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PAPER

Predictive tracking over occlusions by 4-month-old infants

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Abstract

Two experiments investigated how 16–20-week-old infants visually tracked an object that oscillated on a horizontal trajectory with a centrally placed occluder. To determine the principles underlying infants' tendency to shift gaze to the exiting side before the object arrives, occluder width, oscillation frequency, and motion amplitude were manipulated resulting in occlusion durations between 0.20 and 1.66 s. Through these manipulations, we were able to distinguish between several possible modes of behavior underlying 'predictive' actions at occluders. Four such modes were tested. First, if passage-of-time *determines when saccades are made, the tendency to shift gaze over the occluder is expected to be a function of time since disappearance. Second, if* visual salience *of the exiting occluder edge determines when saccades are made, occluder width would determine the pre-reappearance gaze shifts but not oscillation frequency, amplitude, or velocity. Third, if* memory *of the duration of the previous occlusion determines when the subjects shift gaze over the occluder, it is expected that the gaze will shift after the same latency at the next occlusion irrespective of whether occlusion duration is changed or not. Finally, if infants base their pre-reapperance gaze shifts on their ability to represent object motion (*cognitive mode*), it is expected that the latency of the gaze shifts over the occluder is scaled to occlusion duration. Eye and head movements as well as object motion were measured at 240 Hz. In 49% of the passages, the infants shifted gaze to the opposite side of the occluder before the object arrived there. The tendency to make such gaze shifts could not be explained by the passage of time since disappearance. Neither could it be fully explained in terms of visual information present during occlusion, i.e. occluder width. On the contrary, it was found that the latency of the pre-reappearance gaze shifts was determined by the time of object reappearance and that it was a function of all three factors manipulated. The results suggest that object velocity is represented during occlusion and that infants track the object behind the occluder in their 'mind's eye'.*

Introduction

The observation of objects that move in a cluttered environment is frequently interrupted as they pass behind other objects. To keep track of them requires that their motion is somehow represented over such periods of non-visibility. The present article asks whether 4-month-old infants have this ability, and if so, how it is accomplished.

Piaget (1954) was one of the first to reflect on the problem of early object representation and he hypothesized that it would start to evolve from about 4 months of age. Later research supports and expands Piaget's assumptions. One frequently used paradigm has studied looking at displays where the spatio-temporal continuity has been violated with the assumption that infants will look longer at such displays. These experiments strongly suggest that 4-month-olds and maybe even younger infants maintain some kind of representation of the motion of an occluded object. For instance, Baillargeon and associates (Baillargeon & Graber, 1987; Baillargeon & deVos, 1991; Aguiar & Baillargeon, 2002) habituated infants to a tall and a short rabbit moving behind a solid screen. This screen was then replaced by one with a gap in the top. The tall rabbit should have appeared in the gap but did not. Infants from 2.5 months of age looked longer at the tall rabbit event suggesting that they had detected a discrepancy between the expected and the actual event in that display. These studies indicate that infants are somehow aware of the motion of a temporary occluded moving object but not how.

Visual tracking studies are also informative about infants' developing ability to represent object motion. The eyes are not subject to drift under normal circumstances, not even in young infants, and smooth gradual eye movements only appear when a moving object is pursued (von Hofsten & Rosander, 1997; Rosander & von Hofsten, 2002). Tracking is interrupted when the motion is stopped.

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Muller and Aslin (1978) found that 2-, 4-, and 6-month-old infants stopped tracking when an object that moved on a horizontal path stopped just in front of an occluder. When the pursued object is occluded, the smooth eye movements get effectively interrupted (Rosander & von Hofsten, 2004). This is also valid for visual tracking in adults (Lisberger, Morris & Tyschen, 1987; Kowler, 1990). To continue tracking when the object reappears, subjects shift gaze saccadicly across the occluder. As smooth pursuit and saccades are radically different kinds of eye movements requiring different motor programs, the saccades cannot be accounted for by a continuation of the smooth pursuit (see e.g. Leigh & Zee, 1999). If they are elicited before the object reappears they have to be guided by some kind of anticipation of the object's continuing motion. In the past, only a few studies have measured infants' eye movements to determine at what age such anticipations appear. Van der Meer, van der Weel and Lee (1994) found that 5-month-old infants observing a temporarily occluded, linearly moving object looked towards the reappearance side in an anticipatory way. In their study the object was occluded during 0.3–0.6 s.

Two recent studies have addressed the question of when such ability appears and the role of learning in its establishment (Johnson, Amso & Slemmer, 2003; Rosander & von Hofsten, 2004). Rosander and von Hofsten (2004) examined the tracking over occlusion in 7-, 9-, 12-, 17- and 21-week-old infants. The infants viewed an object oscillating on a horizontal track that either had an occluder placed at its center where the object disappeared for 0.3 s, or one at one of the trajectory end points where it became occluded for 0.6 s. In the former case, the object reappeared on the opposite side of the occluder and in the latter case on the same side. The level of performance in the central occluder condition improved rapidly between the ages studied and several of the 17-week-old infants moved gaze to the reappearing side of the occluder from the first passage in a trial. When the object was occluded at the endpoint of the trajectory, there was an increasing tendency with age to shift gaze over the occluder. These results indicate that 4–5-month-old infants have anticipations of where and when an occluded moving object will reappear when moving on a linear trajectory. All the infants in Rosander and von Hofsten (2004) experienced two trials with unoccluded motion before the occlusion trials began.

Johnson, Amso and Slemmer (2003) examined the eye tracking of 4- and 6-month-old infants who viewed an object that oscillated back and forth behind an occluder. Some of the infants experienced an initial period of unoccluded motion and others received no experience of such a stimulus. Johnson *et al*. (2003) reported that 4-month-old infants, who saw the unoccluded motion, showed anticipatory eye movements over the occluder, but not the infants who did not see the unoccluded motion.

One problem with studies of anticipatory gaze shifts at temporary occlusions is that anticipations do not occur on every trial. In Rosander and von Hofsten (2004) the 4-month-old infants moved gaze over the occluder ahead of time in 47% of the trials and in Johnson *et al.* (2003) it happened in 29–46% depending on condition and age. Is it possible that infants stop tracking at the occluder edge when the object disappears, wait there for a while and then shift gaze anyway? Some of those spontaneous gaze shifts might arrive to the other side of the occluder before the object reappears there. Thus, they appear to be predictive although they are not.

In experiments with only one occlusion duration, it is not possible to determine whether the saccades arriving at the reappearance edge before the object are truly predictive or just appear to be so. In order to determine the principles underlying infants' tendency to shift gaze to the reappearing side of an occluder before the object arrives there, a different set of studies is required where occlusion duration is systematically varied. Such manipulations are able to distinguish between several modes of behavior underlying 'predictive' actions at occluders. It is the gaze shifts that arrive before the reappearing object that are informative in this respect. They are here called *pre-reappearance gaze shifts* (*PRGS*). Those that arrive later need to be excluded from this analysis because they may have been elicited by the sight of the reappearing object.

First, let us entertain the possibility that infants stop their gaze at the occluder edge when the object disappears, linger a little there and then shift attention to the other occluder edge. If *passage-of-time* determines when saccades are made, the tendency to shift gaze over the occluder is expected to be a function of time since disappearance. An implication of this mode is that the longer the occlusion duration, the higher the number of these saccades will be counted as predictive purely because the average mean is based on a larger range of values.

