Anim Cogn
DOI 10.1007/s10071-015-0839-3

ORIGINAL PAPER

An automated controlled-rearing method for studying the origins of movement recognition in newly hatched chicks

Jason G. Goldman · Justin N. Wood

Received: 23 July 2014 / Revised: 28 December 2014 / Accepted: 6 January 2015

Abstract Movement recognition is central to visual perception and cognition, yet its origins are poorly understood. Can newborn animals encode and recognize movements at the onset of vision, or does this ability have a protracted developmental trajectory? To address this question, we used an automated controlled-rearing method with a newborn animal model: the domestic chick (*Gallus gallus*). This automated method made it possible to collect over 150 test trials from each subject. In their first week of life, chicks were raised in controlled-rearing chambers that contained a single virtual agent who repeatedly performed three movements. In their second week of life, we tested whether chicks could recognize the agent's movements. Chicks successfully recognized both individual movements and sequences of movements. Further, chicks successfully encoded the order that movements occurred within a sequence. These results indicate that newborn visual systems can encode and recognize movements at the onset of vision and argue for an increased focus on automated controlled-rearing methods for studying the emergence of perceptual and cognitive abilities.

Keywords Controlled rearing · Movement recognition · Newborn · Chicken · *Gallus gallus* · Automation

Electronic supplementary material The online version of this article (doi:10.1007/s10071-015-0839-3) contains supplementary material, which is available to authorized users.

J. G. Goldman · J. N. Wood (✉)
Department of Psychology, University of Southern California, Building SGM, Room 501, 3620 South McClintock Ave., Los Angeles, CA 90089, USA
e-mail: justin.wood@usc.edu

Introduction

The ability to recognize movements is essential for many perceptual and cognitive abilities. For instance, social animals must encode and recognize a diverse range of actions from allies and enemies, in contexts that include imitation, cooperation, teaching, coalitionary violence, territorial defense, and parental care (e.g., Buttelmann et al. 2007; Suchak and De Waal 2012; Warneken and Tomasello 2006; Wood et al. 2007). To date, however, the developmental origins of movement recognition are poorly understood. Does movement recognition have a protracted development, emerging over time as the animal acquires experience with a variety of observed movements? Or can newborn visual systems build accurate movement representations at the onset of vision?

Here, we introduce an automated controlled-rearing method that can be used to study the "initial state" of movement recognition (i.e., the state of movement recognition at the onset of vision). In the current study, we used this method to address three questions about the initial state of movement recognition: (1) Can newborn animals build accurate representations of the first movements they see in their life? (2) Can newborn animals build an accurate representation of the first sequence of movements they see in their life? (3) Can newborn animals encode information about the order in which movements occurred within a sequence?

Chickens as an animal model for studying the initial state of movement recognition

Since the visual system is rapidly shaped by visual experience (e.g., Espinosa and Stryker 2012; Gavornik and Bear 2014; Li and DiCarlo 2008), studying the initial state of

Published online: 11 February 2015

movement recognition requires a controlled-rearing approach with a newborn animal model. By raising animals in controlled environments from the onset of vision, it is possible to determine how specific visual experiences shape newborns' perceptual and cognitive abilities. In the present study, we used domestic chicks (*Gallus gallus*) as an animal model. Four characteristics make newly hatched chicks an ideal model system for studying the origins of movement recognition. First, chicks can extract information from motion patterns—for example, chicks can distinguish between biological and non-biological motion within the first few days of life (e.g., Vallortigara and Regolin 2006; Vallortigara et al. 2005), akin to human infants (e.g., Bertenthal et al. 1984; Fox and Mcdaniel 1982; Simion et al. 2008). The current study builds on these findings by examining whether newly hatched chicks can encode and recognize specific movements, movement sequences, and the order that movements occurred within a sequence. Second, chicks can be raised in strictly controlled environments immediately after hatching (i.e., environments devoid of objects, agents, and movements). Third, chicks imprint to objects and agents seen in the first few days of life. Chicks treat their imprinted agents as social partners; when separated, they will attempt to reunite with the agent by reducing the physical space between themselves and the agent. This imprinting response provides a natural behavioral assay that can be used to test chicks' recognition abilities without training (e.g., Bateson 2000; Horn 2004). Fourth, birds and primates use similar neural mechanisms to process sensory information. For example, both avian and mammalian brains are modular, small-world networks with a connective core of hub nodes that includes prefrontal-like and hippocampal structures (Jarvis et al. 2005; Shanahan et al. 2013). Further, the cells and circuits that populate these networks are generated by homologous genes in birds and mammals and have nearly identical "wiring patterns" (for a side-by-side comparison of avian and mammalian cortical circuity, see Fig. 2 in Karten 2013). Thus, newly hatched chicks are an ideal animal model for studying the development of movement recognition in a biological system.

