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# Development of Object Concepts in Macaque Monkeys

**ABSTRACT:** One of the most interesting questions in cognitive development is how we acquire and mentally represent knowledge about objects. We investigated the development of object concepts in macaque monkeys. Monkeys viewed trajectory occlusion movies in which a ball followed a linear path that was occluded for some portion of the display while their point of gaze was recorded with a corneal-reflection eye tracker. We analyzed the pattern of eye movements as an indicator of object representation. A majority of eye movements of adult monkeys were anticipatory, implying a functional internal object representation that guided oculomotor behavior. The youngest monkeys lacked this strong internal representation of objects. Longitudinal testing showed that this ability develops over time providing compelling evidence that object concepts develop similarly in monkeys and humans. Therefore, the macaque monkey provides an animal model with which to examine neural mechanisms underlying the development of object representations. © 2008 Wiley Periodicals, Inc. *Dev Psychobiol* 50: 278–287, 2008.

**Keywords:** *Macaca nemestrina*; eye movements; object permanence; perceptual completion; comparative study

## INTRODUCTION

Visually normal adults experience a world composed of objects that endure in space and time even when those objects are not fully visible. A central question in cognitive and developmental science is how we come to have these complete mental representations, or concepts, about objects. Researchers have often turned to paradigms that assess perception of object occlusion to investigate object representations. One way to identify the necessary abilities that support veridical object concepts is by studying how they develop. Occlusion perception is relatively trivial for adults, who describe relatable figures as wholes under many conditions (Kellman & Shipley, 1991), but it represents a major challenge for young infants (Slater, Johnson, Brown, & Badenoch, 1996). A systematic approach to studying object concept development was pioneered by Piaget (1954/1937), who intro-

duced a series of tasks posed to his own children in an attempt to gain access to development of object representations, and cognition more generally, across infancy. Following Piaget, in the present article we use the term “object concept” to refer to the ability to represent objects in the absence of direct perceptual support, as when a moving object becomes hidden by an occluding surface.

For Piaget, active search, initiated by the child, was a critical feature of object concepts. Initially in postnatal development (Stages 1 and 2 of Piaget’s 6-stage theory of sensorimotor development), infants exhibited a kind of recognition memory, but this behavior was considered more passive than active. More active search behaviors emerged after 4 months, and marked the beginnings of “true” object concepts during Stage 3. These included “visual accommodation to rapid movements,” when an infant would respond to a dropped object by looking down toward the floor. This behavior became more systematic when the infant himself dropped it, and formed the basis for predictive actions based on the perceived trajectory of the object. During Stage 4, beginning at about 8 months, an infant will search actively for an object that is completely hidden, though she might reach in an incorrect location if there are multiple possible hiding sites. Search errors are gradually overcome across the second year after birth during Stages 5 and 6, as the infant becomes fully cognizant of object identity and permanence.

Received 8 November 2006; Accepted 15 October 2007

Correspondence to: C. Hall-Haro

Contract grant sponsor: NIH

Contract grant numbers: EY05864, R01-HD40432, R01-HD048733

Contract grant sponsor: NSF

Contract grant numbers: BCS-0418103, RR00166

Published online in Wiley InterScience

(www.interscience.wiley.com). DOI 10.1002/dev.20282

Perception of object occlusion has been widely investigated by researchers since Piaget. Slater et al. (1996) used a habituation paradigm to show that newborns do not perceive unity of partly occluded objects, meaning that fragments are processed as unrelated units rather than parts of an object. By 2 months of age, infants provide evidence of unity perception under limited conditions (Johnson, 2004; Johnson & Aslin, 1995), and by 4 months, infants show a strong novelty preference for object parts, indicating their ability for perceptual completion (Johnson & Nanez, 1995; Kellman & Spelke, 1983). Subsequent studies have expanded on this work to show the importance of particular kinds of visual information, such as common motion and alignment of object parts, to successful perceptual completion in young infants (Johnson & Aslin, 1996; Smith, Johnson, & Spelke, 2003).

Other studies of object concept development have examined infants' looking responses to events involving fully occluded objects. The reasoning is as follows: once young infants demonstrate perceptual completion they might be able to keep track of an object's continuous existence when there is no perceptual information about it (i.e., when the object is fully occluded). Baillargeon and colleagues provided positive evidence that 5-month olds maintained a short-term representation for an object when it was out of sight, while 3.5-month olds responded inconsistently (Baillargeon, 1987; Baillargeon, Spelke, & Wasserman, 1985). Rosander and von Hofsten (2004) found a dramatic improvement in oculomotor tracking of an object undergoing occlusion over the same age range, suggesting the development of a persistent representation of the moving object. Johnson, Bremner, Slater, Mason, Foster, and Cheshire (2003) similarly found a developmental trend between 2 and 6 months in the perception of continuity of an object's trajectory. Using oculomotor anticipation as the dependent measure, Johnson, Amso, and Slemmer (2003) showed that 4- and 6-month olds make anticipatory eye movements to the place of an object's reemergence following an occlusion event. Anticipatory eye movements were interpreted as an indication of the infants' expectancy to see the object emerge from behind the occluder. Interestingly, 6-month-old infants made significantly more anticipations than 4-month olds, suggesting a more robust representation of the hidden object in the older infants. However, exposing 4-month olds to the unoccluded trajectory of the object for a short interval improved their perception in the occluded version, shifting their performance to resemble the 6-month-old infants. Thus, perception of object occlusion and continuity develops over time and is enhanced by visual experience.

Despite extensive behavioral evidence showing the developmental course of object concepts in humans, little

is known about the neural mechanisms that support them. Recent studies using noninvasive techniques in human infants have started to look at neural activity correlates of object permanence. For example, Kaufman, Csibra, and Johnson (2005), using a 62 sensor EEG net, identified distinct oscillatory activity over right temporal cortex during an occlusion event. In an intriguing longitudinal study, Baird et al. (2002) measured blood oxygenation using near-infrared spectroscopy and found evidence for increased activation of frontal cortex with the onset of object permanence. Although this approach is promising, these studies are quite rare and the level of analysis is necessarily coarse in scale providing evidence about which broad areas of the brain show changes in activity patterns at key ages. Research using animal models can address developmental questions quantitatively, at a finer scale, for example, the single neuron level or the level of local connectivity. Such studies are needed to help identify the important neural processes that underlie object concepts and other cognitive abilities.

