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CHAPTER 6

Visual tracking and its relationship to cortical development

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Abstract: Measurements of visual tracking in infants have been performed from 2 weeks of age. Although directed appropriately, the eye movements are saccadic at this age. Over the first 4 months of life, a rapid transition to successively smoother eye movements takes place. Timing develops first and at 7 weeks of age the smooth pursuit is well timed to a sinusoidal motion of 0.25 Hz. From this age, the gain of the smooth pursuit improves rapidly and from 4 months of age, smooth pursuit dominates visual tracking in combination with head movements. This development reflects massive cortical and cerebellar changes. The coordination between eyes–head–body and the external events to be tracked presumes predictive control. One common type of model for explaining the acquisition of such control focuses on the maturation of the cerebellar circuits. A problem with such models, however, is that although Purkinje cells and climbing fibers are present in the newborn, the parallel and mossy fibers, essential for predictive control, grow and mature at 4–7 months postnatally. Therefore, an alternative model that also includes the prefrontal cerebral cortex might better explain the early development of predictive control. The prefrontal cortex functions by 3–4 months of age and provides a site for prediction of eye movements as a part of cerebro-cerebellar nets.

Keywords: visual development; vor; cerebellum; infant brain; smooth pursuit; eye–head coordination; predictive models

Introduction

Adult humans track a moving object with eye movements that keep the gaze fixated on the object. Such smooth pursuit (SP) stabilizes the moving object on the retina. When the eye movement is not optimal, saccades quickly adjust the retinal image. The background to this seemingly simple behavior is quite complex. In a natural situation the object is tracked with the head as well as the eyes. This presumes that visual and vestibular information are combined simultaneously to direct

the gaze on the object. When the head moves, gaze will still be on target. This is also the case if the body suddenly turns or moves: the moving object is visually tracked and gaze is on the target. In this situation both the vestibular ocular reflex (VOR) that counter-rotates the eyes when the head moves and the vestibulo-colic reflex (VCR) counter-rotating the head relative to the body (Peterson and Richmond, 1988) must be suppressed. To keep the projection of the moving object on the fovea over changes in its velocity and direction of motion requires that the control of eye rotation compensates for all delays in the motor system. Thus, the oculomotor system that controls the eye muscles must be driven predictively (Pavel, 1990; Leigh

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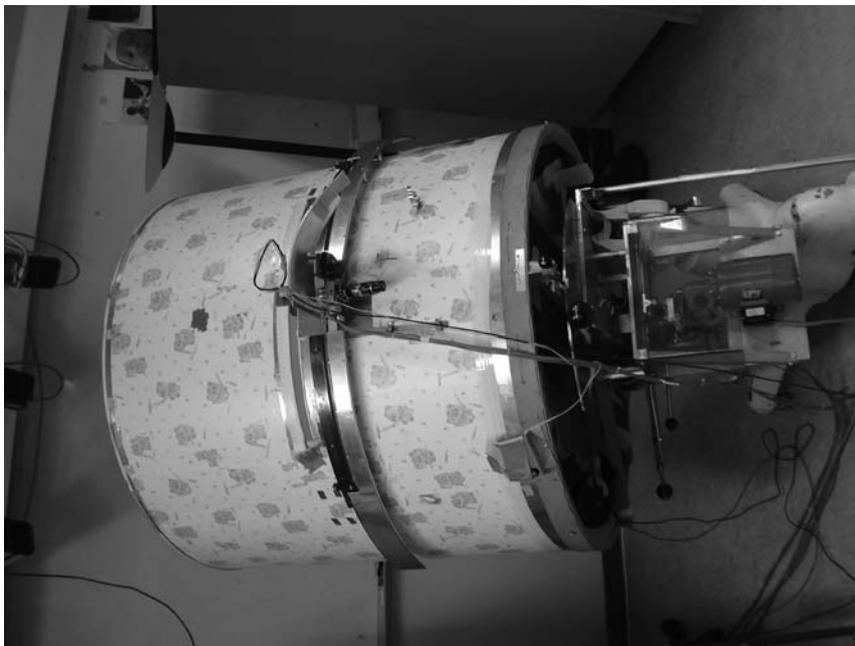
1 and Zee, 1999). That process must, in addition to
 3 the velocity and position of the tracked object and
 5 the delays in the sensorimotor system, involve all
 7 sensory information: visual, vestibular, and prop-
 9 rioceptive. In an experimental situation, when the
 11 lag of the eyes relative to the object motion is less
 13 than 120 ms, we consider the eye movements to be
 15 predictive (Robinson, 1965). The earliest form of
 17 visual tracking is saccadic and it is not until ~7
 weeks of age that smooth eye movements (SEMs)
 are consistently observed. However, already in ne-
 onates, vestibularly controlled eye movements are
 smooth and evidently the eye muscles are ready to
 control such gradual movements (Rosander and
 von Hofsten, 2000). Thus, it is the neural system
 for visual control of SEMs that is the limiting fac-
 tor and not motor system itself.

19 The control of SP eye movements and the com-
 21 plexity of the associated predictive processes are
 23 expressions of cognitive abilities (Kowler, 1990).
 This gives them an important role for understand-
 ing early cognitive development. Successful track-
 ing is realized through a motor command that,

1 similarly to reaching, is regulated with a predictive
 3 model of external and internal factors. In the lit-
 5 erature, the learning of such internal models in
 7 adults has been extensively discussed (i.e., Wolpert
 9 et al., 1998). There is however no such data for
 how and when they appear in development. The
 purpose of this chapter is to relate behavioral data
 from visual and visual-vestibular gaze adjustments
 to neuro-anatomical data relevant for predictive
 models.

