Development of smooth pursuit and predictive eye movements in full-term and preterm infants: An occlusion study

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Abstract

When a moving object disappears behind an occluding surface, the prediction of its reappearance must be made across time and space and this not only requires a maintained representation of the existence but also the representation of the trajectory and future location of the object. Developing stable object representations is a remarkable improvement of infants' capability to coordinate visual perception and motor control in everyday life, where we are constantly surrounded by motion. However, infants born <32 gestational weeks are at high risk of developing later disabilities in such higher brain functions. In view of this (background), the present study investigated the development of infants' understanding of object permanence and the impact of premature birth on the visuo-motor system. This was done by evaluating the infants' capacity to follow, maintain attention and predict the direction of a moving object in an occlusion task. Three groups of normally developing infants including two groups of full-term infants (tested at 5 and 12 months of age), and a group of preterm infants (tested at 12 months of age) were presented with an object moving repeatedly in a linear horizontal path during which it disappeared behind an occluder. Results revealed that full-term infants' ability to smoothly track a moving object undergoing occlusion and to predict its reappearance increases considerably between the ages of 5 and 12 months. These improvements have been attributed to neural maturation in conjunction with an increase in visual experience. Impairments were found in the smooth pursuit systems of 12 month-old preterm infants, while their capacity to make anticipatory eye movements was relatively similar to their full-term term peers. This could be attributed to white matter abnormality related to visual dorsal stream vulnerability or other neonatal complications. It is not evident whether this reflects a delay in dorso-visual pathways in preterm born infants or a persistent functional limitation in visuo-motor capacity.

1.0 Introduction

In order to move and act successfully in the environment one needs to perceive objects as stable entities even when they are temporarily moved out of view. But what factors are necessary for our perceptuo-cognitive system that allow us to perceive objects as continuously existing as they move in and out of sight? One intuitive demand, which immediately comes to mind, is the ability to detect spatiotemporal continuity. In order to perceive one object that we encounter at two different locations at two different points in time to be subsequent stages of the same object, there must be a spatiotemporal continuous path between them (Scholl, 2007). Therefore, to continue tracking an object as it disappears and subsequently reappears from behind an occluder, its spatiotemporal continuity must be preserved over such periods of non-visibility. This includes prediction of the time and position of the object as well as its velocity and direction of motion at the moment of reappearance (Gredebäck and Von Hofsten, 2004). Development of this spatiotemporal coherence is a major improvement in an infant's capability to form a consistent picture of the environment and control prospective actions subsequently which requires a complex system with a tight coupling between action, perception and cognition (Von Hofsten, 2005).

Piaget (1954) who first studied "object permanence" in infants proposed that objects and events can be mentally represented by children even if they are hidden. According to Piaget, infants start to evolve some object representations from about 4 months of age but they fail to retrieve a completely hidden object until they are 8-9 months old. In other words, for such young infants "out of sight appears to be out of mind". In his theory the concept of full object permanence was attributable to infants only around 18 to 24 months. This interpretation has been challenged during the past two decades by numerous researches (Jonsson and Von Hofsten, 2003; see e.g., Baillargeon, 1987; Meltzoff and Moore, 1998; Spelke and Von Hofsten, 2001), suggesting that representation of occluded objects is present in infants much earlier than believed by Piaget. Studies using the violation-of-visual-expectancy paradigm assume that if the infants perceive the continuous motion behind the occlusion, they will look longer at such displays where the object disappears (see e.g., Johnson et al., 2003b). These experiments suggest that infants from 2.5 months of age detect some discrepancy between the actual and expected event (see e.g., Aguiar and Baillargeon, 2002; Baillargeon and DeVos, 1991), but their sensitivity to spatio-temporal violations is suggested to be fairly established by 5 to 6 months of age (Baillargeon, 1986; Baillargeon et al., 1985; Jonsson and Von Hofsten, 2003).

The difference between Piaget’s findings and more recent behavioral studies was generally explained by the fact that Piaget's search task required sophisticated motor skills and efficient memory which is not developed until infants reach about 9 months of age (Berger, 1988). Young infants might fail Piaget's search task, simply because they are unable to perform coordinated actions, and not because they lack object permanence (e.g., Diamond and Goldman-Rakic, 1983). In other words, young infants might show evidence of object permanence but might not be able to perform the specific action operators of pushing aside the obstacle and retrieving the hidden object until a few months later. The validity of this assumption is supported by findings of experiments that investigated infants’ predictive reaching for moving objects. In one of the first of these studies, Van der Meer et al. (1994) reported that 11-month-old infants showed anticipatory reaching and tracking of moving objects in an occlusion task whereas 5-month-old infants anticipated the reappearance of the moving object with their gaze but could not predictively reach for it until about 8 months of age. Therefore, we can conclude that infants’ ability to make anticipatory gaze shifts develops prior to their ability to make anticipatory reaches.

Another set of studies used infants’ predictive tracking of briefly occluded events as a behavioral indicator of their ability to perceive occlusion events. Occluded objects tend to adhere to the principle of inertia, which states that moving objects continue in motion on the same trajectory as before (e.g., Gredebäck and Von Hofsten, 2007). In this paradigm, tracking is assumed to be predictive if, after following a moving target before occlusion, infants shift their gaze 150-200 milliseconds before the object arrives to the other side of the occluder. In contrast, eye movements may be intrinsically reactive when the infants shift theirs gaze across the occluder after the target had been visible for 150- 200 ms after the occlusion event (Gredebäck et al., 2010). Prospective eye movements in infants have been shown to generate different activation patterns than reactive eye movements. These voluntary eye movements are later developed than reactive eye movements, and the control of the different eye movements would follow different pathways through the brain and emerge at different ages (Johnson, 1990). This visuo-motor behavior begins to emerge between 3 and 5 months of age, depending on the occluder width, the occlusion duration, and the target velocity (Johnson et al., 2003a; Jonsson and Von Hofsten, 2003; Rosander and Von Hofsten, 2004; Van der Meer et al., 1994). Given that eye movements are among the first actions available to humans to explore their environment, using anticipatory eye movements could provide a rich source of information for research in infant development of action planning in general (Johnson et al., 1998).