Prior investigations have suggested that the ability for perception of object occlusion and object concepts is not limited to humans. For example, perception of object occlusion can occur very early in development without much visual experience in some species, as demonstrated by studies of newly hatched chicks (Regolin, Marconato, & Vallotigara, 2006; Regolin & Vallotigara, 1995). Classic Piagetian search paradigms have been used to explore the expression of different stages of object permanence in nonhuman primates (e.g., Ha, Kimpo, & Sackett, 1997; Neiworth et al., 2003; see also review in Tomasello & Call, 1997) and other animals (see Gomez, 2005). The data from nonhuman primates suggest that they exhibit all of the object concept stages except Stage 6 (de Blois & Novak, 1994; Gomez, 2005; but see Fillion, Washburn, & Gullede, 1996). In line with the infant studies on perception of object unity described above, Sato and colleagues examined an adult chimpanzee's (*Pan troglodytes*) matching response to a broken or complete rod using partly occluded rods as samples. They showed that the chimpanzee matched the partly occluded figures to the complete rod whenever the alignment and/or movement of the two visible parts were relatable (Sato, Kanazawa, & Fujita, 1997). Similarly, Fujita and Giersch (2005) showed that capuchin monkeys (*Cebus apella*) also perceived unity in a partly occluded rod in a matching-to-sample task as long as the sample stimulus contained relatable parts. Using an overestimation of length illusion, Fujita (2001) tested the capacity for perceptual completion in rhesus monkeys (*Macaca mulatta*). In this illusion, adult humans tend to overestimate the length of a bar that abuts the edge of a large rectangle, suggesting that they believe it continues

behind the rectangle. Rhesus monkeys have a bias for a long bar as the matching-to-sample stimulus suggesting that they extend the length of the rod very much like adult humans do. In a different approach, Churchland, Chou, and Lisberger (2003) studied the smooth pursuit eye movements of adult rhesus monkeys following targets that blinked or were physically occluded. This study showed that eye velocity was greatly reduced when targets blinked, whereas velocity was maintained during the trials in which targets were covered by a physical occluder. This pattern of results suggests that knowledge of object permanence was guiding the monkeys' smooth pursuit when the occluder covered the targets.

These studies suggest that adult nonhuman primates perceive object unity, object persistence following occlusion, and possess classic object concepts, reinforcing their importance as an animal model for human cognition. However, differences in testing approaches make a direct comparison to human infant studies difficult. Instead of habituation or preferential looking type paradigms, in which experimenters test the spontaneous behavior of the infant, these animals were trained to respond either in matching-to-sample type tasks or to pursue a target steadily for reward, both of which require extensive learning and experience. It is not known whether untrained or unrewarded animals would spontaneously behave in a manner consistent with unity perception and perception of object occlusion. Furthermore, in these tasks, monkeys are required to make a decision, which could depend on or be influenced by more factors than the perception of the object and which could be task-specific. Finally, these data are from adult animals only and therefore do not speak to developmental processes.

The few developmental studies about object concepts in monkeys used reaching tasks analogous to those employed by Piaget (plain reach, partial-hide, full-hide, and A-not-B). Two early studies showed that the development of object concepts in rhesus macaques (Wise, Wise, & Zimmermann, 1974) and squirrel monkeys (*Saimiri sciurea*) (Vaughter, Smotherman, & Ordy, 1972) generally follow the sequence of stages described by Piaget for the human infant, although the time of acquisition differs in monkeys and humans. Visually guided reaching appears after about 2 weeks (Boothe, Kiorpes, Regal & Lee, 1982) followed by simple searching for an object by 3–4 weeks (Wise, Wise, & Zimmermann, 1974). Ha, Kimpo, and Sackett (1997) showed that pigtailed macaques (*Macaca nemestrina*) achieve 2-D (screen) versions of classical object concepts before 3-D (well) versions of the same tasks; success on A-not-B was achieved last. Diamond (1990) reported that A-not-B is mastered by infant monkeys by about 4 months. Thus, the

sequence of acquisition of Piagetian object concepts by infant macaques seems to follow a similar sequence to human infants, although age norms for the stages have not been established. The current state of knowledge is limited, and therefore does not permit us to fully understand the development of object concepts nor does it reveal an understanding of the underlying neural limitations on this process.

Most studies in human infants are cross-sectional. Due to the large range of individual differences often observed in behavior across infants of a given age, trends can be lost in the noise in cross-sectional studies. Longitudinal data are of great value to show developmental trends, particularly to identify critical cross-over points, but this approach is often problematic in studies of human infants. Also, sampling the range of performance along a given stimulus dimension for each individual provides information on the strength of a cognitive or perceptual ability. But to accomplish this requires demanding paradigms and multiple test sessions that are difficult to implement in young human infants. These ideals could be met using an appropriate animal model.

Because prior studies suggest that several species of nonhuman primates are capable of unity perception (Fujita, 2001; Fujita & Giersch, 2005; Sato et al., 1997) and some other object concepts (Flombaum, Kundery, Santos, & Scholl, 2004; Hood, Hauser, Anderson, & Santos, 1999; Neiwirth et al., 2003), and the macaque monkey provides a good animal model for development of human visual functions (Boothe et al., 1982; Boothe, Dobson, & Teller, 1985), a nonhuman primate model would be valuable to investigate how object permanence and related concepts develop. In the present study, we examined how object concepts develop over the first 4 months of age in the pigtailed macaque monkey. We implemented an occlusion perception task using the spontaneous behavior of the monkey by tracking their eye movements while they viewed a moving ball undergoing occlusion. In order to fully benefit from comparative studies and document cognitive ability, clear parallels need to be drawn across species using similar paradigms. The task presented in this study is directly comparable to the infant human studies conducted by our group (Johnson, Amso, & Slemmer, 2003). We were particularly interested in implementing a task with no training requirements because, as pointed out before, long training schedules can have a profound effect on results (Pascalis & Bachevalier, 1998). Two animals were studied longitudinally to document at what age they indicate knowledge of object persistence. Our results show that very young monkeys do not consistently anticipate the ball's reemergence following occlusion. However, this behavior changes with age, indicating that this measure of object concepts develops over time.

