



# Using automated controlled rearing to explore the origins of object permanence

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**Abstract**

What are the origins of object permanence? Despite widespread interest in this question, methodological barriers have prevented detailed analysis of how experience shapes the development of object permanence in newborn organisms. Here, we introduce an automated controlled-rearing method for studying the emergence of object permanence in strictly controlled virtual environments. We used newborn chicks as an animal model and recorded their behavior continuously (24/7) from the onset of vision. Across four experiments, we found that object permanence can develop rapidly, within the first few days of life. This ability developed even when chicks were reared in impoverished visual environments containing no object occlusion events. Object permanence failed to develop, however, when chicks were reared in environments containing temporally non-smooth objects (objects moving on discontinuous spatiotemporal paths). These results suggest that experience with temporally smooth objects facilitates the development of object permanence, confirming a key prediction of temporal learning models in computational neuroscience.

**KEYWORDS**

automation, chicks, controlled rearing, newborn, object permanence, smoothness

## 1 | INTRODUCTION

One of the great unsolved mysteries in psychology concerns the origins of object permanence<sup>1</sup> (i.e., the ability to maintain an object representation in memory after the object has disappeared from view). Although object permanence is central to perception and cognition, the field has not yet characterized how this ability emerges in newborn brains. Is object permanence a hardwired property of vision or learned during development? If object permanence is learned, what is the nature of the underlying learning mechanisms?

Some researchers have argued that object permanence is learned during development. For example, according to Piaget's constructionist account (Piaget, 1954), object permanence is constructed progressively over development based on infants' manual exploration of objects. By this account, object permanence begins to emerge around 8–9 months of age, when infants begin to search for hidden objects. More recently, researchers have argued that object

permanence is learned from *visual* experience early in postnatal life (reviewed by Bremner, Slater, & Johnson, 2015). Support for this hypothesis comes from studies showing that young infants gradually develop more advanced object concepts over the first few months of life, before infants have experience manipulating objects (e.g., Bremner et al., 2005; Johnson, Amso, & Slemmer, 2003; Johnson & Aslin, 1996; Johnson, Bremner et al., 2003; Johnson, Bremner, Slater, & Mason, 2000; Slater et al., 1990). For example, infants' ability to perceive object permanence appears to develop gradually, such that older infants perceive object permanence across larger spatial and temporal gaps than younger infants (Bremner et al., 2015). The development of this ability is thought to emerge from domain-general learning mechanisms that encode the spatiotemporal statistics of the visual environment (Bulf, Johnson, & Valenza, 2011; Kirkham, Slemmer, & Johnson, 2002).

Alternatively, other researchers have proposed that knowledge of the physical world is innate (i.e., not learned). According to this

view, infants possess core knowledge about objects (Baillargeon, Spelke, & Wasserman, 1985; Spelke, 1998; Spelke & Kinzler, 2007), including the capacity for object permanence (Baillargeon, 2008). Support for this hypothesis comes from studies showing that infants display knowledge about the continued existence of hidden objects in the first few months of life when tested with methods that do not rely on manual searching for objects (e.g., Baillargeon, 1987; Baillargeon & Devos, 1991; Baillargeon et al., 1985; Spelke, 1990; Spelke, Breinlinger, Macomber, & Jacobson, 1992). For example, in the classic “drawbridge” study, Baillargeon and colleagues reported that 5-month-old infants can reason about both the persistence and solidity of objects (Baillargeon et al., 1985). Similar results have also been obtained with younger (3–4-month-old) infants (Baillargeon, 1987).

How can we distinguish between these alternative accounts? In general, it is not possible to distinguish between nativist and learning accounts with studies of human infants because infants cannot be raised in strictly controlled environments from birth. When infants participate in experiments, they have already been shaped by days, weeks, or months of experience with the natural visual world. This natural visual experience might play an important role in learning object concepts. Thus, for almost any capacity found in young human infants, it is not possible to determine whether the ability is innate or learned from postnatal visual experience. There is also evidence that light can enter the uterus during pregnancy (Del Giudice, 2011) and that the human fetus responds to light (e.g. Eswaran, Lowery, Wilson, Murphy, & Preissl, 2004), allowing for the possibility that even early emerging abilities are shaped by pre-natal visual experience.

In contrast to studies of human infants, controlled-rearing studies of non-human animals can be used to characterize the precise role of visual experience in the development of object perception. By systematically manipulating the pre-natal and post-natal experiences provided to newborn subjects and observing the effects of those manipulations on behavior, it is possible to distinguish the experiences that are causally related to developmental change from those that are not. Controlled-rearing experiments therefore provide an experimental avenue for probing how object perception emerges in newborn brains as a function of specific visual experiences. In the present study, we introduce an automated controlled-rearing method for studying object permanence in newborn animals. We then use this method to examine whether the development of object permanence requires visual experience with (a) object occlusion events (i.e., objects disappearing and reappearing behind other objects) and (b) temporally smooth objects (i.e., objects moving on continuous spatiotemporal paths).

## 1.1 | Automated controlled rearing with newborn chicks

To examine the role of experience in the development of object permanence, we used an automated controlled-rearing method with newborn chicks (Wood, 2013, 2014). This method allows newborn chicks to be raised in strictly controlled virtual environments immediately after hatching (Figure 1). Specifically, we raised chicks in controlled-rearing chambers that contained no movable, real-world

### Research Highlights

- One of the great unsolved mysteries in psychology concerns the origins of object permanence and the role of experience in the development of this ability.
- We introduce an automated controlled-rearing method for studying the development of object permanence in strictly controlled virtual environments, using newborn chicks as a model system.
- We found that object permanence can develop without object occlusion experience, but not without experience of objects moving on smooth, continuous spatiotemporal paths.
- This suggests that experience with temporally smooth objects facilitates the development of object permanence, confirming a key prediction of temporal learning models in computational neuroscience.

objects. To present object stimuli to the chicks, we projected virtual objects on four display walls (LCD monitors) that surrounded the chick. The controlled-rearing chambers recorded all of the chicks' behavior (24/7) using automated image-based tracking software, producing hundreds of hours of behavioral data per chick. Additionally, since the entire data collection process was automated, our method eliminated the possibility of experimenter error and bias when presenting the stimuli and coding the subjects' behavior.