A procedure suitable for investigating gaze control in young infants

15 We have constructed a safe and versatile “mini-
 17 room” that has been used extensively in infants.
 19 The advantage is that the infant can concentrate
 21 on the task, and much data is obtained during a
 23 few minutes. This apparatus has been described
 earlier (von Hofsten and Rosander, 1996, 1997)
 and is shown in Fig. 1. The infant is placed in a
 chair at the centre of a cylinder that constitutes the



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 47 Fig. 1. The drum at the centre of which an infant chair is placed. The surface of the drum is manually rotated 180° when the infant has been safely fastened with attached EOG electrodes and motion markers. An object, usually a 7° happy “face,” is oscillating in a slit in front of the infant. The slit is seen in the middle of the photo.

1 visual field. The inside surface is homogeneously
 3 white or patterned in specific ways and an object is
 5 placed on its inner surface, in front of the infant's
 7 eyes. The object, in most studies an orange-coloured
 9 happy face, has a small video-camera at its
 11 centre, thus allowing continuous monitoring of the
 13 infant's face during the experiment from the point
 15 of view of the stimulus. Other types of objects have
 17 been constructed to replace the routinely used
 19 "happy face." During the experimental trials, the
 21 object is moved by a motor giving an oscillation
 23 according to a sinusoidal or triangular velocity
 function. Another motor controls the oscillation of
 the chair, thus providing a condition for testing the
 vestibular function (VVOR condition). Finally, the
 cylinder and chair can be oscillated in synchrony.
 The last condition gives rise to a conflict between
 visual and vestibular information — the former
 induces visual tracking and the later a counter-
 rotation of the eyes. In order to stabilize gaze on
 the object in this condition, the VOR must be
 completely inhibited (vestibular inhibition (VIN-
 HIB) condition).

Measurements of head, object, and chair motions are performed using a motion analysis system with reflective markers (Qualisys). Small (4mm diameter) markers are placed on the object, the head, and on the upper part of the chair (Rosander and von Hofsten, 2000). Eye movements are registered with pre-amplified EOG (Westling, 1992) and this signal is synchronized with other measurements. In the analysis, the Euclidian coordinates of all markers and the EOG measurements are transformed to angular coordinates. The eye motion data file is then stripped from saccades $>40^\circ/s$ for identifying the smooth tracking component (SEM). Gain is estimated with Fourier analysis and timing with cross correlations. Some examples of eye and head measurements of a 4-week-old infant are shown in Figs. 2(SEM) and 3(VVOR).

The development of visual tracking

Visual tracking of an object is based on the engaging of attention on it and the commands to voluntarily track it. The ability to engage and

disengage attention on targets is present at birth. However, as infants get better at stabilizing gaze on an attractive target, they become less able to look away from it. This phenomenon has been termed "obligatory attention" or "sticky fixation" (Stechler and Latz, 1966; Mayes and Kessen, 1989). It has been suggested that it reflects the early maturation of a basal-ganglia/nigral pathway that induces a nonspecific inhibition of the superior colliculus (SC) (Johnson, 1990). The phenomenon of obligatory attention expresses itself rather dramatically in object tracking. von Hofsten and Rosander (1996, 1997) found that 2- and 3-month-old infants almost never looked away from the moving object they were tracking smoothly even though each trial had a duration of 20–30 s.

Newborns have a very minute ability to track a moving object with SEM. However, it has been shown that if an object with bright contrast is gently moved in front of the infant within reach, he or she will turn the head and eyes towards it and occasionally touch the object (von Hofsten, 1982). Dayton and Jones (1964) observed smooth following of a 15° object in neonates up to velocities of $\sim 15^\circ/s$ and Kremenitzer et al. (1979) observed smooth tracking in newborns for a large, 12° , stimulus moving at 9° – $30^\circ/s$. Bloch and Carchon (1992) used a small ball, 4° in diameter, in their study of visual tracking in neonates of 3 days and 2–4-weeks-old. Although the velocity was low ($8.7^\circ/s$), mostly saccadic tracking and head movements were observed. Phillips et al. (1997) measured 1- to 4-month-old infants' eye movement when they tracked a small (1.7°) red lamp in hold-ramp-hold motion pattern. All infants showed a small amount of SP for the velocity interval 8° – $32^\circ/s$. With increasing age, the number of saccades decreased and the intervals of smooth tracking became longer. At 3 months of age the smooth tracking dominated. A similar result was obtained by Aslin (1981) who used an object, a vertical rod $2^\circ \times 8^\circ$, moving sinusoidally with $10^\circ/s$. He found saccadic tracking up to 6 weeks of age after which SP was observed. We measured eye and head movements for object velocities between 0.1 and 0.4 Hz (von Hofsten and Rosander, 1996, 1997). In one experiment (von Hofsten and Rosander, 1996), an object (size 8°) moved