## METHODS

### Subjects

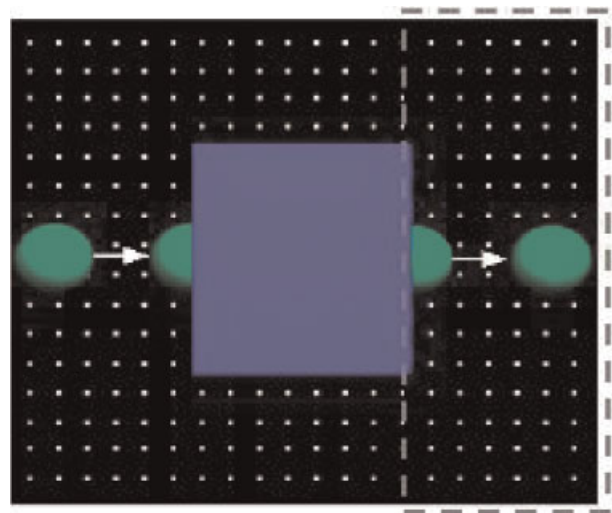
Four pigtailed macaque monkeys (*Macaca nemestrina*) were used in this study. All animals were born at the Washington National Primate Research Center and hand-reared in the nursery facility at the Visual Neuroscience Laboratory at New York University. All experimental procedures and animal care were in accordance with the NIH Guide for the Care and Use of Laboratory Animals and approved by the New York University Animal Care and Use Committee. Two monkeys were tested longitudinally spanning the first 3.5 postnatal months (at 5, 8, and 15 weeks of age). The other two monkeys were tested as adults (mean age = 207 weeks).

### Stimuli

Stimuli were presented on a 21-inch EIZO FlexScan FXE8 monitor. A G4 Macintosh computer controlled stimulus presentation. Viewing distance for infants was 50 cm and for adults it was 100 cm. The stimulus consisted of a 10-s animation showing a 2.5 cm green ball ( $2.9^\circ/1.4^\circ$  visual angle at the infant and adult monkeys' viewing distance, respectively) moving horizontally across the display at 8.4 cm/s. The ball changed its direction of motion at the far right and far left every 2.5 s and the center of its trajectory was occluded by an 8 by 10 cm ( $11.3 \times 9.1^\circ/5.7 \times 4.6^\circ$ ) blue rectangle for .7 s. The ball and rectangle were presented against a 21 cm  $\times$  15 cm ( $22.8 \times 16.7^\circ/11.9 \times 8.5^\circ$ ) textured background. Every animation consisted of two complete cycles of the object's trajectory giving a total of four left-right/right-left excursions per stimulus. We termed these *occlusion events*. Experimental sessions consisted of eight presentations of the occlusion display, each accompanied by a different nonrhythmic sound to maximize attention (as in Johnson, Amso, et al., 2003). Monkeys completed a range of three to eight presentations per testing session.

### Procedure

Each experimental session was conducted in a darkened room. Monkeys were placed in a primate chair that allowed free head and body movement. The monkey's point of gaze was first calibrated by a simple 5-point calibration routine. The animals were shown small pictures of monkey faces at either one of the four corners or in the center of a virtual rectangle. Eye position coordinates were taken when the animal fixated each point. Animals were rewarded with a squirt of age appropriate liquid (infant formula or apple juice) on a constant basis just for directing attention to the screen. Eye position information was obtained with an infrared eye tracking system (ISCAN, Burlington, MA). The point of gaze as computed by the eye tracker was superimposed on the stimuli and recorded on digital video. For offline analysis the screen was divided into two regions, the *emergence zone* and the *occlusion zone* (see Fig. 1). The emergence zone was defined as the area of the display between the edge of the occluder and the edge of the background on the side of the ball's emergence after an occlusion event. The occlusion zone consisted of the remainder of the display.



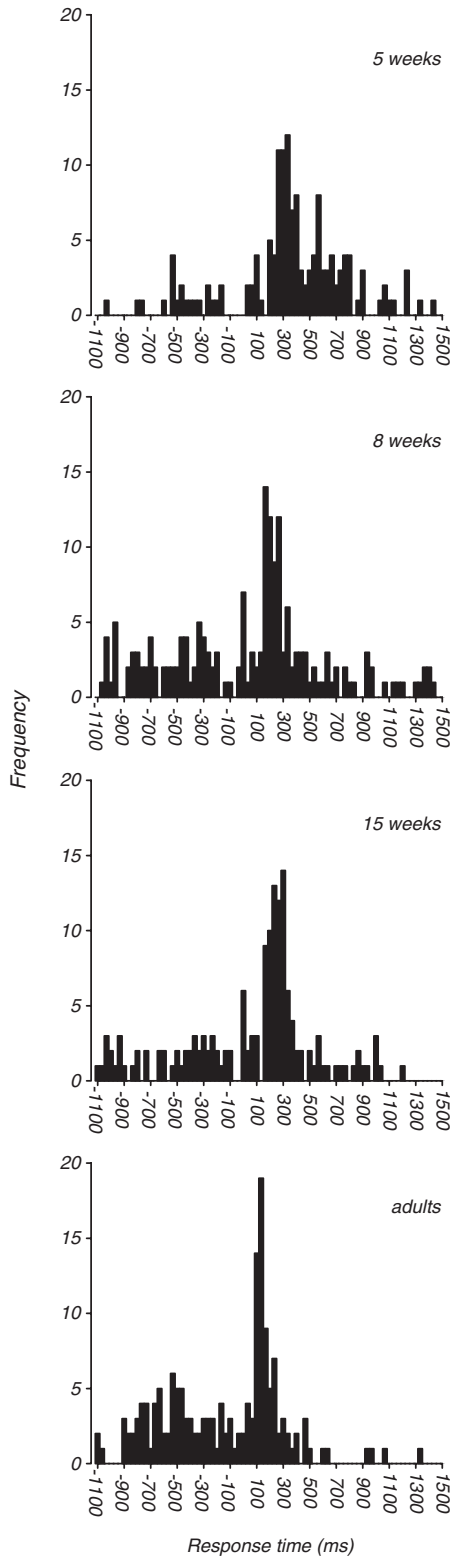
**FIGURE 1** Illustration of the stimulus used in this study. Each stimulus consisted of a 10 s animation showing a green ball moving horizontally across the display. The ball changed its direction of motion at the far right and far left and the center of its trajectory was occluded by a blue rectangle. The dashed area illustrates the *emergence zone* of a right-left occlusion event.

