Running Head: SMOOTHNESS CONSTRAINT

A smoothness constraint on the development of object recognition

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Abstract

Understanding how the brain learns to recognize objects is one of the ultimate goals in the cognitive sciences. To date, however, we have not yet characterized the environmental factors that cause object recognition to emerge in the newborn brain. Here, I present the results of a high-throughput controlled-rearing experiment that examined whether the development of object recognition requires experience with temporally smooth visual objects. When newborn chicks (*Gallus gallus*) were raised with virtual objects that moved smoothly over time, the chicks developed accurate color recognition, shape recognition, and color-shape binding abilities. In contrast, when newborn chicks were raised with virtual objects that moved non-smoothly over time, the chicks' object recognition abilities were severely impaired. These results provide evidence for a "smoothness constraint" on newborn object recognition. Experience with temporally smooth objects facilitates the development of object recognition.

1. Introduction

Object recognition is one of the most important functions of the vertebrate visual system. To date, however, the development of object recognition is poorly understood. What environmental factors cause object recognition to emerge in the newborn brain? Does this ability emerge automatically, or do newborns require a specific type of visual input in order to develop accurate object recognition abilities? These types of questions are difficult to address with humans because human infants cannot be raised in strictly controlled environments from birth. In contrast, questions that concern the role of experience in development can be addressed directly with controlled-rearing studies of newborn animals. Here, I describe a high-throughput controlled-rearing experiment that examined whether the development of object recognition requires experience with temporally smooth visual objects.

Researchers have long theorized that biological visual systems leverage the temporal smoothness of natural visual environments to recognize objects (e.g., DiCarlo, Zoccolan, & Rust, 2012; Feldman & Tremoulet, 2006; Foldiak, 1991; Gibson, 1979; Stone, 1996; Wallis & Rolls, 1997; Wiskott & Sejnowski, 2002). In particular, when an object moves smoothly across the visual field, the object projects a series of gradually changing images on the retina. The visual system might take advantage of this natural tendency for temporally contiguous retinal images to belong to the same object by associating patterns of neuronal activity produced by successive retinal images of an object. When provided with temporally smooth 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).

A wealth of studies provide evidence that mature visual systems use temporal association mechanisms to create object representations. For example, when human adults are presented with objects that rotate in depth, sequential views come to be associated with one another in a manner that aids recognition (Cox, Meier, Oertelt, & DiCarlo, 2005; Liu, 2007; Stone, 1998; Vuong & Tarr, 2004; Wallis, Backus, Langer, Huebner, & Bulthoff, 2009; Wallis & Bulthoff, 2001). Temporal association effects have also been found on the neurophysiological level in adult monkeys (Li & DiCarlo, 2008, 2010; Meyer & Olson, 2011; Miyashita, 1988). In the present study, I examined whether newborn visual systems create more accurate object representations when presented with temporally smooth objects compared to temporally non-smooth objects—as predicted by temporal association models (Wallis, 1998; Wallis & Bulthoff, 2001). Specifically, I examined the *first* visual object representation created by newborn subjects, before their visual systems had been shaped by any prior visual object experience.

1.2. A high-throughput controlled-rearing method

This experiment required controlling all of the subjects' visual experiences from the onset of vision and measuring their object recognition abilities across a range of test trials. To meet these requirements, I used a high-throughput controlled-rearing method (Wood, 2013). The method involves raising newborn chicks in strictly controlled environments and recording their behavior in response to pre-programmed animations (Figure 1A). We use the term "high-throughput" to describe the method because the controlled-rearing chambers record all of the subjects' behavior (24/7).

I used domestic chicks as an animal model because they are an ideal model system for studying the development of vision (Wood & Wood, 2015a). First, chicks can be raised in strictly controlled environments immediately after hatching, which makes it possible to control all of their visual object experiences. Second, chicks imprint to objects seen in the first days of life. This imprinting behavior can be used to test chicks' object recognition abilities without training (Bateson, 2000; Horn, 2004). Third, birds and mammals process sensory input using homologous neural circuits with similar connectivity patterns (reviewed by Jarvis et al., 2005; Karten, 2013). Since birds and mammals use homologous neural mechanisms to process visual input, controlled-rearing studies of newborn chicks can inform our understanding of the development of both avian and mammalian vision. Finally, chicks develop visual recognition abilities rapidly (Vallortigara, 2012). For example, newborn chicks can begin recognizing objects (Wood, 2013, 2015), faces (Wood & Wood, 2015b), and actions (Goldman & Wood, 2015) at the onset of vision. Newborn chicks can also build integrated object representations with bound color-shape units (Wood, 2014).