Visual tracking of moving objects requires the combination of head and eye movements. Two kinds of eye movements make this possible: saccades and smooth pursuit. Saccades are employed to bring images of chosen objects onto the high-resolution fovea and to redirect the eyes to a new part of the surroundings. Smooth pursuit is used to keep the retinal image of a moving object in the fovea (Leigh and Zee, 1999) and is required to attentively predict when and where the object is moving (Rosander, 1996). In newborn infants, the ability to track a moving target occurs only at relatively slow stimulus speeds, and is generally done with saccadic eye movements (Von Hofsten and Rosander, 1997). At this point, saccades are simply reactive to stimulus occurring (Richards, 2001). By 2-3 months of age, infants' ability to discriminate motion direction and to smoothly track moving objects with the head and eyes improves rapidly and attains a level almost equal to that of an adult at about 4–6 months of age (Pieh et al., 2011; Rosander, 1996; Rosander and Von Hofsten, 2002). When the image moves over the retina a prediction for this movement would also be needed and this predictive capacity emerges 4-5 months after birth at which time smooth pursuit has entered in an almost fully developed state (Atkinson, 2000; Rosander, 1996). When a moving object disappears behind an occluder, smooth pursuit gets effectively interrupted. In this case the only way to continue tracking the object is to make large saccades to the place where the object will reappear (Rosander and Von Hofsten, 2004). As smooth pursuit and saccades pertain to two completely different categories of the visuo-motor system, the saccades cannot be accounted for by a continuation of smooth pursuit (e.g., Leigh and Zee, 1999). If saccades occur before the object itself appears, they have to be guided by some kind of prediction of the object's continued movement (Von Hofsten et al., 2007). Such prospective eye movements indicate that some kind of planning should be involved (Richards, 2001). Strong correlation between the development of smooth pursuit and the timing of saccades to track temporarily occluded objects indicates that the onset of predictive smooth pursuit and predictive saccadic tracking might both be related to infants' emerging ability to represent occluded object motion

(Rosander and Von Hofsten, 2004). When smooth pursuit gets interrupted, due to temporary occlusion of the visually tracked object, infants at the age of 4 months start to show the ability of shifting gaze over the occluder, indicating an emerging representation of the spatiotemporal characteristics around this age (Johnson et al., 2003a; Rosander and Von Hofsten, 2004; Van der Meer et al., 1994). Nonetheless, at the age of 6 months, infants make anticipatory eye movements prior to the object's reappearance which suggests that object representation is not robust until that age (Johnson et al., 2003a).

Development of motion sensitivity and smooth pursuit between 2 and 5 months of age corresponds well with the structural maturation of the motion processing area of the cerebral cortex, called middle temporal and middle superior temporal or the MT-MST complex. This area is generally referred to as area V5 or the MT+ and lies at the junction of the occipital, temporal, and parietal lobe. MT+ is activated by visual motion, it contributes selectively to the perception of motion, and plays a crucial role in the control of smooth pursuit eye movements (Rosander et al., 2007). Lesions of MT area produce a selective deficit in motion perception (Zeki, 2004) and impaired smooth pursuit eye movements (Schoenfeld et al., 2002). The signals from visual area MT+ are passed on to frontal areas in the cortex, the frontal eye fields (FEF) which are believed to play a significant role in controlling prospective eye movements and the development of smooth pursuit (Fukushima et al., 2006; Canfield and Kirkham, 2001).

In the visual system of human adults, motion-specific information reaches the MT+ through two parallel visual pathways, the primary pathway and the subcortical pathway. The primary pathway passes the visual information through the lateral geniculate nucleus (LGN) and the primary visual cortex (V1) to the MT+ and further to the visual motor area of the parietal lobe (dorsal stream). The subcortical stream goes to MT+ area via superior colliculus (SC) and pulvinar area (PU) of the thalamus or via LGN (Rosander, 2007; Rosander et al., 2007). This subcortical stream has been found to dominate the immature visual motion processing until around 2 months of age (Atkinson, 2000; Atkinson et al., 2008; Dubowitz et al., 1986). At the postnatal age of 2-4 months, a rapid maturation of the LGN pathways takes place (Garey and De Courten, 1983), and the primary visual pathway -passing through LGN to V1 and further to the MT+ and the dorsal pathways, takes control over subcortical processing and becomes the main pathway of visual motion perception (Atkinson, 2000;

Garey and De Courten, 1983; Rosander, 2007). Moreover, the pathway involving FEF becomes functional by this age (Canfield and Kirkham, 2001). Such developmental changes greatly increase the infant's ability to make anticipatory eye movements.

The complexity of the visual system makes it particularly susceptible to a variety of factors, including growth delay, indirect effects of inflammation, and perinatal brain abnormalities following very premature birth. Several studies have shown that children born very preterm (born before 32 gestational weeks) and/or have a very low birth weight (birth weight < 1500 g) present more deviations in brain structure and function (Munck, 2012). With regard to visual problems, visual deficits may be attributable to brain lesions at different points in the optic pathways and associated areas (Leonhardt et al., 2012), because these undergo significant development during this time and therefore may be vulnerable to disruption by prenatal events (Hou et al., 2011). Prematurity leads to a higher ophthalmological morbidity, e.g. retinopathy of prematurity (ROP), a neovascular retinal disorder whose frequency and severity is inversely related to gestational age and birth weight (Fortes Filho et al., 2009). According to a new study, 60% of the infants with a birth weight lower than 1500 g are diagnosed with some degree of ROP (Zin and Gole, 2013). Another leading cause of brain deficits in infants born preterm is a form of white matter injury which is commonly referred to as periventricular leukomalacia (PVL). In children born before 32 weeks of gestation, PVL is the principal cause of cognitive, behavioral, motor, and sensory disabilities (Volpe, 2003). A conventional MRI study showed that more than half of preterm children had neuro-anatomical abnormalities (Northam, 2013). In addition to PVL and other cerebral deficits, preterm children are at risk of cerebellar lesions that have been shown to cause reduced smooth pursuit velocity, increased pursuit latency and saccadic dysmetria (Newsham et al., 2007).

Even when perinatal brain damages are not detected with conventional brain imaging, disturbed myelin formation and decreased cortical grey and white matter volumes are dominant in preterm children (Inder et al., 1999). A volumetric study has shown that 35% of a cohort of preterm children had reduced occipital regional volumes. These children later exhibited abnormal oculomotor control, including abnormal saccadic movements and smooth pursuit (Shah et al., 2006). Since a substantial part of myelination, neural development, and cortical organization normally takes place in the last weeks of pregnancy (Gressens, 2000), premature birth interrupts the exposure to Intrauterine Growth Factors (IGF) that are facilitating these important processes. Therefore, it is not surprising that prematurity has serious impacts on brain growth and maturation (Counsell et al., 2003).