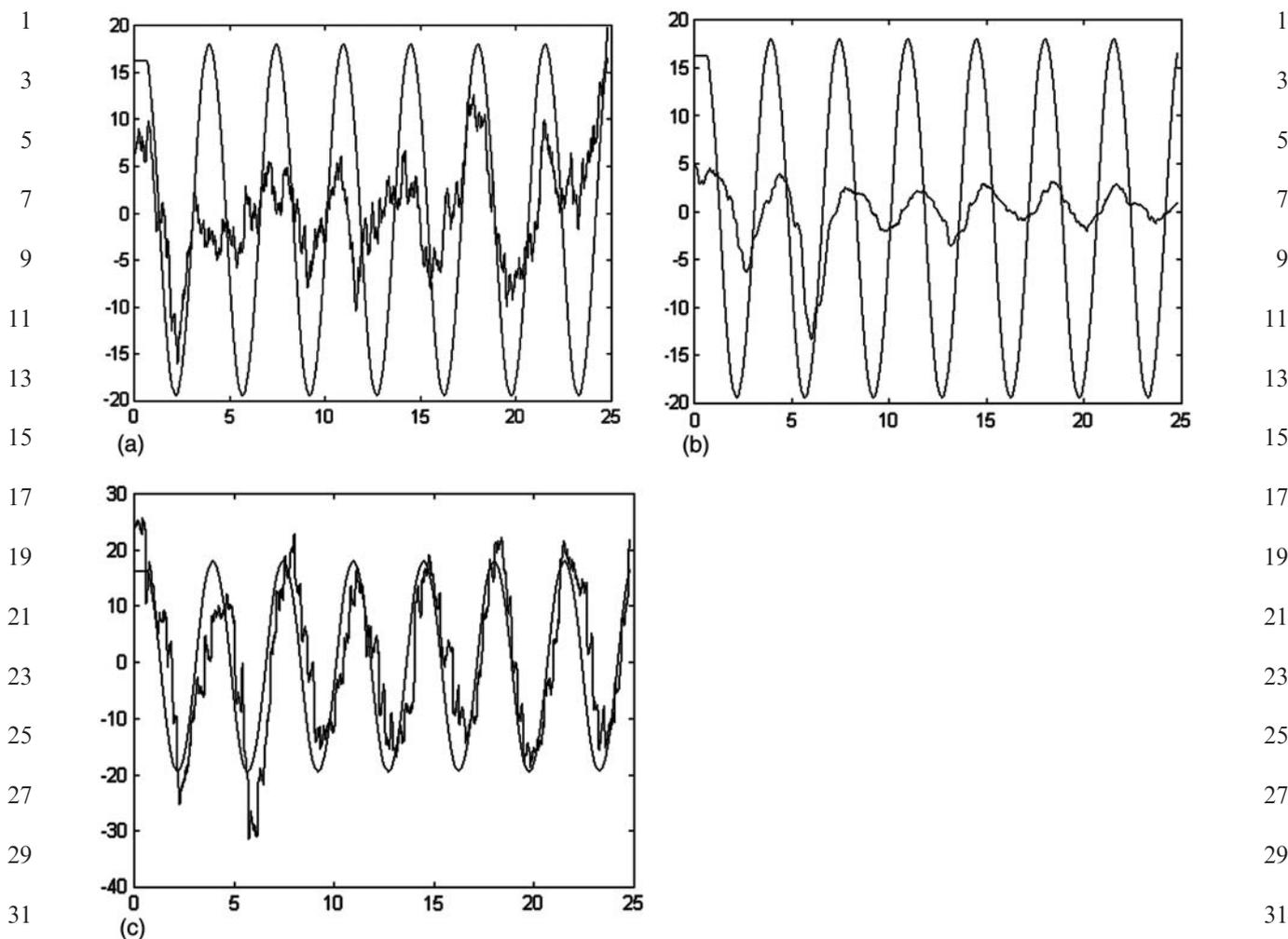


Fig. 2. Measurements of eye, head, and object movements of a 4-week-old infant during a trial of 25 s. Angular position is calculated (y -axis) as a function of time (x -axis); (a) eye-and object movements, (b) head-and object movements, (c) calculated gaze and object motion.

sinusoidally at 0.1, 0.2, and 0.3 Hz, corresponding to 8.9° , 17.8° , and $26.7^\circ/s$, against a red-and-white vertically striped background. Values similar to Phillips et al. (1997) were found for eye gain (saccades plus SP), i.e., close to 0.6 at 1 and 2 months and 0.7–0.8 at 3 months of age.

Smooth pursuit

von Hofsten and Rosander (1997) separated the saccadic and smooth tracking components in a

longitudinal study of infants from 2 to 5 months of age. The infants were shown sinusoidal and triangular oscillations of 0.2 and 0.4 Hz with amplitudes of 10° and 20° corresponding to average speeds of 10, 20, and $40^\circ/s$. They found that SP primarily developed between 2 and 3 months of age (von Hofsten, 2004). All the infants studied showed a similar increase in gain between these two ages. Gain was also dependent on object velocity. At 2 months it was 0.45, on the average, for the $40^\circ/s$ and 0.80 for the $10^\circ/s$ motion. The lag of the SP was less than 100 ms already at 2 months

