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ORIGINAL PAPER

Enhanced learning of natural visual sequences in newborn chicks

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Abstract To what extent are newborn brains designed to operate over natural visual input? To address this question, we used a high-throughput controlled-rearing method to examine whether newborn chicks (*Gallus gallus*) show enhanced learning of natural visual sequences at the onset of vision. We took the same set of images and grouped them into either natural sequences (i.e., sequences showing different viewpoints of the same real-world object) or unnatural sequences (i.e., sequences showing different images of different real-world objects). When raised in virtual worlds containing natural sequences, newborn chicks developed the ability to recognize familiar images of objects. Conversely, when raised in virtual worlds containing unnatural sequences, newborn chicks' object recognition abilities were severely impaired. In fact, the majority of the chicks raised with the unnatural sequences failed to recognize familiar images of objects despite acquiring over 100 h of visual experience with those images. Thus, newborn chicks show enhanced learning of natural visual sequences at the onset of vision. These results indicate that newborn brains are designed to operate over natural visual input.

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Introduction

Natural visual environments vary widely but not without limit. For instance, in natural visual environments, objects tend to move smoothly through space and time while maintaining their three-dimensional shape. This observation raises important questions about the development and flexibility of animal vision. To what extent are newborn visual systems designed to operate over natural visual input? Are there constraints on the types of visual environments that can be successfully understood by newborn visual systems, and if so, what is the nature of these constraints? Addressing these questions requires studying newborn animals at the onset of vision, before the visual system has been shaped and calibrated by natural visual experience. In the present study, we describe a high-throughput controlled-rearing experiment that examined whether newborn chicks show enhanced learning of natural visual sequences at the onset of vision.

Researchers have long theorized that natural visual input plays an important role in the development of object recognition (e.g., DiCarlo et al. 2012; Foldiak 1991; Masquelier and Thorpe 2007; Wallis 2013; Wiskott and Sejnowski 2002; Wyss et al. 2006). For example, according to temporal association models, visual object representations are learned from the temporal contiguity of object features during natural visual experience (e.g., Cox et al. 2005; Li and DiCarlo 2008; Wallis and Bulthoff 2001; Wallis and Rolls 1997). During natural visual experience, objects tend to remain present for seconds or longer. Visual features that covary across short time intervals are therefore more likely to correspond to different images of the same object than to different objects. The visual system might take advantage of this natural tendency for temporally contiguous retinal images to belong to the same object

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by associating patterns of neuronal activity produced by successive retinal images of an object. When an animal receives natural visual input, this temporal association process should create object representations that are selective for object identity and tolerant to identity-preserving image transformations (e.g., changes in viewpoint).

Evidence for temporal association mechanisms comes from both behavioral (Cox et al. 2005; Wallis and Bulthoff 2001) and neurophysiological levels (Li and DiCarlo 2008, 2010). For instance, when adult primates are exposed to an altered visual world where objects change identity across saccades, the neural representations of different objects become associated together, effectively breaking position-invariant object recognition at both the psychophysical and single-cell levels (Cox et al. 2005; Li and DiCarlo 2008). These findings indicate that adult visual systems use the natural temporal contiguity of images on the retina to create accurate visual object representations. To date, however, the origins of this capacity remain largely unknown. Do newborn visual systems create object representations by associating object features over time? If so, are there constraints on the types of visual sequences that can be successfully learned and recognized by newborn animals?

A high-throughput controlled-rearing approach

In the present study, we examined whether newborn animals show enhanced learning of visual images presented in natural versus unnatural temporal sequences. Since this experiment required controlling all of the subjects' visual object experiences from the onset of vision, we used a high-throughput controlled-rearing method with a newborn animal model—the domestic chick (*Gallus gallus*). We use the term "high-throughput" because we recorded the subjects' behavior continuously (9 samples/s, 24 h/day, 7 days/week), producing a complete digital record of each subject's behavior across the test phase. In addition, the entire data collection process was automated. As a result, this method minimized the possibility of experimenter error and bias during data collection.

We used newborn chicks as an animal model because chicks are an ideal model system for studying the development of vision. First, chicks develop object recognition abilities rapidly. For example, previous high-throughput controlled-rearing studies have shown that newborn chicks have advanced visual processing abilities at the onset of vision, including abilities for face recognition (Wood and Wood 2015b), action recognition (Goldman and Wood 2015), color-shape binding (Wood 2014), and viewpoint-invariant object recognition (Wood 2013, 2015; Wood and Wood 2015a). Other controlled-rearing experiments provide evidence that newborn chicks can use symmetry as a

cue to recognize objects (Mascalzoni et al. 2012), recognize partly occluded objects (Regolin and Vallortigara 1995), track and remember the locations of objects (Rugani et al. 2009), and reason about the physical interactions between objects (Chiandetti and Vallortigara 2011). Second, chicks can be raised in strictly controlled visual environments immediately after hatching, which makes it possible to control all of their visual object experiences. Third, chicks imprint to objects seen in the first few days of life; this behavior provides a natural assay for testing chicks' object recognition abilities without using formal training methods (e.g., operant conditioning) (Horn 2004). Fourth, birds and mammals process sensory input using homologous cortical circuits (reviewed by Jarvis et al. 2005; Karten 2013). Both avian and mammalian brains are modular, small-world networks with a connective core of hub nodes that includes prefrontal and hippocampus-like structures (Shanahan et al. 2013). Thus, controlled-rearing studies of newborn chicks can inform our understanding of the development of both avian and mammalian vision.

