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When, Where and What

The Development of Perceived Spatio-Temporal Continuity

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Abstract

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This thesis explored the development of infants' ability to preserve spatio-temporal continuity of moving objects in situations where they disappeared completely (Study I & II) or partially (Study III) behind other objects (occluders). We recorded infants gaze direction with the help of two different techniques: 1) infants' gaze shifts in Study I were measured with electro-oculogram (EOG) in combination with a motion analyzing system (Qualisys) that recorded the reflected infrared light from markers placed on the infant's head and the moving object; 2) in Studies II and III a cornea reflection eye tracker was used (Tobii 1750) .

The results presented in this thesis demonstrate that 4-month-old infants are able to represent the temporal aspects of object motion during different periods of complete occlusion (Study I). At 6 months of age infants are able not only to predict the time when a moving object will reappear after complete occlusion but they are also capable to extrapolate pre-occlusion trajectory of the moving object and, thus, to accurately predict its reappearance (Study II). Moreover, in the situation where a linear pre-occlusion trajectory of the moving object is violated (the object turns by 90 degrees behind the occluder), infants at this age are capable of rapidly learning this new experience and base their future gaze shifts over occluder on the newly acquired knowledge. They are also able to preserve this new experience over a 24-hour period.

In the situations where occlusion is not complete and some visual information is still available (Study III), 9-month-old infants and to a lesser extent 5-month-old infants are able to reconstruct the moving pattern and to follow its direction of motion with the smooth eye movements. Moreover, 9-month-olds are capable to produce such smooth pursuit at an adult-like level.

Keywords: infants, occlusion, incomplete visual information, saccadic gaze shifts, smooth pursuit, temporal, spatial, object representation, learning, extrapolation

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Моему Любимому Олегу

– Щаасс спою!...
– Ну теперь точно спою! – сказал Волк и завыл.

Мультипликационный фильм « Жил-был Пес»

List of papers

I Von Hofsten, C., Kochukhova, O. & Rosander, K. (in press). Predictive tracking over occlusions by 4-month-old infants. *Developmental Science*.

II Kochukhova, O. & Gredebäck, G. (in press). Learning about occlusion: Initial assumptions and rapid adjustments. *Cognition*.

III Kochukhova, O. & Rosander, K. (submitted). Integrated global motion controls smooth pursuit in infants. *Journal of Vision*

Contents

Abbreviations

SP	Smooth Pursuit
PRGS	Pre-reappearance gaze shift
FEF	Frontal Eye Field
MT area	Middle Temporal area
MST area	Medial Superior Temporal Visual area
SEF	Supplemental Eye Field
PEF	Parietal Eye Field
EOG	Electrooculogram

Introduction

From the time of our birth we exist in a world in which objects constantly move in and out of sight or become partly covered by other nearer objects. These constant changes in the observed environment raise several problems which should be solved by our perceptual-cognitive system. Indeed, how do we as adults know that a car driving out of view by disappearing under a bridge will reappear on the opposite side? We pick up a variety of information from the car's motion, but how is this information used in order to perform successful tracking of the car and anticipate its reappearance when it temporarily goes out of sight? The ability to preserve spatio-temporal continuity over periods of non-visibility is crucial for our capability to perform anticipatory and uninterrupted actions. It includes the capability of calculating the approximate velocity of the motion of the object before it disappears so we can anticipate the time of its reappearance. Furthermore, we need to define, approximately at least, the direction of the object motion in order to anticipate where the object actually will reappear.

However, to anticipate *when* and *where* an object will reappear after a period of invisibility is not the only problem that our perceptual-cognitive system resolves.

In everyday life, except in situations where objects completely disappear from sight behind other objects, we are involved in plenty of situations where only fractions of the observed object may be visible. What do we rely on when grouping together some of those visible fractions into one object, and leaving out other parts as individual ones? As adults, we have some assumptions about the real world and the types of objects and motions we can meet there. Here again, the motion of the objects is a critical source of information for our perceptual-cognitive system. All visual information is reflected in 2D patterns of luminance change on the retina of the eyes. Motion of the objects can help us to overcome ambiguity of these images and enable us to construct 3D world representations (Krauzlis & Stone, 1999). We rely on the coherent and incoherent motion of objects and object elements when deciding to group them together as a single unit (representing the motion of one real object) or leave them apart as individual objects. Even when the visible components move orthogonally, our perception has the capability to combine them into a common motion of the whole group and to interpret residual motions as relative motions within the group (Johansson, 1950).

Recovery of the integrated motion of objects by the integration of their component motions is a complex visual task. However, as adults we do not even realize the complexity of these tasks because they are so natural to us. One example that can illustrate this assertion comes from a study of adults' perception of occluded objects by Burke (1952). In this study adults observed an object moving through a tunnel and were subsequently asked to draw the trajectory of the object motion. Almost all adults draw the path of the object motion as if they have never seen the tunnel. The pattern is rather different in young infants. The same types of tasks will be not carried out by them as easily and their performance will be very task dependent and variable (Beer, 2000).

The goal of this thesis is to explore more closely the development of the basic abilities that guide successful tracking of moving objects over periods of partial or complete occlusion. More specifically, this thesis aims to investigate the development of infants' ability to preserve spatiotemporal continuity of moving objects and to define *when* and *where* an object will reappear after completing the occlusion event, as well as *what* can be perceived as an integrated object in situations when only incomplete visual information is available.

Where everything began

Since the first studies by Jean Piaget (1952), the development of infants' ability to represent the permanence of hidden objects has been a hot topic. Indeed, acquisition of ability to preserve objects' spatiotemporal continuity during periods of non-visibility leads to a new level of interplay with the environment; from a segmented world, where, a priori, things only exists if they are visible, to a world where objects are permanent and actions on them can be directed into the future.

Although Piaget claimed that infants cannot represent temporarily occluded objects as adults until their second year of life, he noted that there were indications that infants developed some object representations already during the first 4 to 8 month of life. Piaget observed that during this age period infants will briefly look at the place where an object was hidden but they will not recover it.

Piaget's pioneering research on the development of object representation was further expanded in studies made within the preferential looking paradigm. This paradigm has a different approach to the studies of hidden object representation. Here, infants are presented with situations where objects become repeatedly occluded. After infants became used to the occlusion event and their looking duration has decreased substantially, they are presented with two novel stimuli. One is consistent with the previously observed phenomenon, the so-called "expected event", and another represents a violation of the previous experience (the unexpected event). Infants' looking times at these novel events are measured. If infants increase their looking time at the unexpected event, it is concluded that they have perceived the violation. Such tasks are easier compared to those in Piaget's experiments because they do not require the infant to perform the means-end task of removing the occluder to retrieve the object.

Looking-time experiments strongly suggest that 4-month-olds and even younger infants maintain some kind of representation of a completely occluded object. For instance, several studies carried out in this paradigm demonstrated that 2.5-month-old infants are sensitive to violations in different types of occlusion events (Spelke, Breinlinger, Macomber, & Jacobson, 1992; Wilcox, Nadel, & Rosser, 1996; Aguiar & Baillargeon, 1999; Hespos & Baillargeon, 2001; Wang, Baillargeon, & Paterson, 2005). In all these studies infants increased their looking time at unexpected events. This has been interpreted as evidence that 2.5-month-olds have some representation of totally occluded objects.

Studies carried out with this paradigm have also investigated a somewhat different capability of infants: the reconstruction of occluded portions when a target is only partly hidden by other objects. In other words, these studies asked the question, do infants' have the ability to represent the whole object from only observing its visible parts. Complete occlusion and partial occlusion, despite the fact that both rely on spatiotemporal information, raise slightly different problems for the developing perceptual-cognitive system. In the first case, infants have to keep the hidden object and (or) its trajectory of motion in mind in the absence of any perceptual support. In the second case, some information is continuously available and the infant's task is to fill in the missing part in order to reconstruct what is really observed.

Most of the preferential looking studies that investigated infants' ability to reconstruct objects from the available information, used the "rod-and-box" occlusion displays introduced by Kellman and Spelke (1983). These displays consist of an object with an occluded center, with aligned visible ends undergoing common lateral motion above and below the occluding box. Research carried out within this paradigm could not demonstrate any signs of perceptual completion before 2 month of age (Johnson & Aslin, 1995; Slater, Johnson, Brown, & Badenoch, 1996; Slater, Johnson, Kellman, & Spelke, 1994). However, 2-month-old infants demonstrated fragile object unity perception but only when the rod underwent motion. Perception of object unity in stationary rod-and-box displays was not observed before 5 months of age (Craton, 1994). Unity perception of a moving object became more robust over 4 – 6 months of age (Kellman & Spelke, 1983; Johnson, & Aslin, 1995, 1996; Johnson & Náñez, 1995). As can be seen from these results, coherent motion of the visible parts plays a central role in the perception of object unity in infants. Besides coherent motion, infants often rely on the orientation of visible surfaces relative to each other, and their shape, pattern and proximity (for reviews see Johnson, 2001; Needham, Baillargeon, & Kaufman, 1997).

Of course, one should be careful when interpreting results of preferential-looking experiments especially when the interpretations relate to higher order processes. In principle, longer looking times can be elicited by any kind of changes between the habituation and test parts of the experiment (Haith, 1998; Hood, 2001). At the same time, even if looking-time experiments really reflect infants' ability to represent hidden objects, they still cannot provide information on whether the infants were able to represent the object before the experiment started or whether they learned it during the habituation period. With regard to infants' ability to reconstruct partly occluded objects, preferential looking studies reflect better on infants' ability to fill up spatial gaps in the observed information and which cues are critical for this process. It is still not clear from these kinds of studies whether infants perceive the unity of an object by using several cues and how they pick up this information from the visual scene.

In case of complete occlusion, preferential looking experiments do not require the infants to organize actions related to the anticipation of object reappearance. As a consequence of this, the infants are not required to represent the exact spatiotemporal continuity of the moving object undergoing occlusion. Thus, the only conclusions that can be drawn from the results of preferential looking studies are that infants have some awareness of the temporarily occluded object. However, it is still unclear whether infants know how the object moves behind the obstacle. As a consequence, these studies are unable to inform us of the nature of the infants' knowledge and whether these representations are strong enough to guide actions (Gredebäck & von Hofsten, unpublished manuscript). In addition, these experiments are not able to answer the question of how infants pick up information from visual scenes to form spatiotemporal representations.

Here are two examples showing the discrepancies between the results of a preferential looking study (Spelke, Katz, Purcell, Ehrlich, & Breinlinger, 1994) and a reaching and tracking study (von Hofsten, Vishton, Spelke, Feng, & Rosander, 1998) when the moving object was completely occluded. In Spelke et al. (1994), 6-month-old infants were trained with an object moving on a diagonal linear trajectory from upper right corner of a table and disappearing behind an obstacle placed on the left side of the table (Figure 1). After each trial the obstacle was removed to show the position of the object under the obstacle. In the experimental trials the starting position of the object was changed to the lower right corner. It again moved linearly towards the obstacle. Then the obstacle was removed and the object reappeared in one of two different positions: either in a position inconsistent with previous linear motion but familiar (because of previous training) or in a position consistent with the recently observed linear motion but unfamiliar. Infants looked longer at the unfamiliar event. From these results, the authors proposed that infants were unable to represent the linearity of the object motion behind occluder.

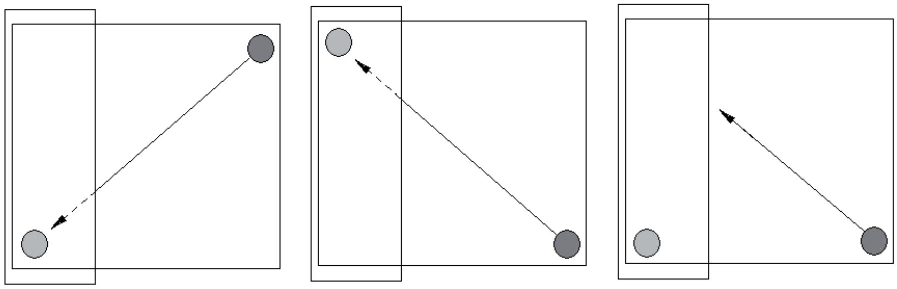

Figure 1. Schematic view of the stimulus events used in one of the experiments in Spelke et al. (1994).

In von Hofsten, Feng, and Spelke (2000), 6-month-old infants showed the opposite result when their head tracking was measured. After watching several blocks of an object moving on a linear or nonlinear trajectory, infants showed a strong tendency to turn their heads along a linear extrapolation of the object's trajectory on the opposite side of the occluding obstacle as if they anticipated that the object would reappear there. The same effect was obtained with reaching in 6-month-old infants, when the motion of the moving object was suddenly perturbed and the object continued along an orthogonal path. The infants then reached toward the continuation of the original path (von Hofsten, Vishton, Spelke, Feng, & Rosander, 1998).

In the latter studies, the infants were not just required to represent the moving object, but also to organize actions (head-turning and reaching) towards it. This action approach can expand our understanding of the early functioning of infants' perceptual-cognitive system. This method links different types of infants' behavioral reactions to the spatiotemporal continuity of the hidden object motion. Furthermore, it can offer a detailed description of how infant's actions, such as gaze shifts, are related to occlusion events. This approach gives us the chance to examine how infants' representations and expectations of *when* and *where* a completely occluded object will reappear develop with experience and age (Gredebäck & von Hofsten, unpublished manuscript). Moreover, it can help us to understand *what* infants perceive and how they pick up information from the visible scene by observing how they act in situations where objects undergo partial occlusions.