Second, it is possible that subjects move gaze over the occluder before the object reappears because of the *visual salience* of the exiting occluder edge. The greater the visual salience of a stimulus, the earlier will gaze be shifted to this stimulus. It is expected that visual salience is greater for high contrast than for low contrast stimuli. As contrast sensitivity decreases with increasing eccentricity in the visual field, it is possible that PRGS in the presence of a wide occluder will have a longer latency, not because the subject expects the object to reappear later, but because the visual salience of the exiting occluder edge is then lower. Thus, varying just the width of the occluder will not distinguish the visual salience hypothesis from a more cognitive one. Another problem with a salient occluder is that it may attract attention to such a degree that tracking is interrupted altogether and instead the child fixates the salient occluder (Muller & Aslin, 1978). To avoid effects of visual salience of the occluder it is therefore of utmost importance to use occluders that deviate from the background as little as possible. In the present experiments both the occluder and the background had the same white color.

If the salience of the exiting occluder edge varies depending on how far into the peripheral visual field it is presented, it is expected that this would also be valid for any salient visual stimulus. The color and luminance of the reappearing object deviated quite distinctly from the background, and saccadic latency to it should therefore be related to its eccentricity in the visual field. If it is, the visual salience hypothesis would be strengthened. If, on the other hand, non-visual factors such as oscillation frequency and object velocity affect the latency of the PRGS, it means that the attractiveness of the exiting occluder edge is, at least, moderated by these other variables. Thus the visual salience hypothesis cannot be properly tested unless both occluder width and object velocity are manipulated. This was done in the present study by varying oscillation frequency and motion amplitude.

Another possible explanation of why PRGS are performed is that it may just be a contingency effect without any anchoring in continuous physical events. The subjects could just remember the duration of the previous occlusion and expect the object to be absent for the same period at the next occlusion (the *memory hypothesis*). Haith and associates (Canfield & Haith, 1991; Haith, 1994; Haith, Hazan & Goodman, 1988) investigated infants' anticipatory saccades to when and where the next picture in a predictable left–right sequence was going to be shown. Saccades arriving at the position of the next picture within 200 ms of its presentation were considered anticipatory. From about 3 months of age, such anticipations were found to be significantly more frequent for a predictable than for an unpredictable sequence (Canfield & Haith, 1991). As the pictures were distinctly different, it is doubtful whether they were perceived as one continuous event. In addition, the left–right sequence of pictures followed an arbitrary rule rather than a physical principle. In spite of this, temporal regularities were rapidly learnt, suggesting that infants are sensitive to spatio-temporal contingencies and use them to predict what is going to happen next. Whether infants' gaze shifts over the occluder are determined in this way cannot be tested with a single duration of occlusion. If several durations are included in the experiment, however, it is expected that the subjects will systematically misjudge the duration every time it is changed. When duration is made shorter, the subjects will overestimate it and consequently shift gaze too late. If the duration is made longer, they will underestimate duration and shift gaze over the occluder too early.

Finally, the PRGS might be based on information about occlusion duration derived from oscillation frequency and amplitude, object velocity, and occluder width. This will be called the *cognitive hypothesis*. Object velocity is linearly related to oscillation frequency and motion amplitude. If frequency or amplitude is doubled, so is velocity. Occlusion duration is obtained by dividing occluder width by object velocity. Instead of having explicit knowledge of this relationship, infants could simply maintain a representation of the object motion while the object is occluded and shift gaze to the other side of the occluder when the conceived object is about to arrive there. In support of this alternative are the findings that object velocity is represented in the frontal eye field (FEF) of rhesus monkeys during the occlusion of a moving object (Barborica & Ferrera, 2003). It is only by simultaneously varying object velocity and occluder width that such a strategy can be revealed.

In the past, there were very few developmental studies that varied both object velocity and occluder width. Muller and Aslin (1978) showed 6-month-old infants a sphere (8 cm diameter) that moved at either 10 or 20 cm/s on a horizontal trajectory and disappeared temporarily behind a 20- or 40-cm wide occluder. They had no opportunity to measure exact timing of the gaze shifts over the occluder, but found that the instances of tracking interruptions larger than 1 s increased dramatically when the complete occlusion duration increased from 0.6 to 1.2 s (i.e. partial occlusion increased from 1 to 2 s). This indicates that the length of the tracking interruptions was related to occlusion duration. Gredebäck, von Hofsten and Boudreau (2002) studied 9-month-old infants who tracked an object moving on a circular trajectory. The results showed that the infants' performance was determined by occlusion duration, that is, by the joint relationship between object velocity and occluder width. For a range of occlusion durations from 0.25 to 5 s, gaze was shifted over the occluder at around 2/3 of the occlusion time. Similar results were obtained by Gredebäck and von Hofsten (2004) with 6-month-old infants and older. In that study, however, occluder width was not varied and the joint effect of these two variables could therefore not be evaluated. The purpose of the present study was to determine how 4-month-old infants behave in a situation with temporarily occluded objects when occluder width and object velocity are simultaneously manipulated.

Two experiments were performed in which infants were presented with objects oscillating on a horizontal trajectory. We created a set of occlusion durations by systematic manipulation of oscillation frequency, occluder width (Experiments 1 and 2), and motion amplitude (Experiment 2). In order to minimize the effect of visual salience of the exiting occluder edge, the occluder had the same white color as the background (the inside of the cylinder). Three oscillation frequencies and three occluders were used in Experiment 1, creating seven different occlusion durations between 0.22 and 0.61 s. In Experiment 2, oscillation amplitude in addition to oscillation frequency and occluder width was varied, creating eight different occlusion durations between 0.2 and 1.66 s. The object velocities used ranged from 15 to 30°/s in Experiment 1 and from 8 to 30°/s in Experiment 2. Earlier research has shown that infants track objects optimally within this interval (von Hofsten & Rosander, 1996; Mareschal, Harris & Plunkett, 1997). The infants were between 16 and 20 weeks of age. Our earlier studies indicate that PRGS emerge during this age period (Rosander & von Hofsten, 2004).

Figure 1 *The experimental situation. The inside of the cylinder and the occluders had matched white colors. The borders of the slit in which the object moved were also white. The slit was 60 cm long and had a movable object placed in it. Note the EOG preamplifier and the reflective markers on the infant's head and the reflective marker on the 'happy-face' object. The object holder visible through the slit in the picture was not visible from the infant's point of view.*

General method

Subjects

Twenty-three 16–20-week-old infants participated in the study. They were all healthy and born within 2 weeks of the expected date. The study was in accordance with the ethical standards specified in the 1964 Declaration of Helsinki.

Apparatus

The experiments were performed with the same apparatus as earlier described in detail (von Hofsten & Rosander, 1996, 1997; Rosander & von Hofsten, 2002, 2004). The infants were placed in a specially designed infant chair positioned at the center of a cylinder, 1 m in diameter and 1 m high. This cylinder shielded off all potentially distracting stimuli around the infant. The chair was positioned in the cylinder in such a way that its axis corresponded approximately to the body axis of the infant. His or her head was lightly supported with pads. In the experiments the setup was comfortably inclined at an angle of 40°. Figure 1 shows a subject in the cylinder.

Stimuli

In front of the infant the cylinder had a narrow horizontal slit where the movable object was placed. A circular orange colored 'happy' face was used as the stimulus to be tracked. It was 5 cm in diameter corresponding to a visual angle of approximately 7°, with black eyes, a black smiling mouth, and a black wide contour around it. In the middle of the schematic face, at the position of the nose, a mini video camera (Panasonic WV-KS152) was placed. Its black front had a diameter of 15 mm or 2.2° of visual angle. Below the face, a red LED was placed. It could be blinked to attract the infant's gaze. The motion of the object was controlled by a function generator (Hung Chang, model 8205A). In the experimental trials, the 'happy face' object oscillated in front of the infant according to a triangular function (i.e. constant velocity that abruptly reversed direction at the endpoints of the trajectory). To minimize visual salience of the non-moving parts of the setup, the moving object was occluded by a rectangular piece of cardboard at the center of its trajectory with the same white color as the inner side of the cylinder (see Figure 1). The edges of the slit in which the object moved were also white. Finally, from the infant's point of view, the background behind the slit was the white ceiling of the experimental room. Different sized occluders were used in the different conditions. They were placed over the motion-trajectory at a distance of 2 cm from the cylinder wall to which it was attached by means of Velcro.