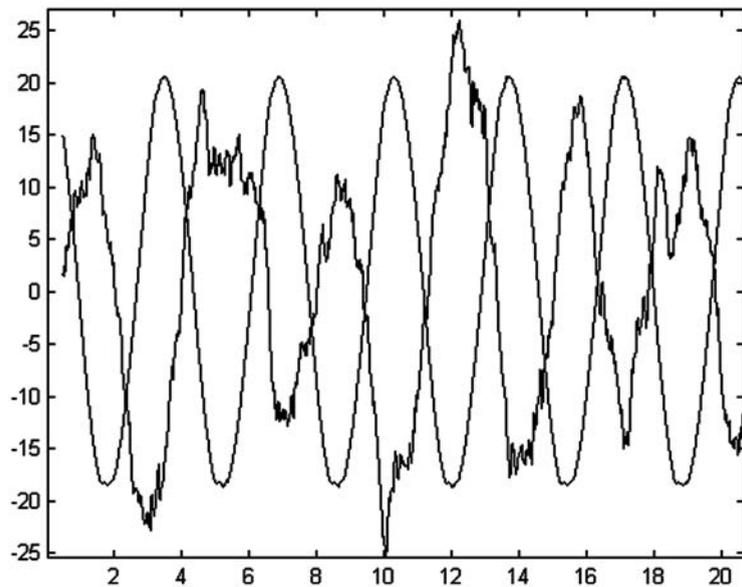


Fig. 3. Measurements of eye and body movements of a 4-week-old infant for a trial of 20 s. The object is stationary (VVOR). Axes as in Fig. 2.

and did not change much over age. At 5 months of age, infants tracked periodic motions up to 0.6 Hz but at higher velocities the gain and phase deteriorated similarly to adults.

Stimulus size

In general, the younger the infant, the larger is the object needed for attentive tracking. Rosander and von Hofsten (2002) measured tracking of objects varying in size between 2.5° and 35° . The infants were studied longitudinally from 6.5–14 weeks. The objects moved sinusoidally at 0.25 Hz. The object size had no effect on SP gain at any of the ages studied. The gain increased with age, independently of object size. At 6.5 weeks of age, it was ~ 0.4 and at 14 weeks it was 0.8. There was an effect of object size in both the 6.5- and 9-week-old infants: smaller objects elicited more saccades. When the SP gain was low, the saccades compensated rather precisely and optimally. Furthermore, while the SP lag was minimal for all the ages and sizes studied, the lag of the raw eye movement, SP+saccades, improved substantially from 6.5 weeks of age where it was 200–300 ms to 12.5

weeks where it was less than 100 ms. There was no effect of object size. This indicates that at 12.5 weeks of age, both these forms of tracking are predictively controlled.

If the background around the object moves with it, this could either enhance or suppress the tracking. A greater extent of motion argues for enhanced tracking and the diminished motion contrast between the fixation object and the background in this condition argues for a suppression of tracking. Rosander and von Hofsten (2000) measured visual tracking for an object moving sinusoidally at 0.25 Hz. The background was a striped pattern and moved with the object. The gain and lag of the eyes relative to the object (alternatively the head slip) was similar for this study and other studies either using no background or a patterned stationary background (von Hofsten and Rosander 1996, 1997). However, the saccades ($> 100^\circ/\text{s}$) were fewer compared to conditions with no moving patterned background (Fig. 4). At 2 weeks of age the eye lagged almost 1.0 s, at 4 weeks 0.2 s, and at 10 weeks of age 0.05 s (Rosander and von Hofsten, 2000). Thus, the timing of the eye is rather precise when the gain of the SEMs start to function.

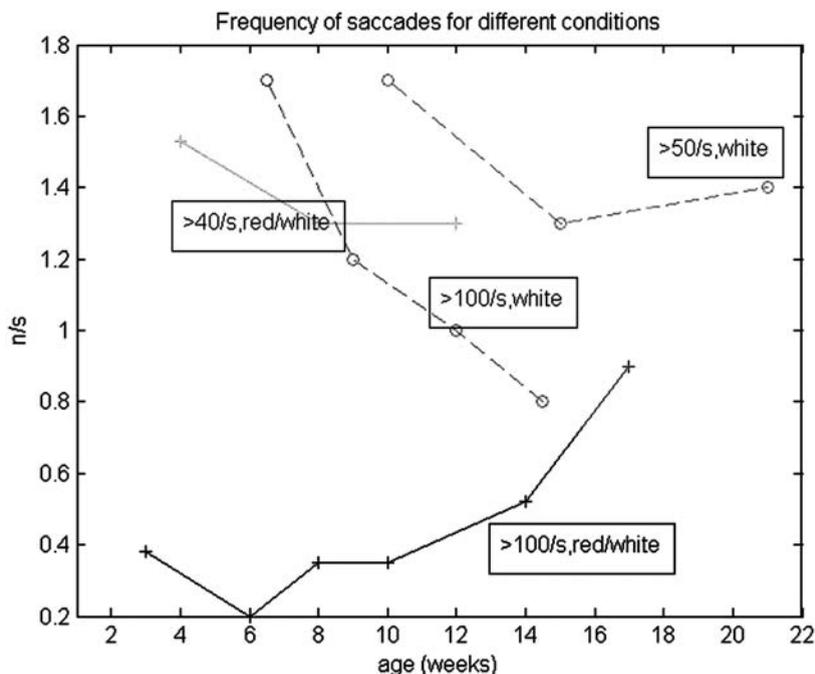


Fig. 4. The number of saccades (y-axis), $>100\text{ s}^{-1}$ and $>40\text{ s}^{-1}$ for visual tracking of a 0.25 Hz moving object if the background is striped (“red/white”) or white.