Infants' ability to represent moving objects undergoing occlusion is revealed by at least three different kinds of actions: reaching, head tracking, and eye/gaze tracking. The first one was already used by Piaget. However, in later studies researchers changed to preferential looking methods because reaching had many constraints that should be overcome during development. First, the onset of reaching in development is quite late because it requires development of body balance and eye-hand coordination, making use of this method impossible for investigating early object permanence (Mareschal, 2000). Measuring head tracking is a better alternative but it still has its own constraints. It is not precise, because infants can move their eyes independently of their head and they may not use head movements when anticipating object reappearance. The third method for studying infants' representation of object motion is gaze tracking. This is very promising for two reasons: first, the tracking of objects with the eyes can be observed from the first days of life (Kremenitzer, Vaughan, Kurtzberg, & Dowling, 1979; Aslin, 1987; Rosander & von Hofsten, 2000). Thus, it can reflect the earliest signs of developing object representation. Second, according to Leigh and Zee (1999), eye movements are easier to interpret than movements of axial or limb muscles because they are actually restricted to rotations in three planes and different classes of eye movements are quite easy to distinguish.

All these methods were used to answer the question of at what age infants begin to anticipate when and where a moving occluded object becomes visible again. This thesis will concentrate on the gaze tracking technique because it can provide the most accurate measurements of spatiotemporal properties of infants' developing representations and because it does not suffer from the same constraints as reaching actions do in young infants.

Gaze tracking

Most of animal and human gaze tracking includes a combination of eye and head movements. It serves at least three purposes (Leigh & Zee, 1999): (1) to bring the image of a detected object to the fovea where it can best be seen, (2) to reorient the eyes and head in space so that new parts of the surroundings can be observed, (3) to fixate moving objects. To attain the first two goals, saccadic eye movements are used, and to attain the third goal smooth pursuit eye movements are used.

Numerous studies of the development of gaze tracking in infants have shown that during the first month of life infants follow moving objects with saccadic eye movements. The very early smooth pursuit in neonates is characterized by low gain[1] and frequent saccadic eye movement intrusions. Smooth pursuit can be observed only in very specific tasks such as the following of a wide angle target moving at a low velocity (Dayton & Jones,

[1] Gain is defined as a ratio of the gaze amplitude to the object motion amplitude

1964; Kremenitzer et al. 1979; Roucoux, Culee, & Roucoux, 1983). However, starting from 1.5-2 months of age, smooth pursuit begins to improve significantly (Aslin, 1981; Shea & Aslin, 1990; von Hofsten & Rosander 1997; Phillips et al. 1997; Richards & Holley 1999; Rosander & von Hofsten, 2002).

Shea and Aslin (1990) observed smooth pursuit for a 2° step-ramp target in 7 to 11-weeks-olds, though the gain of smooth pursuit was found to be very low: 0.11 for a target velocity of 12°/s and 0.25 for a velocity of 6°/s. Von Hofsten and Rosander (1997) studied longitudinally smooth tracking in infants from 2 to 5 months of age. Participants were presented with a 10° target moving with different amplitudes, velocities, and motion patterns. Results of this study revealed that both gain and timing improved in a rapid and consistent way from 2 months of age and most increase was observed between 2 and 3 months. The same improvement in the smooth pursuit tracking between 2 and 3 months of age was observed in another study by Rosander and von Hofsten (2002). Here infants from 7 to 14 weeks of age were exposed to a wide range of stimuli sizes from 2.5 to 35°. Gain of smooth pursuit consistently increased with age independently of the stimuli size.

The earliest expressions of smooth pursuit lag the target motion. Aslin (1981) observed infants tracking pattern in response to a black bar of 2° wide and 8° high, moving sinusoidally with a lowest velocity of 10°/s. When providing a qualitative description of the smooth pursuit in 10-week-old infants he noted that it lagged the object motion somewhat but that this was not always the case for 12-weeks-olds. At this age infants' eyes often remained on the object or, sometimes, they could be slightly ahead of it. In the previously mentioned study by Rosander and von Hofsten (2002) infants were presented with objects moving sinusoidally at 20°/s. Their results revealed that over all ages studied (from 7 to 14 weeks), infants' smooth pursuit component lagged less than 100 ms. Such lag should be considered as predictive according to the criterion by Robinson (1965). Thus, infants' smooth pursuit component was predictive at all ages studied.

To summarize these findings, infants develop a mechanism for the expectations of future target motion or predictive control of smooth eye movements during the first months of life. Without this mechanism it would be impossible to rest the eyes on the moving target in an adult like manner or to lead its motion. Furthermore, tracking of moving objects develops in the direction of increasing smooth pursuit until it reaches an adult-like level of performance around 3 - 4 months of life (von Hofsten & Rosander, 1997; Rosander & von Hofsten, 2002).

Evidence coming from both adult (Skavenski & Steinman, 1970; Kowler & Steinman, 1979) and infant (Rosander & von Hofsten, 2004) studies reveals that we do not voluntarily produce smooth eye movements without a visible moving target to follow. Thus, in the case when the moving object disappears behind an obstacle, smooth pursuit is effectively interrupted and the only ability to continue tracking of the object undergoing occlusion is to use saccadic eye movements. This also means that as soon as we perceive a moving target we can produce smooth pursuit. In other words, it would not be necessary to have a real object to produce smooth following. Instead, smooth pursuit can be initiated by a moving perceived illusory object or object constructed from several coherently moving parts. Indeed, studies of adults by Beutter and Stone (2000) and Stone, Beutter, and Lorenceau (2000) have shown that, when adults recover the motion of an object by integrating the motion of its components, smooth pursuit following the integrated object motion is observed.

But, if an object disappears completely behind an occluder and the only way to continue tracking the moving target is to use saccadic eye movements, this can be accomplished in two alternative ways. First, when the target disappears behind an occluder, we can wait until the target reappears and then make a reactive saccade to catch up with the target. Secondly, the saccades can be programmed before the target becomes visible. Because the brain needs time to program a specific saccade, saccades arriving a short time after the object begins to reappear can be considered predictive. Two studies carried out on adults (Engel, Anderson, & Suechting, 1999) and infants (Gredebäck, Örnkloo, & von Hofsten, 2006) have tried to answer how much time is needed to program a saccade. This is of crucial importance for determining the time threshold between predictive and reactive saccades in situations when the saccade is made when object has already begun to reappear. Engel et al. (1999) have shown that adults had saccadic latencies about 200 ms for unexpected turns of a smoothly tracked moving object. Gredebäck et al. (2006) used a comparable experimental design and they observed infants from 3 to 8 months of age. It was found that infants from all infant groups had saccadic latencies of around 400-500ms on the average. Thus, all saccades that were made by infants to the object reappearance location before the object was visible were planned when the target was still occluded. In other words, these saccades were predictive. In studies I and II presented in this thesis we used more the conservative adult threshold of 200ms in order to separate predictive and reactive saccades.

Neural substrates for eye movements

Saccades

The neural networks for saccadic eye movements include several subcortical and cortical areas. Among them are the superior colliculus, the basal ganglia (caudate putamen and substantia nigra), the FEF, SEF and lateral intraparietal area (LIP). The FEF, SEF, and PEF areas project directly to the superior colliculus. Moreover, FEF projects both directly and via the basal ganglia. Thus, the command by superior colliculus to elicit a saccade is influenced by all of these areas. Most neurons in the putamen that discharge for eye movements do so for memory guided saccades (Hikosaka, Sakamoto, & Usui, 1989) and lesions in this region lead to deficits in anticipatory saccades, though visually guided saccades are still preserved (Vermersch, Müri, Rivaud, Vidailhet, Gaymard, & Pierrot-Deseilligny, 1996). Previous studies have also shown that the frontal and parietal eye fields are involved in voluntary control of saccades (Lynch, 1992; Schiller, Sandell, & Maunsell, 1987). The LIP area activates before a saccadic eye movement is launched (Andersen, 1997). This area is also involved in the coding of direction and amplitude of remembered target locations. Moreover, neurons in this area remain activated until an eye movement is complete, independently of target visibility and time since last sight of target (Gnadt & Andersen, 1988).

All these findings support the statement that the saccadic system is guided by higher-order processes. Recently several physiological and psychophysical studies have provided evidence for a view that pursuit as well as saccades is guided by high-order visual processes, rather than by the raw retinal stimulation (Krauzlis & Stone, 1999; Stone & Krauzlis, 2003).

Smooth pursuit

The hypothetical anatomic scheme for smooth pursuit eye movements includes several subcortical and cortical areas. First, signals encoding retinal image motion pass via the lateral geniculate nucleus to the striate cortex (V1). In this area, the first processing of motion takes place. It is believed to encode direction of local motions because of rather small receptive fields, though directional selectivity is relatively rare here and confounded with one dimensional orientation tuning (Leigh & Zee, 1999). The striate cortex projects to the middle temporal area (MT), which in its turn projects to the medial superior temporal area (MST). Most neurons in the MT encode the speed and direction of moving visual stimuli; they have larger receptive fields and are able to respond to the global direction of the motion of presented two-dimensional stimuli (Rodman & Albright, 1989). According to

Stone and Krauzlis (2003), it is the earliest cortical area within the dorsal stream where nearly all neurons are truly directionally tuned and the true 2D object-motion direction signal first emerges. Neurons in the MST area may differ from those in area MT by taking into account effects of eye movements themselves (Bradley, Maxwell, Andersen, Banks, & Shenoy, 1996). Since MST neurons combine visual and eye movement signals they may encode the motion of the moving visual stimulus in head-centered coordinates rather than eye-centered as in the MT area. Moreover, MST neurons in contrast to neurons in the MT area are highly active during steady-state pursuit (Newsome, Wurtz, & Komatsu, 1988). Furthermore, recent findings by Stone and Krauzlis (2003) suggest that, in adults, MST neurons (or neurons further downstream) are linking perception of veridical motion direction and steady state pursuit. At the same time, target selection or attention may play an important role in linking motion perception and pursuit. When, for example, a subject is less attentive to a stimulus, perceptual judgments of motion direction appear to be more related to retinal motion than to the object motion in the world (Festinger, Sedgwick, & Holtzman, 1976).

The visual areas MT and MST have reciprocal connections with the frontal eye field areas (FEF) and inputs from the MST area also go to the supplementary eye field. Both of them make important contributions to predictive aspects of smooth pursuit (Leigh & Zee, 1999).

The networks mentioned above in relation to control of smooth pursuit and saccades do not, of course, reflect the whole pattern of brain structures involved in their production. In addition, pursuit pathways and pathways controlling saccades do not appear to be completely independent systems. Recent studies have shown that they involve overlapping mechanisms, for example in areas FEF, LIP and MST (Tian & Lynch, 1996), that can be used for coordination of both types of eye movements, at least in the case of tracking a visible object (Krauzlis & Stone, 1999).

Although findings in adults have shown that smooth pursuit and small saccades involve overlapping neural mechanisms, large saccades have separate neural mechanisms (Krauzlis & Stone, 1999). When an object completely disappears, both adults and infants make large saccades to the place of the object reappearance (Kowler, 1990; Rosander & von Hofsten, 2004). In this case, saccades cannot be accounted for by a continuation of the previous motor program. They involve a totally different set of motor commands to smooth pursuit. In the first case, the eye muscle activations are abrupt and fast, and in the second case, they are gradual and continuous. Moreover, if they are elicited before the object reappears they have to be guided by some kind of anticipation of the object's continuing motion.

What do we know about the development of these structures?

Depending on the task, gaze tracking can involve the combination of two eye movement systems: smooth pursuit and saccades. According to Johnson (1990), the pathways guiding infants eye movements develop at different rates during the first months of life. The first pathway, functioning already at birth, involves a direct connection between the retina and the superior colliculus. Its function is to generate saccades to easily detectable targets in the peripheral visual field. During the second month of life, the areas V1 and MT become involved in the control of eye movements. When infants then pursue visible moving objects, they do it with a combination of saccadic eye movements and smooth eye motions (Dayton & Jones, 1964; Aslin, 1981; von Hofsten & Rosander, 1996, 1997; Rosander & von Hofsten, 2002). Before this time almost only saccades are observed. According to Braddick, Atkinson, and Wattam-Bell (2003), this is consistent with the onset of the discrimination of motion direction and with the idea that the neural signal controlling pursuit is closely related to the perception of coherent motion. Moreover, the involvement of V1 and MT areas leads to the development of global motion processing and cortical directional selectivity (Braddick et al. 2003). From about 7 weeks of age, the timing of eye tracking improves dramatically. Von Hofsten and Rosander (2002) have found that already at this age, when infants track a moving object smoothly, their eye movements are closely timed to the motion. However, the amplitude of smooth pursuit at this age is smaller than the object motion. A major increase in the proportion of well timed smooth pursuit to catch-up saccades happens between 2 and 3 months of life. Infants are able to smoothly track a moving object at an adult-like level around 4 months of age (von Hofsten & Rosander, 1997). Moreover, Rosander and von Hofsten (2004) observed that when infants make a saccade over an occluder their initial gaze lag at the object reappearance decreases dramatically between 2 and 3 months of age. The saccadic gaze shifts were predictively timed to the object's reappearance for 5-month-old infants. These findings support the statement that the FEF starts to interconnect with the MT and the superior colliculus around 3 months of age (Johnson, 1990).