In the first week of life (the input phase), we raised newborn chicks in strictly controlled environments that contained no objects other than three virtual sequences (Fig. 1). One group of chicks was raised in an environment containing three natural sequences (i.e., sequences showing different viewpoints of the same real-world object; Natural Sequence Condition), while another group of chicks was raised in an environment containing three unnatural sequences (i.e., sequences showing different images of different real-world objects; Unnatural Sequence Condition). In the second week of life (the test phase), we examined whether the chicks could recognize the images and sequences presented in the input phase.

Importantly, the natural sequences and unnatural sequences were composed of the same nine images (3 images per sequence × 3 sequences; see Fig. 1a, b) and were equally predictive in terms of the transitional probabilities between images. The only difference between the Natural Sequence Condition and Unnatural Sequence Condition was how the nine images were grouped into spatiotemporally defined objects. Thus, any difference in recognition performance between the conditions could not be based on the individual images or the transitional probabilities between images.

Methods

Subjects

Twenty-four Rhode Island Red chicks of unknown sex were tested. The sample size was determined before the experiment was conducted based on previous high-

Fig. 1 The visual sequences. Newborn chicks were raised with three sequences, each consisting of three images. The natural sequences consisted of different images of the same object, separated by 45° rotations in the depth plane. The unnatural sequences consisted of different images of different objects. The natural sequences and unnatural sequences were composed of the same nine images. Half of the chicks were imprinted to the images shown in **a**, while the other half of the chicks were imprinted to the images shown in **b**. **c**, **d** show an example of a natural sequence and unnatural sequence moving across the display wall
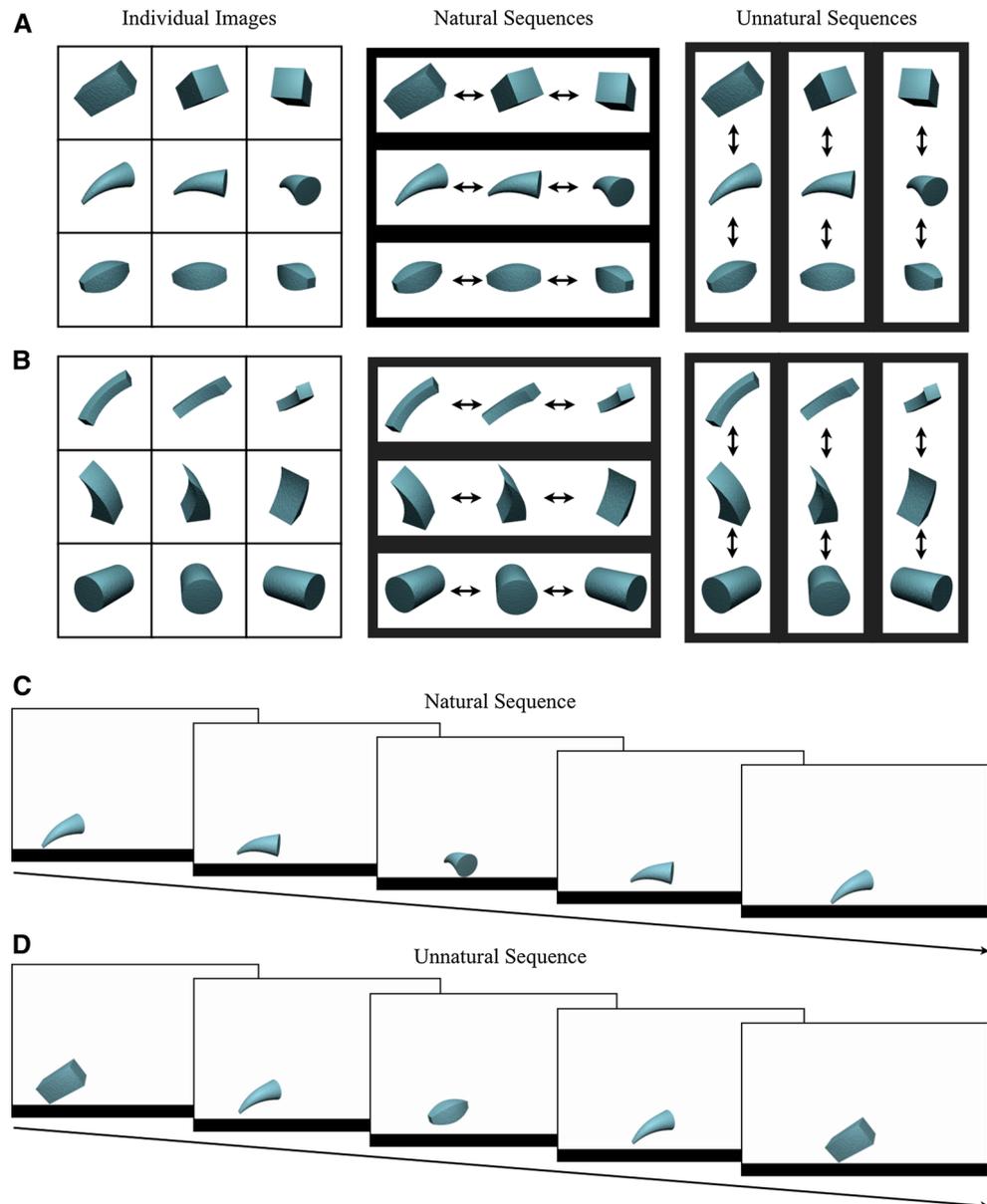
throughput controlled-rearing studies (e.g., Wood 2013, 2014). No subjects were excluded from the analyses.

The eggs were obtained from a local distributor and incubated in darkness in an OVA-Easy incubator (Brinsea Products Inc., Titusville, FL, USA). After hatching, the chicks were moved from the incubation room to the controlled-rearing chambers in darkness with the aid of night vision goggles. Each chick was raised singly within its own chamber. Half of the chicks were raised with the natural sequences, and the other half were raised with the unnatural sequences. This experiment was approved by The University of Southern California Institutional Animal Care and Use Committee. The experimental procedures were consistent with the Association for the Study of Animal Behaviour/Animal Behavior Society Guidelines for the Use of Animals in Research.