Understanding the cognitive abilities of chickens is also important in its own right. From an economic perspective, chickens are a common domestic animal that is used widely as a source of food in many countries. Designing effective animal husbandry procedures for chickens requires understanding the nature of their cognitive capacities. In addition, many scientific fields rely heavily on chickens as an animal model. In developmental biology, for instance, chickens are commonly used as a model of vertebrate development (reviewed by Davey and Tickle 2007). Further, since the sequencing of the chicken genome, many researchers have started using chickens as a model system for studying genetic expression and function (Davey and Tickle 2007). Characterizing chickens' early emerging cognitive abilities will be a critical step for building a unified link between the study of genes and behavior.

From an ecological perspective, chickens are a highly social species. Flocks of chickens have strict dominance hierarchies, with dominant individuals having priority for food and nesting locations (Grandin and Johnson 2005). Accordingly, chickens need to encode and recognize aggressive actions from conspecifics. Chickens can also recognize actions in the context of foraging and mating. For example, to initiate courting, roosters will dance in a circle around or near a hen, often lowering the wing that is closest to the hen (Grandin and Johnson 2005). In addition, after finding food, hens will often pick up and drop food to encourage their chicks to eat: a behavior called "tidbitting" (Stokes and Williams 1972). Tidbitting is a multimodal signal that involves both visual and auditory components (Smith and Evans 2008), and previous studies have shown that chickens can recognize this action on video displays (McQuoid and Galef 1993; Evans and Marler 1991; Evans et al. 1993). In the present study, we used video displays, combined with an automated controlled-rearing technique, to examine the origins of chickens' movement recognition abilities.

An automated controlled-rearing method for studying movement recognition

To study the initial state of movement recognition in newly hatched chicks, we used a "complete data" controlled-rearing method. This method has previously been used to study the initial state of object recognition (Wood 2013, 2014a, b); here, we extend the method to the domain of movement recognition. This automated method involves raising newly hatched chicks in immersive virtual environments and using image-based tracking software to record all of the subjects' behavior (24 h/day, 7 days/week) with high temporal resolution (nine samples/second). We use the term "complete data" because the method produces a complete digital recording of each subject's behavior across their entire lifespan.

This automated method provides several advantages over traditional controlled-rearing methods. First, since the entire data collection process is automated, there is no possibility of experimenter bias (e.g., bias that may occur when presenting stimuli to the subject, coding the subject's behavior, or deciding whether to include the subject in the final analysis). Second, since we record all of the subjects' behavior across their lifespan, it is possible to present each subject with a large number of test trials. In the current study, for example, each chick received over 150 test trials.

Consequently, this method makes it possible to measure each newborn subject's behavior with high precision for an extended period of time within controlled visual environments. Third, image-based tracking is noninvasive, so the subjects do not need to be equipped with bio-loggers or other types of tracking equipment. Importantly, throughout the 2-week duration of the current experiment, the chicks were never manipulated or handled by an experimenter. Fourth, image-based tracking operates over a digital recording of the subjects' behavior, maintaining an objective view of events. This increases the repeatability of analyses and allows researchers to mine data for variables not originally considered.

In the current study, we used this automated controlled-rearing method to examine whether newly hatched chicks can build accurate representations of the first movements they see in their life. Specifically, we raised chicks for 2 weeks within controlled-rearing chambers that provided complete control over all visual object and movement experiences. The chambers contained extended surfaces only (Fig. 1), and agent and movement stimuli were presented to the subjects by projecting animated agents onto two display walls situated on opposite sides of the chamber. In their first week of life (the input phase), chicks were raised in an environment that contained a single virtual agent who repeatedly performed three "input movements" (Fig. 2a, for animations see Supplementary Movies 1–3). In their second week of life (the test phase), we examined whether chicks could distinguish the input movements from novel movements, by using an automated two-alternative forced-choice testing procedure (Fig. 2b).