Although it has been reported by numerous studies that the overall development of preterm infants is comparable to that of their full-term peers, there is still some debate on the issue whether reported differences between term and preterm infants result only from the effects of morbidity (e.g. PVL), or whether premature exposure to the visual environment in itself influences visual development (Hunnius et al., 2008). Different theories exist about how prematurity affects the development of visual abilities in healthy preterm infants (for an overview, see e.g., Madan et al., 2005). Some studies support the notion that earlier extrauterine experience of visual stimuli in preterm infants leads to a favorable effect of earlier development in visual functions. For example, Ricci et al. (2008) reported a more mature visual behavior in preterm infants compared to full-term infants in ocular movements, vertical tracking and arc tracking. Preterm infants are also reported to perform faster in disengaging and shifting their gaze from a stimulus in their central visual field to the periphery until about 16 weeks post-term in a gaze-shifting task (Hunnius et al., 2008). These findings show that extra weeks of postnatal visual experience in preterm infants may have positively influenced the maturation of cortical processes related to ocular stability and tracking. However, preterm infants seem to be affected negatively in other visual areas connected to the dorsal visual system such as selective attention, spatial function and executive control (Atkinson and Braddick, 2007). For example, Rose et al. (2002) reported that 12-month-old preterm infants could make similar anticipatory eye movements compared to their term peers, but had more trouble maintaining anticipatory attention (i.e. maintaining gaze fixation after anticipatory eye movement). Therefore, anticipation problems in early infancy may serve as reliable indicator of brain damages (Kayed and Van der Meer, 2009; Van der Meer et al., 1994)

Overall, these findings suggest that the matureness of preterm infants in specific visual tasks is supposed to be connected to “subcortical” aspects of visual function, which might be accelerated by preterm extrauterine exposure to visual stimuli, whereas preterm infants show a poorer performance in aspects of visual functions that may be mediated by cortical pathways. It is, therefore, very important to develop a greater understanding of the impact of premature birth on the development of the visual system. As suggested by (Strand Brodd, 2011), the assessment of an infant's visual capacity, particularly the infant's capacity to detect motion direction and to smoothly track moving objects, could be a sensitive measure of the preterm infant's developmental status and of the functioning of the visual system.

We used eye tracking in this study to explore infants' ability to track and represent temporarily occluded objects. Eye tracking is a detailed and non-invasive method which provides a detailed description of how infants' actions are directed to ongoing occlusion events. The matureness and effectiveness of the visual system was assessed by analysing predictive eye movements over the occluder as well as the ratio of smooth pursuit eye movements during visual tracking of the moving object. In this regard, three different groups of infants comprising two full-term groups tested at 5 and 12 months of age and a preterm group tested at 12 months of age (corrected for prematurity) were chosen for comparison. The aim was to examine how each of these processes develops over time and with age, and also to investigate how prematurity affects the development of visuo-motor behavior in infants. In accordance with previous research indicating that the ability of anticipatory eye movements improves considerably in the course of the first year of life (Rosander and Von Hofsten, 2004), we expected that infants with increasing age would show more robust evidence of smooth pursuit and make more anticipatory gaze shifts across an occluder. However, considering the fact that early dorsal stream maturation may be perturbed by premature birth, we expected that 12-month-old infants born several weeks before their due dates, would behave less mature compared to their term peers, despite having more visual experience.

2.0 Methods

2.1. Participants

A total of 15 healthy and normally developing infants were selected for final analysis of this cross sectional study. There were 5 subjects in each of three groups: full term infants tested at 5 months of age (FTY) with the mean age of 124 days (SD: 21, range: 94-144, 2 boys), full term infants tested at 12 months of age (FTO) with the mean age of 355 days (SD: 17, range: 329-378, 3 boys) and preterm infants tested at 12 months of age (PTO) with the mean age of 367 days (SD: 7, range: 359-373, 5 boys). In each group, (five) additional infants were tested but eliminated from the study because of eye-tracker calibration difficulties, fussiness or lack of attention. This high attrition rate is not unusual for eye tracking studies (Daum et al., 2012; McMurray and Aslin, 2004).

The preterm infants were recruited with help from the pediatrician in charge at the Neonatal Intensive Care Unit at St Olav's University Hospital (Trondheim, Norway). The preterm infants included in the study were born at ≤ 33 completed weeks gestational age and had a birth weight ≥ 1000 gram (range: 1000-1710). Absence of any major factors such as (ROP), severe brain damage and/or other prenatal issues requiring serious medical intervention) was also an inclusion criterion. However, experimenters were unaware of the infants' neurological status, birth history and any events during their stay at the hospital. The full-term infants were recruited by obtaining their birth announcements from local newspaper and contacting their parents by mail, or by parents showing an interest and making voluntary contact with the laboratory. Those who were willing to participate were then enrolled in the study.

Preterm and full-term 12-month-old infants were matched according to their age in full months. For a valid matching, age corrected for prematurity was calculated for the preterm babies by adding the postnatal age to the gestational age.

Before the experiment began, parents signed the written consent informing them that they can withdraw their infant from the study at any time without giving a reason. Ethical permission for the experimental procedure was provided by the Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences. This study was conducted in the Developmental Neuroscience Laboratory at the Department of Psychology, NTNU, Trondheim, Norway.

2.2. Apparatus

A Tobii systems X50 infrared eye-tracker (<www.tobii.com>) located below the projection screen was used to collect infant's gaze data. This eye tracker calculates gaze based on the infrared corneal reflection at the sampling rate of 50Hz. The signals from the eye tracker were exported through Clear View software and processed on a HP computer.

A Dell computer was used for stimulus decoding and display. The stimulus was generated by E-Prime software (Psychological software Tools, Inc.) and mirror-reversed projected onto a large screen (108 x 67 cm) by means of ASK M2 projector. The signals were also sent to the eye-tracking computer that stored gaze data to indicate when particular events occurred (e.g., the start of the trial). These codes were used to coordinate the infant's eye movements with the stimuli.

To monitor the infant's face and looking behavior during the experiment, two digital video cameras were placed in two different angles in front of the participants. The output from the video cameras was stored for further off-line analysis.