Controlled-rearing chambers

The chambers measured 66 cm (length) × 42 cm (width) × 69 cm (height) and were constructed from white, high-density polyethylene. The chambers were devoid of all real-world (solid, bounded) objects. To present object stimuli to the chicks, we projected virtual objects on two display walls situated on opposite sides of the chamber. The display walls were 19″ liquid crystal display (LCD) monitors (1440 × 900 pixel resolution). Food and water were provided within recessed, transparent acrylic troughs that

measured 66 cm (length) $\times$ 2.5 cm (width) $\times$ 2.7 cm (height). Grain was used as food because a heap of grain does not behave like an object (i.e., grain does not maintain a rigid, bounded shape). The floor was made of wire mesh and was suspended 2.7 cm off the ground by transparent acrylic support beams. The chambers tracked all of the chicks' behavior (9 samples/s, 24 h/day, 7 days/week) during the test phase via micro-cameras in the ceilings and automated image-based tracking software (EthoVision XT, Noldus Information Technology, Leesburg, VA, USA). This high-throughput data collection approach allowed us to collect a large number of test trials (189 trials) from each chick and, consequently, measure each newborn subject's object recognition abilities with high precision.

Procedure

In the first week of life (the input phase), the chicks were imprinted to three visual sequences, each of which consisted of three images (Fig. 1). The natural sequences consisted of different images of the same object. Each image was separated by 45° of rotation in the depth plane. The unnatural sequences consisted of different images of different objects. For both the natural sequences and unnatural sequences, the three images were presented in a predictable order (i.e., 1, 2, 3, 2, 1, 2, 3, 2, 1) at a rate of one image per second. Thus, the transitional probabilities between images were identical for the natural sequences and unnatural sequences. Since the sequences cycled back and forth between the three images, Image 2 was shown twice as often as Image 1 and Image 3. To an adult human observer, the natural sequences appear as rigid 3D objects rotating back and forth 90° in the depth plane, whereas the unnatural sequences appear as non-rigid objects that rapidly change their 3D shape. On average, the objects measured 7 cm (length) $\times$ 5 cm (height) and were suspended 2 cm off the ground. The sequences were displayed on a uniform white background. SI Movies 1 and 2 show sample animations of a natural sequence and unnatural sequence, respectively.

During each minute in the input phase, one of the three imprinted sequences appeared on one display wall by moving from off-screen to the middle of the wall. The sequence then moved back and forth across the display wall, before exiting the display wall at the end of the minute. Only one sequence was presented at a time. The sequences appeared for an equal amount of time on the left and right display walls. The sequences appeared on one display wall for 2 h before switching to the opposite display wall for the next 2 h. The three sequences appeared an equal number of times during the input phase in a randomized order. Both the natural sequences and unnatural sequences moved on a continuous spatiotemporal path across the display wall.

In the second week of life (the test phase), we measured the chicks' object recognition abilities by using an automated two-alternative forced-choice procedure. During each test trial, one of the three imprinted sequences appeared on one display wall and an unfamiliar sequence appeared on the other display wall. If the chicks recognized the imprinted sequence, then they should have spent more time in proximity to the imprinted sequence compared with the unfamiliar sequence. Each test trial lasted 25 min and was followed by a 28-min rest period, with 1 min of darkness between each period. During the rest periods, the sequences from the input phase appeared on one display wall and a white screen appeared on the other display wall. Overall, each chick received 189 test trials during the test phase. The order of the test trials was randomized within blocks.
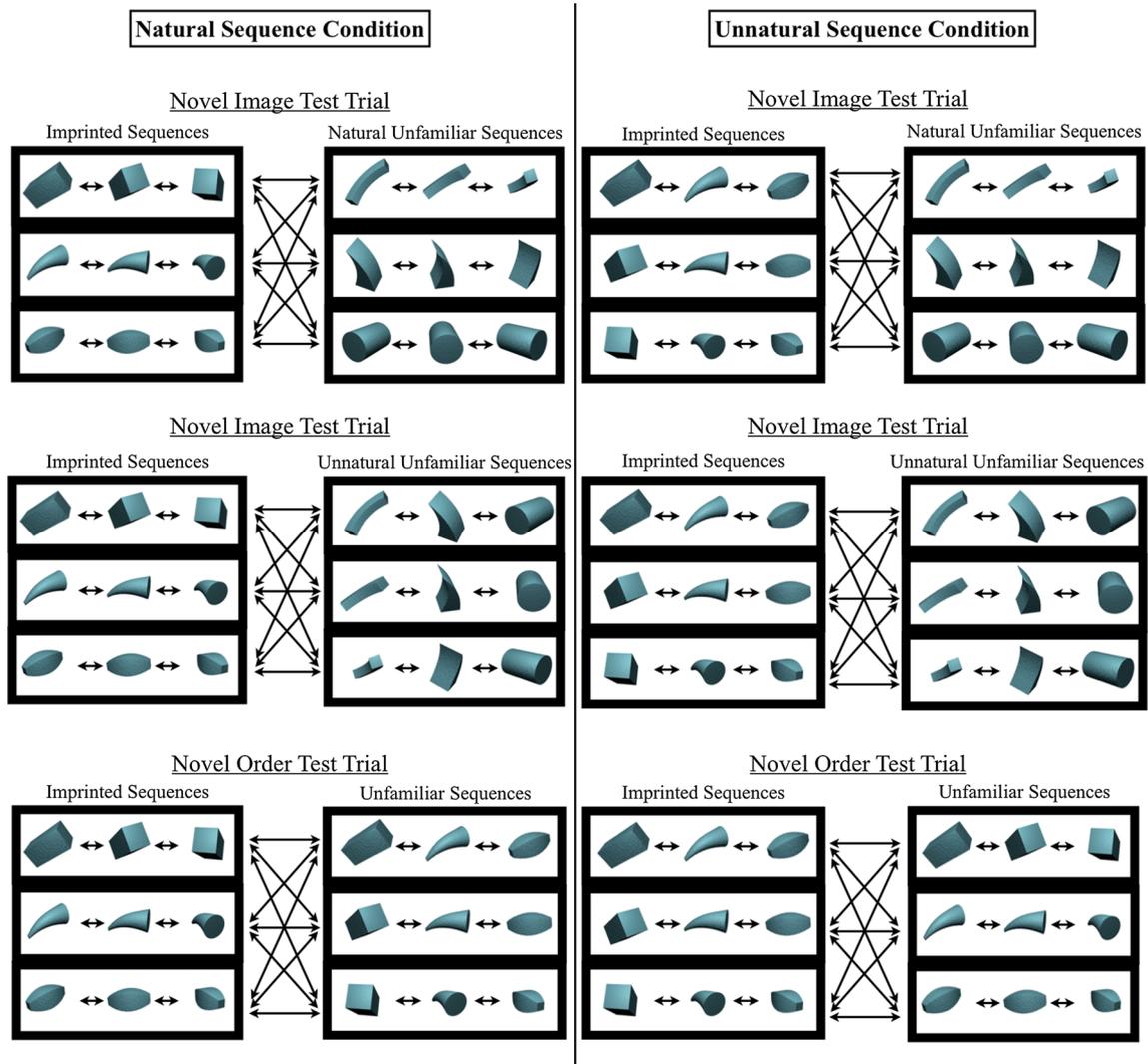
We presented the chicks with two types of test trials (Fig. 2). First, on the Novel Image Test Trials, we examined whether the chicks could distinguish familiar images from novel images. One display wall showed one of the three imprinted sequences (i.e., familiar images), whereas the other display wall showed an unfamiliar sequence (i.e., novel images). On half of the trials, the unfamiliar object was a natural sequence (i.e., consisting of three images of the same novel object), and on the other half of the trials, the unfamiliar object was an unnatural sequence (i.e., consisting of three images each from a different novel object). As a result, the chicks in the Natural Sequence Condition and Unnatural Sequence Condition were presented with the same unfamiliar sequences in the test phase.