In the first week of life (input phase), newborn chicks were raised in environments that contained no objects other than a single virtual object (Figure 1A). For one group of chicks, the virtual object moved smoothly over time (Temporally Smooth Condition), whereas for another group of chicks, the virtual object moved non-smoothly over time (Temporally Non-Smooth Condition). In the second week of life (test phase), I used an automated two-alternative forced-choice procedure to test the chicks' color recognition, shape recognition, and color-shape binding abilities.

2. Method

2.1. Subjects

Twenty-two 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 incubator (Brinsea Products Inc., Titusville, FL). After hatching, the chicks were moved from the incubation room to the controlled-rearing chambers in complete darkness. Each chick was raised singly within its own chamber. Ten chicks were raised with a temporally smooth object and 12 chicks were raised with a temporally non-smooth object.[1] This experiment was approved by The University of Southern California Institutional Animal Care and Use Committee.

2.2. Controlled-Rearing Chambers

The controlled-rearing chambers (66 cm length × 42 cm width × 69 cm height) were constructed from white, high-density polyethylene and were devoid of all real-world (solid, bounded) objects. To present object stimuli to the chicks, virtual objects were projected 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 transparent troughs in the ground (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. The chambers tracked all of the chicks’ behavior (9 samples/second, 24 hours/day, 7 days/week) via micro-cameras in the ceilings and automated image-based tracking software (EthoVision XT, Noldus Information Technology, Leesburg, VA). This high-throughput data collection approach allowed us to collect a large number of test trials (168 trials) from each chick, and consequently, measure each subject’s object recognition abilities with high precision.

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[1] The results from the Temporally Smooth Condition were described previously in Wood (2014). In the present study, I directly contrasted chicks raised with temporally smooth objects and temporally non-smooth objects. While the chicks in the two conditions were not tested concurrently, they were tested with the same automated method. Indeed, one major benefit of this controlled-rearing method is that different groups of subjects can be tested in exactly the same way, since the stimuli presentation and data collection processes are fully automated.

In total, 7,392 hours of video footage (14 days × 24 hours/day × 22 subjects) were collected for this experiment.

2.3. Procedure

In the first week of life (input phase), the chicks were raised in controlled-rearing chambers that contained no objects other than a single virtual object (Figure 1A). The object appeared on one display wall at a time, switching walls every two hours (Figure 2A). On average, the object measured 9 cm (length) × 7 cm (height) and was displayed on a uniform white background. Half of chicks were imprinted to the object shown in Figure 1B and half of the chicks were imprinted to the object shown in Figure 1C.

In the Temporally Smooth Condition (SI Movie 1), the virtual object rotated smoothly around a frontoparallel vertical axis, completing a full rotation every 6 seconds (30 frames/second). The object had two faces, each with a different color and shape (Figure 1B). Since the edges of the object (shown during transitions from one face to the other) were identical in color and shape, the object appeared to change smoothly from one 3-D shape to the other 3-D shape. Using this type of geometrically impossible object allowed two different color-shape units to be presented on a single smoothly moving object. Accordingly, I was able to examine whether the first object representation built by newborn chicks contains integrated color-shape units. The same temporally smooth movie was presented throughout the input phase; thus, the transitional probability between images was 1.0.[2]

[2] The term "transitional probability" refers to the consistency with which the visual images occurred in a particular order. Since the images were presented in a constant order throughput the input phase, the transitional probability between images was 1.0 in both conditions.

In the Temporally Non-Smooth Condition (SI Movie 2), the chicks were shown the same virtual object, but the object images were presented in a scrambled order (Figure 1B). Specifically, I took the 180 unique images (30 frames/second × 6 seconds) from the temporally smooth animations and randomized the order of the images. On average, the successive images differed by 154º and the minimum difference between two successive views was 50º. To make the images more distinct and eliminate flicker, each image was presented for one second. The same non-smooth movie was presented throughout the input phase; thus, the transitional probability between images was 1.0.