2.3. Experimental stimulus

Infants visually tracked a red car moving horizontally in a rectangular path. The car was occluded twice on its way, once when it moved horizontally from lower left to lower right corner and again when it moved horizontally from upper right hand side to upper left corner (Figure 1). The distance between starting and ending point of each trial was 100 cm giving a visual angle of 65 degrees. The length of the car on the screen was 50 pixels or 6.75 cm, and the length of the occluder was 60 pixels which was equivalent to about 10 cm on the screen.

The car started in the lower left hand corner with a speed of 52.3 cm/s for FTY infants and 67.5 cm/s for FTO and PTO infants. The different start speeds were selected to keep the experiment challenging for infants at both ages. According to the start speed the car moved under three different speed conditions, “fast” (10% deceleration), “medium” (50% deceleration) and “slow” (90% deceleration). The three different speed conditions of the car were presented in a random order, so that the infants had to infer in every trial the occlusion duration of the car based on the respective speed. The car started decelerating 500 ms and 250 ms after stimulus onset for the FTY group and FTO and PTO groups, respectively. The car travelled the distance from the start position to the occluder between 1810 and 2210 ms for a start speed of 52.3 cm/s, and between 1230 and 1380 ms for a start speed of 67.5 cm/s. The occlusion duration was between 261 and 556 ms for a start speed of 52.3 cm/s and between 165 and 355 ms for a start speed of 67.5cm/s. Inter-stimulus intervals were fixed at 2000 ms, and prior to each trial a fixation figure appeared on the screen in order to attract the infant’s attention toward the starting position of the car.

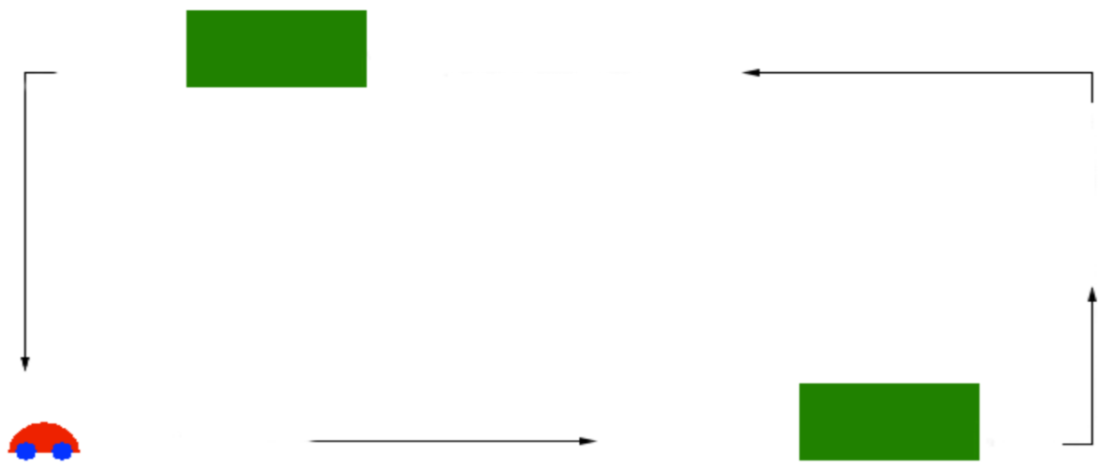


Figure 1: Stimulus setup: The car started from the lower left hand side of the screen and traveled horizontally on a rectangular path under one of the three deceleration conditions. Two green boxes in the lower right and upper left corners temporarily occluded the car. Between trials attention pictures were presented to fixate the infant’s attention to the starting position of the car.

2.4. Procedure

On arrival, parents were informed about the purpose, duration, and experimental procedures and then asked to sign the informed consent form. During that time, the infant was allowed to spend some time playing with toys in order to get familiar with the laboratory surroundings. The infant was then moved to the experimental room and seated comfortably in a baby car seat (at 12 months) or on a parent's lap (at 5 months) 0.8 m away from the screen on which the stimuli were projected. To avoid any stress that parent-infant separation may cause, one parent accompanied the infant during the experiment but was instructed to not interfere unnecessarily. Additionally, an assistant was present in the experimental room to help the infant to stay focused on the screen.

The experiment was performed in a quiet and dimly lit experimental room whilst the infant was being monitored in the control room with computers for stimulus generation and data acquisition. A transparent glass window behind the infant separated the control room from the experimental room. Before starting the experiment, the lights were turned off and the infant’s eye movements in virtual space were calibrated to the Tobii X50 camera.

Immediately after finishing the calibration, presentation of the stimulus material started. A whole experimental session took about 20-30 minutes from start to finish and consisted of three experiments on optic flow, looming, and occlusion, all investigating the development of motion perception in infants. Each experiment lasted for approximately five minutes and the occlusion experiment was usually the last one presented on the screen.

Infants typically completed about 50 to 100 occlusion trials. Testing was conducted in one block. A short break was given if the infant seemed to be bored or disinterested and the parent or the experimental assistant played with the baby for some minutes to revive the level of interest. The experiment was terminated if the infant did not show any more interest or started to fuss.

2.5. Data analysis

The Tobii eye tracker stored coordinates of gaze from both eyes. The gaze calculations were performed based on both eyes in most instances and from one eye only in those instances where the quality of the obtained data from the other eye was poor. Data were analyzed offline by using a custom-written Python script that for each trial plotted eye position and target position as a function of time (see Figure 2)**.**

The eye movement traces were inspected to determine whether the infants attended the occlusion event both prior to, and after the occlusion event for each trial. Trials in which the infant tracked the car before and after occlusion were included in the final sample. This meant two things: target-related eye movements had to be evident before the car became occluded, and the infant had to shift gaze to the side of the occluder where the car reappears and continue tracking the car. Trials contaminated by blinks or head movements were discarded from further analysis. All selected trials were then used to assess the infant's eye movement.

2.5.1 Eye movement analysis

In order to analyze the infant's viewing pattern, trials selected for the final analysis were visually inspected and classified in two categories. The first category was for smooth pursuit trials, which were trials without any saccade in a time interval of [1510; 2315] ms after stimulus onset for FTY infants or an interval of [730; 1275] ms for FTO and PTO infants. The second category was for saccadic trials, which were trials with one or more saccades occurring in the time intervals given above. The time interval was so defined due to the fact that in order for proper analysis to occur, a sufficiently long interval needed to be available in all speed conditions after gaze caught up with car motion and before the car became occluded. In the present study the catch-up saccade occurred at the point in time where the horizontal eye velocity equalled the velocity of the car (target) for the first time (Fuchs, 1967).

