCarlo, J. J. (2008). Unsupervised natural experience rapidly alters invariant object representation in visual cortex. *Science*, *321*, 1502–1507. <http://dx.doi.org/10.1126/science.1160028>
- Mondloch, C. J., Le Grand, R., & Maurer, D. (2010). Development of expertise in face recognition. In I. Gauthier, M. J. Tarr, & D. Bub (Eds.), *Perceptual expertise: Bridging brain and behavior* (pp. 67–106). New York, NY: Oxford University Press.
- Olshausen, B. A., & Field, D. J. (1996). Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature*, *381*, 607–609. <http://dx.doi.org/10.1038/381607a0>
- Pascalis, O., Deschonen, S., Morton, J., Deruelle, C., & Fabregrenet, M. (1995). Mothers face recognition by neonates: A replication and an extension. *Infant Behavior & Development*, *18*, 79–85. [http://dx.doi.org/10.1016/0163-6383\(95\)90009-8](http://dx.doi.org/10.1016/0163-6383(95)90009-8)
- Röder, B., Ley, P., Shenoy, B. H., Kekunnaya, R., & Bottari, D. (2013). Sensitive periods for the functional specialization of the neural system for human face processing. *PNAS Proceedings of the National Academy of Sciences of the United States of America*, *110*, 16760–16765. <http://dx.doi.org/10.1073/pnas.1309963110>
- Rosa-Salva, O., Farroni, T., Regolin, L., Vallortigara, G., & Johnson, M. H. (2011). The evolution of social orienting: Evidence from chicks (*Gallus gallus*) and human newborns. *PLoS ONE*, *6*(4), e18802. <http://dx.doi.org/10.1371/journal.pone.0018802>
- 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. *Developmental Science*, *13*, 565–577. <http://dx.doi.org/10.1111/j.1467-7687.2009.00914.x>

- Rosa-Salva, O., Regolin, L., & Vallortigara, G. (2012). Inversion of contrast polarity abolishes spontaneous preferences for face-like stimuli in newborn chicks. *Behavioural Brain Research*, *228*, 133–143. <http://dx.doi.org/10.1016/j.bbr.2011.11.025>
- Said, C. P., & Todorov, A. (2011). A statistical model of facial attractiveness. *Psychological Science*, *22*, 1183–1190. <http://dx.doi.org/10.1177/0956797611419169>
- Spelke, E. S., & Kinzler, K. D. (2007). Core knowledge. *Developmental Science*, *10*, 89–96. <http://dx.doi.org/10.1111/j.1467-7687.2007.00569.x>
- Srihasam, K., Mandeville, J. B., Morocz, I. A., Sullivan, K. J., & Livingstone, M. S. (2012). Behavioral and anatomical consequences of early versus late symbol training in macaques. *Neuron*, *73*, 608–619. <http://dx.doi.org/10.1016/j.neuron.2011.12.022>
- Sugita, Y. (2008). Face perception in monkeys reared with no exposure to faces. *PNAS Proceedings of the National Academy of Sciences of the United States of America*, *105*, 394–398. <http://dx.doi.org/10.1073/pnas.0706079105>
- Troje, N. F., Huber, L., Loidolt, M., Aust, U., & Fieder, M. (1999). Categorical learning in pigeons: The role of texture and shape in complex static stimuli. *Vision Research*, *39*, 353–366. [http://dx.doi.org/10.1016/S0042-6989\(98\)00153-9](http://dx.doi.org/10.1016/S0042-6989(98)00153-9)
- Vallortigara, G. (2012). Core knowledge of object, number, and geometry: A comparative and neural approach. *Cognitive Neuropsychology*, *29*, 213–236. <http://dx.doi.org/10.1080/02643294.2012.654772>
- Wallis, G. (2013). Toward a unified model of face and object recognition in the human visual system. *Frontiers in Psychology*, *4*, 497. <http://dx.doi.org/10.3389/fpsyg.2013.00497>
- Weigelt, S., Koldewyn, K., Dilks, D. D., Balas, B., McKone, E., & Kanwisher, N. (2014). Domain-specific development of face memory but not face perception. *Developmental Science*, *17*, 47–58. <http://dx.doi.org/10.1111/desc.12089>
- Wilkinson, N., Paikan, A., Gredebäck, G., Rea, F., & Metta, G. (2014). Staring us in the face? An embodied theory of innate face preference. *Developmental Science*, *17*, 809–825. <http://dx.doi.org/10.1111/desc.12159>
- Wood, J. N. (2013). Newborn chickens generate invariant object representations at the onset of visual object experience. *PNAS Proceedings of the National Academy of Sciences of the United States of America*, *110*, 14000–14005. <http://dx.doi.org/10.1073/pnas.1308246110>
- Wood, J. N. (2014). Newly hatched chicks solve the visual binding problem. *Psychological Science*, *25*, 1475–1481. <http://dx.doi.org/10.1177/0956797614528955>
- Wood, J. N. (2015). Characterizing the information content of a newly hatched chick's first visual object representation. *Developmental Science*, *18*, 194–205. <http://dx.doi.org/10.1111/desc.12198>
- Wood, S. M. W., & Wood, J. N. (2015). A chicken model for studying the emergence of invariant object recognition. *Frontiers in Neural Circuits*, *9*. Advance online publication. <http://dx.doi.org/10.3389/fncir.2015.00007>

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