PAPER

Perception of the motion trajectory of objects from moving cast shadows in infant Japanese macaques (*Macaca fuscata*)

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Abstract

The shadows cast by moving objects enable human adults and infants to infer the motion trajectories of objects. Nonhuman animals must also be able to discriminate between objects and their shadows and infer the spatial layout of objects from cast shadows. However, the evolutionary and comparative developmental origins of sensitivity to cast shadows have not been investigated. In this study, we used a familiarity/novelty preferential looking procedure to assess the ability of infant macaques, aged 7–24 weeks, to discriminate between a ‘depth’ display containing a ball and cast shadow moving diagonally and an ‘up’ display containing a ball with a diagonal trajectory and a shadow with a horizontal trajectory. The infant macaques could discriminate the trajectories of the balls based on the moving shadows. These findings suggest that the ability to perceive the motion trajectory of an object from the moving shadow is common to both humans and macaques.

Introduction

A shadow cast on a surface by an object is referred to as a cast shadow (Mamassian, Knill & Kersten, 1998). Human adults (Kersten, Knill, Mamassian & Bülthoff, 1996; Kersten, Mamassian & Knill, 1997), and infants use cast shadows to create three-dimensional shapes and the spatial layout of objects (Imura, Tomonaga, Yamaguchi & Yagi, 2006a; Imura, Yamaguchi, Kanazawa, Shirai, Otsuka, Tomonaga & Yagi, 2006b; Yonas, Goldsmith & Hallstrom, 1978; Yonas & Granrud, 2006). Although the shape and location of a shadow may vary depending on the motion of the light source, casting surfaces, and objects, the assumption that a single light shines from above helps humans to quickly discriminate an object from its shadow and identify the motion of objects from cast shadows (Mamassian *et al.*, 1998; Imura, Shirai, Tomonaga, Yamaguchi & Yagi, 2008a). Given that the abilities to discriminate between shadows and objects and to perceive the spatial arrangements of objects are ecologically important, the human assumption about cast shadows could be an adaptation that is shared with other animals to an environment with a single sun shining from above. However, the evolutionary origin of sensitivity to cast shadows is unknown.

Previous animal behavioral studies have explored the perception of three-dimensional shapes from shading based on the variations of lighting on the surface facing the light source (chicks: Hess, 1950, 1961; Hershberger, 1970; pigeons: Reid & Spetch, 1998; chimpanzees: Tomonaga, 1998). Several physiological studies also suggest that macaques perceive three-dimensional shapes from shading similarly to humans (e.g. Hanazawa & Komatsu, 2001; Smith, Kelly & Lee, 2007; Zhang, Weiner, Slocum & Schiller, 2007). Thus, the ability to perceive three-dimensional shape from shading appears to be common to adult animals of various species. However, few studies have investigated the developmental process of pictorial depth perception.

In humans, the relationship between the development of depth cues in general (e.g. binocular disparity) and pictorial depth cues in particular has been investigated (e.g. Granrud, 1986). Although stereopsis emerges at around 3–4 months (e.g. Braddick, Atkinson, Julesz, Kropfl, Bodis-Wollner & Raab, 1980), the time at which sensitivity to pictorial depth cues develops remains
debatable (see also Brown & Miracle, 2003). Whereas previous studies using a preferential-reaching paradigm have shown that sensitivity to pictorial depth cues such as shading and cast shadows develops at around 6–7 months (e.g. Yonas & Granrud, 2006), a recent meta-analysis of all the preferential-reaching studies on pictorial depth perception suggests that 5-month-old human infants show sensitivity to pictorial depth cues (Kavšek, Granrud & Yonas, 2009). While the studies using looking time as a dependent measure showed that 3- and 4-month-old infants responded to shading and line-junction cues (e.g. Bhatt & Waters 1998; Shuwairi, Albert & Johnson, 2007), the study using the similar paradigm, but using a different type of display, found sensitivity to shading and Y-junctions in infants aged 7 and 8 months but not in infants aged 5 and 6 months (Imura, Tomonaga, Yamaguchi & Yagi, 2008b). These findings suggest that depth perception based on pictorial information develops gradually from 3 to 7 months of age.