By the time of car reappearance, infant’s gaze shift over the occluder was indicated as either predictive or reactive based on the time difference between the reappearance of the car and the arrival of gaze. If the gaze arrived at the reappearance location before the car had been visible for 200 ms, the trial was assumed to be predictive (negative score). In reactive trials, infant’s gaze moved across the occluder after the car had been visible for 200 ms (positive score). The 200 ms threshold was based on the minimum time required to plan and execute a saccade to an unexpected shift in a moving target both in adults (Engel et al., 1999) and infants (Haith et al., 1988). This criterion has been used in previous studies of predictive and reactive eye movements in occlusion tasks (Gredebäck and Von Hofsten, 2004; Gredebäck et al., 2002; Rosander and Von Hofsten, 2004).

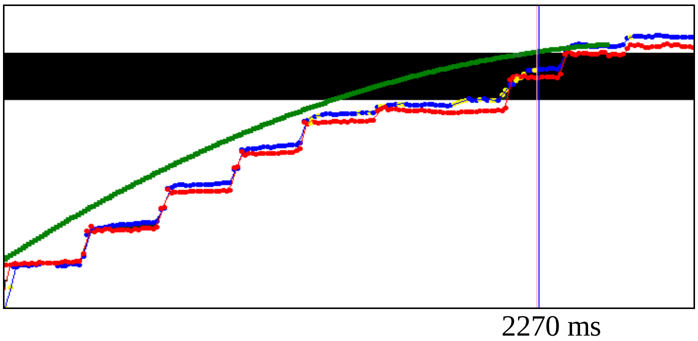
3.0 Results

On average, 36 trials (SD: 14, rang: 21-53) for FTY infants, 43 trials (SD: 12, range: 32-61) for FTO infants and 37 trials (SD: 8, range: 27-48) for PTO infants fulfilled the selection criteria for inclusion in the analysis.

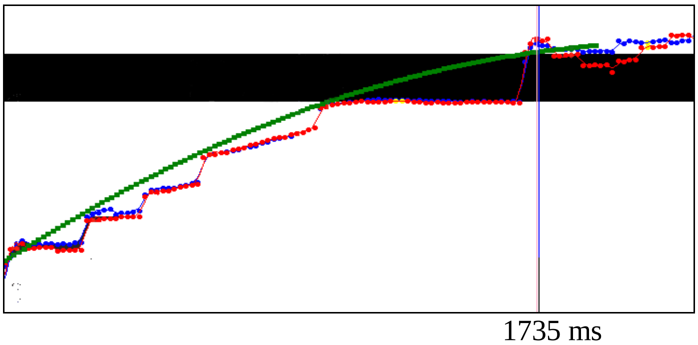
Infants usually started the eye tracking by performing a quick saccade to catch up with the moving car allowing them to follow the target. In Figure 3, typical eye movements of a (a) FTY infant, (b) FTO infant and (c) PTO infant are shown. After catching up with the target, the more mature smooth pursuit predominated the eye responses to the moving car in 64% of all trials for FTO infants (see Figure 3c), whereas the PTO infants as well as the FTY infants used smooth pursuit in only 35% and 9% of the trials, respectively (see Figure 3b and 3a). Still, most infants used both smooth pursuit and saccadic tracking in a given session, but FTO infants performed smooth pursuit more often while FTY and PTO infants predominantly used saccades to follow the car's motion. Only one infant in the FTY group carried out exclusively saccadic eye movements.

Visual tracking of the car was disrupted by an anticipatory saccade to the reappearing side of the occluder in 74% and 62% of all trials for FTO and PTO infants respectively (see Figure 3b and 3c). FTY infants showed mostly reactive saccades by anticipating the car`s reappearance only in 37% of the trials (see Figure 3a).

(a)



(b)



(c)

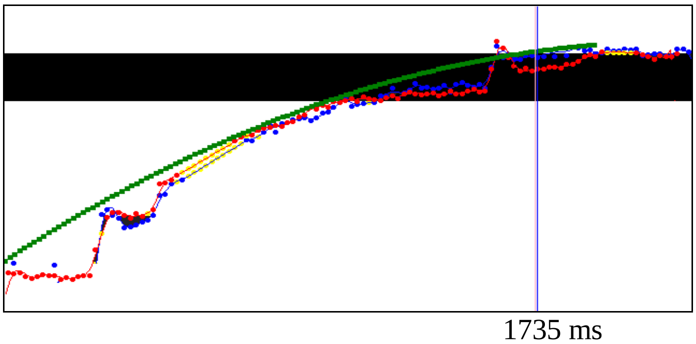


Figure 2: Eye data (↑ position and → time) of a typical trial (car travelling at “slow” deceleration) of a FTY infant (a), PTO infant (b), and FTO (c) infant. In the depicted trials, the occluder is represented by the black bar; the green squares represent car motion; and the red and blue dots represent the right and left eyes respectively, while the yellow dots stand for missing data. The markers to the right represent the point in time at which the car starts to reappear from behind the occluder. The FTY infant (a) and the PTO infant (b) use a series of saccadic jumps to keep up with the car, whereas the FTO infant (c) smoothly tracks the moving target. The PTO infant (b) and the FTO infant (c) shift their gaze to the other side of the occluder when the car is about to arrive there (predictive gaze shift), whereas the FTY infant (a) arrives with his gaze at the opposite side of the occluder slightly after the car has reappeared (reactive gaze shift).

A repeated-measures ANOVA with the dependent variable as the percentage of performed trials, between-subjects factor as infant groups (FTY, FTO, PTO), and within-subjects factors as eye movement types (smooth pursuit, saccadic tracking) and modality of gaze shift (predictive, reactive) was performed.

The analysis revealed a significant interaction effect between eye movement and infant-group, F (2, 12) = 8.704, $p < 0.05$. In the full-term babies an increase in the percentage of smooth pursuit and a decrease in the percentage of saccadic tracking with age were found. FTY infants performed significantly more trials with saccadic tracking than smooth pursuit which was the opposite for FTO infants. At the same time PTO infants still had significantly smaller percentage of smooth pursuit compared to saccadic tracking (see Figure 3).