We used newborn chicks as a model system because they are uniquely suited for studying the earliest stages of visual learning (Wood & Wood, 2015). First, unlike commonly used animal models in psychology (e.g., rats, pigeons, monkeys), newborn chicks are precocial. Chicks require no parental care and can be raised in strictly controlled environments from the onset of vision. Experiments with chicks therefore allow researchers to examine how early visual experience shapes the development of object permanence. Second, previous studies have reported that young chicks can maintain representations of objects that disappear from view (Regolin, Rugani, Pagni, & Vallortigara, 2005; Regolin, Vallortigara, & Zanforlin, 1995; Vallortigara, Regolin, Rigoni, & Zanforlin, 1998). These studies indicate that newborn chicks can develop object permanence abilities within the first few days of life. Third, chicks imprint to objects and attempt to reunite with those objects when separated. This imprinting instinct provides a natural behavioral response that can be used to test chicks' object perception abilities without training (Martinho & Kacelnik, 2016; Wood, 2013). Fourth, birds and mammals use homologous neural cells and circuits to process sensory input (Jarvis et al., 2005; Karten, 2013), and the large-scale network organization of the brain is largely conserved across birds and mammals (Shanahan, 2013). Accordingly, controlled-rearing studies of newborn chicks can inform our understanding of cognitive development across species.

## 2 | EXPERIMENT 1

Our first experiment establishes an automated controlled-rearing method for studying object permanence in newborn chicks. In the first week of life (Input Phase), newborn chicks were reared in strictly controlled environments that contained no objects other than a single virtual object (Figure 1). This object moved smoothly across the four display walls of the chamber (Figure 2a–c, Movie S1). During one-half of the Input Phase, the chicks also received experience with object occlusion events (Figure 2d–f, Movie S2). Eight gray virtual screens were placed around the environment, and the object disappeared and reappeared from behind those screens as it moved around the chamber.

In the second week of life (Test Phase), we used an automated two-alternative forced-choice procedure to test the chicks' object permanence abilities. During the test trials, the chick's imprinted object moved behind one of two virtual screens, and we measured whether the chick spent more time by the correct screen (the screen hiding the imprinted object) compared to the incorrect screen. The object remained hidden for 1–5 min, which allowed us to measure the duration of time the chicks could maintain a representation of their imprinted object after it disappeared from view.

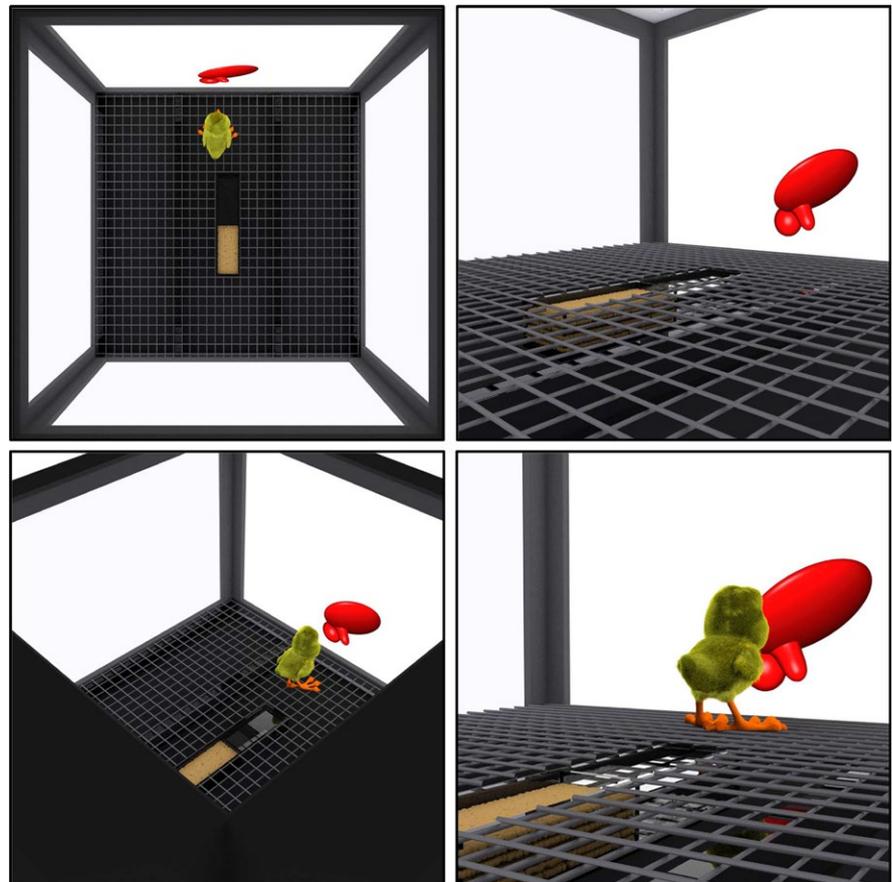
### 2.1 | Method

#### 2.1.1 | Subjects

Six Rhode Island Red chicks of unknown sex were tested. The sample size was determined before the experiment was conducted (based on a pilot study that yielded highly significant results with a similar design). No subjects were excluded from the analyses. The eggs were obtained from a local distributor and incubated in an OVA-Easy incubator (Brinsea Products Inc., Titusville, FL). The eggs were incubated in complete darkness, so no visual input could reach the subjects during their pre-natal development. 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 reared singly within its own chamber. This research was approved by The University of Southern California Institutional Animal Care and Use Committee.

#### 2.1.2 | Controlled-rearing chambers

The controlled-rearing chambers measured 43 cm (length) × 43 cm (width) × 77 cm (height) and contained no real-world objects. To present object stimuli to the chicks, a virtual environment was projected on four display walls surrounding the subject (Figure 1). All four walls



**FIGURE 1** Illustrations of a controlled-rearing chamber. The chick was surrounded by four display walls (LCD monitors) that displayed a pre-programmed virtual world. The chambers contained no objects other than the virtual objects projected on the display walls

of the chamber were 19" LCD monitors (1,440 × 900 pixel resolution). The four monitors were linked into a single continuous virtual space, allowing the imprinted object to move seamlessly across the four display walls. Due to the bevels of the monitors (width = 1.3 cm), the virtual object was partially occluded when it moved across corners of the chamber. From the chick's perspective, the bevels formed a narrow black occluder, and the object appeared to pass behind the occluder.