Critically, the virtual objects presented in the two conditions were composed of the same individual images and were equally predictive in terms of the transitional probabilities between images. Furthermore, the subjects received the same amount of overall time with each individual image across the conditions (despite the images being presented at different rates). Thus, any difference in recognition performance between the conditions could not be based on the amount of exposure to the individual images or the transitional probabilities between images.

In the second week of life (test phase), I examined whether the chicks could recognize their imprinted object across a variety of feature changes. During the test trials, two objects were shown simultaneously, one on each display wall (Figure 2B). One object was the imprinted object from the input phase, and the other object was an unfamiliar object. If the chicks could distinguish their imprinted object from the unfamiliar object, then they should have spent a greater proportion of time in proximity to the imprinted object compared to the unfamiliar object. The chick was considered to be in proximity to an object when the chick occupied a 22 × 42 cm zone next to the display wall showing that object. The test objects moved smoothly in the

Temporally Smooth Condition and non-smoothly in the Temporally Non-Smooth Condition. During the test trials, subjects were presented with the following test trial types:

Color Change Trials: The imprinted object was paired with an unfamiliar object that was identical to the imprinted object except that one or both colors were replaced with novel colors.

Shape Change Trials: The imprinted object was paired with an unfamiliar object that was identical to the imprinted object except that one or both shapes were replaced with novel shapes.

Color-Shape Change Trials: The imprinted object was paired with an unfamiliar object in which one face was replaced with a novel color and shape or both faces were replaced with novel colors and shapes.

Binding Change Trials: The imprinted object was paired with an unfamiliar object that had the same color and shape features as the imprinted object, but in a different configuration (e.g., a yellow triangle and a purple circle vs. a yellow circle and a purple triangle).

During the test phase, subjects received 168 test trials (1 trial per hour). Each test trial lasted 20 minutes and was followed by a 40-minute rest period. During the rest periods, the animation from the input phase was shown on one display wall, and the other display wall contained a white screen.

3. Results

3.1. Recognition Performance

The results are shown in Figure 3. For each test trial type, I computed the percent of time each chick spent with the imprinted object compared to the unfamiliar object. A repeated measures ANOVA with Test Trial Type as a within-subjects factor and Condition (Temporally Smooth vs. Temporally Non-Smooth) as a between-subjects factor revealed a significant main effect of Test Trial Type ($F(6, 120) = 17.08$, $p < .001$). The interaction was not significant ($F(6, 120) = 0.65$, $p = .69$). Recognition performance was significantly higher in the Temporally Smooth Condition than the Temporally Non-Smooth Condition, both for overall recognition performance ($t(20) = 3.44$, $p = .003$, Cohen's $d = 1.54$) and for each of the seven test trial types (see Table 1). In brief, newborn chicks showed superior recognition performance when raised with temporally smooth objects.

3.2 *Measuring the Strength of the Imprinting Response*

One potential explanation for this effect is that the chicks imprinted more strongly to the temporally smooth objects than the temporally non-smooth objects, and were therefore more motivated to approach the temporally smooth objects. To examine whether temporal smoothness influenced the strength of the imprinting response, I examined the proportion of time chicks spent by the imprinted objects during the rest periods. During the rest periods, the imprinted object was projected on one display wall while the other display wall was blank. Thus, the rest periods provided a measure of the amount of time subjects generally preferred to spend in proximity to their imprinted object. The chicks in the Temporally Smooth and Temporally Non-Smooth Conditions spent 86.0% (SEM = 1%) and 86.2% (SEM = 1%) of their time with their imprinted object, respectively. These values did not differ significantly from one another ($t(20) =$

.17, p = .87). The chicks imprinted equally strongly to the temporally smooth and temporally non-smooth objects.

4. Discussion

I used a high-throughput controlled-rearing method to examine whether newborn chicks need experience with temporally smooth visual objects to develop object recognition abilities. The chicks raised with the temporally smooth objects and the chicks raised with the temporally non-smooth objects were exposed to the same individual images, and the objects were equally predictive in terms of the transitional probabilities between images; nevertheless, there were significant differences in recognition performance across the groups. When newborn chicks were raised with a temporally smooth object, they developed accurate color recognition, shape recognition, and color-shape binding abilities. In contrast, when newborn chicks were raised with a temporally non-smooth object, their object recognition abilities were impaired. Thus, there is a "smoothness constraint" on newborn object recognition. Experience with temporally smooth objects facilitates the development of object recognition.