Measurements

Eye movements

Electrooculogram (EOG) was used to measure eye movements. The electrodes were of miniature type (Beckman) and had been soaked in physiological saline for at least 30 minutes before use. They were then filled with conductive electrode cream (Synapse, Med-Tek Corp.) and attached to the outer canthi of each eye. The ground electrode, a standard EEG child electrode, was attached to the ear lobe. The signals from the two electrodes were fed via 10-cm long cables into a preamplifier attached to the head of the infant (see Figure 1). The preamplifier was introduced to eliminate the impedance problems of traditional EOG measurements associated with long wires (Westling, 1992). The amplifier was powered by a battery and completely isolated from the rest of the equipment for safety reasons. The signal was relayed to the outer system by means of optical switches. The EOG signal was low-pass filtered at 20 Hz by means of a third-order Butterworth filter. The position accuracy of the filtered EOG data was $\pm 0.4°$ visual angle or better. This introduced a constant time delay of 0.015 s that was compensated for in the data analysis. As EOG measurements are based on the difference in potential level between the electrodes, it is subject to a slow drift over time. This drift was eliminated before analysis. The drift, however, could cause the amplified potential to reach saturation values in the recording window. Therefore, the base level of EOG was reset between trials. This does not affect the calibration of the EOG or distort the data in any other way (cf. Juhola, 1987). For more detailed information about the EOG setup, see Rosander and von Hofsten (2000, 2002, 2004) and von Hofsten and Rosander (1996, 1997).

Head and object motions

A motion analyzing system, 'Proreflex (Qualisys)', was used to measure the movements in 3-D space. This system uses high-speed cameras that register the position of passive reflective markers illuminated by infrared light positioned around the lens of each camera. In the present setup, three cameras were used, each of which had an infrared light source. Three markers were placed on the head to make it possible to record its translational as well as rotational movements and one marker was placed at the center of the moving object. The position accuracy of each measured marker was 0.5 mm. The markers had a diameter of 4 mm and can be seen in Figure 1. The EOG and the head movement data were recorded in synchrony at 240 Hz.

Procedure

Two experiments with identical procedures were carried out. First, the accompanying parent was informed about the experiment and signed the consent form. Then it was assured that the infant had been recently fed and was in an alert state. The video camera at the center of the stimulus monitored the face of the infant so that the parent and the experimenter could observe the infant during the experiment. As the camera was always directed towards the face of the infant, it gave excellent records of whether the infant attended to the object or not in between occlusions. Each experimental session was video-recorded with this device. If the infant fussed or fell asleep during a trial, the experiment was interrupted temporarily, after which the last trial was repeated and the experiment continued. Such interruptions were uncommon. Before each trial the stimulus parameters were set to the appropriate values. This included changing the occluder and setting the amplitude and frequency of the oscillations to be used on the function generator. The duration of each trial was 25 s and the whole experimental session had a duration of around 7 minutes.

Calibration of EOG

This procedure has been described earlier (Rosander & von Hofsten, 2002, 2004; von Hofsten & Rosander, 1996). The experimenter moved the object swiftly from one extreme position to the middle of the path, and then to the extreme distance on the other side (Finocchio, Preston & Fuchs, 1990). Each position was defined and measured by the motion analyzing system (Qualisys). Each stop lasted 1–2 s and during that time the experimenter flashed the red LED placed below the face. This attracted the infant's gaze. The flashing of the LED also made it possible to determine if the infant fixated the object (Rosander & von Hofsten, 2002). During the 25-s period of calibration, the experimenter covered about four cycles of motion corresponding to 16 fixation stops.

Data analysis

The video records were inspected to determine whether the subjects attended to the object both before and after the occlusion of the object at each passage. Gaze shifts over the occluder launched earlier than 0.3 s before total occlusion or later than 1 s after the object had reappeared were regarded as unrelated to the occlusion event and were therefore not included in the analysis. They constituted merely 2.5% of the total number of gaze shifts. Data were analyzed with programs written in the MATLAB environment. The statistical analysis was performed in SPSS. A specific trial was considered to have started when the infant first directed its gaze toward the object. Thus, if the infant looked somewhere else after the object had started to move and therefore missed one occluder passage, this passage was not included in the analysis of the trial. Instead the second passage was considered as the first. The gaze direction was calculated as a sum of head and eye direction, where the head direction was calculated from the relative positions of the three markers on the infant's head.

Calculation of gaze direction

All calculations were performed in the plane of rotation (xz-plane) of the cylinder which had its origin at the axis of rotation (the y-axis) (see Figure 2). The position of the object on the cylinder was transferred to angular coordinates. We can find the time dependent angles of the head (α_{head}) and the object (β_{object}) using Equations 1 and 2:

$$\alpha_{head} = \frac{1}{2}\arctan\left\{\left[X_A - \frac{1}{2}(X_C + X_B)\right]\Big/\left[Z_A - \frac{1}{2}(Z_C + Z_B)\right]\right\} + \frac{1}{2}\arctan\left\{\left[Z_B - Z_C\right]/\left[X_C - X_B\right]\right\} \quad (1)$$

and

$$\beta_{object} = \arctan\left\{\left[X_D - \frac{1}{2}(X_C + X_B)\right]\Big/\left[Z_D - \frac{1}{2}(Z_C + Z_B)\right]\right\} \quad (2)$$

where X and Z are time dependent coordinates of the markers A, B, C and D (see Figure 2).

The calibration factor of the EOG in mV/deg was obtained by dividing the difference between the values of the EOG signal at different calibration positions with the difference in degrees between head and object at those positions. A linear relation was then assumed between the EOG signal and the radial displacement according to Davis and Shackel (1960), Finocchio *et al.* (1990), and von Hofsten and Rosander (1996). Eye movements were calibrated in the same angular reference system as the head, i.e. in terms of how much head movement would be required to shift gaze an equal amount. Amplitudes of eye movements were regarded as proportional to the corresponding head movements. If the eyes are displaced 6 cm relative to the rotation axis of the head (this value was estimated from measurements on a few of the participating infants) and the object is positioned 44–46 cm from the head axis, as was the case in the present experiment, the exact relationship between head and eye angles deviates from proportionality with less than 0.5% within the interval used (±24°). The gaze was estimated as the sum of eye and head positions. Angular velocities were estimated as the difference between consecutive co-ordinates. The velocities of the eyes, head, and gaze were routinely calculated in this way.

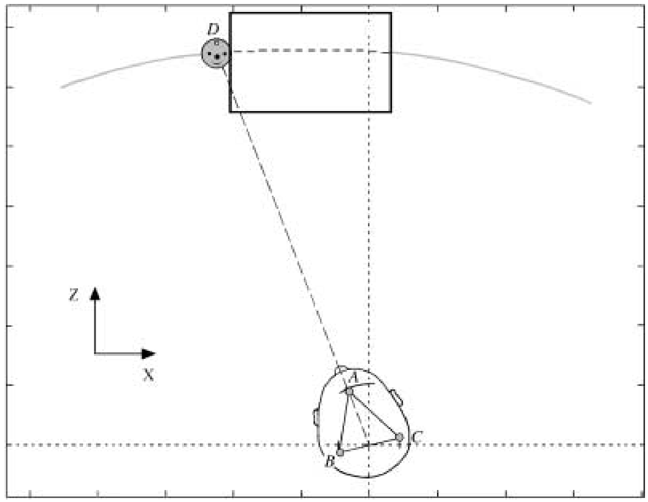

Figure 2 *Illustration of how the positions of the head (markers A, B, C) and object (marker D) were calculated, referring to Figure 1 and Equations 1 and 2.*