Anticipation of reappearance: When

In the past, only a few studies have measured infants' eye movements to determine at what age infants begin to anticipate when the occluded moving object becomes visible again. The first experiments that tried to answer this question studied infants' visual reactions when they observed a toy train moving along a rectangular path and passing through a tunnel (Nelson, 1971, 1974; Meicler & Gratch, 1980). The results of these studies revealed that 9-month-old infants moved their gaze to the other side of the tunnel ahead of the train already in the first presented trial. This was not the case for 5-month-olds. However, after several repetitions they could also learn to anticipate the train reappearance. In a later study, van der Meer, van der Weel, and Lee (1994) presented 5-month-old infants with linearly moving objects that underwent occlusions from 300 to 600ms. They found that infants looked towards the object reappearance side in anticipation of the object's arrival there.

Recently, Johnson, Amso, and Slemmer (2003) recorded eye movements of 4- and 6-month-old infants. They were presented with a linearly moving object that became occluded at the center of its trajectory. Four-month-olds who were presented with non-occluded motion of the object before the occlusion trials were found to be more likely to shift their gaze in anticipation of the object reappearance than the infants of the same age who were not exposed to such motion. Six-month-old infants did not demonstrate the same benefits from seeing non-occluded trials. According to the authors, these results demonstrate that 4-month-old infants do not have robust object representations but that 6-months-olds do.

Moreover, Rosander and von Hofsten (2004) studied tracking development in even younger infants when a moving object underwent occlusion. Seven-, 9-, 12-, 17- and 21-week-old infants viewed an object oscillating on a horizontal track that had an occluder placed either at its center where the object disappeared for 300ms, or at one of the trajectory end points where the object became occluded for 600ms. During the central occlusion the object reappeared on the opposite side of the occluder and in the side occlusion event the object turned back during the period of occlusion and reappeared on the same side. All the infants in Rosander and von Hofsten (2004) also experienced two trials with un-occluded motion before the occlusion trials began. The level of performance in the central occluder condition improved rapidly between the ages studied. Furthermore, several of the 18-week-old infants moved their gaze to the reappearing side of the occluder already at 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 when and where an occluded linearly moving object will reappear.

One problem with studies of anticipatory gaze shifts at temporary occlusions is that predictive saccades over the occluder do not occur on every trial. In Rosander and von Hofsten (2004) the 4-month-old infants moved their 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. Thus, we cannot show that infants, once they have learned to move their gaze in anticipation of object reappearance, will do so on all consecutive trails in the future. In this case, it is 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 at the other side of the occluder before the object reappears there just by accident. Thus, they will be defined as predictive although they are not.

In experiments with only one occlusion duration, it is not possible to resolve whether the saccades arriving at the reappearance edge before the object are really predictive or just appear to be so. In order to understand the basic principles of infants' tendency to shift gaze to the reappearing side of an occluder, we need a different set of studies in which occlusion duration is systematically varied. It can help us to distinguish between several modes of behavior underlying 'predictive' actions at occluders. Here, only the gaze shifts that arrive before the reappearing object will be informative in this respect because those that arrive later are elicited by the sight of the reappearing object.

Attempts to resolve this problem were made previously in three studies by Jonsson and von Hofsten (2003), by Gredebäck, von Hofsten, and Boudreau (2002) and by Gredebäck, and von Hofsten (2004). In the study by Jonsson and von Hofsten (2003), the authors measured head tracking in 6-month-old infants observing a horizontally moving object that was occluded for 400, 800 and 1200ms. They found that infants initially predicted object reappearance only after the 400ms occlusion, but after several trials they began to anticipate the reappearance after the longer occlusion intervals. Unfortunately, the head tracking method does not have the same accuracy as the measurements of gaze tracking. The latter method involves measurements of both head and eye movements. Here it is possible to calculate a veridical direction of infants gaze when eyes and head move in opposite directions or when infants only use the eyes to follow the moving object. The studies by Gredebäck et al. (2002) and by Gredebäck and von Hofsten (2004) employed measurement of gaze tracking to investigate the rate of successful predictions on occlusion durations varying from 250ms to 5000ms (Gredebäck et al., 2002) and from 500ms to 4000ms in Gredebäck and von Hofsten (2004). In both studies infants were presented with circular trajectories of a moving object that became temporarily occluded. It was found that even the 6-month-old infants could predict the time of object reappearance and move gaze to the place where the object would reappear. Moreover, the latency before making a predictive saccade increased with duration of occlusion in all the studied ages (from 6 to 12 months). It was calculated that, in general, infants waited around 2/3 of the occlusion time before making predictive saccades to the future place of object reappearance.

The conclusion that can be drawn from the findings of the previous tracking studies is that infants make predictive saccades over an occluder from at least 6 months of age. A strong relationship between predictive saccade latency and occlusion duration can be interpreted as evidence of it.

What is still unknown is whether such truly predictive anticipations can be seen earlier than 6 months of age. Study I of this thesis attempts to examine the principles underlying 4-month-old infants' ability to shift gaze over occluders in a predictive way. The general question is if we can observe such predictive gaze shifts made in anticipation of object reappearance in infants younger than 6 months of age.

Anticipation of reappearance: Where

In addition to the ability to represent the duration of moving object occlusion, there is another important ability that infants need to develop. In order to be successful in their actions such as shifting gaze over an occluder or stretching a hand in order to grasp a reappearing object, it is important to guess *when* the object will reappear and also *where* it will happen. Thus, a representation of the occluded object should include both when and where the object will reappear.

Reaching experiments using linear trajectories of the moving object show that infants have a tendency to extrapolate this trajectory when trying to catch the object (von Hofsten, Vishton, Spelke, Feng, & Rosander, 1998). Von Hofsten et al. (1998) presented 6-month-old infants with fully visible linear and non-linear trajectories of an object in motion. Infants were placed in front of a vertical screen on which an object was moving. In the case of linear trajectories, the toy started from the upper right or left screen corner and moved diagonally downwards. On the non-linear trajectories the toy began its motion from the same positions but reversed the horizontal direction of its motion at the center of the screen. Infants showed a strong preference to reach for a place which was a linear extrapolation of the currently perceived trajectory. In the following set of studies (von Hofsten, Feng, & Spelke, 2000; Spelke & von Hofsten, 2001) conditions were made more complicated by introducing an occluder at the center of the screen, where the object was changing its direction in the case of the non-linear trials. This decreased the number of performed reaches from around 35% on fully visible trajectories to around 3% on occluded trajectories, making it impossible to decide (based on reaches) if infants have some kind of representation of where the object should reappear. Thus, the measurement of head tracking was a better estimate of infants' ability to represent where the toy should reappear. It was shown that 6-month-olds did not anticipate the reappearance of the toy at the first trial at all. But already from the second trial they learned to move their head to the correct side in anticipation of a continuing linear trajectory. They also learned to anticipate the location of the object's reappearance during non-linear trials but this process took longer. The authors proposed that infants' predictions were originally based on inertia so they extrapolated the pre-occlusion trajectory. However, in the case of non-linear trajectories they needed to inhibit this tendency and use their recent experience to choose where the toy will reappear.

The tendency to predict object reappearance along a linear trajectory was also observed in the previously mentioned study by Rosander and von Hofsten, (2004). They found that infants, at least from 5-months of age, moved their gaze in an anticipatory way over an occluder placed at the very end of the object trajectory. It looked like infants predicted object reappearance along a continuation of its trajectory, though the object never appeared there in this condition. Moreover, at least from 6-months of age infants are also able to anticipate the location of reappearance of objects moving in a circular trajectory (Gredebäck & von Hofsten, 2004).

To summarize, from 5-6 months onward infants develop some kind of representation of *where* an object will reappear and this representation is stable enough to guide predictive gaze shifts but not to guide reaching behavior, at least at 6 months of age. However, although infants develop this representation of where the moving object will reappear, it is still not clear what information they use. From the analysis of the earlier research that examined infants' predictive gaze shifts when a moving object is temporarily occluded, it can be concluded that there are at least two different ways in which infants predict the future trajectory of occluded objects. First, they can extrapolate the pre-occlusion trajectory. Secondly, infants can base their predictions of how the object will continue to move on their recent experience with moving objects. In other words, if infants are provided with enough repetitions of similar events, they can learn trajectories that cannot be easily extrapolated based on the pre-occlusion motion. All occlusion studies mentioned above have presented infants with multiple repetitive trials in which both of these possibilities occurred (Gredebäck & von Hofsten, 2004; Gredebäck et al., 2002; Johnson et al., 2003; Meichler & Gratch, 1980; Nelson, 1971, 1974; Rosander & von Hofsten, 2004; Spelke & von Hofsten, 2001; von Hofsten et al., 2000). The studies allowed infants simultaneously to predict the reappearance location from the current pre-occlusion trajectory and to accumulate experience over time.

In order to understand how infants form representations of *where* to expect occluded objects to reappear, the two possibilities mentioned above should be separated. Firstly, this will give us the opportunity to closely examine how each of these processes develops over time and age by looking at experience based predictions without interference from initial successful extrapolations and vice versa. Secondly, it is also important because many studies of infants' behavior outside the occlusion paradigm have demonstrated that learning is a very important mechanism for picking up information from the world and actions once learnt can be retained over long time periods. For example, Rovee-Collier and colleagues (Hartshorn & Rovee-Collier, 1997; Hartshorn et al., 1998; Hitchcock & Rovee-Collier, 1996) used operant conditioning to assess 2- to 6-month-old infants' ability to associate their own kicking with the motions of a mobile. The results of these studies showed that from 2 months of age infants could show retention for the task for 1 day and 6-month-olds could show retention for 14 days.

In Study II of this thesis we disentangled the two possibilities for representation of *where* an object will reappear after an occlusion event. In this study we examined 6-month-olds because it is well established that infants at this age can already represent moving objects behind occluders. Thus, they can represent *when* an object will reappear, but we were interested in how they form representations of *where* it will reappear. Moreover, we were interested in what roles learning and long term memory play in this process.

Anticipation: What

One of the important problems to be solved by the perceptual-cognitive system is to determine *what* is an integrated object and what cues are utilized in the integration process when only incomplete visual information is available.

Rather few studies have applied gaze tracking techniques in order to investigate development of this ability in infants. Furthermore, there are two approaches in gaze tracking studies that are related to the development of this ability: studies related to the perception of motion coherence and studies highlighting perception of a separate object as a unit in situations when incomplete visual information is available.

The studies of the first kind used a directional eye movement technique (Kowler & McKee, 1987) in which infants' eye movements were judged by an adult observer. Using this technique Manny and Fern (1990) observed that infants from 1 up to 3 months of age showed eye movements in the direction of coherent motion both when they were presented with a single grating viewed through a round aperture and when they observed a grid, composed from two perpendicular gratings. However, a problem with this study was that it was difficult to decide if infants really perceived and tracked coherent motion of a plaid or they followed the gratings' intersections (Dobkins, Fine, Hsueh, & Vitten, 2004), which is commonly observed in adults (for review see Dobkins et al., 2004). In order to eliminate such tracking possibilities in their experiment, Dobkins et al. (2004) presented infants of 2, 3, 4 and 5 months of age with moving gratings spatially separated from each other. The assumption was that, if infants are able to perceive the pattern of motion integration, their gaze direction will represent motion summation across a relatively large area. Results of their study showed that infants of all the ages studied could follow coherent global motion.

The second eye tracking approach has been used as a supplement to preferential looking studies that examined infants' developing ability to perceive a moving object as a unity in different conditions. This method was applied by Johnson and colleagues (Johnson & Johnson, 2000; Johnson, Slemmer, & Amso, 2004). In both of these studies, the authors used the classical "box-and-rod" display, where an inclined rod underwent horizontal translation behind a centrally placed square box. Infants could only directly observe the spatially separated coherently moving ends of the rod. In the first experiment of their study Johnson and Johnson (2000) recorded scanning patterns in 2- and 3.5-month-old infants. The results of this experiment revealed that the older infants scanned between top and bottom halves of the visible rod parts more frequently, as well as in the lower part of the display. It was interpreted as reflecting an ability to pick up relevant visual information concerning edge connectedness in the display. In general, the scanning patterns of older infants were more extensive. In the second experiment of this study Johnson and Johnson longitudinally explored scanning patterns in five infants from 2 to 5 months of age. Though scanning patterns for these infants also appeared to be adapted for effective acquisition of relevant visual information just as in Experiment 1, the result of this experiment revealed that scanning strategies could be very individual for different infants.

Johnson, Slemmer, and Amso (2004) used eye tracking as a comparative measurement for preferential looking outcomes on perception of object unity. Johnson et al. (2004) measured eye scanning patterns during the habituation phase of their experiment on 3-month-old infants. They found that infants whose looking times could be interpreted as indicating an ability to perceive the unity of the moving rod scanned systematically in a way that optimized the intake of important information for unity perception. "Perceivers" scanned more frequently around the rod and across the range of its motion. The authors argued that all these findings support views of perceptual development and stress the importance of information processing skills and self-directed action to the acquisition of object knowledge.

A rather different approach was used to study the perception of object unity, on the basis of coherent motion of several visible components, in adult studies by Krauzlis and Stone (1999) and Beutter and Stone (2000). These studies demonstrated that, if adults really perceive several spatially separated motion elements as parts of a coherently moving object, then they follow its veridical motion direction with smooth pursuit; if not, then the smooth pursuit coincides with the separate motion elements making up the object motion. In their study, the motion of the separate elements did not coincide with veridical motion of the whole object.