Second, on the Novel Order Test Trials, we examined whether the chicks could distinguish between sequences on the basis of the order of the images in the sequence. One display wall showed one of the three imprinted sequences, whereas the other display wall showed an unfamiliar sequence that contained familiar images presented in a novel order (Fig. 2). Specifically, the chicks raised with the natural sequences were presented with an unnatural sequence as the unfamiliar sequence, and the chicks raised with the unnatural sequences were presented with a natural sequence as the unfamiliar sequence. Since the unfamiliar sequence always contained familiar images, the chicks could only distinguish between the sequences by the order of the images.

Results

Overall recognition performance

The results are shown in Fig. 3. For each test trial type, we computed the proportion of time each chick spent with the

Fig. 2 The test stimuli. The chicks were presented with two types of test trials. On the Novel Image Test Trials, we measured whether the chicks could distinguish familiar images from novel images. One display wall showed one of the three imprinted sequences (familiar images), whereas the other display wall showed an unfamiliar sequence (novel images). On half of the trials, the unfamiliar sequence was a natural sequence (i.e., consisting of three images of the same novel object), and on the other half of the trials, the unfamiliar sequence was an unnatural sequence (i.e., consisting of three images from different novel objects). On the Novel Order Test Trials, we measured whether the chicks could distinguish between sequences on the basis of the order of images. One display wall showed one of the three imprinted sequences, whereas the other display wall showed an unfamiliar sequence that contained familiar images presented in a novel order. The chicks raised with the natural sequences were presented with unnatural sequences as the unfamiliar sequences, and the chicks raised with the unnatural sequences were presented with natural sequences as the unfamiliar sequences

imprinted sequence compared with the unfamiliar sequence. We first examined whether the chicks were able to recognize the familiar images on the Novel Image Test Trials when the novel images were presented in both natural sequences and unnatural sequences. A repeated measures ANOVA with Test Trial Type (tested with natural sequences vs. unnatural sequences) as a within-subjects factor and Rearing Condition (raised with natural sequences vs. unnatural sequences) as a between-subjects factor did not reveal a significant main effect of Test Trial Type or an interaction (all ps > .65). The main effect of Rearing Condition was significant [$F(1, 22) = 6.28$, $p = .02$]. As shown in Fig. 3a, the chicks raised with the natural sequences performed better than the chicks raised with the unnatural sequences. Further, both groups performed equally well regardless of whether the novel images were presented in natural sequences versus unnatural sequences [$t(23) = .04$, $p = .97$]. Thus, the data were pooled across these trials for the analyses presented below.