These results accord with previous studies showing that temporal learning abilities can emerge within the first few months of life (e.g., Bulf, Johnson, & Valenza, 2011; Kirkham, Slemmer, & Johnson, 2002; Kirkham, Slemmer, Richardson, & Johnson, 2007), and extend this literature by showing that newborn visual systems use temporal learning mechanisms at the onset of vision when building their first visual object representation. These results also accord with temporal association models in two respects. First, temporal association models predict that smooth changes in an object's appearance over time will result in larger changes in neural selectivity (and hence, discrimination performance) than non-smooth changes in appearance

(Wallis, 1998; Wallis & Bulthoff, 2001). Consistent with these models, newborn chicks developed enhanced object recognition abilities when raised with temporally smooth objects. Second, temporal association models predict that it should be possible to create ‘unnatural’ object representations by exposing subjects to visual worlds with unnatural spatiotemporal statistics (Cox et al., 2005; Li & DiCarlo, 2008, 2010). In the present study, newborn chicks were exposed to an unnatural visual world with a geometrically impossible object; nevertheless, the chicks were able to build a robust representation of the object (provided that the object was temporally smooth).

It is important to emphasize that temporal smoothness is a continuous variable rather than a binary variable. Since chickens have a relatively high flicker fusion rate (~100 Hz), it is possible that even the temporally smooth movies were not perceived as completely smooth by the chicks. Temporal smoothness is also a broad term that can refer to many different types of change across images. Visual sequences can be temporally smooth from a brightness perspective, pixel-level perspective, feature-level perspective, and so forth. It would be interesting for future studies to systematically manipulate the amount and type of temporal smoothness in the visual environment, and examine the effects of those manipulations on chicks’ object recognition abilities.

To what extent do these findings apply to the development of object recognition in humans? In some respects, we should expect differences in the development of object recognition between chickens and humans. For instance, newborn humans are relatively immature at birth and have difficulty detecting the direction and speed of motion (Wattam-Bell, 1991, 1992). Accordingly, newborn humans might process temporally smooth visual input differently than newborn chicks. On the other hand, there is growing evidence in the neurosciences for an evolutionarily ancient cortical circuit for processing sensory information (reviewed by Karten, 2013). This circuit is thought to have evolved in stem amniotes at least 100 million years ago (Jarvis et al., 2005) and to underlie the computations used for visual object recognition (DiCarlo et al., 2012). If mammals and birds share homologous neural circuits for processing visual input, as these findings suggest, then human visual systems should be subject to similar constraints as chicken visual systems. It would be interesting for future studies to examine directly whether object recognition in human infants is subject to a smoothness constraint.

In conclusion, the present study provides evidence for a smoothness constraint on the development of object recognition in a newborn biological visual system. Newborn chicks can develop color recognition, shape recognition, and color-shape binding abilities rapidly (within the first week of life), but these abilities do not emerge automatically. Rather, robust object recognition abilities emerge when newborn chicks are raised with temporally smooth objects.

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Figure Captions

Figure 1: (A) Illustration of a controlled-rearing chamber. The chambers were devoid of real-world objects. To present object stimuli to the chicks, virtual objects were projected on two display walls situated on opposite sides of the chamber. During the input phase (1st week of life), newborn chicks were exposed to a single virtual object that either moved smoothly or non-smoothly over time. Half of the chicks were raised with the object shown in panel **(B)** and half of the chicks were raised with the object shown in panel **(C)**.

Figure 2: The experimental procedure. These schematics illustrate how the virtual stimuli were presented for sample 4-hour periods during the **(A)** input phase and **(B)** test phase. During the input phase, newborn chicks were exposed to a single virtual object with two faces, each with a different color and shape. The object appeared on one wall at a time (indicated by blue segments on the timeline), switching walls every 2 hours, after a 1-min period of darkness (black segments). During the test phase, two virtual objects (one imprinted, one unfamiliar) were shown simultaneously, one on each display wall, for 20 minutes per hour (gray segments). The illustrations below the timeline are examples of paired test objects displayed in four of the test trials. Each test trial was followed by a 40-min rest period (blue segments). During the rest periods, the animation from the input phase was shown on one display wall, and the other display wall was blank. These illustrations show the displays seen by the subjects that were imprinted to Imprinted Object 1 (Figure 1). **(C)** The unfamiliar objects presented in the four test trials depicted in Figure 2B. These illustrations show how the object transitioned from face to face in the Temporally Smooth Condition.