Analysis of visual tracking over the occluder

First, the occluder boundaries were identified from the object motion record. This happened when the reflective marker on the object became occluded and dis-occluded. Then the interval where the object was completely occluded was identified. As the marker on the object was placed at its center, the position in space-time of the full occlusions corresponded to a marker position half an object width inside the occluder (see Figure 3). Gaze was considered to have arrived at the other side of the occluder when it was within 2° of its opposite boundary. The boundary will then be within the foveal region of the infants' visual field (Yudelis & Hendrickson, 1986). The time when gaze arrived at the exiting occluder edge relative to the time when the object started to reappear was defined as the *lag* or *lead* of the gaze shift. The time from the total disappearance of the object to the time when gaze arrived at the opposite boundary was defined as the gaze shift *latency*. When the lag was less than 0.2 s the gaze shift was defined as a pre-reappearance gaze shift (PRGS), as this is the minimum time required to program a saccade to an unexpected event in adults (Engel, Anderson & Soechting, 1999). As PRGS is a

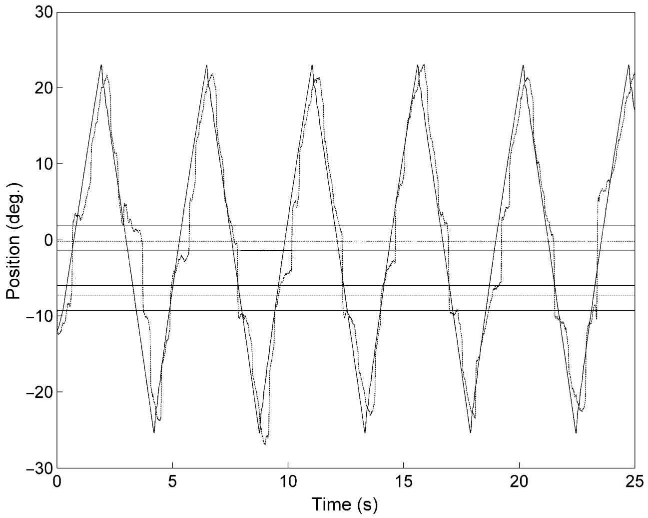

Figure 3 *An example of a trial from Experiment 1 showing gaze tracking plotted together with the object motion. The outer horizontal lines in the figure signify the occluder boundaries. As a centrally placed marker measured the position of the object, only half the object was occluded when the marker passed the occluder boundaries. Therefore the inner horizontal lines are needed to signify the position of the object marker when the object was totally occluded. These are thus positioned half the object width inside the occluder. The horizontal lines in between the inner and outer ones signify the 2° tolerance outside which gaze was considered to have arrived at the other side of the occluder.*

different mode of responding than reacting to the seen object after it has reappeared, separate analyses were conducted on each of these two subsets of data.

Data were evaluated with correlation analysis and general linear model repeated measurement ANOVAS. To control for sphericity the Geisser-Greenhouse correction was used when needed. Individual trial subject means were then used as input.

Experiment 1

The purpose of Experiment 1 was to investigate how 3.5- to 4.5-month-old infants are able to take occlusion duration into account when making *pre-reappearance gaze shifts* (PRGS). Duration was varied by orthogonal manipulation of Oscillation Frequency and Occluder Width. This made it also possible to evaluate each of the four possible strategies outlined in the introduction: the passage-of-time, visual salience, memory mode, and the cognitive mode. Apart from being a determining factor of occlusion duration, object velocity might be of importance for another reason. A higher velocity gives rise to more rapid accretion and deletion of the visible object at the occluder edges. Gradual accretion and deletion has been shown to be of importance for being able to perceive continued motion behind an occluder (Scholl & Pylyshyn, 1999; Kaufman, Csibra & Johnson, 2005). It is therefore possible that the strength and clarity of the represented motion improves when the deletion is made more gradual.

Although earlier research (Johnson *et al.*, 2003; Rosander & von Hofsten, 2004) showed unoccluded motion at the beginning of the experiment, this was not done in the present experiment. Piloting indicated that presenting a trial with unoccluded motion at the beginning of the experiment was not necessary for attaining predictive tracking over occlusion in 4-month-old infants. In experimental situations, young infants tend to get rapidly bored and therefore we wanted to keep the experiment as short as possible. It is important to point out that the calibration procedure does not correspond to a learning trial with unoccluded motion. Instead of being moved with constant velocity as in the experimental trials, the object was moved rapidly between positions where it stopped for 1–2 s. For instance, it stopped at the center of the trajectory. If the infants learned the temporal pattern of this procedure, they would expect the object to stop behind the occluder. However, although the calibration procedure did not provide a learning opportunity for the temporal properties of the oscillatory motion, it made the infants familiar with the horizontal trajectory used.

Method

Experiment 1 included five girls and six boys. Their age varied from 15:6 to 19:5 weeks with a mean age of 18 weeks. The amplitude of the oscillating motion was always the same (24° visual angle). Occluder Width was 8.2, 11 or 14 cm corresponding to 11.6°, 15.5° and 20° of visual angle at a distance of 45 cm from the eyes. Oscillation Frequency was 0.15, 0.21 or 0.30 Hz. Before each trial these values were adjusted by hand on the function generator and occlusion durations could therefore deviate somewhat at a given condition for the different subjects (±8%). The resulting angular velocities of the object were 15°/s, 21.4°/s and 30°/s at 45 cm viewing distance.

Seven combinations of Oscillation Frequency and Occluder Width were included in the experiment instead of the possible nine. The largest occluder was not combined with the slowest velocity and the smallest occluder was not combined with the fastest velocity. The decision to exclude those two conditions was made in order to reduce the number of conditions. It was judged that nine

Table 1 *Average occlusion duration, number of presented occluder passages, number of passages analyzed, number of and percentage of pre-reappearance gaze shifts over the occluder, and mean latency of these gaze shifts for the different conditions in Experiment 1*

Velocity Occluder width		15°/s 0.15 Hz	21.4°/s 0.21 Hz	30°/s 0.30 Hz
11.6°	Occlusion duration (s)	0.31	0.22	
	Passages	64	110	–
	Passages analyzed	54	89	
	Pre-reappearance gaze shifts	27	45	
	Proportion (%)	50	50.6	
	Mean latency (s)	0.26	0.19	
15.5°	Occlusion duration (s)	0.57	0.39	0.28
	Passages	72	85	128
	Passages analyzed	55	67	115
	Pre-reappearance gaze shifts	30	42	50
	Proportion (%)	54.6	62.7	43.5
	Mean latency (s)	0.41	0.29	0.26
20°	Occlusion duration (s)	–	0.61	0.43
	Passages		100	113
	Passages analyzed		83	96
	Pre-reappearance gaze shifts		31	40
	Proportion (%)		37.3	41.7
	Mean latency (s)		0.49	0.35

conditions were going to make the infants too tired and deteriorate their performance. The measured duration of total occlusion was, on average, 0.22, 0.28, 0.31, 0.39, 0.43, 0.56 and 0.61 s. These figures are given in Table 1. The conditions were presented in randomized order. The slowest Oscillation Frequency (0.15 Hz) included 7–8 occluder events per trial, the middle Oscillation Frequency (0.22 Hz) 11–12 occluder events, and the fastest Oscillation Frequency (0.30 Hz) 14–15 occluder events.

Results

One boy did not complete the experiment because of inattention, leaving 10 subjects to be analyzed (five girls and five boys). Seven of the 70 individual trials from these subjects were also excluded for the same reason (four subjects missed one trial and one missed three trials). In the remaining trials, the infants attended to the object both before and after the occlusion in 559 passages (83%), while at 113 passages they were distracted and looked away. In 294 cases, gaze arrived at the reappearance side of the occluder more than 0.2 s after the object had started to reappear and those were considered reactive saccades. The reactive saccades arrived at the reappearance side on average 0.45 s (SD = 0.16) after the object started to appear.