Trials were considered valid if the eye movements met the following criteria: first, they had to show perceptual contact with the ball's trajectory before the occlusion event started; second, they had to originate after the occlusion event began; and third, they had to show perceptual contact with the trajectory subsequent to the occlusion event. Trials were excluded if the monkey's point of gaze remained fixed on any part of the display independently of object excursion. Latency of valid eye movements was determined by coding the digital video frame-by-frame. The first video frame showing the emergence of the ball from behind the occluder was set to 0. Valid eye movements that were initiated 150 ms or more after object's emergence (i.e., time 0) were coded as *reactions* while those initiated before the 150 ms criterion were coded as *anticipations*. The time criterion was based on the assumption that saccadic reaction times in macaques are on the order of 150–200 ms (Krauzlis & Miles, 1996). Since the occlusion event began .4 s before complete occlusion, and the ball was occluded for .7 s, anticipatory eye movements could be initiated up to 1.1 s prior to emergence to count as a valid trial.

## RESULTS

The latency distributions for eye movements relative to the emergence of the ball from behind the occluder are plotted for each tested age as frequency histograms in Figure 2. The two infant monkeys were tested longitudinally at 5, 8, and 15 weeks of age and two additional monkeys were tested as adults.

We divided the eye movements into two classes, anticipations and reactions, on the basis of latency of each

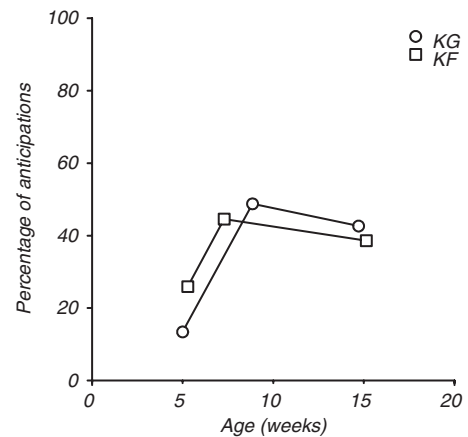


**FIGURE 2** Histograms show the distribution of eye movement latency with respect to the emergence of the ball right after an occlusion event (response time = 0). Combined data from the two infant monkeys tested at several ages is shown in the first three panels. Combined data from two adults is shown in the lower histogram.

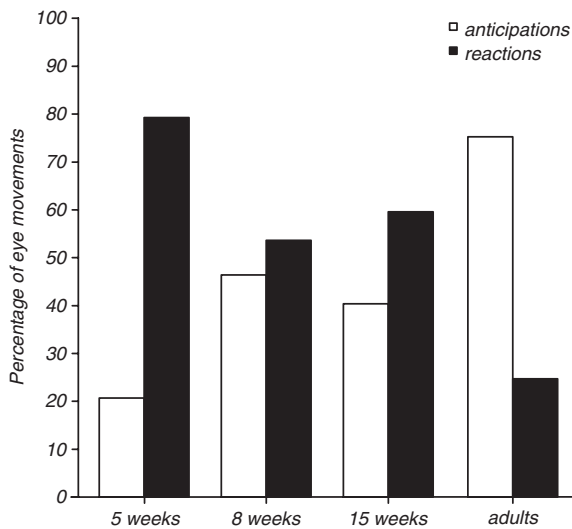
eye movement relative to the reappearance of the moving object from behind the occluder (see detailed description in Methods Section). We first asked whether the two monkeys observed longitudinally exhibited similar performance at each age. As Figure 3 shows the two infant monkeys show a very similar pattern of results over the course of development. There were no statistically reliable differences in the proportions of anticipations versus reactions at any of the three ages tested (5, 8, and 15 weeks),  $\chi^2 < 2.54$ , ns; therefore data from the two infants at each age were combined for subsequent analysis.

Figure 4 shows the difference in proportion of anticipations (open bars) and reactions (black bars) across age. Five-week olds produced 30 anticipations and 115 reactions (20.7% anticipations, 79.3% reactions), 8-week olds produced 85 anticipations and 98 reactions (46.4%, 53.6%), and 15-week olds produced 63 anticipations and 93 reactions (40.4%, 59.6%). Chi-square analyses were used to compare differences in performance at the three ages, and the results are shown in Table 1. Comparisons are also shown between infant monkeys and the two adult monkeys, who produced 125 anticipations and 41 reactions (75.3%, 24.7%).

Evidence was obtained for two notable developmental changes in the proportions of anticipations versus reactions, the first between 5 and 8 weeks, and the second between 15 weeks and adults. These results parallel outcomes from experiments with human infants, although the developmental changes are seen at different ages in the two species. In humans, there is a shift in performance between 4 and 6 months (Johnson, Amso, et al., 2003), and again between 6-month olds and adults, who produce an oculomotor anticipation on nearly every



**FIGURE 3** Similar performance in the proportions of anticipations versus reactions in the two infant monkeys. The percentage of eye movements coded as anticipations is plotted as a function of age in weeks for the two infants that were tested longitudinally (KG and KF).