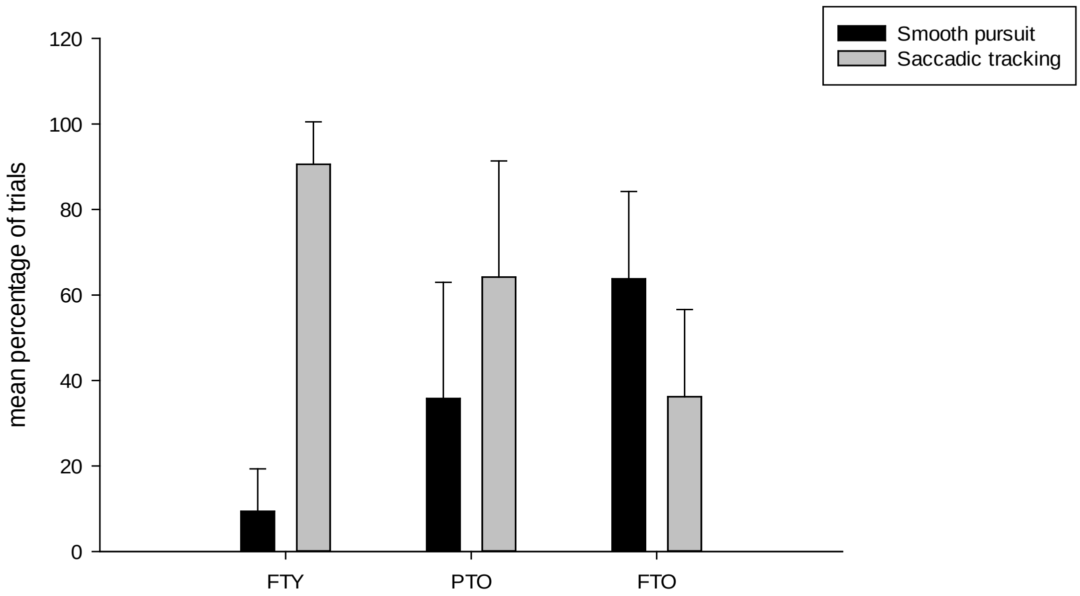


Figure 3: Mean percentage of trials (and standard deviation) performed with smooth pursuit and saccadic tracking in the three groups of infants. FTY infants and PTO infants carried out significantly more trials with saccadic tracking compared to smooth pursuit; whereas, the opposite was true for FTO infants.

The ANOVA also yielded a significant interaction between the modality of gaze shift and infant group, F (2, 12) = 11.319, $p < 0.05$. In the full-term babies there was an increase in the percentage of predictive gaze shifts and a decrease in the percentage of reactive gaze shifts with age. FTY infants performed significantly more reactive tracking over the occluder, whereas the FTO infants performed more trials where they anticipated the reappearance of the car. Similar to FTO infants, PTO infants carried out significantly more trials in which they showed a predictive gaze shift to the other side of the occluder (see Figure 4).

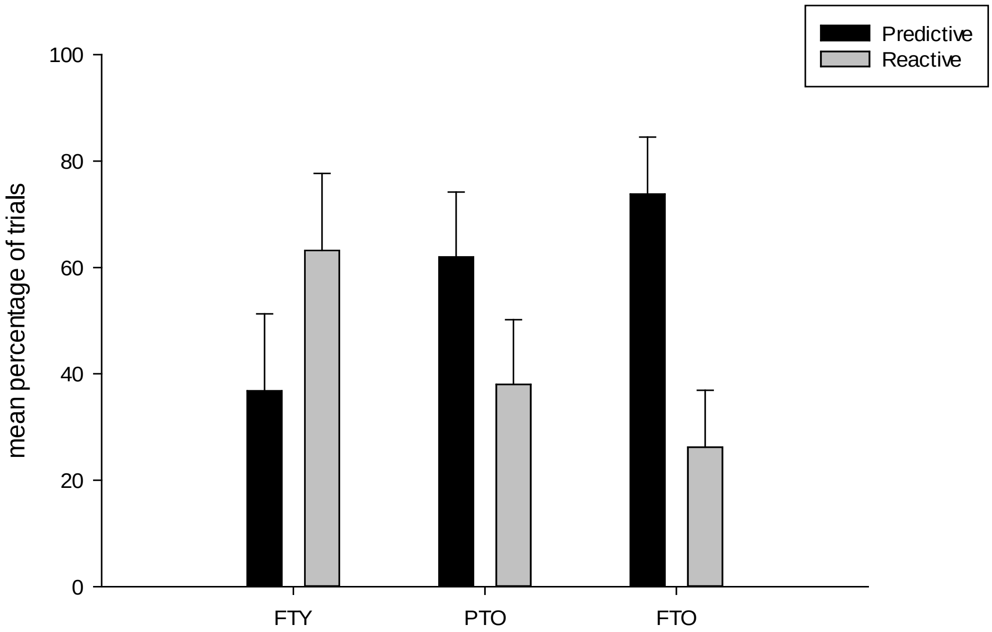


Figure 4: Mean percentage of trials (and standard deviation) performed with predictive gaze shift and reactive gaze shift to the reappearing side of the occluder for three groups of infants. FTO and PTO infants performed significantly more trials with predictive gaze shifts to the reappearing side of the occluder, whereas FTY infants performed significantly more reactive gaze shifts.

There was also a significant interaction between types of eye movement and gaze shift, F (1, 12) = 27.447, $p < 0.05$. Further analysis revealed the interaction effect to be significant for FTY infants, F (1, 4) = 8.660, $p < 0.05$ and FTO infants, F (1, 4) = 64.190, $p < 0.05$, but not for PTO infants, F (1, 4) = 1.830, ns. This finding implies that for FTY and FTO infants, significantly more predictive gaze shits were performed in trials where the car was tracked smoothly, whereas reactive gaze shifts were observed more often in trials where the car was followed by saccades. For PTO infants, on the other hand, relatively the same amount of predictive and reactive gaze shifts were carried out with smooth pursuit and saccadic eye movements.

In addition, significant main effects of eye movement type, F (1, 12) = 6.717, $p < 0.05$, and modality of gaze shift, F (1, 12) = 5.395, $p < 0.05$, were found. However, these were not real main effects since they were caused by the underlying interactions mentioned above.