Experiment 1

Experiment 1 examined whether newly hatched chicks can encode and recognize individual movements (Fig. 2).

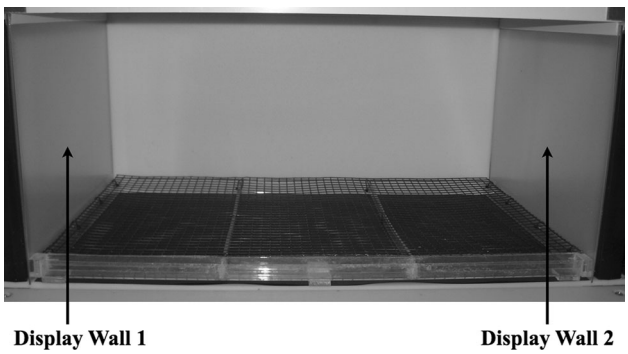

Fig. 1 Interior of a controlled-rearing chamber. The front wall (removed for this picture) was identical to the back wall. These chambers provided complete control over all object, agent, and movement experiences

Method

Subjects

Six domestic chicks of unknown sex were tested. No subjects were excluded from the analyses. The eggs were obtained from a local distributor and incubated in darkness in an OVA-Easy (Brinsea) incubator. The eggs were incubated in darkness to ensure that no visual input would reach the chicks through the shells. For the first 19 days of incubation, the temperature and humidity were maintained at 37.6 °C and 45 %, respectively. The humidity was increased to 60 % on the 19th day of incubation. 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 controlled-rearing chamber.

Controlled-rearing chambers

The chambers (Fig. 1) were constructed from white, high-density plastic and measured 66 cm (length) × 42 cm (width) × 69 cm (height). To present agent and movement stimuli to the subjects, animated stimuli were projected onto two display walls situated on opposite sides of the chamber. The display walls were 19″ liquid crystal display (LCD) monitors (1,440 × 900 pixel resolution). Food and water were provided within transparent troughs in the ground that measured 66 cm (length) × 2.5 cm (width) × 2.7 cm (height). Grain was used as food because it does not behave like an object (i.e., grain does not maintain a rigid, bounded shape). The floors were wire mesh and supported 2.7 cm off the ground by thin, transparent beams. Subjects' movements were tracked by micro-cameras embedded in the ceilings of the chambers and analyzed with automated image-based tracking software (Ethovision XT, Noldus Information Technology). This software calculated the amount of time subjects spent within zones (22 cm × 42 cm) next to the left and right display walls. We considered the chick to be in proximity to the agent on the left versus right display wall when the chick occupied the zone next to the left and right display wall, respectively.

Procedure

During the input phase (the first week of life), we presented subjects with three input movements performed repeatedly by an animated human agent (Fig. 2a, for animations see Supplementary Movie 1). The agent measured 16 cm (height) × 5.5 cm (width) and was displayed on a uniform white background at the middle of the display wall. The movements were dynamic (i.e., they involved fluid,