**FIGURE 4** Two developmental changes in the proportions of anticipations versus reactions, one between 5 and 8 weeks, and the second between 15 weeks and adults. Open bars represent the percentage of eye movements coded as anticipations. Black bars represent the proportion coded as reactions.

trial (unpublished observations). In both monkeys and humans, therefore, the youngest infants observed provide little evidence of object concepts in our anticipatory looking paradigm, and there are rapid developments in this capacity over the first several weeks (monkeys) or months (humans) after birth. Further improvements in performance occur after infancy, perhaps due to a decrease in distractibility, or additional developments in representational capacity.

An alternative explanation for this developmental pattern appeals to the possibility that the higher proportion of anticipations with age stems simply from an overall reduction in oculomotor latency. Such an explanation seems unlikely based upon examination of the frequency histograms for each age (Fig. 2). The distribution of latencies at all four ages is characterized by a marked discontinuity just after time 0 (i.e., when the object reappears), and peaking at 150–300 ms. This implies that the peak is a result of a reaction to the object, and that

**Table 1. Comparisons of Performance (Proportions of Oculomotor Anticipations vs. Reactions) Across Ages**

Comparison	$\chi^2$
5 weeks vs. 8 weeks	23.58, $p < .0001$
5 weeks vs. 15 weeks	13.65, $p < .001$
8 weeks vs. 15 weeks	1.26, ns
5 weeks vs. adults	92.33, $p < .0001$
8 weeks vs. adults	30.24, $p < .0001$
15 weeks vs. adults	40.35, $p < .0001$

latencies prior to this time originate in a representation of the moving object when it is hidden. Furthermore, even the youngest infants produced some eye movements that were initiated with latencies in the range of the adults, and the distributions at the three older age points are similar to one another.

To quantitatively address this alternate possibility, we conducted separate statistical analyses of reactions and anticipations. A one-way ANOVA on latencies of oculomotor reactions yielded a reliable main effect of age (5-, 8-, 15-week olds vs. adults),  $F(3, 343) = 5.39$ ,  $p < .01$ . However, Newman–Keuls tests revealed no significant difference in latencies between 5 and 8 weeks ( $M = 521.7$  ms,  $SD = 279.0$  and  $M = 472.7$  ms,  $SD = 362.2$ , respectively), when a critical change in performance takes place. Latencies were also not reliably different between the 15-week olds and adults ( $M = 380.2$  ms,  $SD = 243.0$  and  $M = 361.8$  ms,  $SD = 271.0$ , respectively), and both were faster relative to the younger ages,  $ps < .05$ . A one-way ANOVA on latencies of oculomotor anticipations across age groups revealed a significant difference,  $F(3, 299) = 3.52$ ,  $p < .05$ , but there was no consistent decrease in latencies with age: Newman–Keuls tests revealed no reliable differences in latencies between any of the groups,  $ps > .05$ . The mean latency across the sample was  $-368.2$  ms ( $SD = 361.4$ ). Taken together, therefore, these results indicate that differences in the proportion of anticipations across age groups were not simply a consequence of a reduction of oculomotor latency with development. We did obtain evidence that older monkeys (beginning at or before 15 weeks) were quicker to produce an eye movement toward a moving target upon its appearance (reactions), but eye movements produced in anticipation of target reemergence were not faster in the older groups. Thus, the reliable shift between 5 and 8 weeks toward a greater proportion of anticipations was presumably based on a developing ability to form a representation of the object while it was out of view.

The final set of analyses addressed the question whether there was progressive learning during the task, which would be reflected in a tendency toward a higher rate of anticipatory looking with the accumulation of trials. Each monkey's performance across trials was examined with a change-point test, which computes the likelihood that up to some point in time the data are generated by one process, and after that time by a different one (Siegel & Castellan, 1988). This analysis was applied to data from the two infants at each of the three ages, as well as the two adults, and there were no statistically reliable outcomes. Moreover, our adult monkeys produced anticipations on the very first trials with the display, revealing no necessity for experience with the display. There is no evidence, therefore, that infant or adult monkeys learned to anticipate during the occlusion

task. This result echoes previous findings with human infants, who were found to exhibit a *decrease* in anticipation proportion across trials (Johnson, Amso, et al., 2003).

In summary, the greatest developmental change in behavior is between 5 and 8 weeks. The number of anticipations more than doubles during this time, and remains constant at 15 weeks, at which point it has not yet reached adult levels. Thus object concepts, as tested in our object anticipation paradigm, develop rapidly over the first 4 months or more after birth in infant monkeys, similarly to humans (Johnson, Amso, et al., 2003), and further development occurs as well after this time.

## DISCUSSION

In the present study we show that adult monkeys, but not young infant monkeys, show evidence of object concepts and continuity of object trajectory over an occlusion event. When monkeys view an occlusion display the pattern of eye movements with respect to the ball's emergence differs in adults and 5-week olds. Moreover, adult monkeys produce mostly anticipatory eye movements while infant monkeys produce mostly reactions. This pattern of results suggests that adult monkeys have a functional internal object representation that guides their oculomotor behavior by producing anticipatory eye movements to the place where the ball will emerge. In contrast, the infant monkeys tested at the earliest age do not provide substantial evidence of an expectation of the ball's emergence indicating that, in early infancy, monkeys lack a strong internal representation of objects.

An alternative explanation for the difference in performance between adult and infant monkeys could be immaturities of the oculomotor system. Lucchetti and Cevolani (1992) used a scleral search coil to measure spontaneous eye movements in 3-month-old monkeys. In comparison to adults, the saccades of 3-month olds were of lower amplitude and slower peak velocity. Since these were spontaneous saccades rather than target driven, it is unclear whether saccade latencies are also longer in infants. Regardless, slower saccade dynamics are unlikely to explain our data since even the youngest infants in our study readily showed some anticipations (20.7% of object-directed eye movements) and latencies in the range of the adult data were recorded. These data imply that their oculomotor system is capable of producing the same swift responses that the adults produce. Furthermore, our statistical analysis showed no significant difference in latency between 5- and 8-week test ages for anticipations or reactions, while this interval showed the greatest change in proportion of anticipations. Also, we categorized eye movements based on time of initiation so slower

eye movements would not affect the analysis. We are confident that the criteria set for including eye movements as valid trials in the analysis (see Methods Section) rules out the added possibility that the difference in performance can be explained by inattentiveness in the 5-week-old monkeys.