In the third study of this thesis we tested infants' ability to integrate the fragments of a partly occluded moving object into perceived global object motion and to use this percept to control smooth pursuit eye movements of the object.

The aims of this thesis

The general aim of this thesis is to explore the development of infants' ability to preserve spatio-temporal continuity of moving objects over periods of non-visibility. This is crucial for accomplishing anticipatory and uninterrupted actions. This problem was approached by studies of how infants come to anticipate *when* and *where* an object will reappear after completing an occlusion event, as well as *what* can be perceived as an integrated object in situations when only incomplete visual information is available.

Study I of this thesis investigated 4-month-old infants' ability to maintain the temporal continuity of a disappearing object. We examined whether 4-month-old infants can shift gaze over an occluder in anticipation of *when* a temporarily occluded object will reappear in the same way as older infants do (Gredebäck & von Hofsten, 2004). This was tested in conditions of different occlusion durations. We also tested alternative explanations of 4-month-old infants' tendency to make predictive gaze shifts over an occluder, such as passage of time from the object disappearance, occluder edge salience, or memory of the occlusion duration on the previous occluder passage.

Study II was focused on infants' ability to maintain spatial continuity of a disappearing object and to predict *where* an object will reappear after an occlusion event. In this study we examined 6-month-olds because it is well established that infants of this age can already time their predictive saccades to the object reappearance. In other words, they can represent temporal continuity of the disappearing object and represent *when* an object will reappear. In this study we investigated how they form representations of *where* the object will reappear. Moreover, we also examined the role of learning and long term memory in this process.

Study III was focused on *what* infants can perceive in a situation where the occlusion is not complete, but only fragments of the object are visible. We investigated *what determines* smooth pursuit tracking of 5- and 9-month-old infants compared to adults in such a situation. Are infants able to perceive and follow the global motion of the object with smooth pursuit movements or only the fragments of the object? If smooth pursuit follows the global motion, the subject can both integrate motion elements into perceived global object motion and use this information to control smooth pursuit.

Method

Participants

For all three studies we contacted families with infants of the appropriate age with a letter describing the study and inviting them to participate. If they decided to take part in the experiment, an appointment was made. Once in the lab, each family was provided with a detailed verbal description of the study, its purpose, and the methods used. The parents signed a consent form before the study began. All studies were approved by the ethics committee of the Research Council in the Humanities and Social Sciences and were in accordance with the ethical standards specified in the 1964 Declaration of Helsinki. Responding families were mostly Caucasian middle class families. As compensation for their participation, each family received either a gift certificate for a CD or a gift certificate for a toy shop; each with a value of 12 €. In Study III, when an adult group was tested every adult participant received a movie ticket with a value of 10 €.

Study I included two experiments in which a total of 23 infants in the age range of 3.5 to 4.5 months participated. The infants (11 girls and 12 boys) were all healthy and born within 2 weeks of the expected date. Out of the total number of participants, 3 boys and 1 girl in Experiment 2 were excluded from the following analyses because of inattention. Study II also included two experiments. In the first experiment, 46 infants (13 boys and 8 girls) with an average age of 26:5 weeks (SD = 3.2 days) took part. In the second experiment 21 infants (13 girls and 8 boys, mean age = 27:4 weeks, SD = 3 days) visited the laboratory twice. The third Study focused on the development of global perception in infancy, and compared infants' performance with the performance of an adult group. In this study we had participants from three age groups: two infant groups and one adult group. Altogether 41 infants in two different age groups were analyzed. Twenty infants (11 girls and 9 boys) were in the age range 36:5 – 39:2 weeks with a mean age of 38:1 weeks, and 9 girls and 12 boys were in the age range 20:6 – 23 weeks with a mean age of 22 weeks. An additional 9 infants were excluded from the experiment due to fussing and 4 due to bad reflection from the eyes. The adult group consisted of 14 "naïve" adults (9 women and 5 men) in age range 23 - 54 years with a mean age of 32.5 years.

Procedure and stimulus presentation equipment

In all three studies, before starting the experiment, the accompanying parent was informed about the experiment and he/she signed a consensus form. It was also checked that the infant had been recently fed and was in an alert state. If the infant fussed during a trial, the experiment was interrupted temporarily. Such interruptions were uncommon. In all three studies infants and adults were presented with different types of moving stimuli, which were temporarily (Study I & II) or partly (Study III) occluded.

Study I

The first study was performed with the same equipment as in the studies by von Hofsten and Rosander (1996, 1997), and Rosander and von Hofsten (2002, 2004). The infants were placed in an infant chair positioned at the center of a cylinder, 1m in diameter and 1m 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. Figure 1 shows the experimental situation setup. In front of the infant the cylinder had a narrow horizontal slit where the movable object was placed. A 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. Infants' eye movements were measured with electrooculogram (EOG). Electrodes of miniature type (Beckman) were 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 10cm long cables into a preamplifier attached to the head of the infant. Prior to the start of the experiment calibration of the EOG was performed. The experimenter moved the object swiftly along the horizontal slit from one extreme position of its path to the middle of the slit, and then to the extreme distance on the other side (Finocchio, Preston, & Fuchs, 1990). On each stop the experimenter flashed a red LED placed below the stimulus to attract the infant's gaze.

During both experiments of Study I, the stimulus was a circular orange "happy" face (diameter = 7°). It oscillated in front of the infant according to a triangular function. It was occluded in the center of its trajectory by a white rectangular piece of cardboard. Occluders of different sizes were used in the different conditions.

To measure the object and head motions of the infant in 3D space a movement analysis system, “Proreflex (Qualisys)” was used. This system uses high-speed cameras that register the position of passive reflective markers illuminated by the infrared light positioned around the lens of each camera. In the present setup, 3 cameras were used. Three markers were placed on the infant’s 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. Marker disposition can be seen on Figure 2. The EOG, the object and the head movement data were recorded in synchrony at 240 Hz.

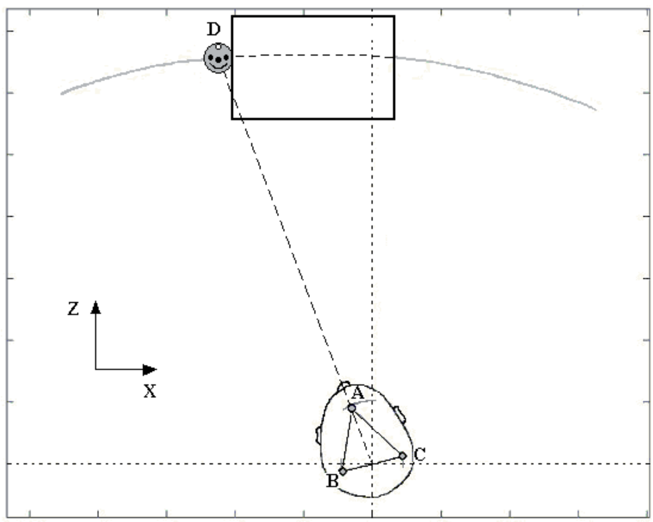

Figure 2. Illustration of the experimental situation setup for Study I. Qualysis system markers were placed on infant’s head (markers A, B, C) and the object (marker D).

Studies II & III

In Studies II & III the gaze was measured with a Tobii 1750 eye tracker (17” monitor) with an infant add-on (www.Tobii.se). Infants were placed in a safety car seat that was positioned on the participating parent’s lap in front of the Tobii eye tracker and the monitor. A calibration procedure was carried out before the experiment. In preparation for the calibration, the experimenter adjusted the eye tracker to make sure that the reflections of both eyes were centered in the field of view of the cameras. During calibration we played a movie showing a blue and white sphere (provided by the courtesy of Scott Johnson) expanding and contracting (extended diameter = 3.3°) in synchrony with the sound. It appeared randomly at one of the 9 screen calibration points. At the end of the calibration a graph appeared that reported how successful the calibration was; any unsuccessfully calibrated points were recalibrated. At the 60 cm viewing distance, the full display measured

24° x 28°. The system recorded the reflection of near infrared light in the pupil and cornea of both eyes at 50 Hz (accuracy = 0.5°, spatial resolution = 0.25°). In between every experimental trial one attention grabber movie was presented. It was chosen from 8 different attention grabbing movies (horizontal and vertical extension = 5.7°) displaying a small toy that moved and sounded in the middle of the screen.

In Study II the experimental stimuli consisted of a bird's eye view of a scene containing a multicoloured ball (radius = 1°) rolling on a blue background. In the middle of the scene a round wooden-textured occluder (radius = 3.5°) covered the ball as it rolled underneath. Both the ball and the occluder cast light shadows on the background and the ball reflected some light (Figure 3); this was done to enhance the perception of a 3D occlusion event. Each experimental session included 8 movies, in which the ball rolled back and forth between the two endpoints according to a triangular function. Two different types of object trajectories were presented: linear ones, and trajectories where the object moving linearly underneath the occluder switched its direction of motion by 90° before reappearing. Each infant was presented with one type of trajectory only.

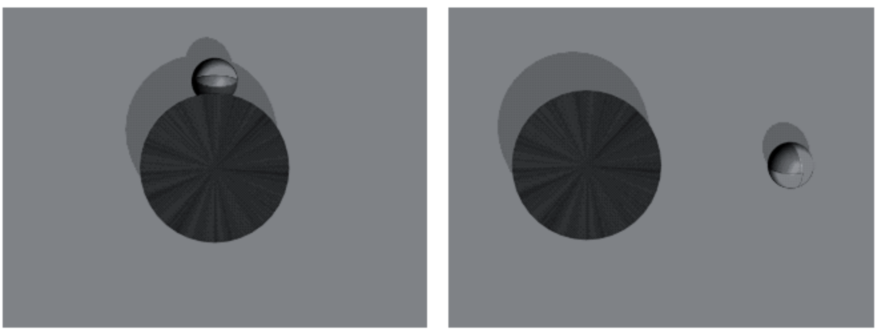

Figure 3. The image of the stimuli in Study II.

In Study III the participants were presented with one session of 8 movies. Each movie contained 8 full cycles of a line-figure rhombus (Figure 4) in motion combined with different kinds of artificial sounds. The rhombus (height = 10°; width = 17.5°; line segments thickness = 0.6°) presented was either in red or in blue color, and was moving horizontally along a sin-modulated linear trajectory on a white background rectangle (22.5° x 22.5°). Its motion was partly occluded by three stationary vertically oriented rectangular occluders. The distance between them was 3.75° and the width of each of them was 5°. The rhombus had vertex angles of 50° and 130° and it was symmetrical about both horizontal and vertical axes. Its vertices were never visible. Thus, only the four line segments falling within the two apertures between the occluders were observable. For each participant two different occluder conditions were presented: visible and invisible. In the *visible occluder* condition the white background rectangle was covered by the three dark grey occluders with two apertures in-between them through which the moving parts of the rhombus were visible (Figure 4A). In the *invisible occluder* condition the covering occluders were of the same white color as the background rectangle (Figure 4B).

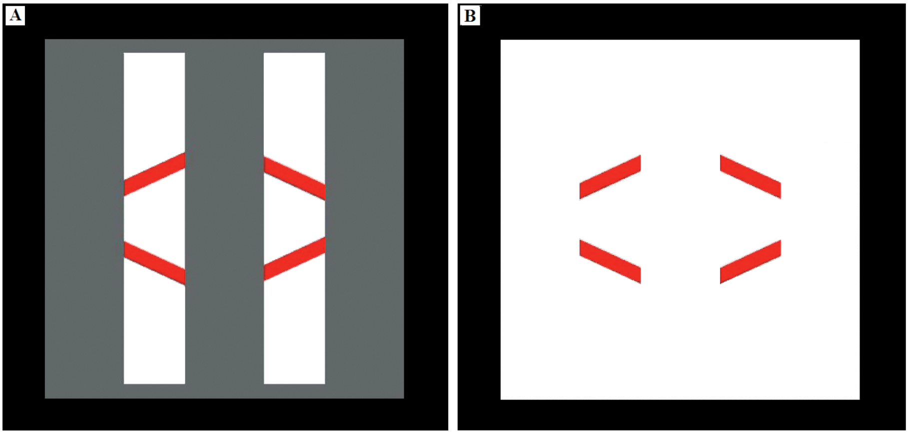

Figure 4. Stimuli used in Study III. Visible occluder (A) and invisible occluder (B) condition.

Data analysis

For the first two studies, the most important aspect was the occurrence of complete occlusion. The analyses were concentrated on the saccadic gaze shifts during the period of occlusion. In Study I it was determined when the gaze reached the reappearance side of the occluder. In Study II we were interested in both when and where the infants' saccades ended. The analysis of the data was done in several steps. The first step in Study I was to calculate the infants' gaze direction. It was calculated as a sum of the head and the eye direction, where the head direction was calculated from the coordinates in space (relative positions) of the three markers on the infant's head. In order to calculate the eye direction, first 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 by the difference in degrees between the head and the object at those positions. A linear relation was then assumed between the EOG signal and the radial displacement (for reviews see Davis & Shackel, 1960; Finocchio, et al., 1990; von Hofsten & Rosander, 1996). Then, the eye movements were calibrated in the same angular reference system as the head – in other words, in terms of how much head movement would be required to shift gaze by an equal amount. The amplitudes of the eye movements were regarded as proportional to the corresponding head movements.