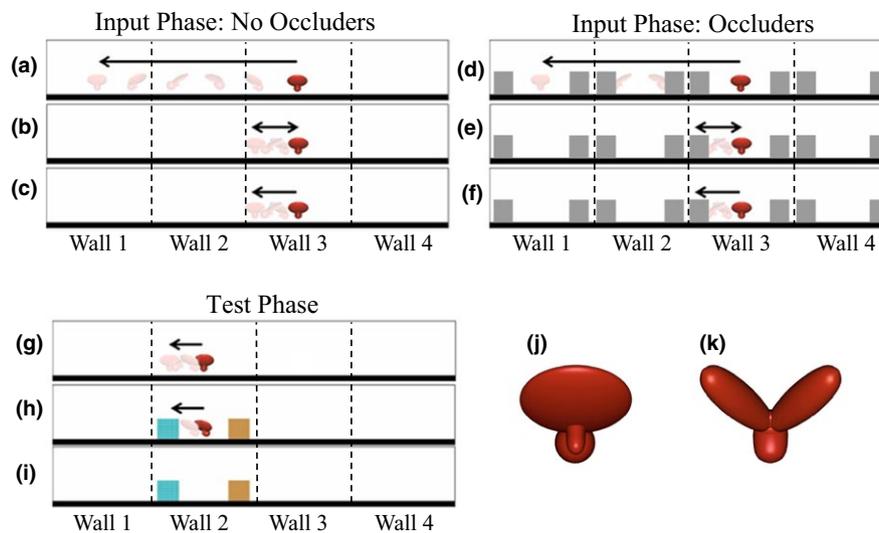
Food and water were provided in a transparent trough in the ground (12 cm length × 4 cm width × 2.5 cm height). Grain was used as food because a heap of grain does not behave like an object (i.e., a heap of grain does not maintain a rigid, bounded shape like real-world objects). The floors were constructed from black wire mesh and supported 2.7 cm off the ground. The chambers tracked all of the chicks' behavior (9 samples/second, 24 hr/day, 7 days/week), via micro-cameras in the chamber ceilings and automated image-based tracking software (EthoVision XT; Noldus Information Technology, Leesburg, VA).

### 2.1.3 | Procedure

In the first week of life (Input Phase), the chicks were raised in controlled-rearing chambers that contained a single virtual object. On average, the object measured 7.5 cm (length) × 6.5 cm (height) and was displayed on a uniform white background. The object rotated continuously around a frontoparallel vertical axis, completing a full rotation every 15 s.

During the Input Phase, the imprinted object moved smoothly across the four display walls. Specifically, during each 1-min period, the object performed one of the following movements (Movie S1): (a) the object moved from the center of one display wall to the center of a different display wall (Figures 2a & 2d); (b) the object moved back and forth repeatedly across the same display wall (Figures 2b & 2e); or (c) the object moved to one side of the display wall, remained in the same location for 45 s, and then returned to the center of the display wall (Figures 2c & 2f). The object moved on continuous spatiotemporal paths at a constant speed (4.3 cm/s), at a rate of 30 frames/s. During one-half of the Input Phase, the chicks also received experience with object occlusion events (Figure 2d–f, Movie S2). Eight gray virtual screens were placed around the environment (two on each display wall), and the object disappeared and reappeared from behind those screens as it moved around the chamber. The screens were present for 60 min and subsequently absent for the next 60 min, in an alternating cycle. During each day in the Input Phase, the chicks were exposed to their imprinted object for 20 hr, followed by 4 hr of darkness.

During the second week of life (Test Phase), we used a two-alternative forced-choice testing procedure to examine whether the chicks could maintain a representation of their imprinted object after it disappeared from view (Movie S3). During the Occluder Trials, the object appeared at the center of a display wall, equidistant between two virtual screens with different colors and textures (Figure 2h). The object then moved behind one of the two screens and remained hidden for 1–5 min (Figure 2i). The chicks received equal numbers of



**FIGURE 2** During the Input Phase, the object performed three types of movements: (a) the object moved from the center of one display wall to the center of a different display wall, (b) the object moved back and forth repeatedly across one display wall, and (c) the object moved to one side of the display wall, remained in the same location for 45 s, and then returned to the center of the display wall. In Experiment 1, the chicks saw the object move behind occluders (d–f), whereas in Experiments 2–4, the chicks did not see the object move behind occluders (a–c). During the Test Phase, the chicks received two types of test trials. (g) On the Visible Trials, the object moved from the center of the display wall to the side of the display wall and then remained in the same location for 1–5 min. (h) On the Occluder Trials, the object moved from the center of the display wall to the side of the display wall (behind a virtual screen) and then remained in the same location for 1–5 min. (i) The object was not visible after it moved behind the screen. In Experiments 1–2, the chicks were reared with the object in panel (j), whereas in Experiments 3–4, one-half of the chicks were reared with the object in panel (j) and one-half of the chicks were reared with the object in panel (k)

test trials in which the object was hidden for 1, 2, 3, 4, or 5 min. As our dependent measure, we measured the amount of time the chicks spent within zones (15 × 12.5 cm) next to each of the two screens. If the chicks could maintain a representation of their imprinted object, then they should have spent more time by the correct screen (the screen hiding their imprinted object) than the incorrect screen in order to stay near their imprinted object.

To measure the strength of the chicks' imprinting response, we also included Visible Trials in which the imprinted object was always in view. During the Visible Trials, the imprinted object performed the same movements as in the Occluder Trials, but there were no virtual screens on the display walls (Figure 2g, Movie S3). If the chicks successfully imprinted to the object, then they should have spent the majority of their time by their imprinted object on the Visible Trials. The chicks received Occluder Trials and Visible Trials in alternating 75-min test blocks. Each test block was followed by a 75-min Rest Period, in which the animations from the Input Phase were displayed.

## 2.2 | Results

To analyze the data, we computed the amount of time the chicks spent in the correct zone versus the incorrect zone on each test trial. We began measuring the time spent in each zone immediately after the object disappeared from view. We then calculated each chick's average performance across the test trials, by dividing the time spent in the correct zone by the time spent in both zones. Scores above 50% indicate more time spent in the correct zone, whereas scores below 50% indicate more time spent in the incorrect zone. All of our statistical tests were two-tailed.

All of the test trials were included in our analyses (i.e., all of the trials presented to the chicks across the 7-day Test Phase). In particular, to avoid the possibility of experimenter error or bias, we did not remove any test trials from the analysis (e.g., based on subjective criteria such as whether the chick seemed alert vs. distracted, fussy vs. relaxed, or awake vs. asleep).