Following the finding that FTO infants performed significantly more saccadic tracking than smooth pursuit tracking, the eye movement data were further explored to see whether a criterion could be found that recognized those preterm infants who were delayed in their performance, and thus struggled to smoothly track the car at 12 months of age. An outlier was defined as values larger or smaller than mean ± 1.5 SD (Field, 2013) based on the mean and standard deviation values of FTO infants for percentage of trials performed with saccadic tracking. The outlier was used as a criterion to specify PTO infants who had remarkably larger percentages of saccadic eye movements. As Table 1 displays, three infants in the PTO group showed outlier values for their percentage of saccadic eye movements, indicating that these infants performed extremely poorly in smooth pursuit eye movements. However, none of these three infants showed dysfunction in making prospective eye movements.

Table 1: Percentage of trials performed with saccadic tracking for both infant groups at 12 months of age. The numbers in bold indicate those PTO infants who showed a value above the mean + 1.5 SD of saccadic tracking values of the FTO group.

FTO infants	Saccades %	PTO infants	Saccades %
FTO1	41	PTO1	**81**
FTO2	32	PTO2	**88**
FTO3	8	PTO3	18
FTO4	65	PTO4	**72**
FTO5	35	PTO5	64
Mean	36		64
SD	20		27
Mean + 1.5 SD	66		

4.0 Discussion

The general aim of this study was to explore infants' ability to preserve spatio-temporal continuity of moving objects over non-visibility periods and also find the effect of preterm birth on this capacity. In this regard, the infants' ability to accomplish anticipatory gaze tracking was evaluated by measuring and calculating the proportion of smooth pursuit eye movements and predictive gaze shifts in an occlusion task. The results obtained in this study provide insights into visual object processing in 5-month-old and 12-month-old full-term infants. Moreover, this study shows delayed development for 12-month-old preterm infants and adds to the understanding of how the visuo-motor system can be affected by preterm birth.

Eye data analysis revealed a considerable improvement of full-term infants' ability to perform smooth pursuit as well as predictive eye movements between the ages of 5 months and 12 months. The proportion of smooth pursuit eye movements on overall performed trials increased from 9% to 64% with age and the proportion of predictive gaze shifts increased from 37% to 74%. This finding is consistent with the existing literature indicating that the ability to make anticipatory eye movements improves considerably in the course of the first year of life (Bertenthal et al., 2013; Bertenthal et al., 2007; Kochukhova and Rosander, 2008; Rosander and Von Hofsten, 2004). These studies indicate that infants' ability to smoothly track a moving object and to predict the reappearance of the object following an occlusion event appears around 4 months of age and clearly improves from 5 to 7 months of age but it is not until 9 months of age that infants display predictive tracking at a level of performance similar to adults.

Our results revealed that FTY infants used significantly more saccades relative to smooth pursuit to follow the moving car. Infants around this age consistently track a small moving target with a combination of saccades and smooth pursuit where the ratio of each is dependent on the age and attentiveness of the infants, and object speed (Fisher et al., 1981; Richards and Holley, 1999). The trend of FTY infants' high saccade ratio in this experiment could be due to infants' foveal, attentional and cortical motion processing immaturity in addition to inadequate conversion of velocity signals into appropriate oculomotor commands (Jacobs et al., 1997). In the immature visual system of young infants, the eyes constantly lag behind the moving target, causing them to make small saccadic movements that rapidly move the gaze from one position to another. As the smooth pursuit system develops, the use of saccades becomes less frequent but infants still use them to catch up if the lag becomes too large. Thus, older infants show more smooth pursuit, and are able to fixate (fast) moving targets more accurately (Richards and Holley, 1999).

Although the majority of the FTY infants showed some evidence of predictive tracking which is expected for infants between 4 and 6 months of age (Rosander and Von Hofsten, 2004; Johnson et al., 2003a), they produced significantly more reactive than predictive gaze shifts to follow the car over the occluder. This could be due to younger infants' difficulties to disengage selective attention from the occluder, which competes with the moving object for attention and representational resources (Gredebäck and Von Hofsten, 2004; Jonsson and Von Hofsten, 2003). It is suggested that by 5 months of age, object representation over occlusion periods is presumably mainly based on the maintenance of spatio-temporal object information. Infants at this age are able to represent a moving object that temporarily disappears behind an occluder by using their perceptual experience of visual motion (Kochukhova and Gredebäck, 2007; Johnson and Shuwairi, 2009). The young infants' visual system gets easily attracted by new and interesting objects and events. By around 5 months of age, infants start to show control of their gaze shifts and move their gaze quickly to disengage from one stimulus to direct attention towards another stimulus (Hood and Atkinson, 1993). This can explain why, when the same stimulus is presented repeatedly, they quickly habituate, lose interest, and stop looking. Therefore, it is not surprising that gaze shifting in young infants is primarily reactive and strongly regulated by novelty (Blaga and Colombo, 2006; Dannemiller, 2005).

Unlike the FTY group, most of the FTO infants could generally anticipate the reappearance of the occluded car by looking at the other side of the occluder ahead of time. This finding confirms the suggestion that infants at around one year of age can use an internal representation to guide their anticipatory gaze shifts (Xu and Baker, 2005; Gredebäck and Von Hofsten, 2004). During the latter half of the first year, visual attention becomes more endogenously controlled (see e.g., Colombo, 2001). Increasing experience and neural maturation of the attention system enables the older infants to perceive an object as a stable entity during object occlusion based on a holistic and sophisticated object representation comprising featural and spatio-temporal properties. Therefore, they are able to keep the object's correct hiding location in mind and form an expectation of where it will reappear.

Eye-movement analysis of PTO infants revealed that preterm infants in this group acted less efficiently than the FTO infants but better than the FTY infants. PTO infants had obvious difficulties to track smoothly, and; therefore they followed the car with more saccades. However, in their overall performance of making anticipatory eye movements over the occluder, PTO infants made considerably more anticipatory gaze shifts compared to reactive ones which was similar to the FTO infants' performance. This finding suggests that preterm birth, in and of itself, does not adversely affect the development of prospective control.