We next examined whether the chicks' rearing condition influenced their ability to recognize familiar objects on the Novel Image and Novel Order Test Trials. As illustrated in
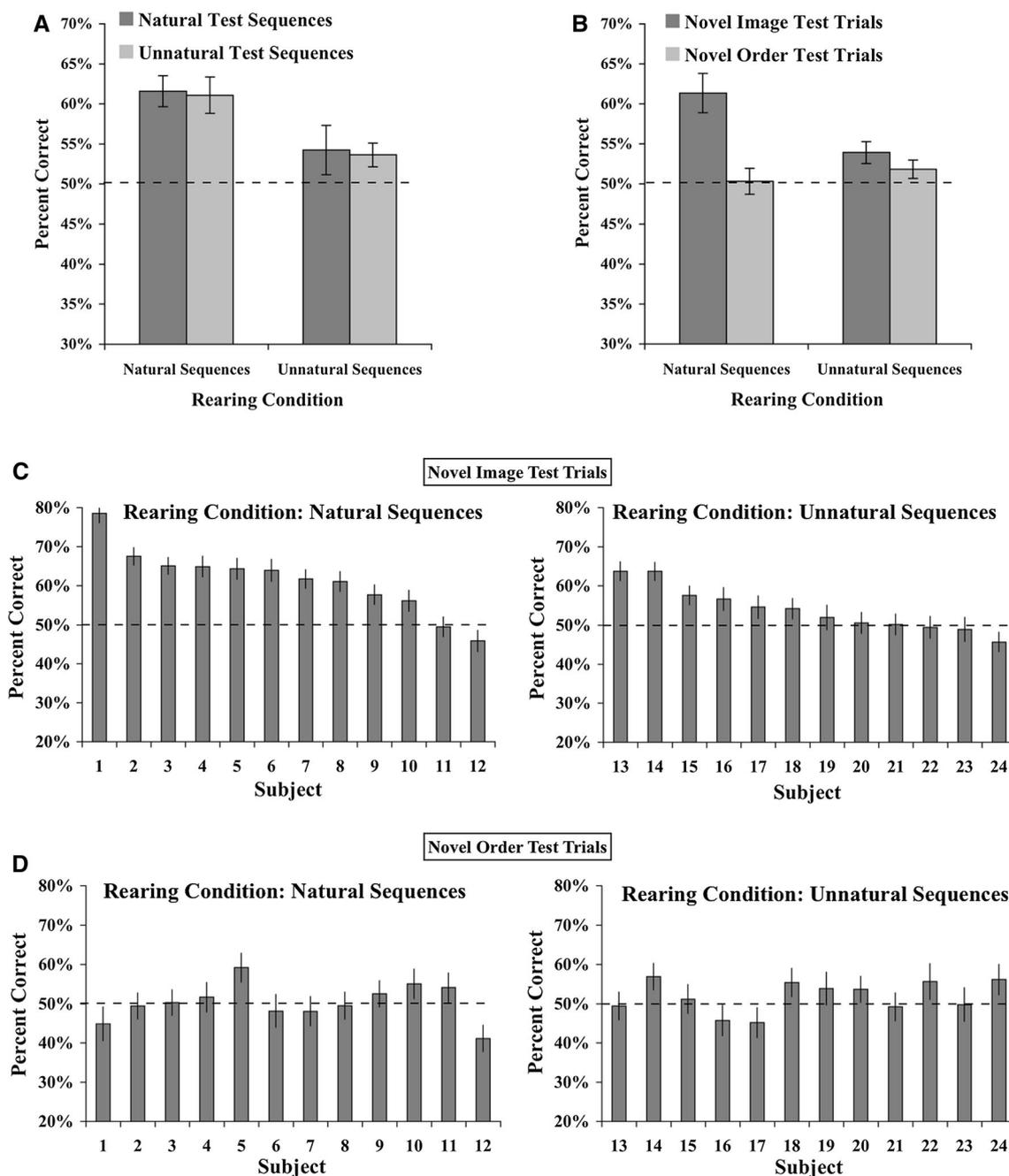
Fig. 3 Results. **a** The chicks' overall recognition performance when the novel images were presented in natural sequences versus unnatural sequences on the Novel Image Test Trials. **b** The chicks' overall recognition performance on the Novel Image Test Trials and the Novel Order Test Trials. The chicks raised with the natural sequences showed enhanced recognition of novel images compared with the chicks raised with the unnatural sequences. **c** Performance of each individual subject on the Novel Image Test Trials (ordered by performance). **d** Performance of each individual subject on the Novel Order Test Trials. The graphs show the percent of time spent with the imprinted sequence compared with the unfamiliar sequence. The *dashed lines* indicate chance performance. The *error bars* indicate standard error

Fig. 3b, the chicks showed enhanced learning of visual images when the images were presented in natural sequences during the input phase. A repeated measures ANOVA with Test Trial Type (Novel Image vs. Novel Order Test Trials) as a within-subjects factor and Rearing Condition (raised with natural sequences vs. unnatural sequences) as a between-subjects factor revealed a significant main effect of Test Trial Type [$F(1, 22) = 13.54$, $p = .001$] and a significant interaction between Test Trial Type and Rearing Condition [$F(1, 22) = 6.28, p = .02$]. In

the Natural Sequence Condition, the chicks spent a greater proportion of time with the imprinted sequences than the unfamiliar sequences on the Novel Image Test Trials [61.3 %, SEM = 2.5 %; $t(11) = 4.62$, $p < .001$, Cohen's $d = 1.33$], but not on the Novel Order Test Trials [50.3 %, SEM = 1.4 %; $t(11) = .25$, $p = .81$, Cohen's $d = .07$]. In the Unnatural Sequence Condition, the chicks also spent a greater proportion of time with the imprinted sequences than the unfamiliar sequences on the Novel Image Test Trials [53.9 %, SEM = 1.6 %; $t(11) = 2.40$, $p = .04$, Cohen's $d = .70$], but not on the Novel Order Test Trials [51.9 %, SEM = 1.2 %; $t(11) = 1.60$, $p = .14$, Cohen's $d = .46$]. Thus, in both conditions, the chicks were able to distinguish familiar images from novel images; however, the chicks' ability to recognize familiar images was significantly higher in the Natural Sequence Condition compared with the Unnatural Sequence Condition [$t(22) = 2.51$, $p = .02$, Cohen's $d = 1.07$].