### 2.2.1 | Performance on visible trials

We first examined whether the chicks in both conditions imprinted to the object. On the Visible Trials, the chicks spent the majority of their time in the zone containing the imprinted object ( $M = 73.84\%$ ,  $SEM = 1.66\%$ ;  $t(5) = 14.37$ ,  $p = 0.00003$ , Cohen's  $d = 5.87$ ). Thus, the chicks successfully imprinted to the virtual object and followed the object around the chamber.

### 2.2.2 | Performance on occluder trials

We next examined whether the chicks preferred to spend time at the location of their imprinted object after the object disappeared from view. Overall, the chicks spent a greater proportion of time by the correct screen compared to the incorrect screen ( $M = 57.75\%$ ,  $SEM = 0.97\%$ ;  $t(5) = 8.02$ ,  $p = 0.0005$ , Cohen's  $d = 3.28$ ). To explore how long the chicks maintained this preference, we pooled the data

based on the duration of time the object had been hidden from view (Figure 3a).<sup>2</sup> Performance exceeded chance level when the object had been hidden for 1 min ( $M = 59.21\%$ ,  $SEM = 1.74\%$ ;  $t(5) = 5.30$ ,  $p = 0.003$ , Cohen's  $d = 2.16$ ), 2 min ( $M = 57.13\%$ ,  $SEM = 0.42\%$ ;  $t(5) = 16.82$ ,  $p = 0.00001$ , Cohen's  $d = 6.87$ ), and 3 min ( $M = 58.53\%$ ,  $SEM = 0.67\%$ ;  $t(5) = 12.67$ ,  $p = 0.00005$ , Cohen's  $d = 5.17$ ). Performance was not significantly higher than chance level when the object had been hidden for 4 min ( $M = 56.10\%$ ,  $SEM = 2.95\%$ ;  $t(5) = 2.06$ ,  $p = 0.09$ , Cohen's  $d = 0.84$ ) or 5 min ( $M = 52.32\%$ ,  $SEM = 3.84\%$ ;  $t(5) = 0.60$ ,  $p = 0.57$ , Cohen's  $d = 0.25$ ).

## 2.3 | Discussion

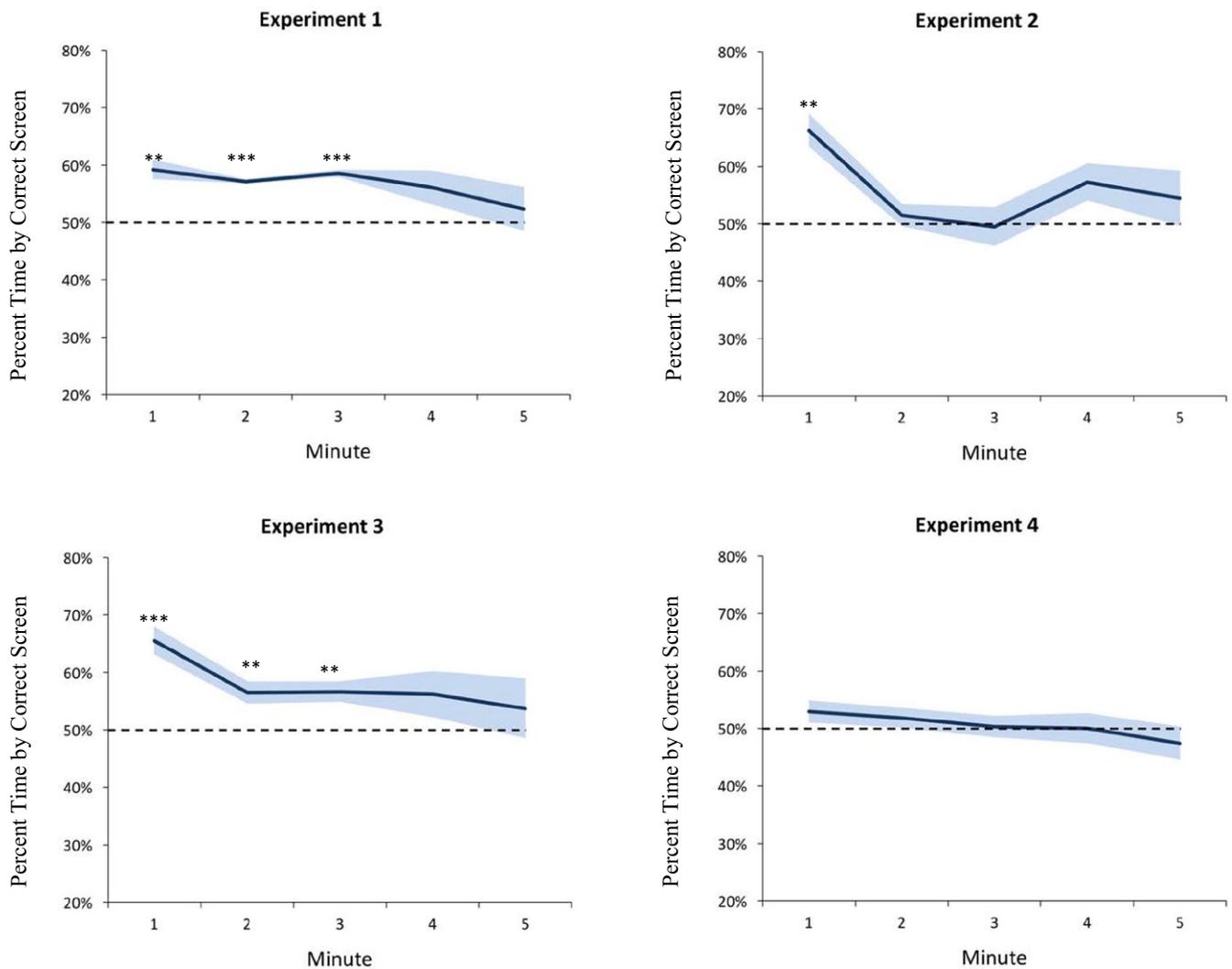
In Experiment 1, we used an automated controlled-rearing method to examine whether newborn chicks can remember the location of an object after the object has disappeared from view. After 1 week of experience with a world containing object occlusion events, we found that the chicks could maintain an object representation for about 3 min after the object disappeared from view. In Experiments 2–4, we used this method to begin exploring the role of experience in the development of this ability.