Because we used a longitudinal paradigm, in which infants were repeatedly exposed to the same object trajectory, one might argue that they could have learned to anticipate in this specific display as a motor habit rather than as a cognitive skill. Although we cannot completely rule out this possibility, it is unlikely this occurred because (1) our adult monkeys showed a large number of anticipations in their first exposure to the display and therefore had no opportunity to learn, and (2) the infants' behavior did not steadily improve with repeated testing—there was no increase in anticipations between 8 and 15 weeks—and they did not achieve adult levels as of the last test age. This analysis is consistent with data from Rosander and von Hofsten (2004) showing little learning across sessions on a similar tracking task with human infants.

Furthermore, our change-point analysis revealed no trend over trials within a session. This suggests that the increase in anticipations following repeated exposure in infants is not due to recurrent experience with a particular occlusion display and instead represents a developing cognitive concept.

Our study shows that the infant monkeys' oculomotor behavior while viewing occlusion events changes over developmental time. Similarly to what Johnson and colleagues reported for human infants, with age infant monkeys produce more anticipatory eye movements. In our study the percentage of anticipations increased dramatically from about 21% in 5-week-old to 45% in 8-week-old monkeys. This rapid increase in anticipations parallels the difference seen in 4- and 6-month-old human infants (Johnson, Amso, et al., 2003); anticipations increased from about 29% to 46% within this age range. Basic visual functions such as acuity and contrast sensitivity in humans and monkeys show a rough equivalence at birth with further development proceeding about four times faster in monkeys (Boothe et al., 1985). It is difficult to know whether object concepts, as tested by our task, would follow the same 4-to-1 rule that other visual functions do since there are only two age points for comparison. There is no a priori reason why the same rule should hold, since perception of our occlusion display probably relies on higher order visual functions such as figure-ground segmentation, motion sensitivity, and visual-motor integration. These higher order visual functions show a protracted developmental course when compared to spatial vision (Kiorpes & Bassin, 2003; Kiorpes & Movshon, 2004). However, speculating based

only on the first two ages in our study, the 5- and 8-week-old monkeys we observed performed similarly to 17- and 26-week-old human infants, respectively, suggesting something closer to a 3-to-1 relationship. This speculation is consistent with data reported by Diamond (1990), showing that young macaques master A-not-B at 4 months while human infants tested in the same way master the task at 12 months; both species pass through the same developmental stages of producing the classic error patterns at earlier ages.

Other studies of the development of cognitive abilities in infant monkeys have found similar developmental trends to those reported in human infants. For example, macaque monkey infants and human infants follow a similar pattern in learning delayed nonmatch-to-sample (DNMS) tasks (Overman, Bachevalier, Turner, & Peuster, 1992). Monkeys were unable to acquire the task before 4 months postnatal, while human infants were unable to do so before 12 months. Human and nonhuman infants thereafter were able to perform well with increasingly long delays. Similarly, infant monkeys and humans demonstrate memory abilities earlier using a visual paired comparisons paradigm (Bachevalier, 1990; Gunderson & Sackett, 1984). Diamond found essentially identical developmental profiles between human and monkey infants on the delayed response memory task as well as A-not-B (Diamond, 1990). As with DNMS, infant monkeys follow a parallel developmental progression with increasing delay periods. Our speculation of a 3-to-1 relationship between monkeys and humans for the development of object concepts is consistent with these comparative studies of cognitive development, suggesting a somewhat slower relative development of cognitive functions in monkeys than simple visual acuity development.

Object recognition and discrimination, and sensitivity to object motion and occlusion, are likely to depend on areas further along the visual pathways than basic spatial or temporal vision. Visual areas in inferior temporal cortex (IT) and dorsal stream areas such as the middle temporal area (MT) have been implicated in encoding object properties and object motion (see Logothetis & Sheinberg, 1996; Schiller, 1995). In humans, cortical areas involved in tracking a target through space and time during brief periods of invisibility include the inferior parietal lobule, superior temporal sulcus (STS) presupplementary motor area, and precentral sulcus (Shuwairi, Curtis, & Johnson, 2007). In nonhuman primates, a number of studies have reported neurons sensitive to occlusion and context in STS, posterior parietal cortex (PP) and inferotemporal cortex (Assad & Maunsell, 1995; Baker, Keysers, Jellema, Wicker, & Perrett, 2001; Duncan, Albright, & Stoner, 2000; Kovacs, Vogels, & Orban, 1995). For example, Baker et al. (2001) reported that neurons of the anterior superior temporal sulcus

(STSa) in the rhesus monkey show activity correlated to occlusion of objects. These responses were hypothesized to contribute to the ability for object permanence. Alternatively, Diamond and Goldman-Rakic (1989) provided evidence for dorsal prefrontal cortex being a necessary area for mastery of A-not-B tasks. There is some evidence for differential, relatively slow development of memory-related areas (Bachevalier, Hagger, & Mishkin, 1991; Distler, Bachevalier, Kennedy, Mishkin, & Ungerleider, 1996) with inferotemporal cortex developing more slowly than dorsal stream areas such as MT (Rodman, Scalaidhe, & Gross, 1993); dorsal prefrontal cortex appears to develop later still (see Guillery, 2005). Future studies in infant monkeys could address, for example, whether neurons in the STS, PP, or IT show a difference in their pattern of responses to occlusion events at different ages. Ultimately such studies can serve as a basis for understanding neural mechanisms of cognitive development more generally.