We also estimated the posterior probability favoring the null hypothesis using the JZS Bayes factor (BF_{01}, calculated from http://pcl.missouri.edu/bayesfactor). The Bayes factor is the odds ratio comparing the likelihood of the data fitting under the null hypothesis to the likelihood of the data fitting under the alternative hypothesis. A BF_{01} of 1 indicates that the null hypothesis and alternative hypothesis are equally likely, while larger values indicate greater evidence for the null hypothesis and smaller values indicate greater evidence for the alternative hypothesis. In the Natural Sequence Condition, the BF_{01} for the Novel Image Test Trials was .02 (i.e., the alternative hypothesis was 51.7 times more likely than the null hypothesis) and the BF_{01} for the Novel Order Test Trials was 3.39 (i.e., the null hypothesis was 3.39 times more likely than the alternative hypothesis). In the Unnatural Sequence Condition, the BF_{01} for the Novel Image Test Trials was .46 (i.e., the alternative hypothesis was 2.17 times more likely than the null hypothesis) and the BF_{01} for the Novel Order Test Trials was 1.27 (i.e., the null hypothesis was 1.27 times more likely than the alternative hypothesis).

Individual subject performance

Since we collected almost 200 test trials from each chick, we were able to measure each subject's object recognition abilities to within a few degrees of error (Fig. 3). Accordingly, we were able to examine whether each subject performed above chance levels. To control for the problem of multiple comparisons, we used a Holm–Bonferroni correction. On the Novel Image Test Trials (Fig. 3c), 9 of the 12 chicks in the Natural Sequence Condition successfully distinguished familiar images from novel images (two-tailed one-sample t tests, 8 subjects, $p < .001$; 1 subject, $p = .003$), whereas only 3 of the 12

chicks in the Unnatural Sequence Condition successfully distinguished familiar images from novel images (two-tailed one-sample t tests, 2 subjects, $p < .001$; 1 subject, $p = .003$). Thus, the majority of the chicks raised with the natural sequences learned to recognize familiar images, whereas only a minority of the chicks raised with the unnatural sequences learned to recognize familiar images.

On the Novel Order Test Trials (Fig. 3d), none of the chicks in the Natural Sequence Condition or Unnatural Sequence Condition (0 of the 24 subjects) successfully distinguished the familiar image order from the novel image order. Thus, the chicks were not capable of learning to distinguish between visual sequences on the basis of the order of the images.

To test whether some sequences were more difficult to recognize than others, we evaluated the inter-subject agreement on each of the test sequence pairings. To measure inter-subject agreement, we (1) measured each subject's performance on each of the 27 unique pairwise combinations of the three imprinted sequences and nine unfamiliar sequences; (2) computed the correlation between the subjects imprinted to each set of images; and (3) calculated the average correlation for each rearing condition. On average, the correlation between subjects was low: .26 (SEM = .05) for the subjects imprinted to the natural sequences and .10 (SEM = .05) for the subjects imprinted to the unnatural sequences. Thus, while rearing condition and test trial type significantly influenced performance, the specific imprinted sequence—unfamiliar sequence combinations were not strong predictors of recognition performance.

Analysis of the virtual objects

Why did these newborn subjects show enhanced learning of natural visual sequences? According to a class of temporal association models, object representations are learned from the smooth temporal progression of images on the retina (e.g., DiCarlo et al. 2012; Foldiak 1991; Stone 1996; Wiskott and Sejnowski 2002). In the present study, neither the natural sequences nor the unnatural sequences were completely smooth from a human perspective, but it is still possible that the natural sequences were more smooth than the unnatural sequences. To test this possibility, we quantified the smoothness of the sequences in three ways.

First, we computed the degree of brightness change across the images in the natural sequences and unnatural sequences. We measured the brightness of each sequence by (1) computing the sum of the pixel intensities for each unique image in the sequence and (2) computing the average difference in brightness across the two image pairs (i.e., Image 1 → Image 2 and Image 2 → Image 3). As shown in Fig. 4, the images in the natural sequences were
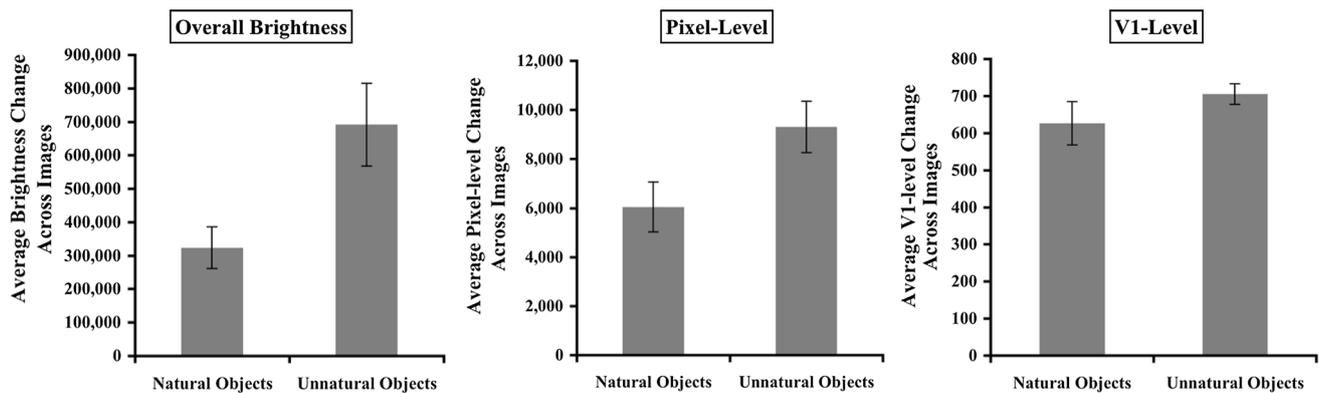
Fig. 4 Results of the analyses of the virtual objects. The graphs show the degree of change across the images in the natural sequences and unnatural sequences from a brightness perspective, retina-like (pixel-level) perspective, and V1-level perspective. The *error bars* indicate standard error

more similar than the images in the unnatural sequences [$t(10) = 2.66$, $p = .02$]. From a brightness perspective, the natural sequences were more temporally smooth than the unnatural sequences.