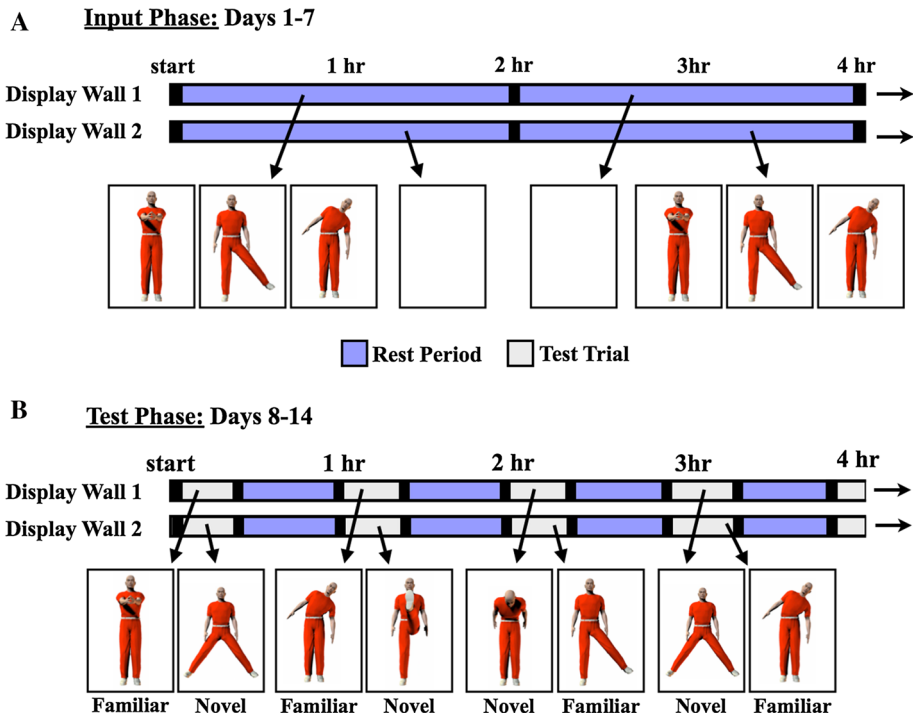

Fig. 2 **a** Schematic showing the presentation schedule of the input movements on the two display walls during a 4-h period in the input phase. **b** A schematic showing the presentation schedule of the input movements and novel movements on the two display walls during a 4-h period in the test phase. The movements were repeated continuously throughout each phase

continuous movement at 24 frames/second). Each movement lasted 1,000 ms and was followed by a 1,000-ms period of stasis (i.e., the agent remained stationary in a neutral position). During each 1-min period in the input phase, we randomly selected one of the three input movements; the agent then performed this movement 30 times in a row within the 1-min period. The input movements were presented continuously (24 h/day) throughout the input phase. The agent appeared for an equal amount of time on the left and right display wall. The agent switched walls every 2 h, following a 1-min period of darkness (Fig. 2a). The same set of input movements were used for all of the chicks. In Experiment 2, we reversed the input movements and novel movements to control for the possibility that chicks have an innate preference for some movements over others.

During the test phase (the second week of life), we examined whether subjects could recognize the input movements by using a two-alternative forced-choice testing procedure. During each test trial, one of the three input movements was displayed on one display wall, and one of three novel movements was displayed on the other display wall (Fig. 2b). Both the input movements and the novel movements were performed by the same agent (the agent from the input phase). If chicks can recognize familiar movements and use this dynamic information as a cue for recognizing their imprinted agent, then the chicks should spend a greater proportion of time in proximity to the input movements versus the novel movements on the test trials.

Like the input movements, the novel movements lasted 1,000 ms and were followed by a 1,000-ms period of stasis. The test trials lasted 20 min and were separated by 33-min rest periods. During the rest periods, the input movements were presented on one display wall and a white screen was projected onto the other display wall (as in the input phase). Rest periods were included in the design to allow subjects to reunite with their imprinted agent without needing to make a choice between two agents. Across the test phase, the input movements appeared an equal number of times on the left and right display wall. Each of the three input movements was paired an equal number of times with each of the three novel movements. The order of the test trials was randomized, with the limitation that any particular "input movement—novel movement" combination could not repeat more than two times in a row. Subjects received 27 test trials every 24 h.

Results and discussion

Test trials were scored as "correct" when subjects spent a greater proportion of time with the input movement compared to the novel movement and "incorrect" when subjects spent a greater proportion of time with the novel movement compared to the input movement. These responses were then analyzed with hierarchical Bayesian methods (Kruschke 2010) that provided probabilistic estimates of recognition performance for both the individual chicks and the overall group. For a detailed discussion of how the Bayesian analyses were conducted, see the SI Appendix (Section 3) in Wood (2013).

The Bayesian analysis required specifying a prior distribution. To be conservative, we used a prior consisting of one correct trial and one incorrect trial. The prior distribution also includes a kappa parameter that represents the consistency across subjects. We used a uniform density kappa 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. The rest periods were expected to produce the greatest consistency across subjects because they presented the easiest choice (i.e., subjects chose whether to spend time with the imprinted agent versus a white screen).

The results are shown in Fig. 4. Subjects successfully recognized the input movement on 65 % (SEM = 6 %) of the test trials. The probability that group performance was above chance was >95 %. Across the six subjects, the probability that individual performance was above chance was >99 % for three of the chicks, 97 % for another chick, and below 75 % for the two remaining chicks. Performance was also significantly above chance when the data were analyzed with a traditional one-sample t test (one-tailed): $t(5) = 2.66$, $p = .02$, $d = 1.09$. In sum, the majority of the chicks were able to recognize the input movements. This experiment indicates that newborn animals can build accurate representations of the first movements they see in their life.