In summary, the results of this experiment establish that the oculomotor behavior of infant monkeys viewing occlusion displays can be used to explore object concepts developmentally. One advantage of using our animal model is that the experimenter has total control over the environment in which the animals grow, making it possible to modify the type of visual experience they receive. Expanding this study to directly assess the role of experience, like the training condition in the Johnson, Amso, and Slemmer (2003) experiments, could provide an interesting contribution to the longstanding debate in developmental psychology centered on whether object concepts follow a nativist or constructivist account (Johnson, 2003). One tentative conclusion arising from our work is that the infant monkeys we observed appeared to develop a robust concept of object permanence over a matter of weeks, and similar changes occur in human infants over a matter of months; it may be, therefore, that cortical maturation within the context of a normal visual environment, rather than a specific period of visual experience, underlies these changes.

## NOTES

This work was supported by NIH grants EY05864 (L.K.) and R01-HD40432 and R01-HD048733 (S.P.J.) and by NSF grant BCS-0418103 (S.P.J.) and RR00166 to the Washington National Primate Research Center. We thank Alexander Gavlin and Kara Stavros for their contributions to this work, and Michael Gorman and Laura Albanese for assistance with animal care.

## REFERENCES

- Assad, J. A., & Maunsell, J. H. (1995). Neuronal correlates of inferred motion in primate posterior parietal cortex. *Nature*, 373, 518–521.



- Bachevalier, J. (1990). Ontogenetic development of habit and memory formation in primates. *Annals of the New York Academy of Sciences*, 608, 457–477; discussion 477–484.
- Bachevalier, J., Hagger, C., & Mishkin, M. (1991). Functional maturation of the occipitotemporal pathway in infants rhesus monkeys. In: N. A. Lassen, D. H. Ingvar, M. E. Raichle, & L. Friberg (Eds.), *Alfred Benzon Symposium 31. Brain work and mental activity*. (Vol. 31, pp. 231–242). Copenhagen: Munksgaard International Publishers.
- Baillargeon, R. (1987). Object permanence in 3. 5- and 4.5-month-old infants. *Developmental Psychology*, 23, 655–664.
- Baillargeon, R., Spelke, E. S., & Wasserman, S. (1985). Object permanence in five-month-old infants. *Cognition*, 20, 191–208.
- Baird, A. A., Kagan, J., Gaudette, T., Walz, K. A., Hershlag, N., & Boas, D. A. (2002). Frontal lobe activation during object permanence: Data from near-infrared spectroscopy. *Neuroimage*, 16, 1120–1125.
- Baker, C. I., Keyser, C., Jellema, T., Wicker, B., & Perrett, D. I. (2001). Neuronal representation of disappearing and hidden objects in temporal cortex of the macaque. *Experimental Brain Research*, 140, 375–381.
- Boothe, R. G., Kiorpes, L., Regal, D. M., & Lee, C. P. (1982). Development of visual responsiveness in *Macaca nemestrina* monkeys. *Developmental Psychology*, 18, 665–670.
- Boothe, R. G., Dobson, V., & Teller, D. Y. (1985). Postnatal development of vision in human and nonhuman primates. *Annual Reviews Neuroscience*, 8, 495–545.
- Churchland, M. M., Chou, I. H., & Lisberger, S. G. (2003). Evidence for object permanence in the smooth-pursuit eye movements of monkeys. *Journal of Neurophysiology*, 90, 2205–2218.
- de Blois, S. T., & Novak, M. A. (1994). Object permanence in Rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, 108, 318–327.
- Diamond, A. (1990). The development and neural bases of memory functions as indexed by the AB and delayed response tasks in human infants and infant monkeys. *Annals of the New York Academy of Sciences*, 608, 267–309; discussion 309–217.
- Diamond, A., & Goldman-Rakic, P. S. (1989). Comparison of human infants and rhesus monkeys on Piaget's AB task: Evidence for dependence on dorsolateral prefrontal cortex. *Experimental Brain Research*, 74, 24–40.
- Distler, C., Bachevalier, J., Kennedy, C., Mishkin, M., & Ungerleider, L. G. (1996). Functional development of the corticocortical pathway for motion analysis in the macaque monkey: A 14C-2-deoxyglucose study. *Cerebral Cortex*, 6, 184–195.
- Duncan, R. O., Albright, T. D., & Stoner, G. R. (2000). Occlusion and the interpretation of visual motion: Perceptual and neuronal effects of context. *Journal of Neuroscience*, 20, 5885–5897.
- Filion, C. M., Washburn, D. A., & Gullledge, J. P. (1996). Can monkeys (*Macaca mulata*) represent invisible displacement? *Journal of Comparative Psychology*, 110, 386–395.
- Flombaum, J. I., Kunder, S. M., Santos, L. R., & Scholl, B. J. (2004). Dynamic object individuation in rhesus macaques: A study of the tunnel effect. *Psychological Science*, 15, 795–800.
- Fujita, K. (2001). Perceptual completion in rhesus monkeys (*Macaca mulatta*) and pigeons (*Columbia livia*). *Perception & Psychophysics*, 63, 115–125.
- Fujita, K., & Giersch, A. (2005). What perceptual rules do capuchin monkeys (*Cebus apella*) follow in completing partly occluded figures? *Journal of Experimental Psychology: Animal Behavior Processes*, 31, 387–398.
- Gomez, J.-C. (2005). Species comparative studies and cognitive development. *Trends in Cognitive Sciences*, 9, 118–125.
- Guillery, R. W. (2005). Is postnatal neocortical maturation hierarchical? *Trends Neuroscience*, 28, 512–517.
- Gunderson, V. M., & Sackett, G. P. (1984). Pattern recognition in infant pigtailed monkeys (*Macaca nemestrina*). *Developmental Psychology*, 20, 418–426.
- Ha, J. C., Kimpo, C. L., & Sackett, G. P. (1997). Multiple-spell, discrete-time survival analysis of developmental data: Object concept in pigtailed macaques. *Developmental Psychology*, 33, 1054–1059.
- Hood, B., Hauser, M. D., Anderson, L., & Santos, L. R. (1999). Gravity biases in a non-human primate? *Developmental Science*, 2, 35–41.
- Johnson, S. P. (2003). The nature of cognitive development. *Trends in Cognitive Sciences*, 7, 102–104.
- Johnson, S. P. (2004). Development of perceptual completion in infancy. *Psychological Science*, 15, 769–775.
- Johnson, S. P., & Aslin, R. N. (1995). Perception of object unity in 2-month-old infants. *Developmental Psychology*, 31, 739–745.
- Johnson, S. P., & Aslin, R. N. (1996). Perception of object unity in young infants: The roles of motion, depth and orientation. *Cognitive Development*, 11, 161–180.
- Johnson, S. P., & Nanez, J. E. (1995). Young infants' perception of object unity in two-dimensional displays. *Infant Behavior & Development*, 18, 133–143.
- Johnson, S. P., Bremner, J. G., Slater, A., Mason, U., Foster, K., & Cheshire, A. (2003). Infants' perception of object trajectories. *Child Development*, 74, 94–108.
- Johnson, S. P., Amso, D., & Slemmer, J. A. (2003). Development of object concepts in infancy: Evidence for early learning in an eye-tracking paradigm. *Proceedings of the National Academy of Sciences (USA)*, 100, 10568–10573.
- Kaufman, J., Csibra, G., & Johnson, M. H. (2005). Oscillatory activity in the infant brain reflects object maintenance. *Proceedings of the National Academy of Sciences (USA)*, 102, 15271–15274.
- Kellman, P. J., & Shipley, T. F. (1991). A theory of visual interpolation in object perception. *Cognitive Psychology*, 23, 141–221.
- Kellman, P. J., & Spelke, E. S. (1983). Perception of partly occluded objects in infancy. *Cognitive Psychology*, 15, 483–524.
- Kiorpes, L., & Bassin, S. A. (2003). Development of contour integration in macaque monkeys. *Visual Neuroscience*, 20, 567–575.