In 265 cases (47.4%) the gaze shifts over the occluder arrived at the opposite side less than 0.2 s after the object arrived there (PRGS). In 234 of these passages (88%) the gaze stopped at the occluder edge until making saccadic shift(s) over to the other side. In the 31 remaining cases (12%), the subject made a gaze shift over to the other side of the occluder and then returned to the original edge where gaze stayed until making a final shift over the occluder. In those cases, it was the second gaze shift that was analyzed. Table 1 shows the average duration of occlusion, number of presented occluder passages, number of passages analyzed, number and percentage of PRGS, and mean latency of these gaze shifts in Experiment 1.

Determinants of gaze shifts over the occluder

The passage-of-time hypothesis

Infants did not show an overall greater tendency to shift gaze over the occluder during occlusion with the passage of time. There was no correlation between occlusion duration and proportion of PRGS for individual subjects ($r = -.02$, $n = 63$). Neither were there significant correlations between proportion of PRGS and Occluder Width ($r = -.192$, $n = 27$) for the middle frequency or between proportion of PRGS and Oscillation Frequency for the middle Occluder Width ($r = .156$, $n = 27$).

The memory hypothesis

To test whether the saccade latencies were based on the remembered duration of the previous occlusion, we compared the performance on the last occlusion in one condition with the first occlusion in the next condition. If infants follow this rule, they should overestimate the occlusion duration and arrive too late every time the duration is made shorter, and underestimate the duration and arrive too early every time the duration is made longer. When the duration of occlusion increased between conditions there were 12 cases of PRGS on the first passage and 14 cases of post-reappearance gaze shifts. When the duration of occlusion decreased between the conditions there were 13 cases of PRGS and 15 cases of post-reappearance ones on the first passage. Thus, altogether there were 27 cases in accordance with the carry-over hypothesis and 27 against that hypothesis. On average, gaze arrived 0.22 s after object reappearance at the first passage after occlusion was made longer and 0.21 s after object reappearance on the first passage after occlusion was made shorter.

The visual salience and the cognitive hypotheses

The effects of occluder width and oscillation frequency on PRGS are related to both of these hypotheses. The

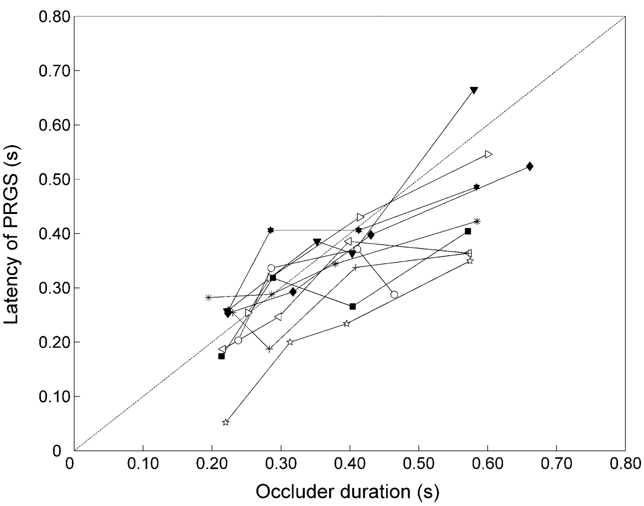

Figure 4 *The relationship between occlusion duration and PRGS for individual subjects in Experiment 1. In the figure the latencies for the following adjacent occlusion durations are averaged (0.28 and 0.31 s, 0.39 and 0.43 s, and 0.57 and 0.61 s) to make the individual curves easier to distinguish. The dashed line shows the hypothetical relationship with saccade latency equal to occlusion duration.*

PRGS were not determined by the time of disappearance but rather by the time of reappearance of the occluded object. This can be seen in Figure 4. The correlation between individual mean latencies for the different conditions and occlusion duration was 0.658 ($p < .001$, $n = 62$). The effects of Occluder Width and Oscillation Frequency were tested in two separate general linear model repeated measurements ANOVAs. Due to the design of the experiment, each variable was tested for the middle condition of the other variable. We tested the effect of Occluder Width on the timing of PRGS for the middle Oscillation Frequency (21°/s). It was found that the effect of Occluder Width was statistically significant ($F(2, 18) = 13.68$, $p < .01$, $\eta^2 = 0.60$). The effect of Oscillation Frequency was tested for the middle Occluder Width (16°). It was found that the effect of Oscillation Frequency was statistically significant ($F(2, 18) = 5.539$, $p < .02$, $\eta^2 = 0.38$).

The reactive saccades

To decide whether visual salience of a stimulus presented at the exiting occluder edge affected the saccade latency to it, a general linear model repeated measurements ANOVA based on the mean individual latencies of post-reappearance saccades for the different Occluder Widths was performed. Only the middle velocity (21°/s) was included in this analysis. It indicated that the eccentricity in the visual field of the exiting occluder edge had no systematic effect on the latency of these saccades ($F(1, 9) < 1.0$). A similar analysis of the effect of velocity for the middle Occluder Width (16°) gave similar non-significant results ($F(1, 9) < 1.0$).

Discussion

The results of Experiment 1 suggested that neither passage-of-time, nor visual salience of the opposite occluder edge, nor memory of the previous occlusion duration determined PRGS. The infants did not show a greater tendency to shift gaze over the occluder before the object reappeared when the occlusion duration was longer. Two kinds of evidence weakened the hypothesis that visual salience of the exiting occluder edge determines the timing of the PRGS. First, it was found that Oscillation Frequency (i.e. Object Velocity) had a significant effect on the timing of PRGS and this effect cannot be derived from visual salience. In addition, the reappearance position in the peripheral visual field of the salient moving object did not have a significant effect on the timing of the post-reappearance saccades. Memory of the previous occlusion neither affected the number of PRGS on the first occlusion in the next trial nor the latency of the saccades to the exiting side of the occluder. In summary, the results of Experiment 1 suggest that the PRGS were determined by the combination of Occluder Width and Object Velocity, i.e. by the Occlusion Duration.

The factorial design of Experiment 1 was incomplete. It was judged that the young infants would not be able to keep optimal attention for more than seven trials. The results, however, proved that failing attention was not a problem with the present experimental setting and design. Therefore a complete factorial design was used in Experiment 2.

Experiment 2

The purpose of Experiment 2 was to expand the range of occlusion durations to confirm the relationships found in Experiment 1 (see Figure 4) and expand them to include faster and slower motions and thus shorter and longer durations. This was made possible by manipulating motion amplitude in addition to oscillation frequency and occluder width. By varying amplitude, object velocity and oscillation frequency could also be disentangled. Furthermore, it is possible that subjects need to view a moving object for a certain distance and/ or time in order to form stable representations that would last over the temporary occlusion. Sekuler, Sekuler and Sekuler (1990) measured response times (RTs) to changes in target motion direction following initial trajectories of varying time and distance. When the initial trajectories were at least 500 ms, the directional uncertainty ceased to affect RTs. Infants may require more time. Two amplitudes were used in Experiment 2. The larger was the same as in Experiment 1 and the smaller was 50% of it. It should be added that the object was never fully visible when the smaller amplitude was used in combination with the larger occluder.

Method

Experiment 2 included six girls and seven boys ranging in age from 17:1 to 20:3 weeks, with a mean age of 18:6 weeks. Altogether eight stimuli were shown to each subject in a factorial design with Occluder Width, Oscillation Frequency, and Motion Amplitude as factors. Occluder Width was either 8.2 or 14 cm, corresponding to 11.6° and 20° of visual angle at 45 cm viewing distance. Oscillation Frequency was 0.15 or 0.30 Hz. Motion Amplitude was 24° or 12.8° at 45 cm viewing distance. Both the oscillation frequency and the motion amplitude were adjusted manually on a function generator before each trial and occlusion durations could therefore deviate somewhat at a given condition for the different subjects (±12%). At the higher amplitude, the velocities were 15 and 30°/s and at the lower amplitude they were 8 and 16°/s on average.