Second, we computed the degree of image change across the images in the natural sequences and unnatural sequences from a retina-like (pixel-level) perspective. For each animation, we (1) measured the brightness level of each pixel in each image, (2) controlled for the overall brightness differences between images by dividing the brightness of each pixel by the mean brightness of the image, (3) compared the successive images (i.e., by comparing the brightness level of each corresponding pixel across the images and taking the absolute difference), and (4) calculated the average pixel-level difference between the two image pairs. As shown in Fig. 4, the images in the natural sequences were more similar than the images in the unnatural sequences [$t(10) = 2.24$, $p = .05$]. From a retina-like (pixel-level) perspective, the natural sequences were more temporally smooth than the unnatural sequences.

Third, we computed the degree of image change across the images in the natural sequences and unnatural sequences from a V1-level perspective. Specifically, we simulated the responses of a population of cells found in the primary visual cortex, the first primate cortical visual processing stage (area V1). Measuring V1-like similarity provides a first-order description of the representations in the early visual system. To compute V1-level similarity, we used the Gabor jet model: a multi-scale, multi-orientation model of V1 complex-cell filtering (Lades et al. 1993). The general parameters and implementation followed those used by Xu and Biederman (2010). For each unique image in each sequence, we measured the magnitude of activation values that the image produced in a set of 40 Gabor jets (8 orientations × 5 scales). We measured the dissimilarity between two images by computing the

Euclidean distance between their Gabor jet activation values. Finally, we calculated the average Gabor jet dissimilarity across the two image pairs. As shown in Fig. 4, the natural sequences and unnatural sequences had similar degrees of V1-level image change. Although the natural sequences were somewhat more temporally smooth than the unnatural sequences from a V1-level perspective, this effect did not approach statistical significance [$t(10) = 1.22$, $p = .25$].

Measuring the strength of the imprinting response

One potential explanation for these findings is that the unnatural sequences were less attractive than the natural sequences, and consequently, the chicks were less likely to imprint to those sequences. We tested this possibility in two ways. First, we examined the proportion of time the chicks spent by the imprinted sequences during the rest periods in the test phase (Fig. 5a). During the rest periods, one of the imprinted sequences was presented on one display wall, while the other display wall was blank. Thus, the rest periods provided a measure of the amount of time the chicks generally preferred to spend in proximity to the imprinted sequences. The chicks raised with the natural sequences and unnatural sequences spent 80.6 % (SEM = 2 %) and 79.3 % (SEM = 2 %) of their time with the imprinted sequences, respectively. These values did not differ significantly from one another [$t(22) = .52$, $p = .61$]. Thus, the chicks imprinted equally strongly to the natural sequences and unnatural sequences.

Second, we examined the rates at which the chicks developed a preference for the natural sequences and unnatural sequences during the input phase (Fig. 5b).[1] A repeated measures ANOVA with Imprinting Day (Days

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[1] Due to an equipment malfunction, we were only able to analyze the imprinting rates from the input phase for half of the subjects (the subjects raised with the sequences shown in Panel B in Fig. 1).
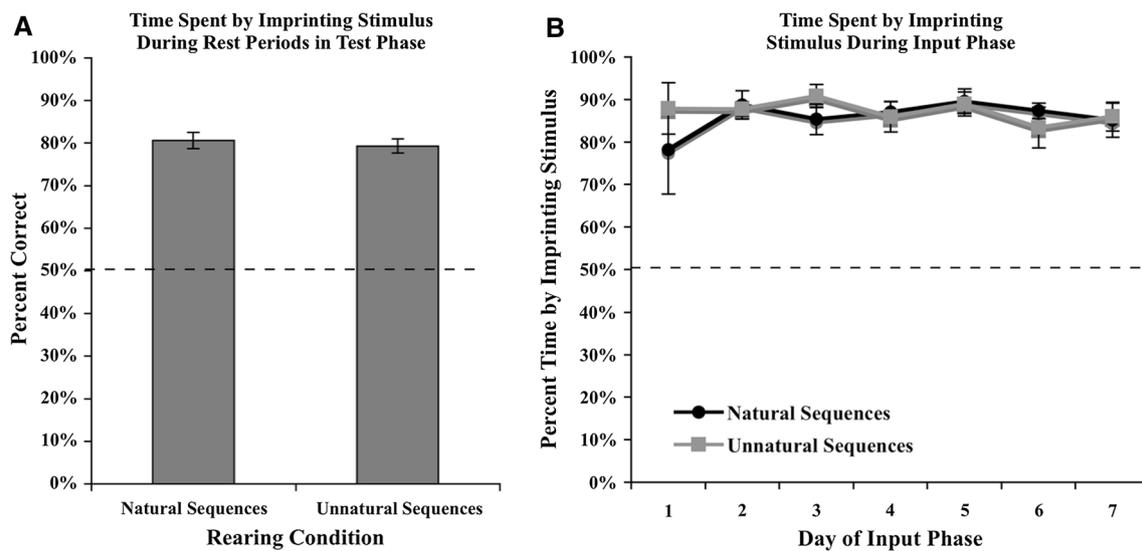
Fig. 5 Results showing the strength of the imprinting response across the conditions. **a** The proportion of time the chicks spent with the imprinted sequences during the rest periods in the test phase. **b** The rates at which the chicks developed a preference for the natural sequences versus the unnatural sequences during the input phase. In general, the chicks imprinted equally strongly to the natural sequences and unnatural sequences