## 3 | EXPERIMENT 2

In Experiment 2, we tested whether the development of object permanence requires visual experience with full object occlusion (i.e., events in which an object completely disappears behind another object). The methods were identical to those used in Experiment 1, except we removed the virtual occluders from the Input Phase. Thus, the chicks never saw their imprinted object disappear and reappear from behind an occluder (the chicks did, however, experience partial occlusion when the object moved from one monitor to the next). If experience with full object occlusion is necessary for the development of object permanence, then the chicks should fail to develop object permanence in this experiment, because their imprinted object was never fully occluded by another object. Conversely, if object permanence can develop in the absence of experience with full object occlusion, then the chicks should successfully develop object permanence.

### 3.1 | Method

The methods were identical to those used in Experiment 1, except in the following ways. First, we tested a new group of six newborn chicks. Second, the chicks were raised with the same virtual object performing the same movements, but there were no virtual occluders during the Input Phase. Thus, the chicks in this experiment never saw their imprinted object disappear and reappear from behind a screen. During the Test Phase, the chicks also never saw their imprinted object reappear after hiding behind one of the two virtual screens (as in Experiment 1). Consequently, in both the Input Phase and Test Phase, there was no opportunity to learn that objects continue to exist after disappearing behind occluders.



**FIGURE 3** Results on the Occluder Trials, as a function of the number of minutes after the object had disappeared from view. In Experiments 1–3, the chicks spent more time by the correct screen than the incorrect screen, indicating that the chicks could remember the location of their imprinted object after it disappeared from view. Conversely, in Experiment 4, the chicks did not spend more time by the correct screen than the incorrect screen. Error bars indicate standard error. The dashed lines show chance performance. Asterisks denote statistical significance: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$  (two-tailed  $t$  tests).

## 3.2 | Results

### 3.2.1 | Performance on visible trials

On the Visible Trials, the chicks spent the majority of their time in the zone containing the imprinted object ( $M = 80.46\%$ ,  $SEM = 3.97\%$ ;  $t(4) = 7.66$ ,  $p = 0.002$ , Cohen's  $d = 3.43$ ). Thus, the chicks successfully imprinted to the virtual object and followed the object around the chamber.

### 3.2.2 | Performance on occluder trials

We next examined whether the chicks preferred to spend time at the location of their imprinted object after the object disappeared from view. One chick's performance was an outlier, and

it was removed from the analysis.<sup>3</sup> Overall, the chicks spent a greater proportion of time by the correct screen compared to the incorrect screen ( $M = 56.97\%$ ,  $SEM = 1.28\%$ ;  $t(4) = 5.45$ ,  $p = 0.005$ , Cohen's  $d = 2.44$ ). When we analyzed the data based on the duration of time the object had been hidden from view (Figure 3b), the chicks spent a greater proportion of time by the correct screen compared to the incorrect screen when the object had been hidden for 1 min ( $M = 66.27\%$ ,  $SEM = 2.92\%$ ;  $t(4) = 5.58$ ,  $p = 0.005$ , Cohen's  $d = 2.49$ ). Performance was not significantly higher than chance level when the object had been hidden for 2 min ( $M = 51.50\%$ ,  $SEM = 1.96\%$ ;  $t(4) = 0.76$ ,  $p = 0.49$ , Cohen's  $d = 0.34$ ), 3 min ( $M = 49.46\%$ ,  $SEM = 3.44\%$ ;  $t(4) = 0.16$ ,  $p = 0.88$ , Cohen's  $d = 0.07$ ), 4 min ( $M = 57.27\%$ ,  $SEM = 3.23\%$ ,  $t(4) = 2.25$ ,  $p = 0.09$ , Cohen's  $d = 1.01$ ), or 5 min ( $M = 54.46\%$ ,  $SEM = 4.85\%$ ;  $t(4) = 0.92$ ,  $p = 0.41$ , Cohen's  $d = 0.41$ ).

### 3.3 | Discussion

In Experiment 2, we examined whether experience with object occlusion events is necessary for the development of object permanence. The results provided evidence that object permanence can develop without full object occlusion experience, but only during the first minute after the object disappeared from view. Thus, before concluding that object permanence can emerge in the absence of object occlusion experience, we attempted to replicate this finding with a larger group of subjects to ensure that this finding is robust.

## 4 | EXPERIMENT 3

### 4.1 | Method

Experiment 3 was identical to Experiment 2, except in the following ways. First, we doubled the sample size to 12 subjects. Second, we reduced the length of the Input Phase and Test Phase to 4 days each. We made this second change to ensure that this automated method could produce similar patterns with shorter Input and Test Phases. Third, we imprinted the chicks to one of two objects to test whether these findings generalize across different objects, rather than being specific to the object used in Experiments 1–2. Half of the chicks were imprinted to the object shown in Figure 2j and half of the chicks were imprinted to the object shown in Figure 2k. These objects were used in previous studies that tested for invariant object recognition in newborn chicks (Wood & Wood, 2015; 2016).

### 4.2 | Results

#### 4.2.1 | Performance on visible trials

On the Visible Trials, the chicks spent the majority of their time in the zone containing the imprinted object ( $M = 80.81\%$ ,  $SEM = 3.31\%$ ;  $t(10) = 9.30$ ,  $p = 0.000003$ , Cohen's  $d = 2.80$ ). Thus, the chicks successfully imprinted to the virtual object and followed the object around the chamber.