In the literature, two kinds of pursuit eye movements have been distinguished: optokinetic response (OKR) and SP. The function of OKR is to enable stabilization of gaze during ego motion while the function of SP is to enable gaze stabilization on a small moving object in a complex visual scene. The OKR is a phylogenetically older system and is present in all mammals while the SP system is only present in primates (Buttner and Buttner-Ennever, 1988; Paigie, 1994). It has been argued that OKR and SP are distinct systems. However, the systems have related neural pathways and both systems are predictive (Krauzlis and Stone, 1999). Our results suggest that both systems are indeed closely connected. There are almost no effects of size. Furthermore, it has been proposed that OKR develops before SP. Our results indicate that there is no shift in control over the age period studied. One might argue then that even the smallest object used activates the OKR system. But a small 2.5° stimulus can hardly be considered to control gaze during ego motion. The question is then whether there is any sense in

distinguishing between OKR and SP. Also experimental data from adults suggest that SP and OKR are parts of a common system (Heinen and Watamaniuk, 1998).

Motion trajectory

In adults several experiments have been performed with unpredictable motion patterns (Barnes and Lawson, 1989), challenging the predictive oculomotor processing. Developmental studies have shown that “biological motion” is detected better than other types of motions early in life (Fox and McDaniel, 1982). One common type of biological motion is the sinus motion, and combinations of such functions. We performed an experiment comparing the sine function with constant object motion that abruptly reversed at the end points of the trajectory (triangular motion). The drum set up was used, and the object was moved horizontally with the two motion patterns and with two amplitudes, 10° and 20° . Two-, 3-, and 5-month-old

1 infants were measured when they were looking at
 3 an object that moved either according to a sinusoidal or a triangular function. Significant differences between motion types were obtained for eye gain, number of saccades, and SP timing. At 5 0.4 Hz the constant velocity motion gave higher gaze and SP gains than the sinusoidal one but very bad timing (around 250 ms). This indicates that 7 because the triangular motion did not give an indication of when the motion would reverse, the tracking continued for a short time in the previous 9 direction after which the eyes caught up with a reactive saccade. Because of this there were also 11 more saccades for the triangular motion as compared to the sinusoidal one. Furthermore, the 13 higher oscillation frequency and/or the higher amplitude induced more saccades. Drastic effects 15 were seen for the timing. At 2 and 3 months of age, the lag was ~ 75 ms for sinusoidal motion, and 17 250 ms for the triangular motion. At 5 months of age all sinusoidal motions were anticipated predictively and the lag for the triangular motion was 19 much reduced. The fact that the reversal of the triangular motion is not predictable from what 21 happens just before (motion is constant), suggests that the reduced lag at 5 months is due to an ability 23 to predict the periodicity of the motion. 25

27 Another question concerns the form of the trajectory. Gronqvist et al. (2006) studied visual 29 tracking of circular, vertical, and horizontal motions in 5-, 7-, and 9-month-olds. They measured 31 gaze movements with an infrared corneal reflection technique (ASL) camera and simultaneously head 33 movements with “Flock of Birds.” Similar to adults, infants tracked horizontal motions better 35 than vertical ones. Learning was also found to improve within trials. Gredeback et al. (2005) 37 found no consistent predictive tracking of a circular path until 8 months of age. 39

41 *Head and eye coordination*

43 In addition to eye movements, head movements are also used to stabilize gaze on a moving object. 45 In 1-month-old infants, Bloch and Carchon (1992) showed that head movements were used more than 47 in newborns. Also Daniel and Lee (1990) found

1 that between 11 and 28 weeks, the head was increasingly used in tracking and some infants used 3 more head than eye movements. von Hofsten and Rosander (1996) found that head gain increased 5 marginally with age from 1 to 3 months for the tracking of an object moving at 0.1, 0.2, or 0.3 Hz. 7 It was below 0.2 for all velocities. This result is similar to those found by von Hofsten and 9 Rosander (1997). They found that the head made up around 10% of the gain at 2 and 3.5 months of 11 age. However, at 5 months of age, almost 50% of the gain was accounted for by head movements. 13 This can be seen in Fig. 5 that shows how the change in head movement gain is balanced with a 15 change in gain for the eye movements. The resulting gaze is still on target. We found that it was 17 convenient to relate eye position and eye velocity to the difference between object and head, i.e., the 19 head slip. During tracking with both eye and head it means that the eye movement gain should optimally 21 be equal to the head slip. von Hofsten and Rosander (1997) measured the lag of the head 23 movements and found it to be considerable (~ 0.4 s). However, the lagging head did not deteriorate 25 gaze tracking. Instead the eyes were compensating for the lagging head in such a way that 27 the resulting gaze lag was close to 0. This means the head movements are taken into account in the 29 programming of the eye movements. However, for high oscillation frequencies, the lag of the head 31 and the lead of the eyes tended to counteract each other. For instance, at 0.6 Hz a 0.4 s lag corresponds 33 to almost a 90° phase lag. Thus the combined gain was less than the gain of either single 35 head or eyes. In such cases the subject would fill in the smooth tracking with saccades. 37

39 Although the head contributes to the tracking of moving objects, it also moves for other reasons. 41 One of the most important functions of the vestibular system is to compensate head movements 43 unrelated to the tracking task by counter-rotating the eyes in equal amount in synchrony with the 45 head movements (VOR). This keeps the image stable on the retina in spite of the fact that head 47 movements always include some fast head oscillations (Skavenski et al., 1979; Gresty, 1992). In adults, VOR is very effective for high frequencies in the interval 1–6 Hz. We found that this kind of

