Newborn chickens generate invariant object representations at the onset of visual object experience

Justin N. Wood

Department of Psychology, University of Southern California, Los Angeles, CA 90089

Edited by Susan E. Carey, Harvard University, Cambridge, MA, and approved July 8, 2013 (received for review May 3, 2013)

To recognize objects quickly and accurately, mature visual systems build invariant object representations that generalize across a range of novel viewing conditions (e.g., changes in viewpoint). To date, however, the origins of this core cognitive ability have not yet been established. To examine how invariant object recognition develops in a newborn visual system, I raised chickens from birth for 2 weeks within controlled-rearing chambers. These chambers provided complete control over all visual object experiences. In the first week of life, subjects’ visual object experience was limited to a single virtual object rotating through a 60° viewpoint range. In the second week of life, I examined whether subjects could recognize that virtual object from novel viewpoints. Newborn chickens were able to generate viewpoint-invariant representations that supported object recognition across large, novel, and complex changes in the object’s appearance. Thus, newborn visual systems can begin building invariant object representations at the onset of visual object experience. These abstract representations can be generated from sparse data, in this case from a visual world containing a single virtual object seen from a limited range of viewpoints. This study shows that powerful, robust, and invariant object recognition machinery is an inherent feature of the newborn brain.

Newborn cognition | animal cognition | avian cognition | imprinting

Human adults recognize objects quickly and accurately, despite the tremendous variation in appearance that each object can produce on the retina (i.e., a result of changes in viewpoint, scale, lighting, and so forth) (1–4). To date, however, little is known about the origins of this ability. Does invariant object recognition have a protracted development, constructed over time from extensive experiences with objects? Or can the newborn brain begin building invariant representations at the onset of visual object experience?

Because of challenges associated with testing newborns experimentally, previous studies of invariant object recognition were forced to test individuals months or years after birth. Thus, during testing, subjects were using visual systems that had already been shaped (perhaps heavily) by their prior experiences. Natural scenes are richly structured and highly predictable across space and time (5), and the visual system exploits these statistical redundancies during development to fine-tune the response properties of neurons (6–8). For example, studies of monkeys and humans show that object recognition machinery changes rapidly in response to statistical redundancies present in the organism’s environment (9, 10), with significant neuronal rewiring occurring in as little as 1 h (11, 12). Furthermore, there is extensive behavioral evidence that infants begin learning statistical redundancies soon after birth (13–15). These findings allow for the possibility that even early emerging object concepts (e.g., abilities appearing days, weeks, or months after birth) are learned from experience early in postnatal life (16).

Analyzing the development of object recognition therefore requires an animal that can learn to recognize objects and whose visual environment can be strictly controlled and manipulated from birth. Domestic chickens (Gallus gallus) meet both of these criteria. First, chickens can recognize objects, including 2D and 3D shapes (17–21). Second, chickens can be raised from birth in environments devoid of objects (22, 23). Unlike newborn primates and rodents, newborn chickens do not require parental care and, because of early motor development, are immediately able to explore their environment. In addition, newborn chickens imprint to conspicuous objects they see after hatching (24–26). Chickens develop a strong social attachment to their imprinted objects, and will attempt to spend the majority of their time with the objects. This imprinting response can therefore be used to test object recognition abilities without training (18, 19). Together, these characteristics make chickens an ideal animal model for studying the development of core cognitive abilities (for a general review, see ref. 27).

To investigate the origins of invariant object recognition, chickens were raised from birth for 2 wk within novel, specially designed controlled-rearing chambers. These chambers provided complete control over all visual object experiences from birth. Specifically, the chambers contained extended surfaces only (Fig. 1A). Object stimuli were presented to the subjects by projecting virtual objects onto two display walls situated on opposite sides of the chamber (Fig. 1B). Food and water were available within transparent holes in the ground. Grain was used as food because it does not behave like an object (i.e., the grain was nonsolid and did not maintain a rigid, bounded shape). All care of the chickens (i.e., replenishment of food and water) was performed in darkness with the aid of night vision goggles. Thus, subjects’ entire visual object experience was limited to the virtual objects projected onto the display walls.

The virtual objects were modeled after those used in previous studies that tested for invariant object recognition in adult rats (28, 29). These objects are ideal for studying invariant recognition because changing the viewpoint of an object can produce a greater within-object image difference than changing the identity of the object while maintaining its viewpoint (see SI Appendix, Section 1 for details). Distinguishing between these objects from novel viewpoints therefore requires an invariant representation that can generalize across large, novel, and complex changes in the object’s appearance on the retina.