Results

Three boys and one girl provided data in less than six of the eight conditions and were therefore excluded from the data analysis. The data from the remaining nine subjects (five girls and four boys) were analyzed. Three of the 72 individual trials of these subjects were excluded because of fussing or inattention. On the remaining occluder passages, infants attended to the object both before and after the occlusion in 559 cases (77%), while in 167 cases they were distracted and looked away. There were 287 gaze shifts over the occluder that arrived more than 0.2 s after the object had started to reappear.

There were 280 cases of PRGS (50%). In 249 of these passages (89%) the gaze stopped at the occluder until a saccadic shift was made over to the other side. In the 31 remaining cases (11%) the subject made a gaze shift over to the other side of the occluder just after the object disappeared and then returned to the original edge where gaze stayed until making a final shift over the occluder. In these cases, the second shift was analyzed. Table 2 shows the average occlusion duration, number of presented occluder passages, number of passages analyzed, number and percentage of PRGS and mean latency of these gaze shifts for the different conditions in Experiment 2.

Table 2 *Average duration of occlusion, number of presented occluder passages, number of passages analyzed, number and percentage of pre-reappearance gaze shifts over the occluder and mean latency of those gaze shifts for the different conditions in Experiment 2*

		0.15 Hz		0.30 Hz	
Occluder width		8°/s small amp	15°/s large amp	16°/s small amp	30°/s large amp
11.6°	Occlusion duration (s)	0.64	0.35	0.34	0.20
	Passages	64	65	112	126
	Passages analyzed	49	60	88	117
	Pre-reappearance gaze shifts	24	35	55	50
	Proportion (%)	49	58	63	43
	Mean latency (s)	0.35	0.25	0.36	0.27
20°	Occlusion duration (s)	1.66	0.88	0.86	0.48
	Passages	63	58	126	112
	Passages analyzed	38	49	74	84
	Pre-reappearance gaze shifts	22	33	31	30
	Proportion (%)	58	67	42	36
	Mean latency (s)	1.37	0.59	0.77	0.43

Determinants of gaze shifts over the occluder

The *passage-of-time* hypothesis was not supported by Experiment 2 (see Table 2). There was no significant correlation between occlusion duration and proportion of PRGS (r = .116, n = 69, p = .34). The proportion of PRGS was not greater for the longer occlusions than for the shorter ones. The *visual salience* hypothesis stating that the timing of PRGS is determined by Occluder Width was further weakened. Strong effects of Oscillation Frequency and Motion Amplitude on the timing of PRGS were obtained. Furthermore, it was shown that there was an effect of visual salience of the reappearing moving object on the saccadic reaction time to it, but that this effect was small compared to the effect of occluder width on PRGS. The *memory* hypothesis stating that PRGS is determined by the memory of the previous occlusion duration did not receive any support from the results of Experiment 2. The proportion of PRGS at the first occlusion when its duration was increased was not greater than when it was decreased and the timing relative to object reappearance was unaffected. Finally, the *cognitive* hypothesis was strengthened. It was found that the timing of the PRGS was strongly determined by the time of reappearance of the object. Figure 5 shows the relationship between PRGS and

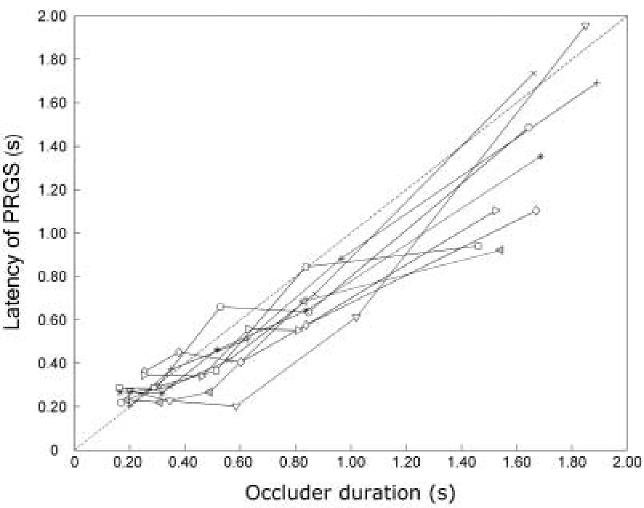

Figure 5 *The relationship between occlusion duration and PRGS for individual subjects in Experiment 2. In the figure the latencies for the following adjacent occlusion durations are averaged (0.34 and 0.35 s, 0.48 and 0.64 s, and 0.86 and 0.88 s) to make the individual curves easier to distinguish. The dashed line shows the hypothetical relationship with saccade latency equal to occlusion duration.*

occlusion duration for individual subjects. The correlation between individual mean latencies for the different conditions and occlusion duration was very high (r = .902, p < .0001, n = 66). The analysis of the relative timing of PRGS (independent of occlusion duration) showed that subjects shifted gaze to the exiting side after, on average, 89% of the occlusion interval. The analysis of the relative timing also showed that PRGS were elicited relatively earlier for the longer than for the shorter occlusions (r = −.35, p < .01, n = 66). The statistical analyses of these effects are further elaborated below.

The passage-of-time hypothesis

A general linear model repeated measurements ANOVA showed that there were no main effects of either Occluder Width, Oscillation Frequency, or Motion Amplitude (all Fs < 1.0). At the high and low frequency, the proportion PRGS was 0.48 and 0.53, respectively. At the high and low amplitude the proportion PRGS was 0.50 and 0.51, respectively. Finally, for the narrow and wide occluder the proportion PRGS was 0.49 and 0.53, respectively. The same analysis showed that there were no interactions except for the one between Oscillation Frequency and Motion Amplitude ($F(1, 8) = 8.01$, $p < .05$, $\eta^2 = 0.50$). At the lower frequency, there was a greater average proportion of PRGS for the higher (0.55) than for the lower amplitude (0.51). At the higher frequency, there was a greater proportion of PRGS for the lower (0.54) than for the higher amplitude (0.42).

The memory hypothesis

The results of Experiment 2 did not support the memory hypothesis. Gaze did not arrive at the exiting side of the occluder systematically later when the duration was made shorter and systematically earlier when it was made longer. When the duration of occlusion increased between conditions there were 18 PRGS on the first passage and 16 post-reappearance gaze shifts. When the duration of occlusion decreased between the conditions there were 13 PRGS and 14 cases of post-reappearance ones on the first passage. Thus, altogether there were 32 cases in accordance with the carry-over hypothesis and 29 against it. On average, gaze arrived 0.21 s after object reappearance when occlusion was made longer and 0.20 s after object reappearance when occlusion was made shorter. This difference was not statistically significant (p = .9).