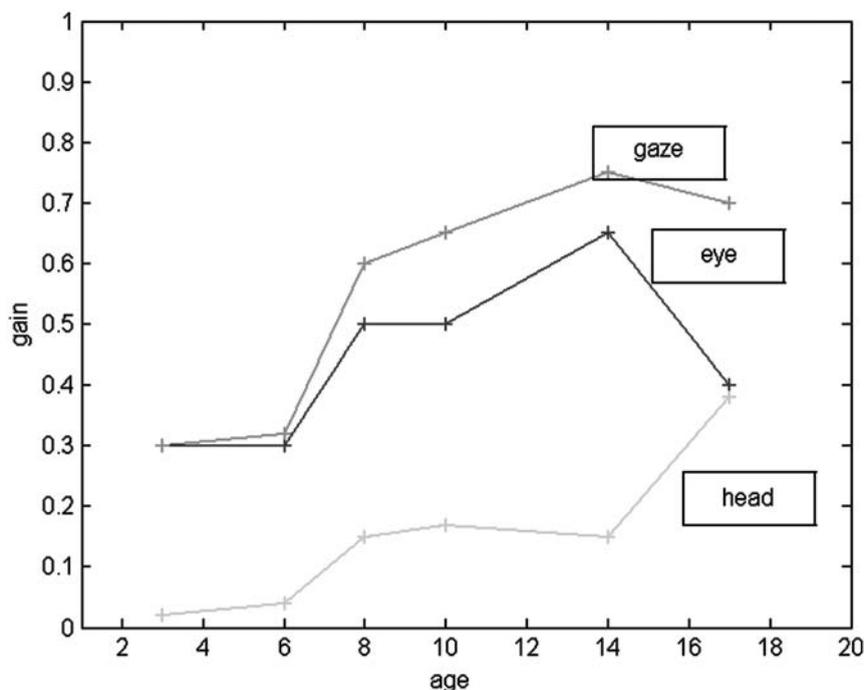


Fig. 5. Eye, head, and gaze position gain for tracking a 0.25 Hz moving object as a function of age in weeks.

compensatory eye movements appear very early in development (von Hofsten and Rosander, 1996). They are present in 1-month-old infants but the amplitude of the compensating eye movements is generally much higher than the inducing head movements. By 3 months of age the head and eye movements are much better scaled to each other and the compensation is much more effective.

Before 5–6 weeks of age essentially all head movements are compensated, even those that may contribute to the tracking. The problem that has to be solved in the development of eye–head coordination is how to separate the head movements that contribute to gaze tracking from the head movements that have to be compensated. It has been proposed that such smooth tracking with eye and head requires a suppression of the VOR (cf. Fukushima, 2003a). At the age when SP appears, the oculomotor system begins to utilize head movements in the tracking task, but sometimes the head movements involved in the tracking are compensated giving the paradoxical effect that the head tracking is totally ineffective. The VOR for

the head movements involved in the tracking must not be compensated but a general suppression of VOR includes the compensations of head movements unrelated to the tracking task and they still need to be compensated if gaze is to be stabilized on the moving target. Separating the head movements that contribute to gaze tracking from those that need to be compensated is a problem that is solved at around 3 months of age (Fig. 6).

Apart from the vestibular system, several other systems are involved in the stabilization of body and gaze in space and the coordination between eyes and head. The vestibulo-collic response (VCR) will induce counter-rotation of the head to keep it stable in space in response to body rotation. The collic-ocular response, guided by proprioceptive information from the neck will initiate a counter-rotation of the eyes to compensate for neck-rotation. The final solution of the problem of coordinating head and eye movements needs to take all these different systems into account and has to be based on predictive control of intentional movements.

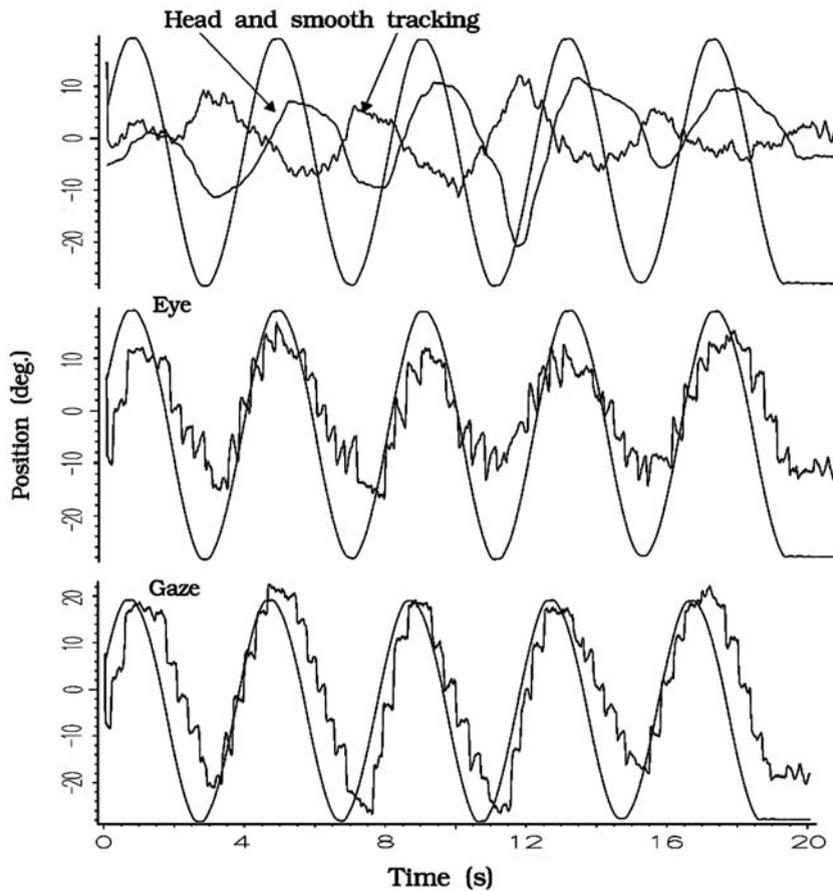


Fig. 6. Measurements of eye movements for an infant (3 months of age) that was not able to suppress VOR during the trial. The upper figure shows measured head and object movements together with calculated smooth eye movement component. The middle figure shows measured eye and object movements, and the lower figure the calculated gaze.