Figure 3: Results from the test phase. The bar graph shows the mean proportion of time spent by the imprinted object compared to the unfamiliar object for each test trial type. Error bars denote ±1 SE. Chance performance (dashed lines) was 50%.

Tables

Trial Type	***t*-score**	***p*-value**	**Cohen's *d***
1 Color Change	2.25	.04	1.01
2 Color Changes	2.05	.05	.92
1 Shape Change	2.84	.01	1.27
2 Shape Changes	2.99	.007	1.34
1 Color-Shape Change	2.19	.04	.98
2 Color-Shape Changes	2.13	.05	.95
Binding Change	3.30	.004	1.48

Table 1: Results of two-tailed, independent samples *t*-tests comparing object recognition performance across the Temporally Smooth and Temporally Non-Smooth Conditions for the seven trial types.

Figure 1

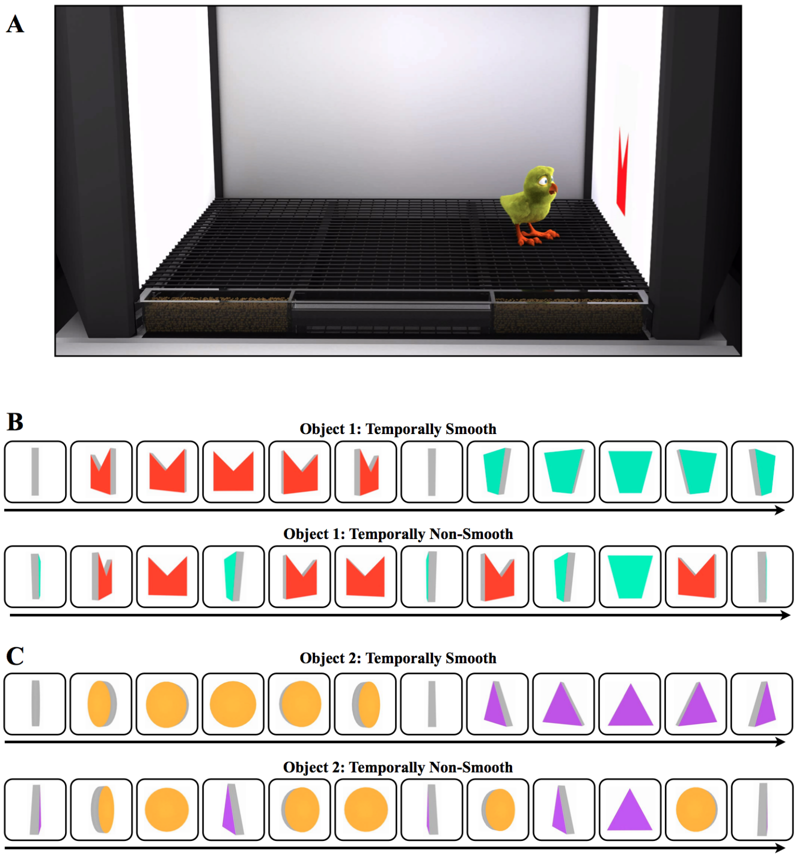

A
B
Object 1: Temporally Smooth
Object 1: Temporally Non-Smooth
C
Object 2: Temporally Smooth
Object 2: Temporally Non-Smooth