In the first week of life (the input phase), subjects’ visual object experience was limited to a single virtual object rotating through a 60° viewpoint range. In the second week of life (the test phase), I probed the nature of the object representation generated from that limited input by using the two-alternative forced-choice test. During each test trial, the imprinted object was presented onto one display wall and an unfamiliar object was presented onto the other display wall. If subjects recognize their imprinted object, then they should spend a greater proportion of their time with the imprinted object. To test this prediction, I used a forced-choice test. During each test trial, the imprinted object was projected onto one display wall and an unfamiliar object was projected onto the other display wall. If subjects recognize their imprinted object, then they should spend a greater proportion of their time with the imprinted object. To test this prediction, I used a forced-choice test. During each test trial, the imprinted object was projected onto one display wall and an unfamiliar object was projected onto the other display wall. If subjects recognize their imprinted object, then they should spend a greater proportion of their time with the imprinted object.

Author contributions: J.N.W. designed research, performed research, analyzed data, and wrote the paper.

The author declares no conflict of interest.

This article is a PNAS Direct Submission.

1 E-mail: justin.wood@usc.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1308246110/-/DCSupplemental.
time in proximity to the imprinted object compared with the unfamiliar object during the test trials (24–26).

All of the subjects’ behavior was tracked by microcameras embedded in the ceilings of the chambers and analyzed with automated animal tracking software. This made it possible to: (i) eliminate the possibility of experimenter bias, (ii) sample behavior noninvasively (i.e., the subjects did not need to be moved to a separate testing apparatus and there were no visual interactions between the subjects and an experimenter), and (iii) collect a large number of data points from each newborn subject across multiple testing conditions. Specifically, I was able to collect 168 test trials from each newborn subject across 12 different viewpoint ranges. This process allowed for a detailed analysis of object recognition performance for both the individual subjects and the overall group.

Results

Exp. 1. Exp. 1 examined whether newborn chickens can generate invariant object representations at the onset of visual object experience. In the first week of life (the input phase), subjects were raised in an environment that contained a single virtual object (Fig. 2A). This object moved continuously, rotating through a 60° frontal viewpoint range about a vertical axis passing through its centroid (see Movies S1 and S2 for animations). The object only moved along this 60° trajectory; subjects never observed the object from any other viewpoint in the input phase.

In the second week of life (the test phase), I examined whether subjects could recognize their imprinted object across changes in viewpoint. The test phase was identical to the input phase, except every hour subjects received one 20-min test trial (Fig. 2B). During the test trials, a different virtual object was projected onto each display wall and I measured the amount of time subjects spent in proximity to each object. One object was the imprinted object from the input phase shown from a familiar or novel viewpoint range, and the other object was an unfamiliar object. The unfamiliar object had a similar size, color, motion speed, and motion trajectory as the imprinted object from the input phase. Specifically, on all of test trials, the unfamiliar object was presented from the same frontal viewpoint range as the imprinted object from the input phase (Fig. 3). Consequently, on most of the test trials, the unfamiliar object was more similar to the imprinting stimulus than the imprinted object was to the imprinting stimulus (from a pixel-wise perspective). To recognize their imprinted object, subjects therefore needed to generalize across large, novel, and complex changes in the object’s appearance. Object recognition was tested across 12 viewpoint ranges. Each viewpoint range was tested twice per day.

Test trials were scored as “correct” when subjects spent a greater proportion of time with their imprinted object and “incorrect” when they spent a greater proportion of time with the unfamiliar object. These responses were then analyzed with hierarchical Bayesian methods (30) that provided detailed probabilistic estimates of recognition performance for both the individual subjects and the overall group (see SI Appendix, Sections 3 and 4 for details).

Subjects successfully recognized their imprinted object on 71% (SEM, 5%) of the test trials (Fig. 3). Overall, the probability that performance was above chance was greater than 99.99% (SI Appendix, Fig. S6). Across the 12 subjects, the probability that performance was above chance was 99.99% or greater for nine of the subjects, 97% for one of the subjects, and 89% for another subject. The remaining subject scored below chance level. Across the 24 viewpoint tests (i.e., 12 viewpoint tests for each of the two imprinted objects), the probability that performance was above chance was 99% or greater for 13 of the viewpoint ranges, 90% or greater for 19 of the viewpoint ranges, and 75% or greater for all 24 of the viewpoint ranges (SI Appendix, Figs. S9 and S10). Thus, these newborn subjects were able to recognize their imprinted object with high precision across the majority of the viewpoint ranges, despite never having observed that object (or any other object) move beyond the limited 60° viewpoint range seen in the input phase.