The generally low proportion of smooth pursuit (35%) performed by preterm infants at 12 months of age, shows that the smooth pursuit system was not functioning well in the PTO group. This could be caused by disturbances in the development of motion perception which is necessary for smooth pursuit (Rosander, 2007). It is possible that the origin of this disturbance could be located in the cortical pathways and specifically in the dorsal stream, which is the dominating pathway for motion processing in late infancy. Dorsal system responsible for smooth pursuit runs between the occipital lobe, the median temporal lobe, the posterior parietal lobe and the frontal lobe in a complex network, which makes it particularly susceptible to impairment (Lekwuwa and Barnes, 1996). Theoretically therefore, the unusually early visual stimulation that premature infants are exposed to may, in itself, play an important role in dorsal stream vulnerability. This may be due to the fact that the dorsal stream motion-processing systems are undergoing rapid development during the perinatal period (see e.g., Atkinson and Braddick, 1992; Braddick et al., 2005). In this regard, magnocellular-dominated (M) cells of the dorsal stream seem to be particularly vulnerable (Atkinson and Braddick, 2010; Grinter et al., 2010) and their development has been found to be disrupted by premature birth (Hammarrenger et al., 2007; Tremblay et al., 2014). One possible cause can be a reduced uptake of omega-3 docosahexaenoic acid (DHA), -a major structural component of cell membranes in the cells of the retina and the brain- which facilitate the growth and functioning of M pathway of the visual system (Stein, 2001). DHA is being transferred from the mother to the fetus at a high rate during the last three months of pregnancy when the dorsal pathway development is thought to occur. Premature infants who are born < 32 weeks of pregnancy are reported to be deficient in DHA **s**torage compared with their term peers (Agostoni et al., 2008). Limited DHA accumulation explains abnormal functioning of M pathway and reduced visual acuity which is strongly affecting the accuracy of smooth pursuit eye movements. Jacobson et al. (2008) reported the association of higher cord DHA concentration with better visual acuity and novelty preference in infants at 6 months of age, and also better mental and psychomotor performance at 11 months. In accordance, a better visual acuity has been reported in premature infants fed formulas containing DHA from the time of first enteral feeding to 12 months. Thus, ‘DHA gap of prematurity’ appears to alleviate the rate of visual impairment and neuro-developmental comorbidity in preterm infants (Harris and Baack, 2015).

Although it is suggested that the M pathway maturational delay gradually resolves with age (Tremblay et al., 2014), a decreased smooth pursuit still remains at school age. Studies involving preterm children between the ages of 5 and 7 years have reported impaired smooth pursuit during tracking of a moving object which is attributed to a delayed development of visual areas responding to smooth tracking (Atkinson and Braddick, 2007; Langaas et al., 1998).

Despite the delayed smooth pursuit development because of prematurity, the neonatal complications related to preterm birth excreting inflammatory, circularity, and nutritional complications could also affect the specific and vulnerable areas in the brain responsible for smooth pursuit. Although none of the PTO infants in our experiment were diagnosed with ROP or other lesions like PVL, it cannot be ruled out that other types of visual dysfunctions were present that influenced motion tracking. Such ophthalmological complications have been found up to 10 years of age in preterm infants (Holmström and Larsson, 2008).

All the infants studied except one infant in the FTY group, displayed predictive eye movements and smooth pursuit to some extent, although the relative amount varied between subjects and with age. This finding indicates that infants’ ability to smoothly track a moving object undergoing occlusion and to predict its reappearance, is not an all or none response that infant either lack or possess. Rather, it is a gradual progressing achievement which highly depends on parameters of current occlusion situation and previous experiences with similar events (Gredebäck and Von Hofsten, 2007).

FTY and FTO infants performed significantly more predictive eye movements in the trials that they smoothly tracked the car and in accordance, more reactive eye movements in the trials that they followed the car with saccades. This seems logical since only predication mechanisms behind smooth pursuit tracking are able to disengage attention from a moving object and redirect gaze in a predictive manner. In other words, smooth pursuit eye movements make it possible to anticipate the spatio-temporal characteristics of the object before it gets occluded. As mentioned earlier, representations of occluded objects are initially weak and gradually strengthen across the first 12 months of age. So, it was not unexpected to observe overall smaller ratios of predictive gaze shifts in FTY infants, because their abilities to internally represent occluded objects are still developing and therefore too fragile to be acted upon in a consistent anticipatory manner.

In this regard, relatively similar distribution of predictive and reactive gaze shifts carried out with smooth pursuit and saccadic eye movements in the PTO group, and also their overall greater proportion of predictive relative to reactive eye movements, indicates that preterm infants at 12 months of age are developed enough to disengage their attention from tracking the apparent moving object to re-orient gaze in a predictive manner over an occluder, but they still have problems to track a moving object with smooth pursuit. This result is in accordance with the finding of Rose et al. (2002) who reported that 12-month-old preterm infants could make anticipatory eye movements similar to their term peers, but had more trouble maintaining anticipatory attention (Stroganova et al., 2005). It has been suggested that preterm infants use saccades and head movements to correct their less functioning smooth pursuit to track moving objects (Grönqvist et al., 2011). The consequences of this compensatory mechanism can be less functional smooth pursuit tracking, despite the normal capacity to predictively track the moving object.

When exploring the developmental characteristics of the visuo-motor system and the effects of prematurity thereon, an outlier criterion was suggested to identify those PTO infants with extremely low ability to make smooth pursuit eye movements, and who might be at risk of developmental disorders. Although three PTO infants employed extremely low ratios of smooth pursuit (instead displaying more saccades), their otherwise normal capacity to perform predictive gaze shifting could represent a developmental delay to be recovered as they grow older. In order to evaluate whether measures of smooth pursuit could be used as an early screening tool for later visuo-motor impairments, it would be necessary to complete a longitudinal follow-up on these preterm infants.

In conclusion, the findings of this study suggest that visuo-motor capacity measured by smooth pursuit and anticipatory eye movements develops considerably in the course of the first year of life. Infants during the first months of life rely heavily on spatio-temporal object information to fill perceptual gaps over the transient disappearance of a visual target. Infants at the end of the first year, on the other hand, possess advanced knowledge reflected by the incorporation of object features into perceptual representations, which in turn can be acted upon. However, the visuo-motor system seems to follow a different developmental path in preterm infants. 12- month-old preterm infants employed considerably less smooth pursuit on average, although they could make anticipatory eye movements close to full-term infants' level. Whether these differences are caused by delayed development because of premature birth per se or by focal implications during the neonatal period remains to be investigated. For future research, the preterm infants can be followed longitudinally to see if they eventually will reach the full-term level or if they continue to perform less well, possibly even after starting school.

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