The first step in Study II and the second step in Study I was to define which trials should be included in the analysis. First of all, in the trials to be included, the infants had to be attentive to the occluder event both prior to and after the occlusion for at least 200ms. In other words, the infants should track the target for at least 200ms prior to its disappearance. Moreover, infants had to fixate the reappearance location before the target emerged there or continue to track the target after its reappearance for an equal amount of time. The infants' gaze arrived to the reappearance location of the occluder when it came within 2° inside of the object's reappearance boundary. The boundary is then within the foveal region of the infants' visual field (Yudelis & Hendrickson, 1986). If these criteria were not fulfilled, the trial was excluded from the analysis.

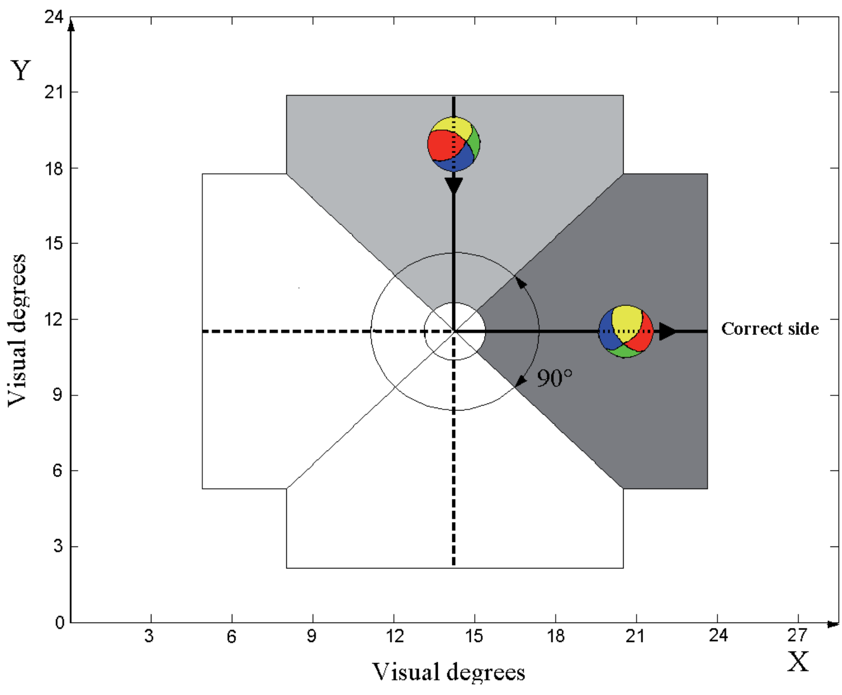

Figure 5. The different areas covered by the analysis of a typical nonlinear object trajectory in Study II. The thick solid line depicts the current trajectory being analyzed and the outer circle indicates the location of the occluder. The four large areas (not including the area covered by the inner circle) define the four possible reappearance locations of the target. The light gray area represents the disappearing edge and the dark grey area the reappearance edge.

In the next step of both Study I and II, the infant's response to each occlusion passage was dichotomized as either predictive or reactive. During the reactive responses the gaze moved across the occluder after the object had been visible for 200ms. The predictive responses included all passages in which the gaze moved before the target had been visible for 200ms. This criterion was based on the average reactive saccadic latency to moving targets in adults (Engel et al. 1999) and infants (Gredebäck et al. 2006). Thus, in Study I and II the prediction rate was calculated. The prediction rate reports how often infants succeed in predicting the reappearance of the target relative to the total number of attended passages (number of predictive responses/number of predictive and reactive responses). While Study I focused on the temporal characteristics of the infants' predictive and reactive gaze responses, Study II involved one additional measurement, namely the accuracy rate (the number of accurate predictions divided by the number of accurate and inaccurate predictions). This measurement takes into account where along the occluder edge infants predicted the target to reappear. This measurement reports whether infants' predictive responses terminated near the actual reappearance location of the target (as defined by the dark grey area in Figure 5) or at some other part of the occluder's edge (white areas in Figure 5).

Whereas Study I and II focused on measurements of saccadic eye movements during complete occlusion, Study III measured the smooth pursuit component of the eye movements when a moving object underwent partial occlusion. In this study, in order to be included in the analysis, participants were required to be attentive at least 1/3 of the time in each of two experimental conditions. Then the gain of the smooth pursuit and its timing were calculated for these trials.

To calculate the smooth pursuit, eye movement velocities higher than 25°/s were eliminated from the raw gaze tracking record. This was done separately for the horizontal and vertical component of the gaze tracking. The Tobii eye tracker does not separate the eye and the head movements. In order to decide if the was an influence of head movements on the smooth pursuit we checked the distances from each eye to the display screen. If the head turns, the relation between these distances will change. It was found that this was not the case and therefore, it was concluded that the smooth gaze movements registered by the eye tracker were smooth pursuit eye movements.

At the next step, the smooth pursuit gain was calculated as a ratio of the smooth pursuit amplitude to the object motion amplitude at every half of the motion cycle of the object (referred to as a passage below). It was also decided that a participant followed the motion on the display with smooth pursuit if the peak to peak amplitude for at least one of the above mentioned dimensions was greater than 1°. If the amplitude was lower, the passage was excluded from the analysis. In the beginning and end of each movie, the first and the last quarters of the object motion cycles were excluded, leaving 15 full object passages for the analysis.

Direction of smooth pursuit was defined as the ratio between the horizontal gain and vertical gain at every passage of the object motion included in the analysis. If the ratio was greater than 1, the smooth tracking direction was considered to be horizontal; otherwise the subject had tracked the object vertically. Depending on the tracking direction the data were divided into one of two categories: following global motion of the integrated object (horizontal direction) and following local motions of the object's parts (vertical direction).

The timing of smooth pursuit was calculated for every trial and for both the horizontal and vertical directions as the median of the time shift between the sine approximation of the eye movement and the object motion at the passages included in the analysis.

The eye and head tracking in all three studies were analyzed in space and time with programs written in the Matlab environment (Mathworks Inc.). The statistical analysis was performed in SPSS. For Study I and III, the analysis was performed using ANOVAs with Tukey HSD post hoc comparisons (Study III). All three studies used regression analyses to reveal the changes of predictive passages (Study I & II) or accuracy rate (Study II) and the amount of global vs. local smooth tracking (Study III) with time.

Study I (When)

In Study I infants in the age range of 3.5 to 4.5 months visually tracked a horizontally moving object that was temporary occluded in the middle of its trajectory. The aim of this study was to determine the principles underlying infants' ability to anticipate reappearance of the temporarily occluded moving objects. For this purpose, two experiments were performed with a wide variety of conditions where velocities, amplitude of the moving object, as well as occluder width, were systematically manipulated. Such manipulations help to distinguish between several modes of cognitive mechanisms underlying 'predictive' actions at occluders. In this respect, most informative are the gaze shifts that arrive before the object reappears from behind the occluder (pre-reappearance gaze shifts (PRGS)).

In the first experiment infants were presented with occlusion durations ranging from 220 ms to 610 ms. These were obtained through combination of 3 different velocities of the object and 3 different occluder widths. The purpose of Experiment 1 was to investigate how infants around 4 months of age are able to take occlusion duration into account when making PRGS and what strategy they use in doing it.

In the second experiment of Study I two different amplitudes of object motion were introduced. Besides giving broader range of occlusion durations (from 200ms to 1660ms), introducing different amplitudes of object motion helped to disentangle effects of the object velocity and oscillation frequency on infants' tracking.

We tested four different hypotheses regarding modes of making PRGS. The first of them, the passage of time hypothesis, stated that the more time that passed from the moment of object disappearance the greater the chance that infants just accidentally shift gaze over the occluder. An implication of this mode is that the longer the occlusion duration, the higher the number of saccades will be counted as predictive purely because the average mean is based on a larger range of values.

The second hypothesis tested stated that participants move gaze over the occluder before the object reappears because of the visual salience of the exit occluder edge.

The third hypothesis stated that predictive gaze shifts over the occluder were determined by the remembered duration of the previous occlusion. In this case, correct anticipation of when the object will reappear does not require the participants to represent the moving object behind the occluder. What would be needed is just an assumption that the object would to be absent for the same period at the next occlusion.

The fourth hypothesis tested stated that the PRGS were determined by some kind of representation of the occluded object motion. Information about occlusion duration may be derived from the oscillation frequency, object velocity, and occluder width. If the subject has knowledge of the occluder width and the object velocity, then the occlusion duration could be obtained through mental arithmetic, that is, by dividing occluder width with object velocity. However, instead of having explicit knowledge of this multiplicative 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.

Design

In the first experiment seven combinations of oscillation frequency and occluder width were included, instead of the nine possible. The largest occluder was not combined with the slowest velocity and the smallest occluder was not combined with the fastest velocity (see Table 1, Experiment 1). At every trial the object always started and finished its trajectory behind the occluder. Each trial lasted 25s, thus, the number of times the object went behind the occluder varied from 7-8 passages for the lowest object motion frequency to 14-15 passages for the highest one. An example of an infant's performance can be seen in Figure 6.

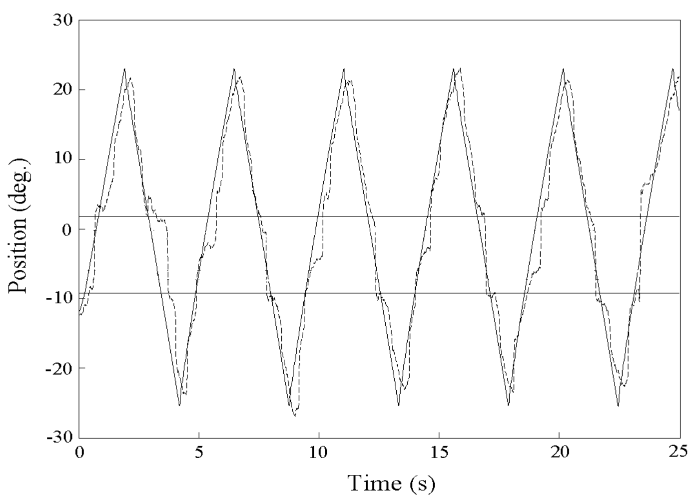

Figure 6. An example of a trial showing an infant's gaze tracking at a frequency of 0.21Hz over an 11.6° wide occluder with 24°amplitude of motion. The horizontal lines in the figure show the occluder boundaries (i.e. positions where half of the object has become occluded or already reappeared from behind the occluder).

Table 1. The average occlusion duration and the number of occluder passages per trial for the different conditions in Experiment 1 and Experiment 2.

Experiment 1

Occluder Width		Frequency / Velocity	0.15Hz / 15°/s	0.21Hz / 21.4°/s	0.30Hz / 30°/s
11.6°	Occlusion duration (s)		0.31	0.22	—
	Passages per trial		7-8	11-12	
15.5°	Occlusion duration (s)		0.57	0.39	0.28
	Passages per trial		7-8	11-12	14-15
20°	Occlusion duration (s)		—	0.61	0.43
	Passages per trial			11-12	14-15

Experiment 2

Frequency		0.15 Hz		0.30Hz	
Occluder Width	Velocity	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 per trial	7	7-8	7-8	14-15
20°	Occlusion duration (s)	1.66	0.88	0.86	0.48
	Passages per trial	7	7-8	7-8	14-15

Results

In the first experiment, 47.4% of the gaze shifts were made as PRGS on the attended passages of the object motion. In most of them (88%) the gaze stopped at the occluder edge when the object disappeared there, and subsequently made a saccadic shift to the other side.

The PRGS were not determined by the duration since disappearance, but rather by anticipation of the time of object reappearance from behind the occluder. This can be seen in Figure 7. Independently of condition, infants displayed sensitivity to the occlusion duration. The correlation between individual mean latencies of PRGS and the occlusion duration was 0.658 ($p < 0.001$).

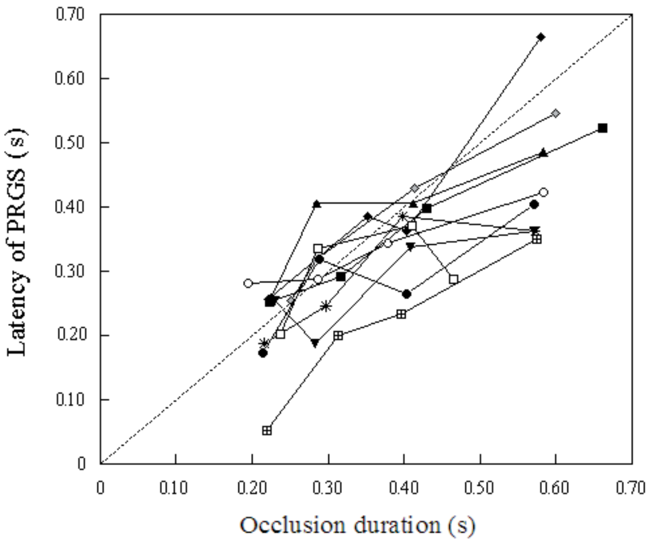

Figure 7. The relationship between the occlusion duration and PRGS for individual participants in Experiment 1. In the figure the latencies for the adjacent occlusion durations (0.28 and 0.31s, 0.39 and 0.43s, and 0.57 and 0.61s) are averaged to make the individual curves easier to distinguish. The dotted line shows the hypothetical relationship with the saccade latency equal to the occlusion duration.