- Kiorpes, L., & Movshon, J. A. (2004). Development of sensitivity to visual motion in macaque monkeys. *Visual Neuroscience*, 21, 851–859.
- Kovacs, G., Vogels, R., & Orban, G. A. (1995). Selectivity of macaque inferior temporal neurons for partially occluded shapes. *Journal of Neuroscience*, 15, 1984–1997.
- Krauzlis, R. J., & Miles, F. A. (1996). Decreases in the latency of smooth pursuit and saccadic eye movements produced by the “gap paradigm” in the monkey. *Vision Research*, 36, 1973–1985.
- Logothetis, N. K., & Sheinberg, D. L. (1996). Visual object recognition. *Annual Reviews Neuroscience*, 19, 577–621.
- Lucchetti, C., & Cevolani, D. (1992). The effects of maturation on spontaneous eye movements in the macaque monkey. *Electroencephalography and Clinical Neurophysiology*, 85, 220–224.
- Neiworth, J. J., Steinmark, E., Basile, B. M., Wonders, R., Steely, F., & DeHart, C. (2003). A test of object permanence in a new-world monkey species, cotton top tamarins (*Saguinus oedipus*). *Animal Cognition*, 6, 27–37.
- Overman, W., Bachevalier, J., Turner, M., & Peuster, A. (1992). Object recognition versus object discrimination: Comparison between human infants and infant monkeys. *Behavioral Neuroscience*, 106, 15–29.
- Pascalis, O., & Bachevalier, J. (1998). Face recognition in primates: A cross-species study. *Behavioural Processes*, 43, 87–96.
- Piaget, J. (1954). *The construction of reality in the child*. (M. Cook, Trans.). New York: Basic Books. (Original work published 1937).
- Regolin, L., & Vallotigara, G. (1995). Perception of partly occluded objects by young chicks. *Perception & Psychophysics*, 57, 971–976.
- Regolin, L., Marconato, F., & Vallotigara, G. (2006). Hemispheric differences in the recognition of partly occluded objects by newly hatched domestic chicks (*Gallus gallus*). *Animal Cognition*, 7, 162–170.
- Rodman, H. R., Scalaidhe, S. P., & Gross, C. G. (1993). Response properties of neurons in temporal cortical visual areas of infant monkeys. *Journal of Neurophysiology*, 70, 1115–1136.
- Rosander, K., & von Hofsten, C. (2004). Infants’ emerging ability to represent occluded object motion. *Cognition*, 91, 1–22.
- Sato, A., Kanazawa, S., & Fujita, K. (1997). Perception of object unity in a chimpanzee (*Pan troglodytes*). *Japanese Psychological Research*, 39, 191–199.
- Schiller, P. H. (1995). Effect of lesions in visual cortical area V4 on the recognition of transformed objects. *Nature*, 376, 342–344.
- Shuwairi, S. M., Curtis, C. E., & Johnson, S. P. (2007). Neural substrates of dynamic object occlusion. *Journal of Cognitive Neuroscience*, 19, 1275–1285.
- Siegel, S., & Castellan, N. J. (1988). *Nonparametric statistics for the behavioral sciences*. New York: McGraw-Hill.
- Slater, A., Johnson, S. P., Brown, E., & Badenoch, M. (1996). Newborn infant’s perception of partly occluded objects. *Infant Behavior & Development*, 19, 145–148.
- Smith, W., Johnson, S. P., & Spelke, E. S. (2003). Motion and edge sensitivity in perception of object unity. *Cognitive Psychology*, 46, 31–64.
- Tomasello, M., & Call, J. (1997). *Primate Cognition*. New York: Oxford University Press.
- Vaughter, R. M., Smotherman, W., & Ordy, J. M. (1972). Development of object permanence in the infant squirrel monkey. *Developmental Psychology*, 7, 34–38.
- Wise, K. A., Wise, L. A., & Zimmermann, R. R. (1974). Piagetian object permanence in the infant rhesus monkey. *Developmental Psychology*, 10, 429–437.