Experiment 2

Experiment 1 shows that newly hatched chicks can recognize individual movements. During everyday visual experience, however, individual movements are often embedded together within larger movement sequences, with few pauses to mark boundaries between distinct movements (e.g., Heider 1958; Newtson and Engquist 1976). Thus, in Experiment 2, we examined whether newly hatched chicks can also recognize movement sequences (see Fig. 3, for animations see Supplementary Movie 2).

Methods

The methods were identical to those used in Experiment 1, with the following exceptions. First, we tested a new group of chicks ($n = 6$). Second, we switched the input movements and novel movements: The input movements from Experiment 1 were used as the novel movements, and the novel movements from Experiment 1 were used as the input movements. We switched the input movements and novel movements to ensure that the results from Experiment 1

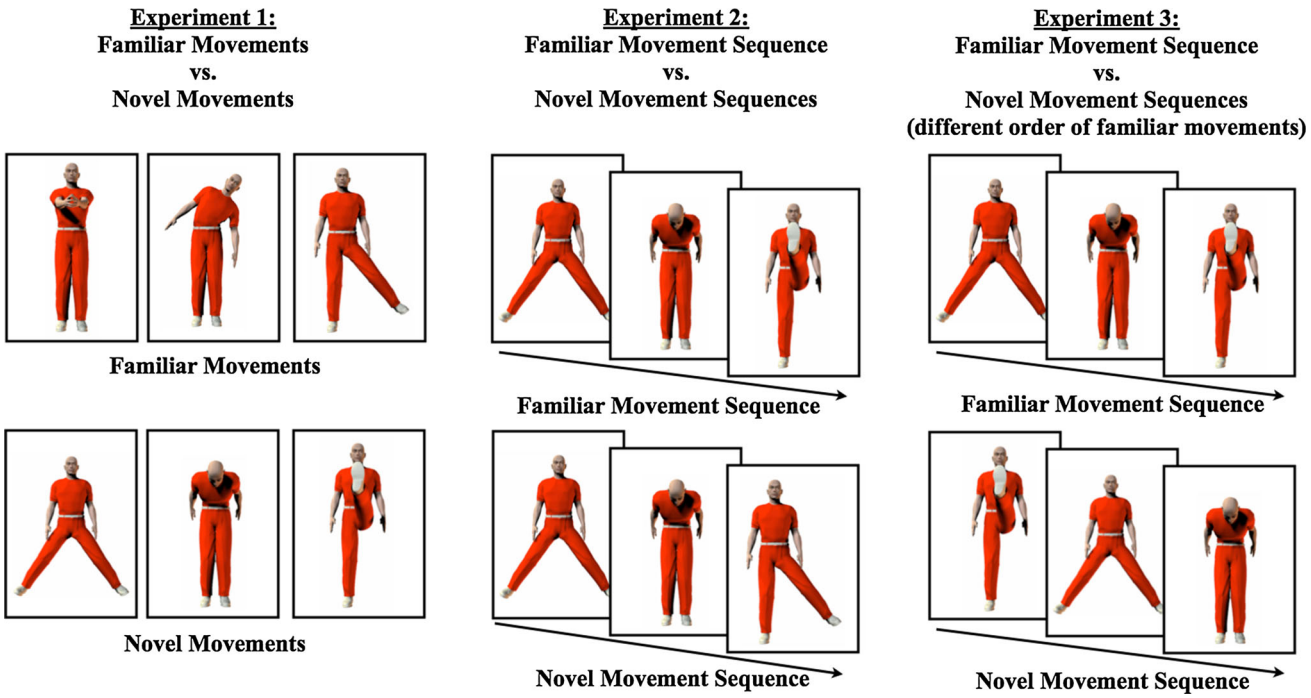

Fig. 3 Stimuli used in Experiments 1–3. During the input phase, chicks were shown individual movements (*left column*) or a sequence of movements (*middle* and *right columns*). During the test phase, we tested whether chicks could distinguish the familiar movements from novel movements. Experiment 1 tested whether chicks could recognize individual movements, Experiment 2 tested whether chicks could recognize movement sequences, and Experiment 3 tested whether chicks could recognize movement sequences on the basis of the order that the movements occurred within the sequence. Animations of the stimuli are provided in Supplementary Movies 1–3