Figure 2

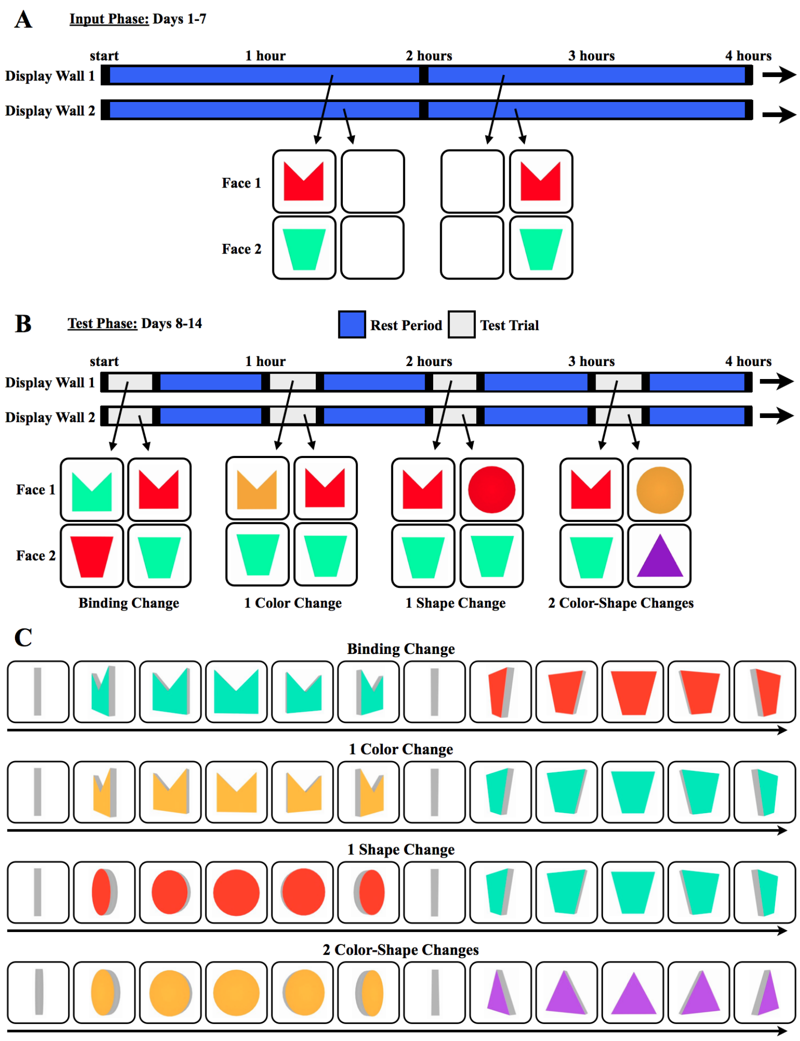
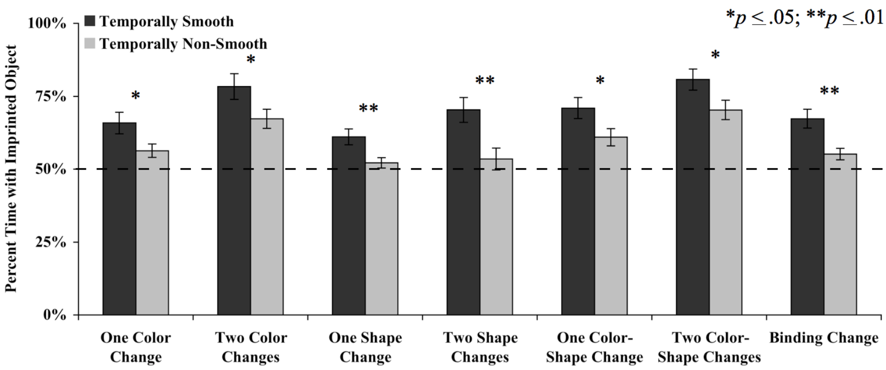

A
Input Phase: Days 1-7
start
1 hour
2 hours
3 hours
4 hours
Display Wall 1
Display Wall 2
Face 1
Face 2
B
Test Phase: Days 8-14
Rest Period
Test Trial
start
1 hour
2 hours
3 hours
4 hours
Display Wall 1
Display Wall 2
Face 1
Face 2
Binding Change
1 Color Change
1 Shape Change
2 Color-Shape Changes
C
Binding Change
1 Color Change
1 Shape Change
2 Color-Shape Changes

Figure 3



Temporally Smooth
Temporally Non-Smooth
*p ≤ .05; **p ≤ .01
Percent Time with Imprinted Object
100%
75%
50%
25%
0%
One Color Change
Two Color Changes
One Shape Change
Two Shape Changes
One Color-Shape Change
Two Color-Shape Changes
Binding Change