To confirm that subjects generated invariant representations, I computed the pixel-level similarity between the imprinted object presented in the input phase and the test objects presented in the test phase (see SI Appendix, Section 1 for details). Because a retinal image consists of a collection of signals from photoreceptor cells, and each photoreceptor cell registers the brightness value from a particular region in the image, a pixel-level description of a stimulus provides a reasonable first-order approximation of the retinal input (31). The within-object image difference (i.e., the pixel-level difference between the test animation of the imprinted object and the input animation of the imprinted object) was greater than the between-object image difference (i.e., the pixel-level difference between the test animation of the unfamiliar object and the input animation of the imprinted object) on 68% of the novel viewpoint test trials (SI Appendix, Fig. S2). Furthermore, subjects’ object recognition performance did not vary as a function of the pixel-level similarity between the test animation of the imprinted object and the input animation of the imprinted object (Pearson correlation: r = −0.17, P = 0.44). Thus, for the majority of these newborn subjects, the outputs of object recognition generalized well beyond the input coming in through the senses.

Exp. 2. In Exp. 2 I attempted to replicate and extend the findings from Exp. 1. The methods were identical to those used in Exp. 1, except subjects were presented with a different viewpoint range of the imprinted objects during the input phase. Specifically, subjects viewed a side viewpoint range of the imprinted object rather than a frontal viewpoint range (see Movies S3 and S4 for animations). This side viewpoint range increased the pixel-level similarity between the imprinted object presented during the input phase and the unfamiliar object presented during the test
phase. Consequently, the within-object image difference was greater than the between-object image difference on 100% of the novel viewpoint test trials (SI Appendix, Fig. S3). This experiment thus provided a particularly strong test of newborns’ ability to generate invariant object representations from sparse visual input. Subjects successfully recognized their imprinted object on 76% (SEM, 3%) of the test trials (Fig. 3). Overall, the probability that performance was above chance was greater than 99.99% (SI Appendix, Fig. S7). The probability that performance was above chance was also 99.99% or greater for all of the 11 subjects. Across the 24 viewpoint tests, the probability that performance was above chance was 99% or greater for 23 of the viewpoint ranges, and 75% or greater for all 24 of the viewpoint ranges (SI Appendix, Figs. S11 and S12). Furthermore, as in Exp. 1, subjects’ object recognition performance did not vary as a function of the pixel-level similarity between the test animation of the imprinted object and the input animation of the imprinted object (Pearson correlation: \( r = -0.07, P = 0.75 \)). These results replicate and extend the findings from Exp. 1. Newborns can generate viewpoint-invariant representations that support object recognition across large, novel, and complex changes in the object’s appearance.

Exp. 3. In Exps. 1 and 2, the unfamiliar object was always presented from the same viewpoint range in the test phase, whereas the imprinted object was presented from 12 different viewpoint ranges. Thus, subjects might simply have preferred the more novel test animation, without necessarily having generated an invariant representation of the imprinted object. This alternative explanation is unlikely because many studies have shown that chickens prefer to spend time with their imprinted objects rather than novel objects (24–27). Nevertheless, it was important to

---

**Fig. 3.** Results from Exps. 1–3. The Upper part of each panel shows the viewpoint range of the imprinted object presented during the input phase. The Lower part of the panel shows the viewpoint ranges of the imprinted object presented during the test phase, along with the percentage of test trials in which the subjects successfully distinguished their imprinted object from the unfamiliar object. Chance performance was 50%. To maximize the pixel-level similarity between the unfamiliar object and the imprinted object, the unfamiliar object (Inset) was always presented from the same viewpoint range as the imprinted object from the input phase in Exps. 1 and 2. In Exp. 3, the unfamiliar object and the imprinted object were presented from the same viewpoint range on each test trial to minimize the pixel-wise image differences between the two test objects and to equate the familiarity of the test animations.
control for this possibility within the context of the present testing methodology. To do so, I conducted an additional experiment (Exp. 3) in which the unfamiliar object was presented from the same viewpoint range as the imprinted object on each of the test trials (see Movies S5 and S6 for animations). This aspect made the two test animations equally novel to the subjects on each test trial, while also minimizing the pixel-level image difference between the two test animations. The experiment was identical to Exp. 1 in all other respects.