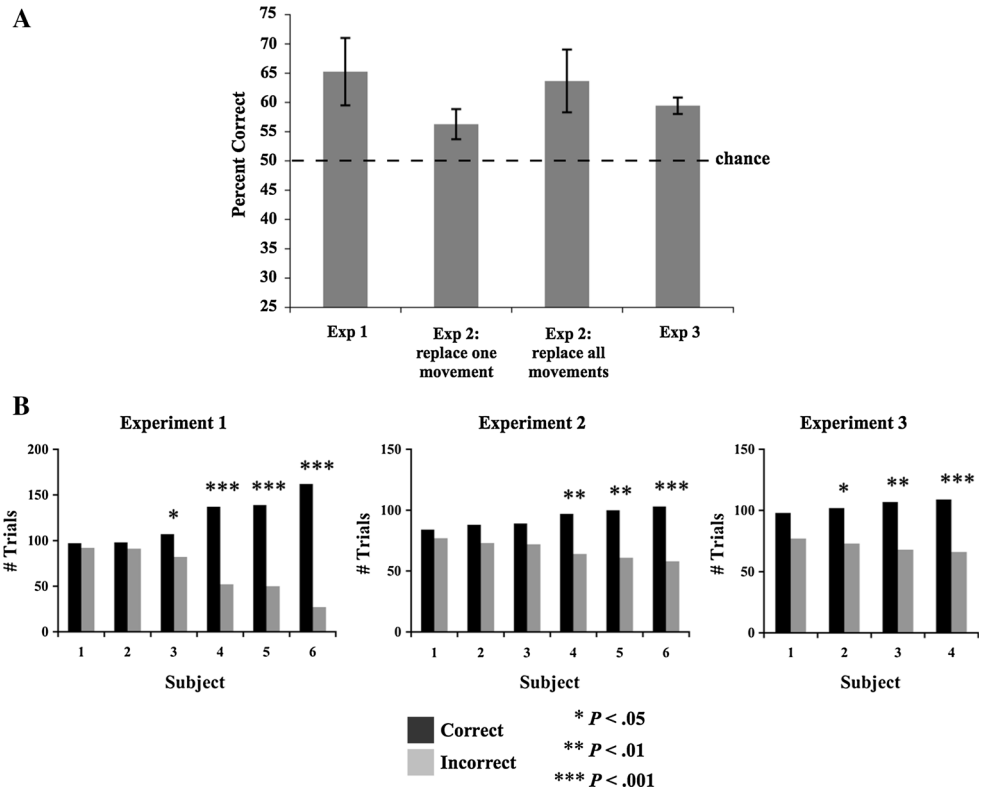

Fig. 4 Results from Experiments 1–3. **a** Subjects' average movement recognition performance in the three experiments. Chance performance was 50 %. *Error bars* denote standard error. **b** Performance of each individual chick (ordered by performance). The *graphs* show the total number of correct and incorrect test trials for each chick across the test phase. *p* values denote the statistical difference between the number of correct and incorrect test trials, as computed through one-tailed binomial tests

reflected the ability to encode and recognize specific movements, as opposed to chicks simply showing an innate preference for the input movements over the novel movements. Third, the input movements were presented in a fixed order (movement 1 → movement 2 → movement 3) with no pause between movements. The 3,000-ms sequences were separated from one another by 3,000-ms periods of stasis. The sequence was repeated 10 times per minute continuously (24 h/day) throughout the input phase.

During each test trial in the test phase, the input movement sequence was displayed on one display wall and a novel movement sequence was displayed on the other display wall. We presented two types of novel movement sequences. In the "Replace One Movement" condition, the sequence contained two input movements and one novel movement (see Fig. 3). The position of the novel movement was counterbalanced across the three possible positions within the sequence (first, second, or third position). In the "Replace All Movements" condition, all three of the input movements were replaced with novel movements. The test trials lasted 20 min and were separated by 40-min rest periods. Subjects received 24 test trials every 24 h.

Results and discussion

The results are shown in Fig. 4. In the Replace One Movement condition, subjects successfully recognized the input movement sequence on 56 % (SEM = 3 %) of the test trials. The probability that group performance was above chance was >95 %. Across the six subjects, the probability that individual performance was above chance was >99 % for two of the chicks, between 92 and 95 % for two other chicks, and 88 % for a fifth chick. The probability that performance was above chance was below 50 % for the remaining subject. Performance was also significantly above chance when the data were analyzed with a traditional one-sample *t* test (one-tailed): $t(5) = 2.46$, $p = .03$, $d = 1.00$.