A comparative developmental study showed that chimpanzee infants aged 4–5 months preferred reaching photographic convexity over photographic concavity defined by the shading pattern, although the images were actually flat. Thus, chimpanzee infants appear to discriminate three-dimensional shapes based on the shading pattern (Imura & Tomonaga, 2003). Human 7-month-old infants showed a reaching preference for photographic convexity over photographic concavity under a similar experimental procedure (Granrud, Yonas & Opland, 1985). Another comparative developmental study of pictorial depth perception revealed that 7- and 8-week-old pigtail macaque infants reached more often toward the closer of two objects based on linear perspective and relative size, which refer to pictorial depth cues, as well as on shading (Gunderson, Yonas, Sargent & Grant-Webster, 1993). Previous comparative studies have demonstrated that a variety of visual functions such as acuity, contrast sensitivity, and stereocuity emerge approximately four times faster in macaques than humans (Boothe, Dobson & Teller, 1985; O’Dell & Boothe, 1997). Inasmuch as visual function develops at different rates in different species, these studies suggest that the sensitivity to pictorial depth cues emerges with similar developmental timing across primate species. Additional comparative developmental studies of different kinds of pictorial depth cues would allow us to elucidate the developmental origins of visual perception.

We examined the sensitivity to moving cast shadows in Japanese macaque infants aged 7 to 24 weeks. Our previous study showed that 6- and 7-month-old human infants could discriminate the motion trajectories of objects based on different types of cast shadow motion (Imura et al., 2006b). In contrast, 4- and 5-month-old infants did not detect any differences defined by the moving cast shadows in the test events. We compared the results with macaques with those from our previous study of human infants (Imura et al., 2006b).

General methods

Participants

The sample for this experiment consisted of a total of 32 Japanese macaque (Macaca fuscata) infants including separate groups of infants for Experiment 1 (aged 7–24 weeks, \(N = 16, \text{ mean age } = 118.4 \text{ days, } SD = 34.6\); nine females, seven males) and Experiment 2 (aged 12–24 weeks, \(N = 16, \text{ mean age } = 123.0 \text{ days, } SD = 25.7\) days; nine females, seven males).

All of the infants were born at the Primate Research Institute, Kyoto University, Aichi, Japan, and were raised by their mothers. Twenty-eight of the 32 monkeys lived in a large social group in an outdoor enclosure, and the other four were moved to indoor cages soon after birth, where they lived with their mothers.

All of the monkeys were healthy at the time of testing. The care and use of the macaques followed the guidelines of ‘Guide for the Care and Use of Laboratory Primates’ (Primate Research Institute, Kyoto University, 2002). Our research design was approved by the institute Animal Welfare and Animal Care Committee.

Apparatus

For each test session, a monkey was wrapped in a blanket and brought to the testing room. One experimenter held the monkey in front of a 19-inch LCD monitor (Nanao, Flexscan S190) located approximately 40 cm away. The visual fixation of the monkey was recorded via a video camera (Panasonic, NV-GS150) on top of the monitor. Another experimenter presented the stimuli. The presentation of stimuli and sounds was controlled by a personal computer (Panasonic CF-Y2).

Experiment 1

Experiment 1 investigated whether infants could discriminate the motion trajectories of a ball from those of cast shadows. We created two kinds of events: one was perceived by adults as moving in ‘depth’, and the other was perceived as flowing ‘up’. These stimuli were produced by manipulating only the motion trajectories of a cast shadow.
Figure 1a shows examples of the stimuli in Experiment 1. The stimuli consisted of a light-blue disk (subtending 2.7 deg x 2.7 deg visual angle), a computer-generated cast shadow (subtending 2.7 deg x 0.9 deg visual angle), and a checkerboard background with linear perspective indicative of a floor with a depth dimension. During the familiarization trials, a ball and cast shadow were moved from the bottom left diagonally upward and to the right against the checkered background over a period of 2.4 sec. To adult humans, the ball appeared to move in depth. In the test trials, two kinds of cast-shadow motion events were prepared. In the ‘depth’ event, a cast shadow moved upward from the right bottom to the left parallel to a ball. The trajectories of the ball and cast shadow were symmetrical to that of the familiarization trials, and adult humans perceived the ball as moving in depth. In the ‘up’ event, the cast shadow trajectory was horizontal, but the ball moved diagonally. To adult humans, the ball appeared to float up above the floor, and the trajectory of the ball did not change. All of the stimuli were produced with Adobe Photoshop and Macromedia Flash MX; these were based on our previous study of human infants (Imura et al., 2006b).