Subjects successfully recognized their imprinted object on 61% (SEM = 4%) of the test trials (Fig. 3). Overall, the probability that performance was above chance was greater than 99% (SI Appendix, Fig. S8). Across the 12 subjects, the probability that performance was above chance was 99% or greater for eight of the subjects and 92% for another subject. The remaining three subjects scored at or below chance level. Across the 24 viewpoint tests, the probability that performance was above chance was 99% or greater for 7 of the viewpoint ranges, 90% or greater for 13 of the viewpoint ranges, and 75% or greater for 16 of the viewpoint ranges (SI Appendix, Figs. S13 and S14). Performance was at or below chance for the remaining eight viewpoint ranges. In general, subjects were able to recognize their imprinted object across novel viewpoint ranges, even when the test animations were equally novel to the subjects. Furthermore, because presentation order of the viewpoint range minimized the pixel-level image difference between the two test animations, these results also show that newborn chickens can distinguish between test objects that produce similar retinal projections over time.

**Change Over Time Analysis.** Imprinting in chickens is subject to a critical period, which ends approximately 3 d after birth. Thus, subjects’ representation of their imprinted object was not expected to change over the course of the test phase (which began 7 d after birth). To test this assumption, I analyzed the proportion of time subjects spent in proximity to their imprinted object as a function of trial number (e.g., first presentation, second, third, etc.). For all experiments, performance was high and significantly above chance even for the first presentation of the novel stimuli (one-tailed t tests, all P < 0.002), and remained stable over the course of the test phase (SI Appendix, Fig. S4) with little variation as a function of presentation number (one-way ANOVAs, all P > 0.57). The test-retest reliability was also high in all experiments (Cronbach’s α = all 0.89 or greater). These analyses showed that objects’ viewpoints were sufficiently consistent and robust, and cannot be explained by learning taking place across the test phase. Newborn chickens immediately achieved their maximal performance and did not significantly improve thereafter.

**Analysis of Individual Subject Performance.** With this controlled-rearing method it was possible to collect a large number of data points from each newborn subject across multiple testing conditions. This process allowed for a detailed analysis of the performance of each individual subject. I first examined whether all of the subjects were able to build an invariant representation from the sparse visual input provided in the input phase. To do so, I computed whether each subject’s performance across the test trials exceeded chance level. Twenty-nine of the 35 subjects successfully generated an invariant object representation (Fig. 4).

The six subjects who did not generate an invariant representation could have failed in this task for two reasons. First, the subjects may have failed to imprint to the virtual object presented in the input phase, and thus lacked motivation to approach either of the virtual objects presented in the test phase. Second, the subjects may have successfully imprinted to the virtual object, but nevertheless failed to generate a viewpoint-invariant representation of that object. To distinguish between these possibilities, I examined whether subjects showed a preference for the imprinted object during the rest periods in the test phase. During the rest periods, the input animation was projected onto one display wall and a white screen was projected onto the other display wall (Fig. 2B). All 35 subjects spent the majority of the rest periods in proximity to the imprinting stimulus (mean = 92% of trials; SEM = 1%; one-tailed Binomial tests, all P < 10−8), including the six subjects who failed to generate an invariant representation of the imprinted object. Thus, it is possible to imprint to an object but fail to generate a viewpoint-invariant representation of that object. More generally, these results suggest that there can be significant variation in newborns’ object recognition abilities, even when raised from birth in identical visual environments.

To test for the presence of individual differences more directly, I examined whether the identity of the subject was a predictor of object recognition performance. In all experiments, one-way ANOVAs revealed that subject identity was a strong predictor of performance: Exp. 1, F(11, 167) = 29.54, P < 0.001; Exp. 2, F(10, 153) = 8.65, P < 0.001; and Exp. 3, F(11,167) = 29.54, P < 0.001. Despite being raised in identical visual environments, there were significant individual differences in the object recognition abilities of these newborn subjects.

All 17 of the subjects who were imprinted to object A successfully generated a viewpoint-invariant representation, whereas only 12 of the 18 subjects imprinted to object B successfully did so (Fig. 4). Furthermore, all six of the unsuccessful subjects were imprinted to the frontal viewpoint range of object B (as opposed to the side viewpoint range). Why did subjects have greater difficulty generating a viewpoint-invariant representation from this particular set of visual input? Although this experiment was not designed to address this question, a study with adult rats who were trained to distinguish between these same two objects indicates that object B contains greater structural complexity than object A (29). Specifically, the frontal viewpoint range of object B presents three fully visible, spatially separated, and approximately equally sized lobes, whereas object A has one large lobe and two smaller, less salient lobes. These feature differences strongly influence performance, causing high intersubject variability in recognition strategies for object B and low intersubject variability for object A (for details, see ref. 29). It would be interesting for future research to examine systematically which objects and viewpoint ranges are better and which are worse for generating viewpoint-invariant representations in a newborn visual system, because these input-output patterns could then be used as benchmarks for assessing the accuracy of computational models of invariant object recognition.