In the Replace All Movements condition, subjects successfully recognized the input movement sequence on 64 % (SEM = 5 %) of trials. The probability that group performance was above chance was >99 %. Across the six subjects, the probability that individual performance was above chance was >99 % for three of the chicks and 95, 89, and 72 % for the remaining three chicks. Performance was also significantly above chance when the data were analyzed with a traditional one-sample *t* test (one-tailed): $t(5) = 2.55$, $p = .03$, $d = 1.05$.

This experiment indicates that newly hatched chicks can recognize movement sequences. Chicks distinguished between the familiar movement sequence and novel movement sequences, both when the sequences differed by three movements or just a single movement.

Experiment 3

In the final experiment, we examined whether newly hatched chicks can encode the order that movements occurred within a sequence.

Methods

The methods were identical to those used in Experiment 2, with the following exceptions. First, we tested a new group of subjects ($n = 4$). Second, in the test trials, we presented subjects with novel movement sequences that contained the same individual movements as the input movement sequence but in different orders (see Fig. 3, for animations see Supplementary Movie 3). The movement sequence from the input phase was displayed on one display wall, and a novel sequence (consisting of the same movements but in a different order) was displayed on the second display wall. We tested subjects with all possible order combinations of the individual movements. The test trials lasted 20 min and were separated by 37-min rest periods. Subjects received 25 test trials every 24 h.

Results and discussion

The results are shown in Fig. 4. Subjects successfully recognized the input movement sequence on 59 % (SEM = 2 %) of the test trials. The probability that group performance was above chance was >99 %. The probability that individual performance was above chance was also >99 % for all four of the chicks. Performance was also significantly above chance when the data were analyzed with a traditional one-sample t test (one-tailed): $t(3) = 6.64$, $p < .005$, $d = 3.36$. Chicks were able to distinguish between movement sequences on the basis of the order of the movements within the sequence.

Additional analyses

Analysis of change in performance over time

To test whether performance changed over the course of the test phase, we examined whether subjects' performance (i.e., the proportion of time chicks spent in proximity to the input movements versus the novel movements) was correlated with test trial number (e.g., first test trial, second test trial). The correlation was not significant in Experiment 1 ($r = .07$, $p = .33$), Experiment 2 ($r = .16$, $p = .34$), or Experiment 3 ($r = -.15$, $p = .06$). Further, chicks' movement recognition performance did not differ significantly across the first day of the test phase and the last day of the test phase: $t(5) = 1.48$, $p = .20$ (Experiment 1); $t(5) = 1.46$, $p = .20$ (Experiment 2, Replace One Movement condition); $t(5) = 0.03$, $p = .98$ (Experiment 2, Replace All Movements condition); and $t(3) = 1.47$, $p = .24$ (Experiment 3). Thus, chicks' recognition performance was stable and cannot be explained by learning taking place across the test phase.

Analysis of individual subject performance

With this automated method, we were able to collect a large number of test trials from each subject. Thus, we were able to examine whether each chick was able to build accurate representations of the input movements. To do so, we computed whether each subject's performance across the test trials exceeded chance level. Ten of the 16 subjects successfully distinguished the input movements from the novel movements (see Fig. 4b).

The subjects who failed to recognize the input movements could have failed in this task for two reasons. First, the chicks might have failed to imprint to the animated agent. Second, the chicks might have successfully imprinted on the agent, but nevertheless failed to build accurate representations of the agent's movements. To distinguish between these possibilities, we examined whether subjects showed a preference for the agent during the rest periods in the test phase. During the rest periods, the agent was projected onto one display wall and a white screen was projected onto the other display wall (Fig. 2b). All 16 chicks spent the majority of the rest periods in proximity to the agent (mean = 94 % of trials; SEM = 2 %; one-tailed Binomial tests, all $p < 10^{-7}$), including the six chicks who failed to distinguish the input movements from the novel movements. Thus, it is possible to imprint on an agent but fail to build accurate representations of the agent's movements. Alternatively, it is possible that these chicks successfully encoded the agent's movements, but nevertheless failed to use movement information as a cue for recognizing their imprinted agent. Importantly, these results show that there can be significant individual variation in newly hatched chicks' movement recognition abilities and behavior, even when raised from birth in identical visual environments.