Procedure

A familiarity/novelty preferential looking procedure was used to test the ability of the monkeys to discriminate. Previous studies have demonstrated that nonhuman mammalian species such as pigs (Wood-Grush, Vestergaard & Petersen, 1990) and primates (e.g. Adachi, Chou & Hampton, 2009; Kaneko & Tomonaga, 2008; Munakata, Santos, O’Reilly, Hauser & Spelke, 2000; Murai, Kosugi, Tomonaga, Tanaka, Matsuzawa & Itakura, 2005) also exhibited a preference for novelty, whereas some studies, especially those using social information as stimuli, have found a familiarity preference among nonhuman primates (Myowa-Yamakoshi & Tomonaga, 2001; Myowa-Yamakoshi, Yamaguchi, Tomonaga, Tanaka & Matsuzawa, 2005).

Each trial began with the presentation of a sound and a fixation figure at the center of the monitor to attract the subject’s attention. Once the monkey looked at the monitor, the fixation image disappeared, and the stimulus was presented. The experimental session consisted of four familiarization trials and two test trials per monkey. The duration of each familiarization and test trial was 20 sec.

Each monkey was familiarized to a ‘depth’ event. After the familiarization trials, each monkey was tested with two novel events, with the order of conditions counterbalanced across subjects. In the ‘depth’ event, the trajectory of the ball and cast shadow was completely novel and symmetrical to that in the habituation event. In the ‘up’ event, the ball motion was identical to that in the familiarization event, but the cast shadow moved horizontally. If a monkey discriminated differences in the three-dimensional motion of the ball based on the trajectory of a cast shadow under the ‘shadow’ condition, it should look longer at the ‘up’ event than at the ‘depth’ event.

Figure 1  Example of familiarization and test stimuli in Experiment 1 (a), and Experiment 2 (b). The solid arrow illustrates the motion trajectory of the ball, and the dashed arrow illustrates that of the cast shadow.
Data coding and analysis

One observer measured the looking time of the monkeys during the familiarization and test events from an off-line video. The observer, who was naive to the order of the two test events, recorded the time spent looking by pressing a key when the infant looked at the event. The looking time for each trial was calculated based on these coded data. To compare the looking times between two events during the test trials, we performed two-tailed paired-comparison t-tests. To control the experimentwise error rates across Experiments 1 and 2, we corrected alpha levels using Bonferroni’s procedure. Another naive experimenter coded the performance of four randomly chosen participants for each experiment. The Pearson correlation between the two observers’ scores was .94 for total looking time from the three events.

Preliminary correlation tests between looking time and age were conducted in familiarization and test trials. The trends toward decreasing looking times between the first and the last two familiarization trials showed no correlation with age (Pearson’s correlation coefficient for Experiment 1: r = -0.13, p = .64; Experiment 2: r = 0.39, p = .70). We also found no systematic trends with respect to the looking times during test trials (Pearson’s correlation coefficient: Experiment 1: r = 0.09, p = .74; Experiment 2: r = 0.19, p = .47).

Based on these results, we pooled the data for all of the monkeys for each experiment.

Results

The looking times for the first two and the last two familiarization trials revealed significantly decreasing trends under both conditions (means of first two trials = 10.74 s (SD = 4.80), means of last two trials = 8.83 s (SD = 4.35), t(15) = 2.27, p = .084).

Figure 2a shows the mean looking time during the test trials in Experiment 1. Macaque infants looked longer at the ‘up’ event than at the ‘depth’ event. The paired comparison t-test showed a significant difference in looking times between the ‘up’ and ‘depth’ events (t (15) = 3.449, p = .007, two-tailed). These results suggest that macaque infants discriminated between the motion trajectories of objects based on the motion of cast shadows. Furthermore, the same analyses for looking times of macaque infants aged 12 to 24 weeks revealed a significant difference in the looking times in response to the up and depth events (t(12) = 3.27, p = .0068, two-tailed). It suggests that the findings in Experiment 1 are directly comparable to those of macaque infants of the same age in Experiment 2.

Experiment 2

In Experiment 1, macaque infants discriminated between two test events based on moving shadows. However, it is possible that the infants preferred the ‘up’ event just because it included two-dimensional motion in which two ‘objects’ were approaching and moving away. Experiment 2 examined whether the discrimination observed in Experiment 1 was based on the three-dimensional motion of objects. The macaque infants habituated to and were tested with events in which the spatial relationship between the ball and shadow was reversed from that used in Experiment 1. These events never induce the impression of depth among human adults and infants (Imura et al., 2006b). If macaque infants responded to three-dimensional motion and not to two-dimensional motion, we would expect that they would look at both test events equally.
Stimuli

Figure 1b shows examples of the stimuli used in Experiment 2, which were identical to those used in Experiment 1, except for the cast shadow above the ball. In the ‘no-depth’ event, the cast shadow and the ball moved diagonally, with the shadow above the ball. In the ‘no-up’ event, the cast shadow trajectory was horizontal, whereas the ball moved diagonally. These events never produced a depth impression for adult humans, as the spatial relationship between the cast shadow and the object was unnatural. The two different objects seemed to move independently.