Due to the design of Experiment 1 we could test the effects of occluder width on the timing of PRGS only for the intermediate values of oscillation frequency and vice versa. Both changes in occluder width for 0.21Hz of oscillation frequency and changes in oscillation frequency for 15.5° of occluder width influenced the timing of PRGS [occluder width: $F(2, 18) = 13.68$, $p < 0.01$, $\eta^2 = 0.60$; oscillation frequency: $F(2, 18) = 5.539$, $p < 0.02$, $\eta^2 = 0.38$].

In the second experiment we observed pre-reappearance gaze shifts in 50% of attended passages of the object motion. And again in 89% of the cases the gaze stopped on the object disappearance side of the occluder before making a saccadic shift over to the other side.

The second experiment also confirmed the result of Experiment 1 that the timing of the PRGS was not determined by the time of disappearance of the object, but rather by the time of its reappearance. Figure 8 shows the relationship between pre-reappearance gaze shifts and the occlusion duration for individual participants. The correlation between individual mean latencies for the different conditions and occlusion duration is 0.9 ($p = 0.00$).

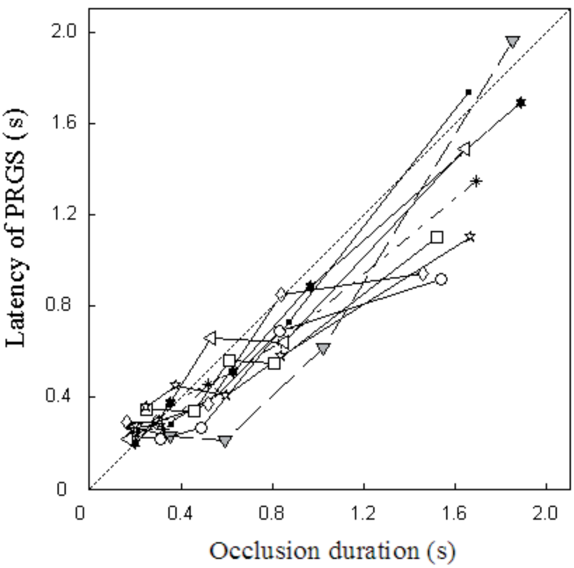

Figure 8. The same as Figure 7 but for Experiment 2. Occlusion durations averaged (0.34s and 0.35s, 0.48s and 0.64s, 0.86s and 0.88s).

Repeated measures ANOVA performed on the PRGS latencies confirmed the significant effects of occluder width ($F (1, 8) = 120.2$, $p < 0.00$, $\eta^2 = 0.94$) and oscillation frequency ($F (1, 8) = 15.20$, $p < 0.00$, $\eta^2 = 0.66$) observed in Experiment 1. Moreover, motion amplitude also showed significant influence on the timing of the pre-reappearance gaze shifts ($F (1, 8) = 87.35$, $p < 0.00$, $\eta^2 = 0.92$). While occluder width had a direct effect on the average latency of PRGS, oscillation frequency and motion amplitude had inverse effect on it. In addition, there was a significant interaction between occluder width and oscillation frequency ($F (1, 8) = 16.35$, $p < 0.00$, $\eta^2 = 0.67$), motion amplitude and occluder width ($F (1, 6) = 28.28$, $p < 0.00$, $\eta^2 = 0.78$), and oscillation frequency and motion amplitude ($F (1, 6) = 9.483$, $p < 0.02$, $\eta^2 = 0.54$).

Conclusions

Of the four modes tested the study gives strong support only for the cognitive mode hypothesis. 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 was determined by the duration of the occlusion. Indeed, 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 match between the latency of PRGS and occlusion duration. It is possible that separate interacting mechanisms are responsible for these effects.

Another possibility is that the object velocity is somehow represented while the object is occluded. If the infants are able to imagine the motion behind the occluder, they could simply track the object in their "mind's eye". This representation might not, however, 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 located at the specific time behind the occluder. It could rather be expressed as preparedness for the object reappearance on the other side of the occluder. Support for the hypothesis that infants represent the velocity of the occluded object can be found in the results of studies which show 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 may represent object motion during occlusion in a similar way. The critical stimulus variable for preserving a representation of object motion over occlusion could be the 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 had 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.

When does such intelligent behaviour appear in the child's 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. Thus, the developmental onset of predictive smooth pursuit and predictive saccadic tracking might both be related to the onset of the 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.

Study II (Where)

Study II of this thesis included two experiments. The purpose of Experiment 1 was to examine the ability of 6-month-old infants to make temporal and, more importantly, spatial representations of an object completely disappearing behind the occluder, based on either its pre-occlusion trajectory or on recent experience with the event. Experiment 2 investigated more deeply the effect of recent experience and training on the robustness of the object representation in temporal and spatial domain over longer time periods.

Design

In contrast to Study I, in this study we separated the linearity of the moving object trajectory and its repetitiveness. This time the infants were presented with movies where a multicolored ball rolled back and forth and underwent occlusion. Both the ball and the occluder cast light shadows on the background and the ball reflected some light; this was done to enhance the perception of a three-dimensional occlusion event. Moreover, to be sure that infants did not use the occluder sides in order to get landmarks that might help them to associate the object disappearance with object reappearance location, we changed occluder form from the classical rectangular used also in Study 1 to a circular one.

In Experiment 1 6-month-old infants were presented with one of two conditions: variable-linear or fixed nonlinear. In every condition 8 movies were presented, each comprised two complete occlusion events. Thus, every infant was presented with 16 complete occlusion events. The total duration of each movie equaled 9s. The duration of the full occlusion period was 700 ms and the accretion/deletion period lasted 333 ms.

In the first condition (below referred to as variable-linear condition) the infants were presented with multiple linear trajectories whose starting position (and thereby disappearance and reappearance locations) were randomized between movies. Thus, the ball started to move up, down, left or right and rolled back and forth between 2 endpoints, always starting to move from and finishing behind the occluder, completing 2 full occlusion passages. Here, we estimated infants' ability to extrapolate pre-occlusion trajectories of the object, independently of recent experience. One example of a linear trajectory is presented in Figure 9A.

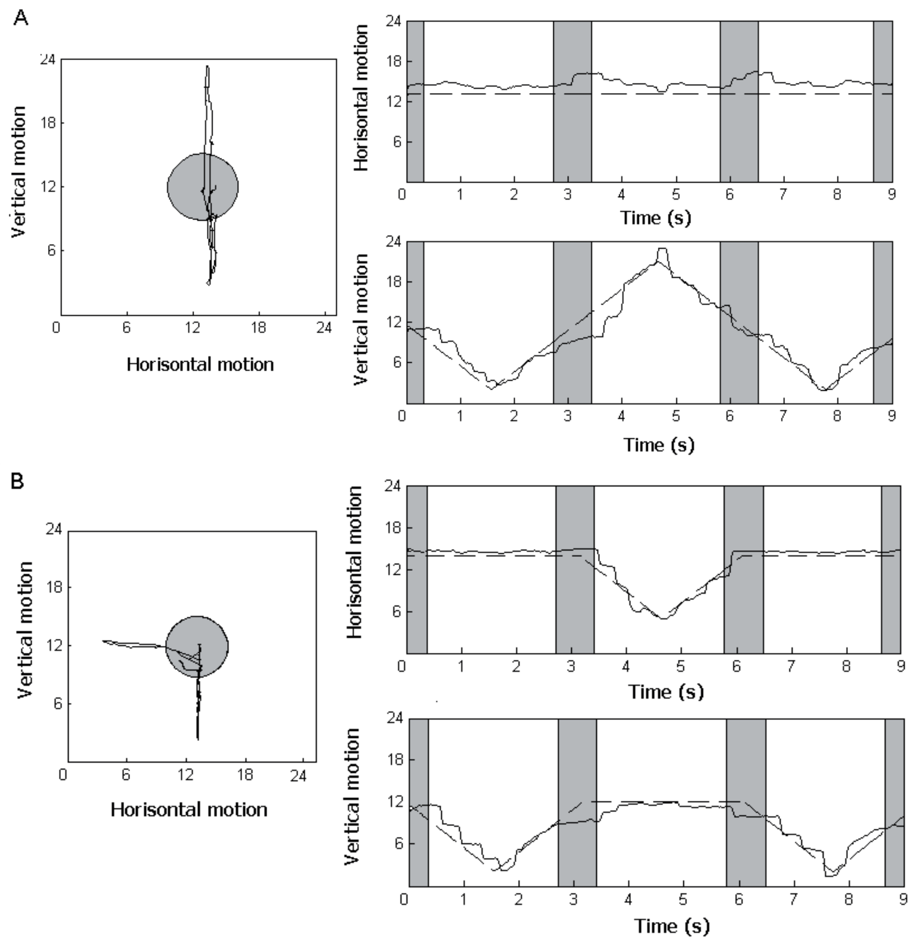

Figure 9. Examples of the target trajectory and the infants' gaze in one linear (A) and one non-linear (B) movie. Grey areas indicate the location of the occluder. The solid line represents gaze and the dashed line represents the target.

The individual stimuli presented to infants in the second condition (fixed non-linear condition) were identical to the stimuli in the variable linear condition with one exception. During each occlusion passage the ball did not continue along the linear extension. Instead its direction of motion shifted 90° when it was behind the occluder. One example of such a trajectory can be found in Figure 9B. Each infant was presented with only one of the eight possible trajectories: the ball could start in any of the four directions - up, down, left, and right - and could shift ±90° with respect to initial direction.

In Experiment 2 the infants were presented only with fixed non-linear condition. Each infant viewed three identical experimental sessions: the first two sessions were presented during the infant's first visit to the lab, with a 15 min pause in-between, and the third session was presented 24 hours later.

Results

Neither the amount of predictive responses to the occlusion event nor the amount of accurate predictions showed any differences between two conditions in Experiment 1. Infants were predictive in 47 ± SE 3.7% of the occlusion passages in the fixed non-linear and in 43 ± SE 2.1% of the occlusion passages in the variable linear condition. They also had comparable levels of accurate predictions (66 ± SE 0.7% during non-linear passages and 76 ± SE 0.25% during linear passages), except for the two very first passages of occlusion [$t(34) = 2.7$, $p < .01$]. Thus, in the variable linear condition infants' accuracy level did not change over successive occluder passages (see Figure 10A). However, infants presented with the fixed non-linear condition rapidly improved their accuracy from 0% correct predictions on the first occlusion passage to 63% on the third passage. Such rapid learning was best described by a logarithmical model ($y = 17.3 + 25.2 \ln(x)$, $R^2 = .45$, $F(1, 14) = 11.37$, $p < .005$, see Figure 10B). In this condition, the object trajectory changed unexpectedly when it was moving behind the occluder, so it was impossible to make correct predictions from the very beginning. What was possible was to extrapolate the linear pre-occlusion path and this is what infants did in the beginning. However, extrapolations dropped rapidly with more experience of the non-linear object trajectory ($R^2 = .34$, $F(1, 14) = 7.1$, $p < .02$).

During the first session of Experiment 2 we replicated the effect of rapid improvement in the correct anticipation of reappearance position, and decrease of the predictive linear gaze shifts over the occluder, observed in the fixed non-linear condition of Experiment 1.

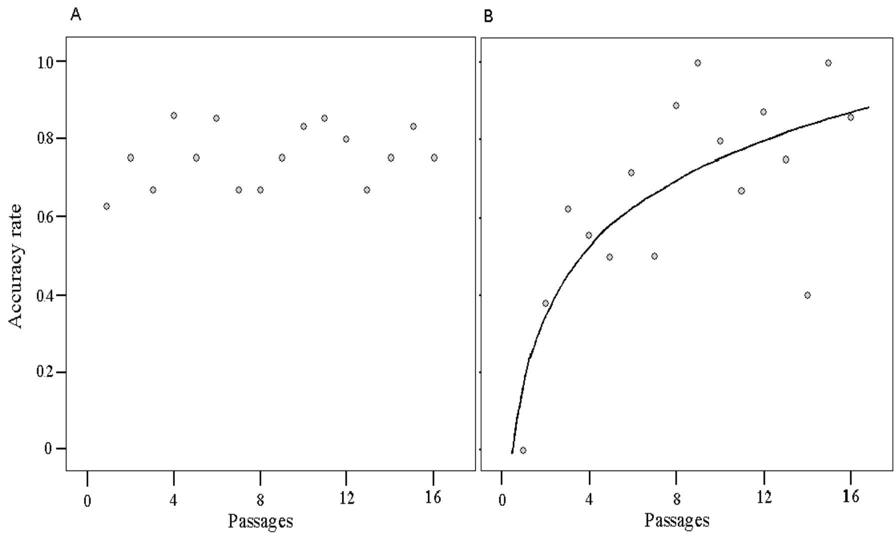

Figure 10. Accuracy rates (number of accurate predictions / (number of accurate + inaccurate predictions)) over successive occlusion passages in the variable linear (A) and fixed non-linear (B) conditions of Experiment 1. The X-axis shows each occlusion passage during one experimental session. The solid curve depicts the regression line with most explained variance. Note that no significant regression line exists for the variable linear condition.

Here again, rapid increase in the accuracy rate occurred over the first few trials[2] (see Figure 11, left panel). Moreover, during the second session, after a 15 min break, the infants continued to improve their accuracy rate[3] (see Figure 11, middle panel) and finally, 24 hours later, the infants' accuracy was still significantly better than during the very first 8 occlusion events the day before ($p < .05$).

Rapid decrease of predictive linear gaze shifts over the occluder was only observed during the first session of Experiment 2. No such effect could be detected during the later sessions.