#### 4.2.2 | Performance on occluder trials

We next examined whether the chicks preferred to spend time at the location of their imprinted object after the object disappeared from view. One chick's performance was an outlier, and it was removed from the analysis.<sup>4</sup> Performance was similar whether the chicks were reared with Object 1 or Object 2 (two-sample  $t$  test;  $t(9) = 0.71$ ,  $p = 0.50$ , Cohen's  $d = 0.44$ ). Overall, the chicks spent a greater proportion of time by the correct screen compared to the incorrect screen ( $M = 59.38\%$ ,  $SEM = 1.37\%$ ;  $t(10) = 6.85$ ,  $p = 0.00004$ , Cohen's  $d = 2.06$ ). To explore how long the chicks maintained this preference, we pooled the data based on the duration of time the object had been hidden from view (Figure 3c). Performance exceeded chance level when the object had been hidden for 1 min ( $M = 65.48\%$ ,  $SEM = 2.46\%$ ;  $t(10) = 6.29$ ,  $p = 0.00009$ , Cohen's

$d = 1.90$ ), 2 min ( $M = 56.48\%$ ,  $SEM = 2.00\%$ ;  $t(10) = 3.25$ ,  $p = 0.009$ , Cohen's  $d = 0.98$ ), and 3 min ( $M = 56.65\%$ ,  $SEM = 1.79\%$ ;  $t(10) = 3.71$ ,  $p = 0.004$ , Cohen's  $d = 1.12$ ). Performance was not significantly higher than chance level when the object had been hidden for 4 min ( $M = 56.22\%$ ,  $SEM = 4.05\%$ ;  $t(10) = 1.54$ ,  $p = 0.16$ , Cohen's  $d = 0.46$ ) or 5 min ( $M = 53.74\%$ ,  $SEM = 5.23\%$ ;  $t(10) = 0.72$ ,  $p = 0.49$ , Cohen's  $d = 0.22$ ).

### 4.3 | Discussion

This experiment replicates the main finding from Experiment 2 with a larger group of subjects and shorter Input and Test Phases. Together, Experiments 2 and 3 indicate that object permanence can develop in the absence of experience with full object occlusion. During the Input Phase, the chicks never saw their imprinted object disappear and reappear from behind an occluder. Moreover, in the Test Phase, the chicks never saw their imprinted object reappear after moving behind one of the virtual screens (and thus had no opportunity to learn that objects continue to exist after disappearing behind screens). Nevertheless, after 4 days of experience with a world containing no object occlusion events, the chicks were able to maintain an object representation for about 3 min after the object disappeared from view.

It is important to emphasize that the chicks did receive experience with partial object occlusion when the object moved from one monitor to the next (across the bevels of the monitors). Additional research is needed to determine whether this partial object occlusion experience facilitates the development of object permanence.

## 5 | EXPERIMENT 4

The results from Experiments 1–3 provide evidence that (a) newborn chicks can develop object permanence within the first few days of life and (b) object permanence can develop in the absence of visual experience with full object occlusion. In the final experiment, we tested whether visual experience with smooth, continuous object motion facilitates the development of object permanence. A wealth of studies in developmental psychology and vision science indicate that infants and adults expect objects to move continuously, following connected paths through space and time (e.g., Bremner et al., 2015; Feldman & Tremoulet, 2006; Scholl, 2001; Spelke, 1990). Similarly, researchers in computational neuroscience have long theorized that biological visual systems leverage the temporal continuity of natural visual environments to develop stable object representations (e.g., DiCarlo, Zoccolan, & Rust, 2012; Foldiak, 1991; Gibson, 1979; Stone, 1996; Wallis & Rolls, 1997; Wiskott & Sejnowski, 2002). A key assumption underlying these models is that perceptually salient visual parameters vary smoothly over time in natural visual environments. Thus, in principle, newborn brains could build up stable object representations by encoding temporally smooth changes in the environment. This view predicts that if a newborn's environment lacks temporally smooth object motion, then the newborn should

fail to build stable object representations that persist over time. To test this prediction, we examined whether visual experience with smooth, continuous object motion facilitates the development of object permanence.

## 5.1 | Method

Experiment 4 was identical to Experiment 3, except in the following ways. First, we tested a new group of 12 subjects. Second, rather than presenting an object moving on a smooth (continuous) spatiotemporal path, the chicks were shown the same virtual object, but the object moved on a non-smooth (discontinuous) spatiotemporal path (Movie S4). To create the non-smooth motion, we reduced the frame rate of the animations to 0.33 frames per second (i.e., the virtual environment updated every 3 s rather than 30 times per second). Reducing the frame rate of the animations caused the virtual object to move on a discontinuous spatiotemporal path, such that—when the object was moving—there was no overlap between the pixels of the object across successive images. In addition, for one of the two objects (the object in Figure 2J), we scrambled the order of the successive object views. This manipulation has been used to reduce temporal smoothness in studies of object recognition (Wood & Wood, 2018). The object moved on a discontinuous spatiotemporal path in both the Input Phase (Movie S4) and Test Phase (Movie S5).

## 5.2 | Results

### 5.2.1 | Performance on visible trials

On the Visible Trials, the chicks spent the majority of their time in the zone containing their imprinted object ( $M = 76.57\%$ ,  $SEM = 2.31\%$ ;  $t(11) = 11.49$ ,  $p = 0.0000002$ , Cohen's  $d = 3.32$ ). Despite the discontinuous motion, the chicks successfully imprinted to the virtual object and followed the object around the chamber.

### 5.2.2 | Performance on occluder trials

We next examined whether the chicks preferred to spend time at the location of their imprinted object after the object disappeared from view (Figure 3d). Performance was similar whether the chicks were reared with Object 1 or Object 2 (two-sample  $t$  test;  $t(10) = 1.52$ ,  $p = 0.16$ , Cohen's  $d = 0.88$ ). Overall, the chicks did not spend a greater proportion of time by the correct screen compared to the incorrect screen ( $M = 51.42\%$ ,  $SEM = 1.61\%$ ;  $t(11) = 0.88$ ,  $p = 0.40$ , Cohen's  $d = 0.25$ ). The chicks also did not perform above chance level when the object had been hidden for 1 min ( $M = 52.93\%$ ,  $SEM = 1.97\%$ ;  $t(11) = 1.49$ ,  $p = 0.16$ , Cohen's  $d = 0.43$ ), 2 min ( $M = 51.84\%$ ,  $SEM = 1.76\%$ ;  $t(11) = 1.04$ ,  $p = 0.32$ , Cohen's  $d = 0.30$ ), 3 min ( $M = 50.33\%$ ,  $SEM = 1.91\%$ ;  $t(11) = 0.17$ ,  $p = 0.87$ , Cohen's  $d = 0.05$ ), 4 min ( $M = 50.03\%$ ,  $SEM = 2.67\%$ ;  $t(11) = 0.01$ ,  $p = 0.99$ , Cohen's  $d = 0.003$ ), and 5 min ( $M = 47.43\%$ ,  $SEM = 2.90\%$ ;  $t(11) = 0.89$ ,  $p = 0.39$ , Cohen's  $d = 0.26$ ).