1–7) as a within-subjects factor and Rearing Condition (raised with natural sequences vs. unnatural sequences) as a between-subjects factor did not reveal a main effect of Imprinting Day or Rearing Condition, and the interaction was not significant (all ps > .62). Thus, the chicks imprinted equally well to the natural sequences and unnatural sequences. Together, these analyses indicate that enhanced learning of natural visual sequences in newborn chicks cannot be explained by appealing to differences in the strength of the imprinting response to natural versus unnatural sequences.

Discussion

We used a high-throughput controlled-rearing method to examine the mechanisms that underlie object recognition at the onset of vision, before the visual system has been shaped by natural visual experience. Specifically, we examined whether newborn chicks show enhanced learning of natural visual sequences. The chicks raised with the natural sequences and the chicks raised with the unnatural sequences were exposed to the same individual images, and the sequences were equally predictive in terms of the transitional probabilities between images; nevertheless, there were significant differences in recognition performance across the conditions. When raised in virtual worlds containing natural sequences, the majority of the chicks developed the ability to recognize familiar visual images. Conversely, when raised in virtual worlds containing unnatural sequences, the chicks' ability to recognize

familiar images was severely impaired. In fact, the majority of the chicks raised with the unnatural sequences failed to learn to recognize familiar images despite acquiring over 100 h of experience with those images during the 1-week input phase. Thus, newborn chicks show enhanced learning of images presented in natural temporal sequences. These results indicate that newborn visual systems operate most effectively over natural visual input.

It is worth emphasizing that the chicks raised with the unnatural sequences failed to develop accurate object recognition abilities despite being raised in environments that contained some natural features. For example, these chicks did acquire visual experience with continuous and solid extended surfaces (i.e., the walls and floor of the chamber). These chicks also acquired visual experience with non-solid grain during feeding. Nevertheless, when raised with unnatural visual sequences, the chicks were unable to build accurate representations of the images. This finding suggests that the development of object recognition requires experience with natural visual objects.

Our exploratory analyses suggest that this effect may result from the temporal smoothness of the images. We found that the natural sequences were more temporally smooth than the unnatural sequences both from a brightness perspective and from a retina-like (pixel-wise) perspective. This finding provides suggestive evidence that newborn visual systems are designed to operate over temporally smooth visual object input, as predicted by temporal association models of visual object recognition (e.g., Stone 1996). Of course, we do not claim this to be an exhaustive characterization of all possible factors that lead

to enhanced learning of natural visual sequences, but rather a starting point toward that greater goal. It would be interesting for future studies to systematically manipulate the properties of the successive images and examine the effects of those manipulations on chicks' emerging object recognition abilities.

These results support previous studies showing that adult pigeons learn visual events more effectively when presented with temporally smooth sequences compared with temporally non-smooth sequences (e.g., Cook et al. 2001; Cook and Roberts 2007). In these previous studies, the pigeons had acquired a lifetime of experience with a natural (temporally smooth) visual world. Thus, the present study extends these findings by showing that enhanced learning of natural visual sequences is not simply the product of experience with a temporally smooth visual world. Rather, newborn animals show enhanced learning of natural visual sequences at the onset of vision.

The present results also provide evidence for a dissociation between encoding and recognition in newborn chicks. Manipulating the order of the images influenced chicks' ability to *encode* the images (i.e., chicks built more accurate representations of images when raised with natural sequences vs. unnatural sequences), but not their ability to *recognize* the images (i.e., chicks did not distinguish between natural sequences and unnatural sequences during the Novel Order Test Trials). This dissociation between encoding and recognition is consistent with a large body of work in the neurosciences showing that encoding (pattern separation) and recognition (pattern completion) depend on computationally distinct processes (e.g., Duncan et al. 2012; Hasselmo and Schnell 1994; O'Reilly and McClelland 1994). It would be interesting for future research to examine why the chicks had difficulty encoding the images in the unnatural sequences. One possible explanation is that for the natural sequences, the three images of each real-world object were concentrated over time, whereas for the unnatural sequences, the three images of each real-world object were distributed over time. Accordingly, the visual features that define real-world objects remained stable over time in the natural sequences, but changed rapidly over time in the unnatural sequences. Thus, the visual stability of object features might be important for the development of object representations in the newborn brain.

Finally, these results indicate that newborn chicks recognize objects primarily in a bottom-up manner (i.e., each image is analyzed independently from the previous image). Specifically, on the Novel Order Test Trials, all of the chicks failed to distinguish between the imprinted sequences and the unfamiliar sequences. Despite having observed the image transitions in the imprinted sequences thousands of times during the input phase, none of the chicks learned to distinguish between the test sequences on

the basis of the familiarity of the image transitions. Newborn chicks therefore appear to recognize objects primarily by analyzing individual images rather than the order of the images in the sequence. This result is consistent with feed-forward models of visual object recognition, in which objects are recognized largely through a cascade of rapid, feed-forward computations (e.g., DiCarlo et al. 2012; Hung et al. 2005; Serre et al. 2007; Yamins et al. 2014).

In conclusion, understanding the flexibility of biological vision and the constraints on that flexibility is a major goal in the cognitive sciences. While animals can learn about a wide range of visual environments, the present results suggest that there are constraints on the types of visual sequences that can be successfully learned. Newborn visual systems appear to learn best in natural visual environments.

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