**Discussion.** This study examined whether newborns can generate invariant object representations at the onset of visual object experience. To do so, newborn chickens were raised in environments that contained a single virtual object. The majority of subjects were able to generate a viewpoint-invariant representation of this object. This result shows that newborns can build an invariant representation of the first object they see.

This finding does not necessarily imply that newborns build 3D geometric representations of whole objects (28). Chickens could generate invariant object representations by building invariant representations of subfeatures that are smaller than the entire object. These feature detectors might respond to only a portion of the object, or be sensitive to key 2D, rather than 3D, features. Indeed, many leading computational models of invariant object recognition in humans and monkeys explicitly rely on such subfeatures (32, 33). Remarkably, at least some of these invariant feature detectors appear to be present at the onset of visual object experience. It will be interesting for future studies to examine the specific characteristics of these feature detectors.

This study extends the existing literature concerning chickens’ visual abilities (17–21, 34–36). Although previous studies show that chickens are proficient at using vision to solve a variety of tasks, they did not look at invariant object recognition specifically. Previous studies primarily used 2D shapes or simple 3D objects as stimuli, so there was little variation in the individual
on the neurophysiological level, researchers have identified the physical interactions between objects (37). Similarly, identifying and remembering the locations of objects (34), and reasoning ref. 27), such as recognizing partly occluded objects (19), tracking and chickens have similar core cognitive abilities (reviewed by (40). This discovery that mammals and birds share homologous cells and circuits suggests that their brains perform similar, or even identical, computational operations (41).

In sum, this study shows that (i) the first object representation built by a newborn visual system can be invariant to large, novel, and complex changes in an object’s appearance on the retina; and (ii) this invariant representation can be generated from extremely sparse data, in this case from a visual world containing a single virtual object seen from a limited 60° viewpoint range. From a computer vision perspective, this is an extraordinary computational feat. Viewpoint-invariant object recognition is widely recognized to be a difficult computational problem (42, 43), and it remains a major stumbling block in the development of artificial visual systems. While many previous studies have emphasized the importance of visual experience in the development of this ability (44–47), the present experiments indicate that the underlying machinery can be present and functional at birth, in the absence of any prior experience with objects.

**Materials and Methods**

**Subjects.** Thirty-five domestic chickens of unknown sex were tested. The chicken eggs were obtained from a local distributor and incubated in darkness in an OVA-Easy (Brinsea) incubator. For the first 19 d of incubation, the temperature and humidity were maintained at 99.6 °F and 45%, respectively. On day 19, the humidity was increased to 60%. The incubation room was kept in complete darkness. After hatching, the chickens were moved from the incubation room to the controlled-rearing chambers in darkness with the aid of night vision goggles. Each chicken was raised singly within its own chamber.

**Controlled-Rearing Chambers and Task.** The controlled-rearing chambers measured 66 cm (length) × 42 cm (width) × 69 cm (height) and were constructed from white, high-density plastic. The display walls were 19” liquid crystal display monitors (1,440 × 900 pixel resolution). Food and water were provided within transparent holes in the ground that measured 66 cm (length) × 2.5 cm (width) × 2.7 cm (height). The floors were made from wire mesh, and the objects were suspended 2.7 cm off the ground by thin, transparent beams; this allowed excrement to drop away from the subject. Subjects’ behavior was tracked by microcameras and Ethovision XT 7.0 software (Noldus Information Technology) that calculated the amount of time chickens spent within zones (22 cm × 42 cm) next to the left and right display walls.

On average, the virtual objects measured 8 cm (length) × 7 cm (height) and were suspended 3 cm off the floor. Each object rotated through a 60° viewpoint range about an axis passing through its centroid, completing the full back and forth rotation every 6 s. The objects were displayed on a uniform white background at the middle of the display walls. All of the virtual object stimuli presented in this study can be viewed in Movies S1–S6.

In the input phase, the imprinted object was displayed from a single 60° viewpoint range and appeared for an equal amount of time on the left and right display walls. The object was suspended 3 cm off the floor. Each object rotated through a 60° viewpoint range about an axis passing through its centroid, completing the full back and forth rotation every 6 s. The objects were displayed on a uniform white background at the middle of the display walls. All of the virtual object stimuli presented in this study can be viewed in Movies S1–S6.