Procedure

The procedure used in this experiment was identical to that used in Experiment 1. After each monkey infant was familiarized with a ‘no-depth’ event, each monkey was tested with a novel ‘no-depth’ event and a ‘no-up’ event.

Data coding and analysis

The data coding and analysis were the same as those used in Experiment 1. The Pearson correlation between the two observers’ scores was .94.

Results

The looking times in the first and last two familiarization trials showed significantly decreasing trends under both conditions (mean of first two trials = 13.45 s (SD = 4.82), mean of last two trials = 9.10 s (SD = 4.68), t(15) = 5.69, p = .0002).

Figure 2b shows the mean duration of looking during the test trials in Experiment 2. Paired-comparison t-tests revealed no significant difference in looking times between ‘no-up’ and ‘no-depth’ events (t(15) = 0.60, p = .555). These findings suggest that macaque infants did not discriminate a no-up event from a no-depth event, although the difference between habituation and test events was identical to that in Experiment 1 except that the cast shadows were above the ball.

Discussion

We examined the sensitivity of infant macaques aged 7 to 24 weeks to moving shadows cast by objects to clarify the early development of the perception of spatial layout from cast shadows. The findings of Experiment 1 suggest that infant macaques discriminate an ‘up’ event from a ‘depth’ event. In Experiment 2, the macaques showed no evidence of discrimination between such events when a shadow appeared above a ball. These findings suggest that infant macaques discriminated between test events based not on the differences in two-dimensional feature such as two balls’ approaching and separating (in the up and no-up events) but rather based on the differences in a three-dimensional feature. The findings of Experiment 1 in this study are consistent with those of previous studies in 6-month-old human infants (Imura et al., 2006b), 5-month-old macaque infants (Imura et al., 2006a), and an adult chimpanzee (Imura et al., 2006a). The findings of Experiment 2 provide additional evidence that the ability to perceive depth from a moving cast shadow is shared by the primate species.

Furthermore, the infant macaques looked for a long time at an event when a cast shadow made an object appear to float up and down in space with no support. It is possible that an understanding of gravity and the need for support may have contributed to the preference for the up event. Previous studies have provided evidence that nonhuman primates possess knowledge about physical phenomena such as support relations between objects (chimpanzees (Pan troglodytes): Cacchione & Krist, 2004; Murai, Tanaka & Sakagami, 2011; Tomonaga, Imura, Mizuno & Tanaka, 2007; rhesus macaques (Macaca mulatta): Hauser & Carey, 1998; Munakata et al., 2000). Previous developmental studies in human infants using the expectancy-violation paradigm have shown that initial concepts of support are acquired at 3 months of age (Baillargeon, Kotovsky & Needham, 1995; Baillargeon, 2002). In contrast, Van de Walle, Rubenstein and Spelke (1998) provided evidence that 5- and 8-month-old human infants tended to overgeneralize their knowledge of object motion to shadow motion. For example, infants were familiarized with a stationary event including a ball and a shadow and then tested with two displays. One display was of the ‘natural event’ in which the ball and the shadow moved conjointly, and the other was of the ‘unnatural event’ in which the ball moved while the shadow remained at rest. Adults understand that an object moves with its shadow despite the absence of contact. However, human infants looked longer at the motion of the natural shadow, which violated the ‘contact principle’ that applies to relationships between the movements of solid objects. These findings suggest that knowledge of shadows remains immature in 5- and 8-month-old human infants and may be acquired later than knowledge of objects. Indeed, it would have been surprising if the infant macaques in our study had shown sensitivity not only to spatial arrangements but also to support relations between objects.
Finally, the current findings suggest that infant macaques may process shadow information based on the same assumption that humans use concerning a light source. In humans, the assumptions that a single light source shines from above and that it is static make discriminating three-dimensional shapes from shading (e.g. Kleffner & Ramachandran 1992) and perceiving the spatial arrangement of objects from shadows (Mamaisian et al., 1998) much quicker and easier. Our previous human study also suggested that these assumptions may assist 6- and 7-month-old infants to determine the spatial layout of objects (Imura et al., 2006b). However, little evidence has been adduced to suggest that other animals may process shading and shadow information based on assumptions about a light source similar to those held by humans (Hess, 1950, 1961; Hershberger, 1970; Tomonaga, 1998). Our findings here support the position that light-source assumptions are shared by macaques and humans.

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