The visual salience and the cognitive hypotheses

The visual salience and the cognitive hypotheses are both addressed by the analyses of absolute and relative latency of the PRGS. Because the proportions of PRGS for the different conditions were not significantly different, it was possible to compare their timing (with the exception of the interaction between Oscillation Frequency and Motion Amplitude). A general linear model repeated measurements ANOVA was performed on the PRGS latencies. Significant effects were obtained of Occluder Width ($F(1, 8) = 120.2$, $p < .0001$, $\eta^2 = 0.94$), Motion Amplitude ($F(1, 8) = 87.35$, $p < .0001$, $\eta^2 = 0.92$), and Oscillation Frequency ($F(1, 8) = 15.20$, $p < .005$, $\eta^2 = 0.66$). The average latency of PRGS for the narrow and wide occluder was 0.33 s and 0.79 s, respectively. Corresponding figures for the high and low frequency were 0.46 and 0.66, and for the high and low amplitude 0.39 and 0.73. There was a significant interaction between Occluder Width and Oscillation Frequency ($F(1, 8) = 16.35$, $p < .005$, $\eta^2 = 0.67$). While the latency of the PRGS for the wider occluder decreased with oscillation frequency, this was not the case for the narrow occluder. There also an interaction between Motion Amplitude and Occluder Width ($F(1, 6) = 28.28$, $p < .001$, $\eta^2 = 0.78$). The effect of amplitude was greater for the wide than for the narrow occluder. Finally, there was an interaction between Oscillation Frequency and Motion Amplitude ($F(1, 6) = 9.483$, $p < .02$, $\eta^2 = 0.54$). The effect of Oscillation Frequency was smaller for the large amplitude than for the small one.

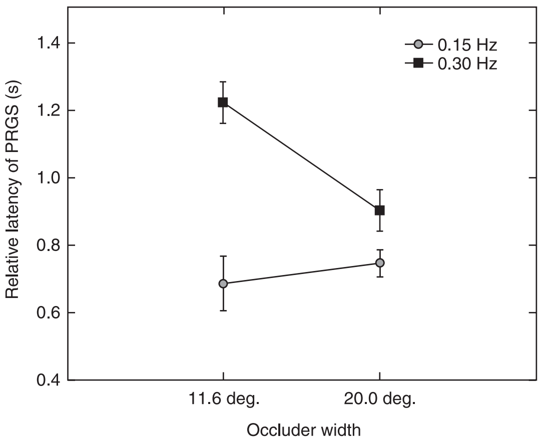

Figure 6 *The relative latency of PRGS for the combinations of occluder width and oscillation frequency.*

To determine how the PRGS were distributed within the occlusion interval, their relative timing was analyzed by dividing PRGS by occlusion duration. This set of analyses shows the relative distribution of PRGS independent of occlusion duration. If the PRGS were completely determined by the reappearance time of the object, the relative latencies would be the same independently of the condition. This was not the case. A general linear model repeated measurements ANOVA tested these relative latencies. Significant effects were obtained for Occluder Width ($F(1, 8) = 9.296$, $p < .02$, $\eta^2 = 0.54$) and Oscillation Frequency ($F(1, 8) = 29.07$, $p < .001$, $\eta^2 = 0.78$), but not for motion amplitude. On average, gaze arrived at the reappearance side of the occluder after 0.96 of the occlusion duration for the narrow and at 0.83 for the wider occluder. Corresponding figures were 0.72 for the lower frequency and 1.06 for the higher one. An interaction was obtained between Occluder Width and Oscillation Frequency ($F(1, 8) = 9.779$, $p < .02$, $\eta^2 = 0.55$). For the low frequency, the relative latency of PRGS was similar for the wide and the narrow occluder, but for the high frequency, the relative latency was larger for the narrow occluder than for the wide one. This is depicted in Figure 6. There was also an interaction between Occluder Width and Motion Amplitude ($F(1, 8) = 5.791$, $p < .05$, $\eta^2 = 0.42$). For the small amplitude, the relative latency of PRGS was the same for both the wide and the narrow occluder (0.85), but for the large amplitude the relative latency was larger for the narrow (1.06) than for the wide occluder (0.80). Another way to describe these interactions is to say that the shortest occlusion durations produced relatively longer relative latencies.

The reactive saccades

A general linear model repeated measurements ANOVA was performed on the reactive saccades (latencies 0.2 s longer than the occlusion duration). Significant effects were obtained only for Occluder Width ($F(1, 8) = 11.46$, $p < .01$, $\eta^2 = 0.56$). The average reaction time for the narrow occluder was 0.45 s and for the wider one 0.54 s. The difference in reaction time for the narrow and wide occluder was much smaller than the difference in PRGS for the same occluders ($F(1, 8) = 71.72$, $p < .0001$, $\eta^2 = 0.90$).

General discussion

When 4-month-old infants visually track an object that moves behind an occluder, they tend to shift gaze to the reappearing side ahead of the object. The present experiments asked whether the PRGS reflect an ability to preserve information about the moving object while it is hidden or if they are just an expression of low-level visual processing or a randomly determined process. The PRGS cannot just be a continuation of the pre-occlusion visual tracking, because the smooth pursuit used to track a visible object and the saccades used to reconnect to the object on the other side of the occluder are radically different modes of eye movements (see e.g. Lisberger *et al.*, 1987; Leigh & Zee, 1999). None of the infants pursued the object smoothly over the occluder. They all used saccades to shift gaze to the other side.

The determinants of PRGS

The passage-of-time hypothesis

The PRGS could not be explained in terms of passage-of-time. The subjects' gaze did not just linger at the disappearing edge after the object disappeared and then, after a random time interval, turn to the next thing along the path – the reappearing edge. If this had been the case, proportionally more saccades would end up on the other side of the occluder within the occlusion interval for the longer occlusions. On the contrary, the proportion of PRGS showed no such relationship with occlusion duration in either Experiment 1 or 2. Furthermore, there was no indication that either Occluder Width and Oscillation Frequency or Occluder Width and Motion Amplitude had opposite effects that counteracted each other.

Visual salience hypothesis

What is the likelihood that Occluder Width has an effect on 'predictive saccades' purely because of the visual salience of the exiting occluder edge and not because a wider occluder implies a longer occlusion? This is not easily tested because both hypotheses have the same implications on the latency of saccades over the occluder but for different reasons. The most important precaution to ensure that salience does not determine saccade latency is to make the occluder as non-salient as possible. In the reported experiments this was done by matching the white color of the occluder to the white background (the inside of the cylinder). Thus, although it can be argued that the exiting occluder edge is visible, it was not *salient*.

One argument against the visual salience hypothesis comes from the reactive saccades. They are by definition elicited by the detection of the reappearing object in the periphery of the visual field. The results indicate that the latency of those saccades is influenced by the eccentricity in the visual field of the reappearing stimulus. It can thus be argued that although efforts were made to make the occluder edges as non-salient as possible, the visibility of the exiting occluder edge could have influenced the effects of Occluder Width on PRGS. However, the difference in reactive saccade latency for the two occluders in Experiment 2 was small (0.45 s for the narrow and 0.54 s for the wide) in comparison to the difference in the latency of the PRGS (0.33 s for the narrow and 0.79 s for the wide occluder). It is therefore unlikely that visual salience of the exiting occluder edge is the only determinant of the difference in saccade latency for the different occluder widths. One can, of course, argue that a non-salient stimulus in the periphery of the visual field like the occluder edge will take longer to detect than a salient one like the reappearing object. However, the results show that the latency of PRGS for the narrow occluder is shorter than the reaction time to the salient reappearing object in the same condition.

A second argument against the visual salience hypothesis comes from the relative latencies of PRGS. They showed that gaze arrived proportionally later in the occlusion interval for the narrow occluder than for the wide occluder. This is contrary to what would be expected from the visual salience hypothesis. Visual salience of the occluder may also have a different effect on tracking over occlusion. Muller and Aslin (1978) found that a salient occluder made infants interrupt tracking and look at the occluder instead.

Finally and most importantly, visual salience could not be the only determinant of PRGS. The effects of oscillation frequency and motion amplitude were found to be just as important. Motion amplitude and oscillation frequency refer to variables that are not visually present during occlusion and therefore it is inevitable that some information from the seen pre-occlusion motion is preserved during occlusion.

The memory hypothesis

Neither of the two experiments supported the hypothesis that infants remembered the duration of the previous occlusion and expected the object to be absent for the same period at the next occlusion. The saccade latency at the first passages of a new condition was not influenced in a systematic way by the last occlusion of the previous condition with a different duration.