In the input phase, the imprinted object was displayed from a single 60° viewpoint range and appeared for an equal amount of time on the left and right display walls. The object switched walls every 2 h, following a 1-min period of darkness. One-half of the subjects were imprinted to object A (with object B serving as the unfamiliar object), and the other one-half of the subjects were imprinted to object B (with object A serving as the unfamiliar object) (Fig. 3). In the test phase, subjects received one 20-min test trial every hour, followed by one 40-min rest period. During each rest period, the input animation from the input phase appeared on one display wall and a white screen appeared on the other display wall. The 12 viewpoint ranges were tested 14 times each within randomized blocks over the course of the test phase.

These experiments were approved by The University of Southern California Institutional Animal Care and Use Committee.
ACKNOWLEDGMENTS. I thank Samantha M. W. Wood for assistance on this manuscript and Aditya Prasad, Tony Bouz, Lynette Tan, and Jason G. Goldman for assistance building the controlled-rearing chambers. This work was supported by the University of Southern California.

Newborn chickens generate invariant object representations at the onset of visual object experience

Supplementary Information

Sections

1. Definition of object recognition and description of the virtual objects.................................2
2. Change in performance over time...............................................................................................6
3. Description of the hierarchical Bayesian analyses.....................................................................7
4. Results of the Bayesian analyses for all experiments and viewpoint ranges............................9
5. References..................................................................................................................................19
1. Definition of object recognition and description of the virtual objects

Following previous research (1), object recognition was defined as the ability to discriminate an object from other objects, and to do so over a range of identity-preserving transformations of the retinal image of that object (e.g., image transformations resulting from changes in viewpoint). This definition is useful for two reasons. First, it focuses attention on the computational hallmark of object recognition—the ability to identify objects over a large range of viewing conditions. Although each encounter with an object is almost entirely unique (in terms of the image projected onto the retina), the visual system is able to link these unique patterns of retinal activity to the same object stored in memory. This so-called “invariance problem” is the computational crux of object recognition (2), and the primary obstacle in the development of artificial object recognition systems (3). Second, by focusing on the invariance problem, this definition provides an objective measure of having “solved” object recognition. An organism can be said to have solved object recognition if it can recognize objects across large and complex changes in their pixel-level appearances.

The two virtual objects (Fig. S1) were modeled after those used in a previous study that tested for invariant object recognition in adult rats (4). These objects are ideal for studying invariant recognition because changing the viewpoint (i.e., azimuth and elevation rotation) of a given object can produce a greater within-object image difference than changing the identity of the object while maintaining its viewpoint. Thus, distinguishing between these objects from novel viewpoints requires an invariant representation that can generalize across large, novel, and complex changes in the object’s pixel-level appearance.

To confirm that subjects were able to recognize their imprinted object across large and complex changes in its pixel-level appearance, I measured the amount of image variation produced by the virtual objects. A retinal image consists of a collection of signals from photoreceptor cells. Each photoreceptor cell registers the brightness value from a particular region in the image. Thus, it is possible to regard a retinal image as a matrix of numbers, each specifying light intensity at an image pixel (5). To compare the pixel-wise similarity of the virtual objects, I converted each object animation into a sequence of images (at 24 frames per second) and measured the brightness level of each pixel in each image. For each corresponding set of frames (e.g., the 1st frame of the input animation and the 1st frame of the test animation, the 2nd frame of the input animation and the 2nd frame of the test animation, etc.), I compared the brightness level of each corresponding pixel. I then added together the absolute differences in brightness values obtained for all corresponding pixels, across all corresponding frames, to obtain a single measure of the overall pixel difference between the test animation and the input animation. This analysis confirmed that changing the viewpoint of the imprinted object could produce a larger pixel-wise image change than manipulating the identity of the object while maintaining its viewpoint. As shown in Figures S2 and S3, the within-object image difference (i.e., the pixel-level difference between the test animation of the imprinted object and the input animation of the imprinted object) was greater than the between-object image difference (i.e., the pixel-level difference between the test animation of the unfamiliar object and the input animation of the imprinted object) on 15 of the 22 novel viewpoint tests in Experiment 1, and 22 of the 22 novel viewpoint tests in Experiment 2. These results supplement the analyses of Zoccolan and colleagues (4), who also measured the amount of image variation produced by changing the viewpoint and
identity of these two objects. Importantly, they showed that when these objects are presented from the same azimuth and elevation positions, the between-object image difference is smaller than the within-object image distance obtained when the same object is presented from different azimuth and elevation positions. These researchers measured image variation in several ways, including (a) computing the pixel-wise Euclidean distance between the different images of the objects, and (b) computing image difference by using the responses of a population of simulated V1-like simple cells (simulated using a bank of Gabor filters). These two measurements yielded similar within- and between-object image differences (4).