Brain development from the perspective of visual tracking

The visual pathways

In the human neonate two neural pathways have been suggested to process visual motion information. The primary pathway from the retina via the lateral geniculate nucleus (LGN) to visual cortex and MT+, and the secondary one via the SC and pulvinar to MT (Atkinson, 2000). The visual cortex is the cornerstone of visual processing. In primary visual area v17 (V1) Layer 4, most visual input comes from the LGN. The extrastriate areas, primary visual area v18 (V2), primary visual area

v19 (V3), V4, and V5 (MT), process and distribute visual information further. For example, it has been suggested that the V3 processes large pattern coherent motions, as the striped pattern described earlier.

There are a few studies in humans on the development of neural growth between layers in the visual cortex. Prenatally, the intracolumnar connections between layers 2/3 and 5 develop, and the first intercolumnar connections are observed within layers 4 and 5 (Burkhalter et al., 1993). Burkhalter et al. (1993) also conclude that the intracolumnar connections develop before the intercolumnar ones reflect the processing of local features in the visual field. The magnocellular

1 pathway characterized by the fibers from the LGN
 3 reaching Layer 4C in the V1, continue to Layer 4B
 5 and further towards the MT area. Sandersen
 7 (1991) (referring to Rakic, 1976) reported that
 9 the neuro-genesis in primate area 18 (V2) is slightly
 11 ahead of area 17 (V1), and that area 19 (V3) is
 13 ahead of area 18. Becker et al. (1984) studied the
 dendritic development in the visual cortex and
 found that at 4 months of age the dendritic length
 in Layer 5 had reached its maximum. Burkhalter
 (1993) report that at 4 months of age forward
 connections from V1 to V2 are well matured.
 Taken together, at 4 months the maturation of the
 visual cortex is well on its way.

15 The maturation of the LGN in humans was
 17 studied by Garey and de Courten (1983). Their
 19 study concerns the dendritic and somatic spines,
 21 both common at 4 months of age. At 9 months of
 23 age, such spines have disappeared and the cells
 look like those in adults (Garey, 1984). Further-
 25 more, the volume of the LGN doubles between
 birth and 6 months of age, after which no changes
 in volume are observed. In macaque infants Mo-
 vshon et al. (2005) concluded that the maturation
 of neurons in the LGN is driven by that of the
 retinal cells. From 1 week of age, the spatial and
 temporal resolutions increase (Movshon et al.,
 2005).

29 The visual cortex increases 4-fold in size be-
 31 tween birth and 4 months of age (see Garey, 1984).
 33 Huttenlocher et al. (1982) investigated the synap-
 35 togenesis in the primary visual cortex (V1) and
 37 found that it increases rapidly between 2 and 4
 months of age reaching a peak at 8 months of age.
 Such high production of synapses during the 2–4
 month period is rather general and is found in
 visual, prefrontal, somatosensory, and motor parts
 of the cerebral cortex (Rakic et al., 1986). After 1
 year of age, the synaptic density decreases to adult
 values at 11 years of age, a process that permits
 plasticity or individual differences (Sandersen,
 1991). For the development of SEM and for per-
 43 ception of motion direction, the V5/MT+ area,
 45 downstream from the primary visual cortex is es-
 47 sential. It has been suggested that the development
 of visual motion perception and SP between 2 and
 5 months of age reflects the onset of functioning of
 the MT+ area. Kiorpes and Movshon (2004)

1 measured receptive-field properties in infant mac-
 3 aques and found direction-sensitivity in the ma-
 5 jority of MT cells at 1 week of age, (corresponding
 7 to 1 month in humans) although the neuronal dyn-
 9 amics was not adult-like. According to a histol-
 11 ogy study by Flechsig (1905), the MT+ area
 13 becomes myelinated during the first month in hu-
 man infants. Rosander et al. (2007) reported that
 the evoked response potential (ERP) for motion
 stimulus in this area was discernable at 2, distinct
 at 3, and massive at 5 months of age. The mat-
 uration of the MT+ structure may be compared
 to the development of motion perception and SP
 gain.

15 An alternative visual pathway from the retina
 17 via SC has by some authors been suggested to be
 19 exuberant (Sandersen, 1991). However, for motion
 21 stimuli, this pathway that bypasses V1 still remains
 23 in adults and is active for non-conscious fear
 25 (Morris et al., 1999) and fast moving stimuli
 (ffytche et al., 1995; Buchner et al., 1997; Sincich
 et al., 2004). The subcortical, collicular pathway is
 considered to dominate motion processing until
 around 2 months of age (Dubowitz et al., 1986;
 Snyder et al., 1990; Martin et al., 1999; Atkinson,
 2000).