## 5.2.3 | Comparison between experiments 3 and 4

Experiments 3 and 4 were identical, except that the chicks were reared with temporally smooth objects in Experiment 3 and temporally non-smooth objects in Experiment 4. Performance was significantly higher on the Occluder Trials in Experiment 3 compared to Experiment 4 (two-sample  $t$  test;  $t(21) = 3.74$ ,  $p = 0.001$ , Cohen's  $d = 1.57$ ). This difference was particularly pronounced during the first minute after the object had disappeared from view ( $t(21) = 4.01$ ,  $p = 0.0006$ , Cohen's  $d = 1.67$ ).

## 5.3 | Discussion

Across Experiments 3 and 4, we examined whether visual experience with continuous object motion facilitates the development of object permanence. When newborn chicks were reared with an object moving on smooth (continuous) spatiotemporal paths, the chicks developed object permanence for that object (Experiment 3). In contrast, when newborn chicks were reared with an object moving on non-smooth (discontinuous) spatiotemporal paths, the chicks did not show evidence of object permanence (Experiment 4). Thus, visual experience with smooth, continuous object motion facilitates the development of object permanence.

It is worth emphasizing that the chicks reared with the non-smooth object motion did not show evidence for object permanence despite being raised in environments that contained some temporally smooth features. For example, the chicks acquired visual experience with temporally smooth extended surfaces (i.e., the walls and floor of the chamber). The chicks also acquired visual experience with temporally smooth heaps of grain during feeding. Nevertheless, when reared with an object that moved non-smoothly over time, the chicks failed to develop object permanence for that object. This finding suggests that the development of object permanence is facilitated by visual experience with *objects* moving on smooth, continuous spatiotemporal paths, rather than visual experience with temporally smooth features more generally.

Finally, an important feature of our design is that the movements in Experiments 3 and 4 were equally predictable (from a statistical perspective). Since we created the temporally non-smooth animations by reducing the frame rate of the temporally smooth animations, the transitional probability (i.e., the consistency with which the images occurred in a particular order) was the same in both experiments. Thus, it was not the case that the object's motion was more random or ambiguous in Experiment 4. It is, however, possible that the temporally non-smooth motion was harder to track than the temporally smooth motion. Like the development of object permanence, the development of object tracking might be facilitated by visual experience with smooth object motion. This possibility would accord with the theoretical view that object tracking and object permanence depend on the same underlying mechanisms (e.g., Leslie, Xu, Tremoulet, & Scholl, 1998).

One potential limitation of Experiment 4 is that the chicks were not presented with both continuous and discontinuous motion

during the test trials, so we cannot determine whether the low performance in Experiment 4 was due to the discontinuous motion during the Input Phase or the discontinuous motion during the test trials. We designed our experiment this way because if we had presented both types of motion during the test trials, then the chicks reared with the discontinuous motion could have learned from the continuous motion during the test trials. Nevertheless, it would be interesting in future work to present chicks with a variety of motion types during the test trials to more precisely characterize the role of continuous object motion in the development of object permanence.

## 6 | GENERAL DISCUSSION

What role does visual experience play in the development of object permanence? In this study, we used an automated controlled-rearing method to examine whether experience with object occlusion events and smooth (continuous) object motion influences the development of object permanence. Across four experiments, we found that object permanence can develop rapidly in newborn chicks, within the first few days of life. This ability developed even when newborn chicks were reared in impoverished visual environments containing no full object occlusion events. However, when chicks were reared in environments with temporally non-smooth objects (objects moving on discontinuous spatiotemporal paths), they did not show evidence of object permanence. These results suggest that experience with natural (temporally smooth) objects facilitates the development of object permanence.

Our study replicates previous studies showing that newborn chicks can develop object permanence abilities rapidly (Regolin et al., 2005, 1995; Vallortigara et al., 1998) and extends this research by revealing an experiential factor (temporal smoothness<sup>5</sup>) that facilitates the development of object permanence. These results also complement controlled-rearing experiments showing that the development of object recognition requires visual experience with temporally smooth objects (Wood, Prasad, Goldman, & Wood, 2016). In particular, newborn chicks develop more accurate color recognition, shape recognition, and color-shape binding abilities when reared with temporally smooth objects versus temporally non-smooth objects (Wood, 2016). Newborn chicks also develop more accurate view-invariant object recognition abilities when reared with temporally smooth objects (Wood & Wood, 2018). Together, these findings indicate that the development of at least two foundational cognitive abilities—object recognition and object permanence—is facilitated by visual experience with natural object motion (i.e., smooth and continuous spatiotemporal changes).

### 6.1 | Implications for human development

To what extent do these results inform our understanding of the development of object permanence in humans, given that we used an imprinting method with a distantly related species? Ultimately, imprinting is the acquisition of a preference: chicks build a visual

representation of an object/agent in their environment, and that representation becomes linked to the neural systems controlling preferences and behavior (Horn, 2004). Thus, the extent to which studies of imprinting can inform the development of object permanence in humans depends on whether chicks and humans use homologous neural mechanisms to build visual object representations. If chicks and humans use homologous neural mechanisms, then object permanence may develop in similar ways across species. If chicks and humans use different neural mechanisms, then object permanence may develop differently across species.

While additional research is needed to distinguish between these possibilities, there is growing evidence that birds and mammals use homologous neural circuits to process sensory input and build enduring representations of the environment (reviewed by Karten, 2013). This circuit is thought to have evolved in stem amniotes at least 300 million years ago (Jarvis et al., 2005) and to underlie the computations used for building visual object representations (DiCarlo et al., 2012). Given the structural and functional similarities between the neural circuits found in mammals and birds, controlled-rearing studies of newborn chicks may therefore illuminate the development of object permanence in humans.

Of course, we should also expect some differences in the development of object permanence across species. First, chickens have much smaller brains than humans, which might influence the development of object permanence in important ways (e.g., in terms of how long an object can be maintained in memory and how long the ability takes to develop). Second, chicks, unlike humans, begin exploring their environment at the onset of post-natal experience. This active motor exploration might play an important role in the development of object permanence. Third, chicks and humans receive different pre-natal experiences, which might influence the development of object permanence. One benefit of our controlled-rearing approach is that we can systematically manipulate both the pre-natal and post-natal experiences of newborn animals, providing an experimental avenue for probing the respective roles of these different types of experiences in cognitive development. Fourth, we used a locomotion-based search method to probe chicks' object permanence abilities, whereas studies with young human infants typically rely on looking time methods. In humans, looking time and search methods often yield different patterns of performance, with infants showing an earlier understanding of physical events with looking time (Baillargeon, 1987; Spelke et al., 1992) compared to manual search (Berthier, DeBlois, Poirier, Novak, & Clifton, 2000; Hood, 1995; Hood, Carey, & Prasada, 2000). Comparisons of object permanence performance across species should therefore account for differences in how subjects are tested across experiments.