Figure S1: (A) The two virtual objects used in the study. (B) When presented with four novel test stimuli of these objects, a human observer can easily recognize the test stimuli as being “Object A, Object A, Object B, Object B” (from left to right). In contrast, an ideal observer having access to all available image information, but lacking knowledge of the geometry of identity-preserving transformations (i.e., a classification based on a pixel-by-pixel comparison), would incorrectly judge the test stimuli to be “Object B, Object A, Object B, Object A” (example adapted from ref. 9).
Figure S2: Results of the pixel-by-pixel comparisons of the virtual objects presented in the test phase and the virtual object presented in the input phase for Experiment 1. The dashed line shows the image difference between the unfamiliar object and imprinting stimulus (i.e., the input animation). Critically, for most of the test trials, the unfamiliar object was more similar to the imprinting stimulus than the imprinted object was to the imprinting stimulus.
Figure S3: Results of the pixel-by-pixel comparisons of the virtual objects presented in the test phase and the virtual object presented in the input phase for Experiment 2. The dashed line shows the image difference between the unfamiliar object and imprinting stimulus (i.e., the input animation). Critically, for all of the novel viewpoint test trials, the unfamiliar object was more similar to the imprinting stimulus than the imprinted object was to the imprinting stimulus.
2. Change in performance over time

**Figure S4**: Change over time results. The graphs illustrate group mean performance over the full set of viewpoint ranges shown during the test phase, computed for the first, second, third, etc., presentation of the viewpoint ranges. The y-axis indicates the proportion of time subjects spent with the imprinted object versus the unfamiliar object. Chance performance was 50%. Error bars denote standard error.
3. Description of the hierarchical Bayesian analyses

To analyze the data, I first computed the number of test trials in which subjects preferred their imprinted object over the unfamiliar object. The subject was rated to have preferred their imprinted object on a trial if their object preference score was greater than 50%. The object preference score was calculated with the formula:

\[
\text{Object Preference Score} = \frac{\text{Time by Imprinted Object}}{\text{Time by Imprinted Object + Time by Unfamiliar Object}}
\]

Test trials were thus scored as “correct” when subjects spent a greater proportion of time with their imprinted object and “incorrect” when they spent a greater proportion of time with the unfamiliar object. These responses were then analyzed using hierarchical Bayesian methods (6) that are able to account for the hierarchical dependencies in the data (shown in Fig. S5).

Bayesian methods offer many advantages over traditional null hypothesis significance testing (7). For instance, with a Bayesian analysis, it is possible to calculate the actual probability that performance was above chance levels (an intuitive statistic to interpret), rather than a p-value that calculates the probability of getting data as extreme as the data actually obtained assuming that the null hypothesis is actually true (a less intuitive statistic to interpret). For the current

Figure S5: A Bayes net diagram depicting the hierarchical dependency of the data.
study, Bayesian analyses provided detailed probabilistic estimates of success for each newborn subject as well as the underlying probability of success for each condition and experiment (for results, see section 4).

This Bayesian analysis first requires specifying a prior distribution that represents the current uncertainty in performance. I used a prior consisting of one correct trial and one incorrect trial. This is a highly conservative prior because it consists of just two trials at chance level (50%). The prior distribution also includes a parameter, K, that represents the consistency across subjects. To be conservative, I used a uniform prior (8) that ranged from 0.000001 (i.e., very little consistency across subjects) to the maximum reasonable kappa. The maximum reasonable kappa was estimated from subjects’ performance during the rest periods in the test phase. During the rest periods, the input animation from the input phase was projected onto one display wall and a white screen was projected onto the other display wall. These rest periods were expected to produce the greatest consistency across subjects because they presented the easiest choice: subjects chose whether to spend time with the imprinting stimulus versus a white screen. Critically, all of these prior distribution parameters were both broad and vague, thereby expressing great prior uncertainty in the values of the parameters. This type of prior has minimal influence on the estimates of success and is quickly overwhelmed by even a modest amount of data with Bayesian parameter estimation (6).