The cognitive hypothesis

This hypothesis states that the subjects moderate their PRGS from information that is not visually present during the occlusion. The cognitive hypothesis was strongly supported by the results. There was not a single stimulus variable like Occluder Width, Oscillation Frequency, or Motion Amplitude that determined the latency of the PRGS. On the contrary, the timing of the PRGS was determined by a combination of these variables that resulted in a rather close fit between the latency of PRGS and occlusion duration. Occlusion duration could be obtained by dividing occluder width by object velocity but it seems more parsimonious to assume that the infants maintained a representation of the object motion while the object was occluded and shifted gaze to the other side of the occluder when the conceived object was about to arrive there. Thus, instead of tracking the moving object visually, the infants could track it in their 'mind's eye'. If object velocity is represented in this way while the object is occluded, the effects of Occluder Width, Oscillation Frequency, as well as Motion Amplitude, could all be explained. However, this representation might not have anything to do with the notion of a permanent object that exists over time or with infants' conscious experience of where the occluded object is at a specific time behind the occluder. Object velocity may rather be represented by some kind of buffer during visible as well as non-visible parts of the motion. This would also explain why the timing of PRGS could be so good, irrespective of whether the occlusion duration was 0.2 or 1.6 s. In support of this hypothesis are the findings that object velocity is represented in the frontal eye field (FEF) of rhesus monkeys during the occlusion of a moving object (Barborica & Ferrera, 2003). Four-month-old infants might represent object motion during occlusion in a similar way. The critical stimulus variable for preserving a representation of object motion over occlusion could be accretion-deletion of the seen object at the occluder edges as suggested by Kaufman, Csibra and Johnson (2005). If this is the case, the accretion and deletion used in the present experiments was never too rapid or too slow to be perceived by the infants. The most rapid accretion-deletion had a duration of 0.23 s and the slowest one a duration of 0.87 s in the present experiments. The results also suggest that such a representation is by no means perfect. There was a clear tendency to overestimate the duration of short occlusions and underestimate the duration of long ones.

Other issues

The reactive gaze shifts

The subjects failed to predict the reappearance of the object on about half the occlusions. On some of those passages the subjects might have expected the object to reappear at a later time. However, the fact that the proportions of reactive gaze shifts were not systematically greater for the short occlusions than for the long ones argues against this suggestion. On average, the reactive gaze shifts arrived almost half a second after reappearance of the object. This is in accordance with other reaction time studies on infants (Aslin & Salapatek, 1975; Canfield, Smith, Brezsnyak & Snow, 1997; Gredebäck, Örnkloo & von Hofsten, 2006).

Motion amplitude

The low motion amplitude in Experiment 2 did not result in impaired timing of the PRGS. It should be noted that in the conditions with low amplitude, the object was only visible for 50% of the total viewing time, corresponding to about 0.8 and 1.6 s exposure on each side of the occluder. In the small amplitude and large occluder condition the object was never fully visible. The results suggest that infants do not require much more prolonged exposure of the moving object to anticipate its reappearance than adults do (cf. Sekuler *et al.*, 1990).

Effects of earlier exposure to visual motion

Johnson *et al.* (2003) reported that such experience was of critical importance for 4-month-old infants' ability to predict the reappearance of an occluded object. In the present study, the subjects had only initial experience with the stimulus at the calibration procedure. Then the object was rapidly transferred between the extreme positions of the trajectory and the center of it. If this in any way primed the infants, it would be to expect the object to stop at the middle of the trajectory, i.e. behind the occluder as it did at the calibration. Thus, it is unlikely that presentation of unoccluded motion before a set of occlusion trials is necessary for eliciting PRGS in 4-month-old infants.

Attention effects

Comparing the present results with those of Johnson *et al.* (2003) strongly suggests that their experimental situation was more distracting than the present one. First, the proportion of passages included and the proportion of predictive gaze shifts over the occluder were much lower in their study. The proportion of 'predictive' gaze shifts in their baseline condition was 29% compared to 47% in Experiment 1 and 50% in Experiment 2 of the present study. The obtained proportions are comparable to those found for older infants. Gredebäck *et al.* (2002) found that 9-month-olds tracked predictively over occlusion in 52% of the trials. Second, the number of predictive gaze shifts over the occluder decreased substantially over the experiment in Johnson *et al.* (2003). Such a deterioration of performance is a clear sign of distraction and it was not observed in the present study. At the transition age to predictive tracking over occlusion, it is expected that the expression of the ability is crucially dependent on the experimental setting. The present procedure of placing the infant in a sheltered environment apparently provided more optimal conditions for attentive tracking than in Johnson *et al.* (2003). Another difference that might have an effect on attention is the fact that Johnson *et al.* (2003) used 2-D images while the present study used real objects.

Future research

The next set of questions that need to be answered concerns the role of learning and neural maturation in the development of these abilities. While experience, no doubt, plays an important role in the development of predictive tracking over occlusion, it is also important to investigate the importance of the maturation of specific neural structures associated with this ability. In adults, the representation of occluded objects involves several specific parts of the cerebral cortex. These areas include the frontal eye field (Barborica & Ferrera, 2003), the temporal area (Baker, Keysers, Jellema, Wicker & Perrett, 2001) and especially the middle temporal region (MT/MST) (Olson, Gatenby, Leung, Skudlarski & Gore, 2004), the intraparietal sulcus (IPS) (Assad & Maunsell, 1995) and the lateral intraparietal area (LIP) (Tian & Lynch, 1996). When and how do the different parts of this network become engaged in the neural processing of occlusion? Kaufman *et al.* (2003, 2005) have led the way by showing that the temporal areas of 6-month-old infants are activated when they view object occlusion.

Conclusions

When 4-month-old infants track an object over occlusion and shift gaze to the exiting side of the occluder ahead of time, the latency of these gaze shifts is primarily determined by the duration of occlusion. It may be argued that because PRGS is never longer than the occlusion interval (plus 0.2 s), they are inevitably related to it. There are several arguments against such a conclusion. The first has to do with the proportions of PRGS in the different conditions. If the tendency to shift gaze ahead of time to the exiting side of the occluder was independent of occlusion duration, there would have been much more PRGS for the long occlusions than for the short ones. The results show that the proportions of PRGS were similar over a range of occlusion durations from 0.2 to 1.6 s. It is, of course, possible that all PRGS have shorter latencies than the shortest occlusion interval. Then the proportions would be independent of occlusion duration. The results show that this was not the case. On the contrary, the PRGS arrived close to the reappearance time independently of occlusion duration (r = .902). This tendency could not be explained by the visual salience of the exiting occluder edge. In addition, Oscillation Frequency and Motion Amplitude were equally important determinants of PRGS latency. Neither could it be explained in terms of a memory for the previous occluder duration. This suggests that object velocity is represented during occlusion and that the infants track the object behind the occluder in their 'mind's eye'. This brings continuity to events in a world where vision of moving objects is frequently obstructed by other objects. Seeing the object for an extended distance before each occlusion did not make these gaze shifts more precisely timed.

When does such intelligent behavior appear in development? Rosander and von Hofsten (2004) found that smooth pursuit gain and the timing of saccades when tracking a temporarily occluded object were highly correlated (r = .85). Thus the developmental onset of predictive smooth pursuit and predictive saccadic tracking might both be related to the onset of ability to represent occluded motion. Rosander and von Hofsten (2002) found that by 12 weeks of age both modes of tracking are predictive. The present results show that it takes at least another month before these predictive abilities manifest themselves in the launching of predictive saccades over occlusion.

Finally, the present results demonstrate the advantages of using parametric studies in infant research. A design with only one occlusion condition could not have determined whether the pre-reappearance saccades over the occluder were predictive or not. Neither could a design where only occluder width is manipulated. To answer the questions posed, both occluder width and object velocity had to be manipulated.

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