[2] Best data fit ($R^2 = .58$, $F(1,14) = 19.4$, $p < .001$) by the logarithmic model: $y = 1.0 + 29\ln(x)$

[3] Learning was best described by linear regression model: $y = 43.4 + 3.2x$, $R^2_{adj} = .45$, $F(1, 14) = 13.4$, $p < .003$

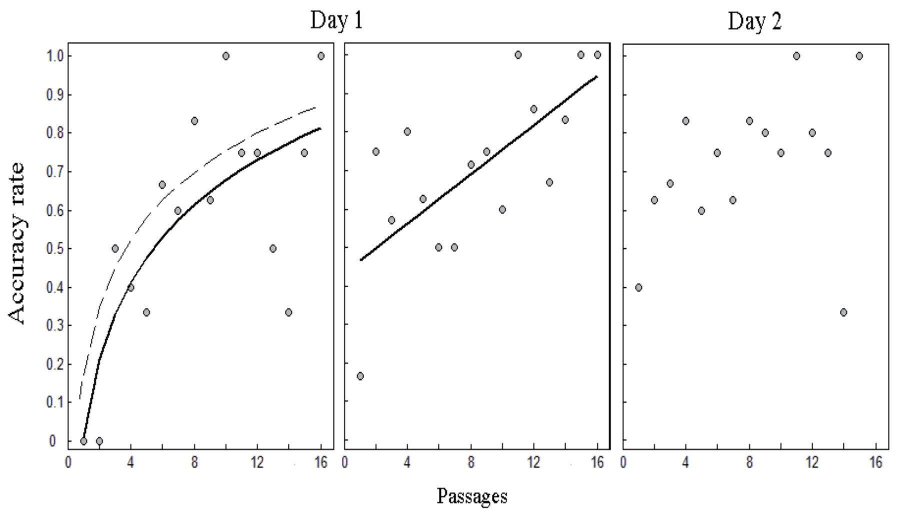

Figure 11. Accuracy rates (number of accurate predictions/(number of accurate + inaccurate predictions)) over successive occlusion passages in each block of Experiment 2. The left panel shows the initial testing session; the middle plot shows the second experimental session which took place after a 15 min break. The right panel depicts the third experimental session after a 24 h break. The solid curve shows the regression line which explains most of the variance. The dashed line shows the regression curve in the fixed nonlinear condition of Experiment 1. Note that no significant regression line exists for the third session.

Conclusions

In the first experiment, we demonstrated that 6-month-old infants can predict both when and where the moving object would reappear. They did it in two different ways, depending on the object trajectory. In the very beginning, before seeing where the object would actually reappear, the infants tended to extrapolate the pre-occlusion trajectory of the object, and continued to do so unless an alternative experience became available to guide predictions. The infants' initial reliance on the extrapolations of pre-occlusion trajectory is equally prominent in both conditions. If initial extrapolations accurately predict where the target will reappear (as in the variable linear condition) the infants will continue to extrapolate the pre-occlusion trajectory, thus maintaining initial asymptotic performance. However, if the same extrapolations provide an unreliable predictor of future outcomes (the fixed non-linear condition) then infants rapidly learn to rely on the alternative sources of information.

Thus, it can be concluded that 6-month-old infants possess a good understanding of the basic physical constraints that govern object motion. This understanding is easily generalized to novel situations. As a consequence, the infants display accurate linear predictions from the very first occlusion passage. In addition, 6-month-olds showed a remarkable ability to adjust their expectations to accommodate unexpected events. After being presented with only two fixed non-linear occlusion events the infants adjusted their predictions accordingly.

The second experiment confirms this later finding. Another group of 6-month-old infants tested with the same nonlinear object trajectories showed results comparable to the previous group (see Figure 10). This finding corroborates our conclusion that 6-month-olds are able to use recent experience to form new expectations, and these predictions are formed very rapidly once a new repetitive pattern appears. Moreover, the 2nd and 3rd sessions of Experiment 2 provide evidence that 6-month-olds are able to preserve this newly learned information in memory. At the same time, the infant's ability to maintain these novel expectations is easily disrupted by temporal delays. Only after multiple sessions will the infants' new experiences stabilize long enough to withstand a 24 h break.

Thus, it can be suggested that in order to guide their actions infants form new expectations by perceiving reoccurring events and generalize these events to novel situations. The infants' rapid learning in predicting non-linear trajectories suggests that this ability plays an important role in how we perceive occluded objects.

Comparing the results of the different conditions of the two experiments we can suppose the following. Although linear trajectories are extrapolated, whereas non-linear trajectories are predicted through an accumulation of the recent experiences, these two abilities may have a common ontology because of the rapid long-term learning effects demonstrated in the second experiment. It is possible that the infant's initial tendency to extrapolate and their ability to generalize from recent experience both stem from past experience. This does not mean that there are no differences between the two conditions. Instead, it is possible that existing differences arise from variations in the frequency of exposure to these different constraints.

Thus, the infant's tendency to extrapolate is closely related to the natural constraints governing the object motion. This means that infants have had ample experience of these constraints. In contrast, the non-linear trajectory is governed by the novel constraints that infants have little or no experience with.

Study III (What)

This study takes a slightly different approach to exploration of the infants developing representation of moving objects. Instead of a complete occlusion event as in previous studies, we introduced a partial occlusion. Here, the whole moving object was never seen, but instead only parts of it appeared and disappeared behind multiple occluders. We explored 5- and 9-month-old infants' ability to track perceived object unity with smooth pursuit. According to previous adult studies (Beutter & Stone, 1999; Stone, Beutter, & Lorenceau, 2000), the smooth pursuit measurement would reflect ability to separate object and background only on the basis of the object's coherent motion even if it was never fully seen. This developing ability was compared to the performance of an adult group.

Design

In this study all three age groups were presented with a line-figure rhombus moving sinusoidally behind 3 vertical occluders separated with gaps. Through these gaps four moving figure segments were visible but the vertices of the figure were always behind the occluders. Every subject was presented with 8 trials of object motion, each lasting 24s. During every trial the object completed 8 full horizontal cycles. The order of the trial presentation counterbalanced two different types of occluders (visible and invisible), two different colors of the moving object, and left- and rightward initial object motion.

The *visible* and *invisible occluder* conditions were obtained by changing color contrast between background and occluders, so that in the invisible condition their colors coincided. Previous adult studies (Beutter & Stone, 1999; Stone, Beutter, & Lorenceau, 2000) showed that saliency of occluder edges would emphasize different terms for perceiving global motion, making it impossible to perceive coherent motion when no salient occluder edges are visible. Moreover, the same studies have shown that the process of perception is interlinked with smooth pursuit tracking in adults. Thus, smooth following of the integrated object's veridical motion will reveal an ability to perceive the object as an integrated unity in adults. In infants smooth following of the direction of integrated motion of the objects' parts will also show the degree to which the smooth pursuit is controlled by world-centered coordinates.

In order to explore the infants' developing ability to smoothly track an object as a united pattern, we calculated the amount of smooth pursuit in the horizontal and vertical directions and its distribution over the exposure time in every condition.

Results

We found that in the *visible occluder* condition the smooth pursuit following of the object coherent motion increased with age ($F (2, 52) = 6.8$, $p < .003$). The most rapid change in the amount of smooth tracking of the coherently moving object happened between 5 and 9 months of age (Tukey HSD $p < .002$). Moreover, the level of global smooth tracking in 9-month-old infants did not differ from adults. No such improvement was observed in the *invisible occluder* condition.

Actually, the amount of coherent smooth tracking observed in 5-month-old infants in the *visible occluder* condition was not different from smooth pursuit following in the *invisible occluder* condition in all three age groups. The only difference we could observe here was the development of the smooth tracking with increased time of exposure. While smooth pursuit in the *invisible occluder* condition did not change over time, smooth pursuit tracking of the global pattern of motion in the *visible occluder* condition increased in 5-month-olds over the trial ($F (1, 20) = 6.1$, $p < .02$, Tukey HSD, $p < .05$). Furthermore, both 9-month-old infants and adults showed an increase within trials of smooth coherent tracking, which was very similar to the performance of 5-month-olds in the *visible occluder* condition. All three groups became better tuned to the global motion of the object with increasing exposure time. This relation is illustrated in Figure 12.

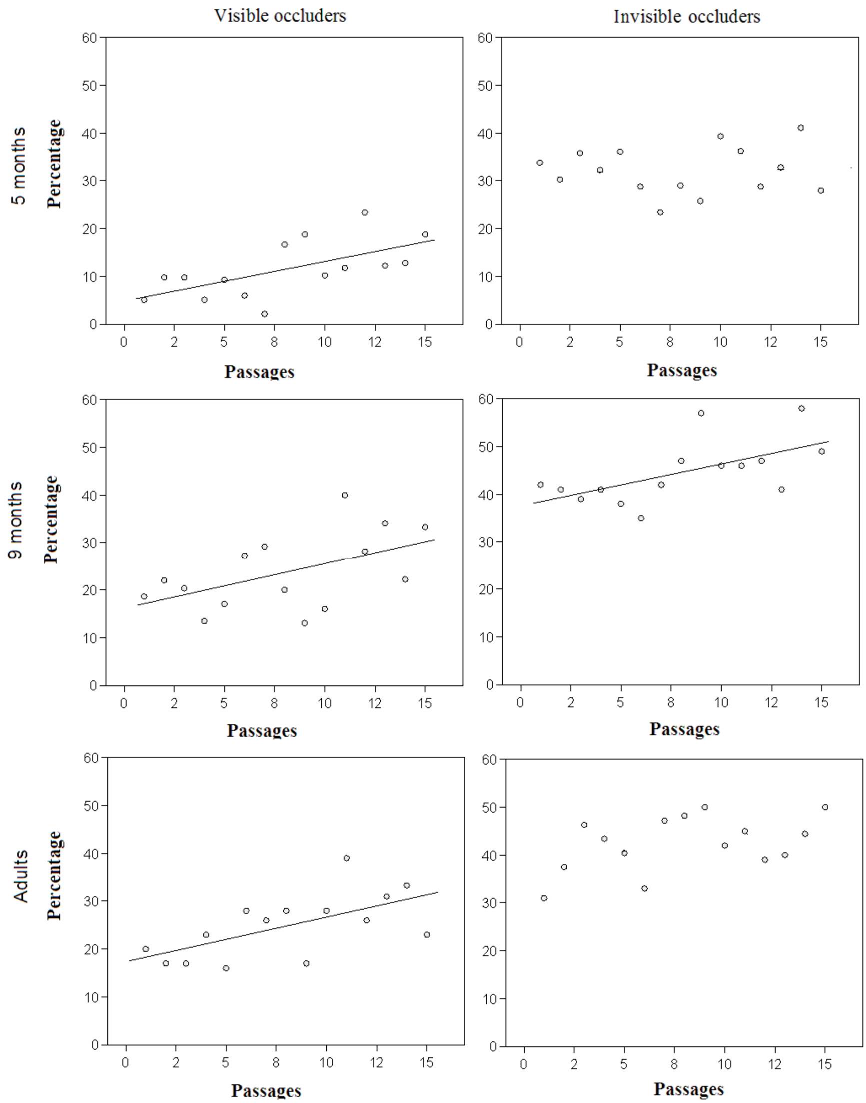

Figure 12. The fraction of smooth pursuit on every object passage as a function of number of passages performed by infants and adults in both conditions. Solid lines show statistically significant regression.

Conclusions

The results of this study indicate that both 5- and 9-month-old infants can combine incompletely visible information in order to follow motion of an integrated object with smooth pursuit. Moreover, 9-month-old infants are able to control direction of their smooth pursuit according to perceived global motion of an integrated object at the same level as adults. Although 5-month-old infants control smooth pursuit tracking of the global motion of an integrated pattern to a lesser degree than 9-month-old infants and adults, the similarity of the increase in smooth pursuit over the exposure time in all age groups confirms that the same neural mechanisms might be involved in this process for all age groups.

To perceive *what* is really moving on a display where only incompletely visible information is presented, and, moreover, to follow it with smooth pursuit, infants have to develop an ability to refer to head- or world-centered coordinates. In this case, the representation of the whole object, and smooth pursuit in direction of its motion, cannot be explained just by the retinal slip of single motion elements. The visible elements of the presented object move in different directions so slips on the retina are happening in different directions at the same time. Thus, to produce smooth pursuit in the direction of the integrated object motion, a mechanism which takes into account all these directions is needed. It will calculate motion of the whole entity in world centered coordinates. In adults the MST area is involved in combining such information (Stone & Krauzlis, 2003).

Thus, it can be assumed that the MST area starts to be involved in this process at 5 months of age but that it continues to develop over the first year of life. Significant shift in control of smooth pursuit by world-centric coordinates happens between 5 and 9 months of age. Despite this, observing continuously moving visible parts of the object in the *visible occluder* condition strengthens control of smooth pursuit into direction of more frequent tracking of the perceived global motion in both infants and adult groups.

General Discussion

The studies included in this thesis focused on the three different aspects of the development of object representation in infancy. The first study explored infants' ability to maintain temporal continuity of a disappearing object. Study II concentrated on the spatial aspects of such representations and Study III examined what is actually represented. Although the focuses of these object representation studies were different, the results showed that learning of some kind was involved in all cases. It was somewhat unexpected because only the design of Study II was in fact adapted to learning. Below I will address more closely the studied aspects of the object representation and the role of learning in the process of its development.