All analyses were performed using R version 2.15.0 (http://www.r-project.org/), JAGS (http://mcmc-jags.sourceforge.net/), and adaptation of code from Dr. John Kruschke (6). The hierarchical Bayesian model used Markov Chain Monte Carlo (MCMC) sampling to approximate the posterior distribution of the parameters for each individual subject and the hyperparameter for each condition. The analysis used a burn-in of 10,000 steps, with a total of 100,000 steps after burn-in.
4. Results of the Bayesian analyses for all experiments and viewpoint ranges

This section provides a graphical depiction of performance for each experiment and viewpoint test. Figures S6-S8 provide the probability density graphs for the group and the probability density graphs for each subject. Figures S9-S14 provide the probability density graphs for the group for all of the viewpoint tests in Experiments 1-3. The graphs show an estimate of the 95% highest density interval (HDI). The 95% HDI is an interval that spans 95% of the distribution, such that every point inside the interval has higher believability than any point outside of the interval (6). Chance performance (50%) is indicated by the vertical dashed line on each graph.
Figure S6: The probability density graphs for the group and each subject in Experiment 1.
Figure S7: The probability density graphs for the group and each subject in Experiment 2.
Figure S8: The probability density graphs for the group and each subject in Experiment 3.
**Figure S9:** The probability density graphs for the group for each viewpoint test in Experiment 1. These subjects were imprinted to Object A.
Figure S10: The probability density graphs for the group for each viewpoint test in Experiment 1. These subjects were imprinted to Object B.
Figure S11: The probability density graphs for the group for each viewpoint test in Experiment 2. These subjects were imprinted to Object A.
Figure S12: The probability density graphs for the group for each viewpoint test in Experiment 2. These subjects were imprinted to Object B.
Figure S13: The probability density graphs for the group for each viewpoint test in Experiment 3. These subjects were imprinted to Object A.
Figure S14: The probability density graphs for the group for each viewpoint test in Experiment 3. These subjects were imprinted to Object B.
5. References

Movie S1. The object stimuli used in Exp. 1. The Upper part of the frame shows the animation of the imprinted object presented during the input phase. The Lower part of the frame shows the animations of the imprinted object and unfamiliar object presented during each of the 12 viewpoint tests in the test phase. The bar graphs show the total number of trials in which subjects preferred the imprinted object over the unfamiliar object. These subjects were imprinted to object A in the input phase, with object B serving as the unfamiliar object in the test phase.
Movie S2. The object stimuli used in Exp. 1. The upper part of the frame shows the animation of the imprinted object presented during the input phase. The bottom part of the frame shows the animations of the imprinted object and unfamiliar object presented during each of the 12 viewpoint tests in the test phase. The bar graphs show the total number of trials in which subjects preferred the imprinted object over the unfamiliar object. These subjects were imprinted to object B in the input phase, with object A serving as the unfamiliar object in the test phase.

Movie S3. The object stimuli used in Exp. 2. The upper part of the frame shows the animation of the imprinted object presented during the input phase. The lower part of the frame shows the animations of the imprinted object and unfamiliar object presented during each of the 12 viewpoint tests in the test phase. The bar graphs show the total number of trials in which subjects preferred the imprinted object over the unfamiliar object. These subjects were imprinted to object A in the input phase, with object B serving as the unfamiliar object in the test phase.

Wood, J. N. (2013). Newborn chickens generate invariant object representations at the onset of visual object experience. PNAS.
Movie S4. The object stimuli used in Exp. 2. The Upper part of the frame shows the animation of the imprinted object presented during the input phase. The Lower part of the frame shows the animations of the imprinted object and unfamiliar object presented during each of the 12 viewpoint tests in the test phase. The bar graphs show the total number of trials in which subjects preferred the imprinted object over the unfamiliar object. These subjects were imprinted to object B in the input phase, with object A serving as the unfamiliar object in the test phase.

Movie S5. The object stimuli used in Exp. 3. The Upper part of the frame shows the animation of the imprinted object presented during the input phase. The Lower part of the frame shows the animations of the imprinted object and unfamiliar object presented during each of the 12 viewpoint tests in the test phase. The bar graphs show the total number of trials in which subjects preferred the imprinted object over the unfamiliar object. These subjects were imprinted to object A in the input phase, with object B serving as the unfamiliar object in the test phase.

Wood, J. N. (2013). Newborn chickens generate invariant object representations at the onset of visual object experience. *PNAS.*
Movie S6. The object stimuli used in Exp. 3. The Upper part of the frame shows the animation of the imprinted object presented during the input phase. The Lower part of the frame shows the animations of the imprinted object and unfamiliar object presented during each of the 12 viewpoint tests in the test phase. The bar graphs show the total number of trials in which subjects preferred the imprinted object over the unfamiliar object. These subjects were imprinted to object B in the input phase, with object A serving as the unfamiliar object in the test phase.

Movie S6

Other Supporting Information Files

SI Appendix (PDF)