### 6.2 | Limitations of this study and directions for future research

It is important to emphasize the limitations of this study and directions for future research. First, these newborn chicks were raised

with a single object. As a result, these data do not reveal whether experience with temporally non-smooth motion inhibits chicks' object permanence abilities in general, or whether this effect is specific to objects that follow temporally non-smooth paths. Future studies could distinguish between these possibilities by rearing chicks with multiple objects—some that move smoothly and others that move non-smoothly—and then testing whether the chicks develop object permanence for all of the objects or only the objects that move along temporally smooth paths. In addition, the chicks in our experiments were reared with the virtual object for 7 days (Experiments 1–2) or 4 days (Experiments 3–4) before being tested in the object permanence task. In future work, it would be interesting to measure chicks' object permanence abilities from the onset of vision, as the chicks are actively imprinting to the stimulus.

Second, we contrasted chicks raised with highly smooth object motion (i.e., objects that moved at 30 frames/s) versus highly non-smooth object motion (i.e., objects that moved every 3 s). Thus, additional research is needed to characterize the precise amount of motion continuity that is needed for the development of object permanence. Moreover, future studies are needed to determine how different types of experiences interact in the development of object permanence. For instance, while we found that experience with smooth object motion facilitates performance in the absence of object occlusion experience, we do not yet know whether object occlusion experience facilitates performance in the absence of smooth object motion.

Third, we tested newborn chicks in virtual environments. While there are many benefits to using virtual stimuli in controlled-rearing experiments (e.g., it is possible to both automate experiments and raise chicks in environments with discontinuous object motion), there may be some costs to presenting object information in a virtual format. In the case of object recognition, newborn chicks seem to have no impairment processing virtual stimuli. For example, newborn chicks can build view-invariant representations of virtual objects that generalize across large, novel, and complex changes in the object's appearance on the retina (Wood, 2013, 2015; Wood & Wood, 2016). In addition, previous studies have found that newborn chicks develop object permanence abilities even when they receive no tactile information from the object (i.e., when the object is presented behind a transparent screen, Chiandetti & Vallortigara, 2011).

Finally, while the present results provide evidence that experience with temporally smooth objects facilitates the development of object permanence, additional research is needed to characterize the precise nature of this developmental process. Specifically, our results are consistent with two possibilities. First, experience with smoothly moving objects might be needed to *maintain* object permanence abilities in newborn brains. According to this view, object permanence is present at the onset of vision, but the underlying mechanisms require visual experience with smoothly moving objects in order to be maintained across development. Second, experience with smoothly moving objects might be needed for the *emergence* of object permanence in newborn brains. According to this view, the neural mechanisms that support object permanence

require input from smoothly moving objects to develop spatial and temporal receptive fields that can sustain object information over time. Evidence for this second hypothesis comes from studies in computational neuroscience suggesting that temporally smooth visual input plays a central role in the development of visual processing machinery (Franzius, Sprekeler, & Wiskott, 2007; Wyss, König, & Verschure, 2006). There is also growing neurophysiological and computational evidence that temporally smooth visual input allows the brain to achieve a stable representation of sensory input (reviewed by DiCarlo et al., 2012). It would be interesting for future studies to directly link controlled-rearing experiments with newborn animals to biologically plausible computational models, in order to formally characterize the mechanisms underlying object permanence in newborn brains.

In summary, a deep understanding of object permanence requires understanding the role of experience in the development of this ability. Here, we show that newborn chicks can develop object permanence rapidly, within the first few days of life. However, this ability does not emerge automatically. Rather, visual experience with temporally smooth objects facilitates the development of object permanence. This study sheds light on how a foundational ability develops in newborn animals and opens new experimental avenues for drawing causal links between the particular experiences encountered by newborn organisms and the development of their object concepts.

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## CONFLICTS OF INTEREST

We have no conflicts of interest to report.

## ENDNOTES

<sup>1</sup>Researchers have used a variety of terms to describe the ability to maintain object information in memory, including “visual working memory” (Luck & Vogel, 1997), “object persistence” (Bremner, Slater, & Johnson, 2015), and “object continuity” (Spelke, Kestenbaum, Simons, & Wein, 1995). We use the term “object permanence” because of its historical significance (Piaget, 1954) and widespread use in developmental psychology and cognitive science.

<sup>2</sup>Since the design included equal numbers of trials in which the object was hidden for 1, 2, 3, 4, and 5 min, the shorter time bins included more data (i.e., the test trials in which the object was hidden for 1–5 min all included a 1-min time bin, whereas only the trials in which the object was hidden for 5 min included a 5-min time bin).

<sup>3</sup>We determined outliers as more than 1.5 times the interquartile range below the 1st quartile or above the 3rd quartile (Tukey, 1977). This method is applicable to most data ranges since it is not dependent on distributional assumptions. It also ignores the mean and standard deviation, making it resistant to being influenced by extreme values in the range.

<sup>4</sup>We used the same criteria to determine outliers as in Experiment 2 (more than 1.5\*IQR below the 1st quartile or above the 3rd quartile). The outlier in Experiment 2 was below this threshold range, and the outlier in Experiment 3 was above this threshold range.

<sup>5</sup>*Smoothness* and *continuity* are separate, but highly related concepts. *Smoothness* is used in the computational neuroscience literature to refer to the amount of image change across successive frames in a sequence, such that smoother sequences contain less change across successive frames than non-smooth sequences (Stone, 1996; Wiskott & Sejnowski, 2002). Similarly, *continuity* is used in the developmental psychology literature to refer to the amount of location change across time (Spelke, Kestenbaum, Simons, & Wein, 1995). An object that moves on a continuous spatiotemporal path accumulates small spatial perturbations over time, whereas an object that moves on a discontinuous spatiotemporal path accumulates large spatial perturbations over time. An object that moves on a continuous path is therefore more temporally smooth than an object that moves on a discontinuous path.

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## SUPPORTING INFORMATION

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