General discussion

We used an automated controlled-rearing method to examine whether newly hatched chicks can encode and recognize the first movements they see in their life. Specifically, we raised chicks within controlled-rearing chambers that contained no objects other than a single virtual agent who repeatedly performed three movements. The majority of the chicks were able to distinguish the

familiar movements from the novel movements, both when the movements were presented separately and when they were presented together within a sequence. Further, chicks were able to encode the order that the movements occurred within the sequence. These results show that movement recognition abilities can be present and functional in newborn visual systems.

These results extend the existing literature concerning the development of visual learning in newly hatched chicks. Previous studies provide evidence that chicks have powerful object recognition abilities. For example, chicks can bind color and shape features into integrated object representations at the onset of vision (Wood 2014a) and can build a viewpoint-invariant representation of the first object they see in their life (Wood 2013, 2014b). The current study shows that chicks can also encode and recognize dynamic visual information such as observed movements. These chicks' visual movement experiences were limited to just three movements, all of which could be observed from a single viewpoint; nevertheless, the majority of the chicks were able to encode and recognize the agent's movements.

These results also converge with previous controlled-rearing experiments showing that chicks have a preference for some motion patterns over others (e.g., Vallortigara and Regolin 2006; Vallortigara et al. 2005). The current study extends these findings by using an automated method and by testing recognition of individual movements, movement sequences, and the order of movements within a sequence. This automated method made it possible to examine each chick's performance with high precision and was thus able to reveal a surprising range of individual variation in chicks' movement recognition abilities (see Fig. 4b).

We would like to point out two potential limitations of the current study. First, these chicks observed each of the input movements a large number of times throughout the input phase and test phase. Thus, additional studies are needed to determine whether newly hatched chicks can build accurate movement representations after seeing a movement just a few times, akin to human adults (Urgolites and Wood 2013), or whether they need to see a movement many times. Second, these movements were more simple than those typically encountered in the natural visual world. Indeed, studies of action understanding with human infants typically present more complex actions that contain multiple movements (e.g., Woodward and Sommerville 2000) and are directed toward explicit goals (e.g., Woodward 1998). In contrast, the stimuli used here consisted of simple movements of body parts. Using simple movements as stimuli has been a productive approach for studying the nature of the movement representations stored in visual working memory (Wood 2007) and visual long-term memory (Urgolites and Wood 2013) as well as for studying the statistical learning mechanisms that integrate movements into action sequences (Endress and Wood 2011). Likewise, we suggest that studying how newborn visual systems encode and recognize simple movements provides an important first step in characterizing the nature of the representations produced by the initial state of movement recognition. It would be interesting for future studies to gradually increase the complexity of the movements presented to chicks to examine how newborn visual systems learn to recognize more natural actions. Further, it would be interesting to examine whether chicks show enhanced learning of species-typical movements (e.g., ground scratching, tidbitting) compared to movements performed by other animals such as humans.

More generally, these methods and results raise new questions about the initial state of movement recognition. For example, what visual features do newborn visual systems use to distinguish movements from one another? How do these visual features change with growth and experience? What is the nature of the temporal learning mechanisms that integrate individual movements into action sequences? And how do movement recognition mechanisms and object recognition mechanisms relate to one another (e.g., for linking actions to goals and for binding actions to agents in memory)?

In sum, our study provides systematic evidence that newly hatched chicks are capable of encoding and recognizing movements. Impressively, chicks can encode and recognize individual movements and movement sequences soon after hatching, which shows that experience with a rich visual world filled with a diverse range of actions is not necessary for developing movement recognition. This automated controlled-rearing approach opens up largely unexplored experimental avenues for probing the initial state of movement recognition and examining how the initial state changes a function of specific visual experiences.

Acknowledgments We thank Samantha M. W. Wood for assistance on this manuscript and Aditya Prasad, Tony Bouz, and Lynette Tan for their assistance building the controlled-rearing chambers. This research was funded by National Science Foundation CAREER Grant BCS-1351892 to J. N. W. The experiments were approved by The University of Southern California Institutional Animal Care and Use Committee.

Conflict of interest The authors declare that they have no conflict of interest.

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