Time representation

Although we tested several alternative hypotheses in the first study in order to explain 4-month-olds' ability to make predictive gaze shifts over an occluder, only the hypothesis that object motion is represented over occlusion received support from the collected data and could explain the infants' ability to time their PRGS to the object reappearance.

The results of Study I indicate that infants can represent the temporal characteristics of the disappearing object already at 4 months of age. In this study, infants had a tendency to time their anticipatory gaze shifts to the time of object reappearance in the same way as was previously observed in 6-month-old infants (Gredebäck & von Hofsten, 2004). The close timing was observed in different infant groups in both the experiments of Study I.

The range of the occlusion durations presented to infants in both experiments of Study I varied from 220ms (200) to 1660ms. Although infants had individual differences in timing of their PRGS, on average, PRGS were performed when around 70-80% of the occlusion time had passed. At the same time, we observed a clear tendency to overestimate the duration of short occlusions and underestimate the duration of long ones. Such discrepancy implies that, although infants at this age are able to represent object velocity and prepare their gaze shifts for the reappearance of the object, the representation of the reappearance time is not perfect and is influenced by stimulus conditions. This assumption is supported by the previous results of

Johnson et al. (2003). They found that showing unoccluded object motion before exposing 4-month-old infants to an occlusion event could significantly increase the amount of PRGS. This effect was not present in 6-month-olds.

Although representation of the temporal characteristics of object motion in 4-month-old infants is not as robust as at 6-months of age, 4-month-olds can develop more stable representation of object temporal continuity with experience. We found that infants in Study I significantly increased the amount of PRGS towards the end of individual trials at 0.3Hz frequency (Figure 13). In these trials, performance began less well geared to the reappearance of the object but, by the end of the trials, the infants predicted the object's reappearance as well as they did for lower frequencies. Here 4-month-olds could produce PRGS from the beginning of the trial but towards the end they improved the timing of their PRGS relative to object reappearance.

These results support finding by Rosander and von Hofsten (2004). These authors also saw strong learning effects during single trials in infants from 7 to 21 weeks of age. In that study infants were exposed to an object moving repetitively at 0.25Hz. PRGS were observed only from around 18 weeks of age, but the younger infants decreased their reaction times to the object reappearance over the repetition period.

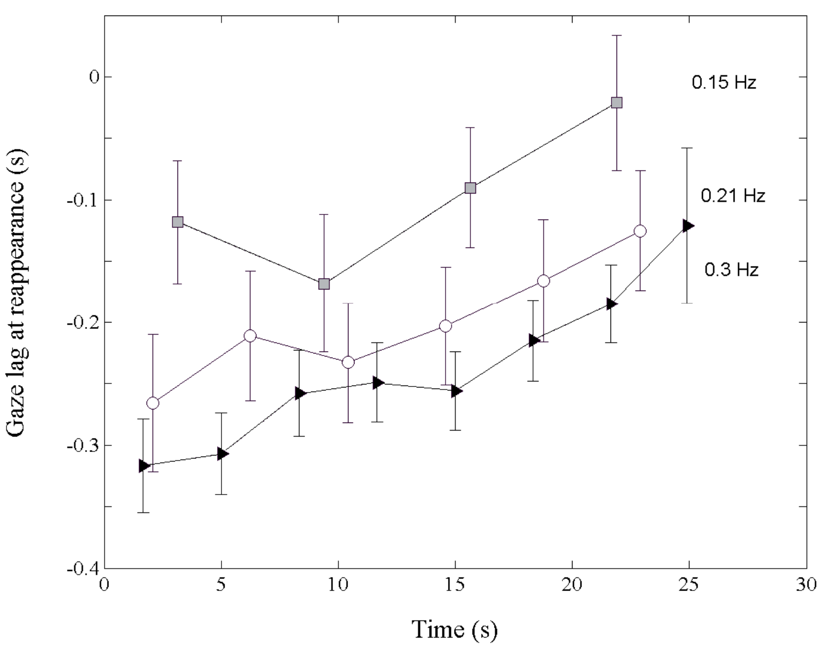

Figure 13. Mean gaze lag at reappearance for each passage within single trials of Experiment 1 and 2 of Study I plotted as a function of elapsed time during trials. Separate curves are shown for each oscillation frequency.

In the first experiment of this Study I we also observed a learning effect over the whole experiment. This learning was observed despite the fact that infants were randomly exposed to the different occlusion durations during the experiment. Moreover, the increase in PRGS was confined to the first 2 trials of the experiment (see Figure 14).

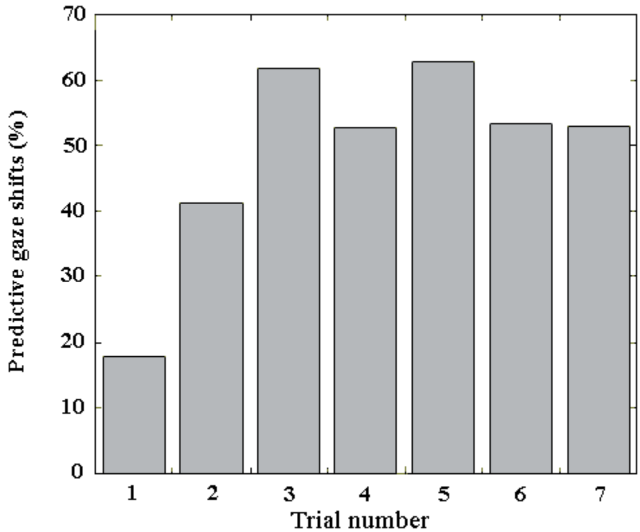

Figure 14. Learning between trials had a significant effect on the latency of PRGS ($R^2 = 0.68$, $F(1,6) = 10.5$, $p = 0.023$) in the first experiment of Study I. This dependence is best described by equation $y = 26.45 + 18.57 \ln(x)$.

The learning effects in 4-month-old infants observed in the present study, taken together with previous results by Rosander and von Hofsten (2004) and Johnson et al. (2003), reveal that infants at this age are able to learn from experience with moving objects in order to develop stable representations of object continuity over periods of occlusion.

Space representation

The second study of this thesis focused on 6-month-old infants' ability to form spatial representations of where a moving object will reappear after occlusion. Moreover, we also examined the role of learning and long term memory in this process.

To be able to address these questions, we presented infants with two sets of stimuli that can only be correctly predicted through linear extrapolations or through recent experience. Infants could not simultaneously use both these mechanisms as in previous studies (Gredebäck & von Hofsten, 2004; Gredebäck et al., 2002; Johnson et al., 2003; Meichler & Gratch, 1980; Nelson, 1971, 1974; Rosander & von Hofsten, 2004; Spelke & von Hofsten, 2001; von Hofsten et al., 2000). This separation helped to reveal that infants at this age are able to extrapolate the initial pre-occlusion trajectory of the moving object. In other words, infants at this age can represent spatial continuity of the object moving on a linear path and they do not need previous experience of where the object will disappear and reappear. In parallel to this well-established mechanism, 6-month-old infants also learned rapidly from new experiences *where* the moving object reappeared when its linear trajectory suddenly changed under the occluder. However, before infants could acquire this new experience, they used extrapolation mechanisms for future expectation of the object reappearance location.

When infants at this age learn new locations of the object reappearance, the learning process is very rapid. The actual learning primarily occurs during the first two trials of object motion. After this, infants' correct localization of the object reappearance position is highly comparable with their performance when using the extrapolation mechanism. This pattern of learning was observed to be the same for different groups of infants tested with the same task in experiments 1 and 2 of this study.

This learning of the object reappearance position at 6 month of age can be compared with learning of temporal continuity of the object behind the occluder at 4 months of age over the entire first experiment of Study I. Although 4-month-old infants needed more experience with a stimulus, both learning patterns reflect the same curve-linearity principle in which the major increase in correct performance is concentrated in the beginning of the session. This pattern may reflect a basic ability of infants to pick up new information.

Further exploration of the 6-month-olds representation of the object reappearance location included the study of their capability to maintain the new pattern of object motion over long-term breaks. We found that infants at this age are able to remember the learned pattern of the object motion over a 24 hour break. This effect is quite remarkable given the massive flow of visual information that infants are bombarded during this period.

Thus, we can conclude that 6-month-olds have an initial tendency to predict the reappearance location of temporarily occluded objects by extrapolating the pre-occlusion trajectory. Moreover, they also demonstrate a remarkable ability to absorb information from recent events and maintain this information to predict the outcome of future occlusion events. The initial tendency to extrapolate the object trajectory and the learning from new experiences have different patterns of development, but it can be assumed that these two abilities have a common ontology.

It is here suggested that infant’s initial tendency to extrapolate and their ability to generalize from recent experience both stem from past experience. Differences in infants’ performance observed when they are exposed to linear and curvilinear object motion can arise from variations in the frequency of exposure to such patterns of object motion in the past. Infant’s tendency to extrapolate is closely related to the natural constraints governing object motion. This means that infants have had ample experience with such motion. In contrast, the non-linear trajectory is governed by novel constraints that infants have little or no experience with.

Object representation

In the first two studies of this thesis, we found that in situations of complete occlusion infants at 4 months of age are able to represent temporal continuity of the object motion. Infants at 6 months of age show evidence of representation of object motion in both time and space. The third study presented in this thesis focused on *what* infants can perceive in a situation where the occlusion is not complete but only fragments of the moving object are visible.

The results of Study III reveal that the smooth pursuit tracking of 9-month-old infants and, to a lesser degree, of 5-month-old infants is determined by the global motion direction of a partly occluded object. At 5 months of age infants begin to perceive and follow the global motion of the integrated object with smooth eye movements. The major improvement in this ability occurs between 5 and 9 months of age. Nine-month-old infants follow the global motion of the integrated object with smooth pursuit at a level comparable to the level of performance in an adult group.

At the same time, all three age groups showed similar tuning patterns to the coherent object motion during single experimental trials. This similarity suggests that if motion of an integrated object is perceived, it is processed by the same neural mechanisms in all three age groups. Moreover, the perception of global motion of an integrated object is subject to learning effects at all ages studied.

The ability to follow the motion of an integrated object with smooth pursuit implies the ability to process motion of the entire object in world-centric coordinates. According to Stone and Krauzlis (2003), the MST brain area plays a role in the process of transition from the retino-centric coordinate system to the world-centric one. Thus, we can assume that MST is involved in the control of global smooth pursuit already at 5 months of age. Moreover, the process of transition from smooth pursuit, controlled by displacements of stimuli on the retina, to the perceived external motion of the object took time in all age groups. In other words, the smooth pursuit system becomes better tuned to the perception of global motion with increasing time.

The notion that the same neural mechanisms are involved in the control of the global smooth pursuit does not answer the question of why 5-month-old infants had more difficulty in following the integrated object motion than the two other age groups. One possible explanation may be related to the combination of the object velocity used in this study and the point in the infants' development when the MST area becomes functional.

In this study, object velocity was relatively low, only 3.4°/s, which is half of the velocity used by Dobkins et al. (2004), and only 1/3 of the object velocity used in the study by Beutter and Stone (2000). Such low velocity was chosen to minimize the portion of saccades in participants' tracking patterns, but it was also crucial for calculating coherent global motion. In fact, both 9-month-olds and adults followed global motion of the object only around 1/5 to 1/ 4 of time. But for 5-month-old infants the effect of velocity was most critical. If the MST area only begins to function around 5 months of age, then the pathways from this area might not be mature enough to handle a wide range of velocities over which global motion of stimuli can be integrated and tracked with smooth pursuit. As a result, we observe much lower performance for global following in 5-month-old infants.

This hypothesis finds support in the amount of smooth pursuit elicited in response to the incoherent motions of visible fragments of the object. In this case all three groups of participants tracked them for 1/2 - 1/3 of the time.

Conclusions and future research

The general aim of this thesis was to explore the development of infants' ability to preserve spatio-temporal continuity of moving objects over periods of non-visibility by observing infants' ability to accomplish anticipatory gaze tracking in these conditions.

The conclusions from the work presented in this thesis can be organized according to the ages at which certain aspects of this ability were observed:

1) Four-month-old infants are able to represent object velocity during occlusion and predict when the object will reappear.

2) At 5 months of age, the ability to perceive *what* is moving and track the direction of motion with smooth pursuit in situation of partial occlusion is first observed. Note, however, that in the current experimental conditions of low object velocity it is fragile.

3) Six-month-old infants represent object motion in both time and space, and they still remembered the motion constraints 24h later.

4) Nine-month-old infants are able to reconstruct partly occluded moving objects and track the motion of integrated objects with smooth pursuit at an adult-like level.

Independently of what was studied and at what age, all the above mentioned aspects of infants' developing ability to represent objects over periods of non-visibility included some kind of learning. At all ages across the different conditions infants formed more stable representations with increased task experience. The exception was only observed at 6-month of age in the situation where infants extrapolated linear motion of the object. There they performed at an asymptotic level already from the beginning.

Taking into account that only Study II had a clear training design, these findings are impressive and demonstrate what an important role learning plays in the development of object representation.

In the light of these findings it would be worthwhile to further explore the role of learning in the acquisition of object representation. If object representation improves with experience, to what extend can it be trained? Future training studies could address this issue more carefully. Moreover, it would be worthwhile to apply a developmental perspective in such training studies. Comparative analysis of the differences in object representation formation in infants of different ages that are presented with the same training sequences can give us new insights into the ontogeny of object representation. In other words, we will be able to answer questions of when different aspects of object spatio-temporal continuity appear in development, and how they are acquired.

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