27 The neural pathways for visual motion are il-
 29 lustrated in Fig. 7. As observed in Fig. 7, one im-
 31 portant connection is MT+ to frontal eye field
 33 (FEF). In adults, O'Driscoll (2000) found that the
 35 gain of SP is set in the FEF area. At 4 months of
 37 age the prefrontal cortex is functioning (Csibra et
 al., 1997), as shown by the ERP for anticipatory
 or reactive saccades. In their discussion of such
 prospective control Canfield and Kirkham (2001)
 suggest that FEF may function even earlier, i.e.,
 at 3 months of age. For language perception,
 Dehaene-Lambertz et al. (2002) obtained MRI re-
 39 sponse in the right prefrontal area of 3-month-old
 41 infants. The fact that the prefrontal and FEF areas
 may function at such young age is supported by
 the reported neural development by Mrzljak et al.
 (1990). During the postnatal period of 0–6 months
 most types of projections and local circuits are
 developed. Successive functioning may then take
 45 place to process SP gain for oculomotor function-
 47 ing according to the compartment model in Fig. 7.
 Fukushima (2003b) suggests that caudal neurons

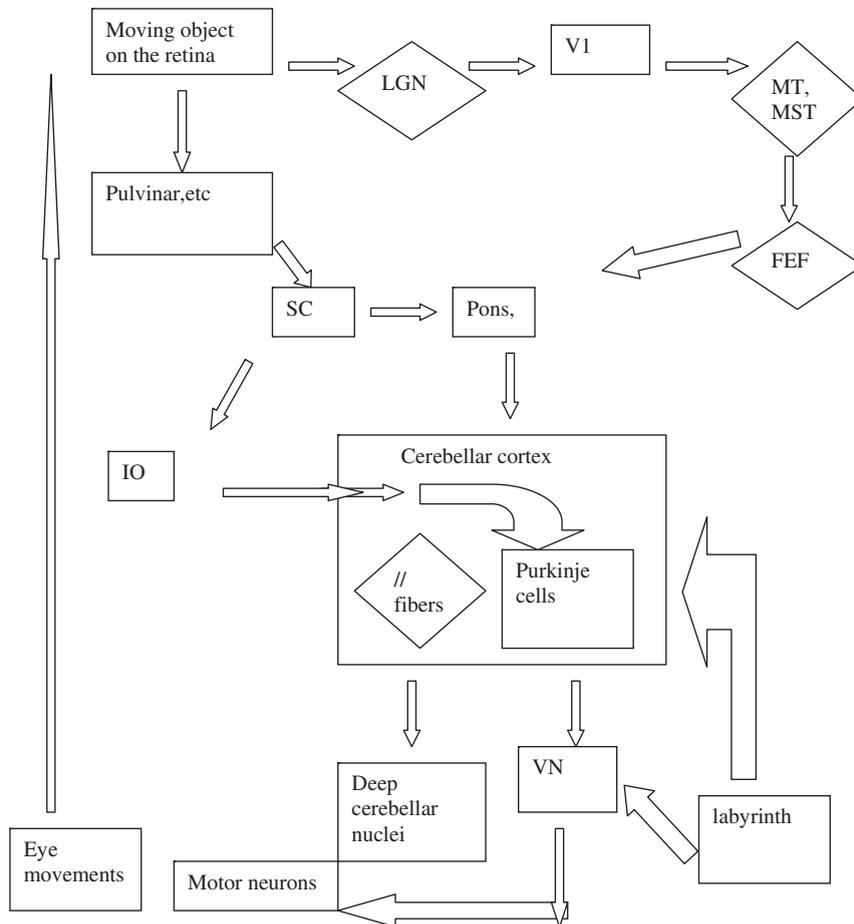


Fig. 7. An illustration of neural visual motion pathways. (square = functions from birth, and rhombus = functions from 3 to 4 months of age.) Adapted with permission from Atkinson (2000), Fukushima, (2003a), Krauzlis and Stone (1999), and Leigh and Zee (1999).

in the FEF set the SP gain as well as maintaining a prediction of the eye movement. Furthermore, also head movements are involved in gaze estimates (see Fig. 1 in Fukushima, 2003b).

Cerebellum

The structure of cerebellum differs from that of cerebrum, consisting of three lobes and an underlying deep cerebellar nuclei (the fastigial, interpositus, and dentate). One lobe, the flocculus in the vestibulo-cerebellum is of special interest as it is essential for VOR and SP. This is a phylogenetic

old part of cerebellum. There are two major inputs to cerebellum: one via the mossy fibers (MFs) and one via the climbing fibers (CFs) from the inferior olive (IO). MFs also branch to the deep nuclei.

The cerebellum has a central role in motor regulation, learning, memory, and action planning. The key loop includes the IO, the CFs, the Purkinje cells (PCs), plus the connecting MFs and parallel fibers (PF), the signals of which constitute the Purkinje output to the cerebellar nuclei (Miall, 1998). The MFs provide, from the pontine nuclei in the brainstem, information about the external world and intended and actual movements. The CFs from the IO to cerebellar cortex provide

1 error signals related to movement production. All
 3 output from the cerebellum go via PCs to deep
 5 nuclei and VN for further distribution over the
 brain. The output to the cerebral cortex via the
 thalamus is massive.

7 There is some data on the maturation of CFs,
 MFs, and PFs. At birth, the CFs from the IO are
 9 connected to the PCs (Gudovic and Milutinovic,
 1996). These cells, that form the cerebellar output,
 11 are then in their 3rd stage of maturation (Zecevic
 and Rakic, 1976) and especially their dendritic tree
 13 expands slowly during the first year of life. As
 pointed out (Zecevic and Rakic, 1976) this is a
 15 complex process, as the PFs connect to the PCs.
 These fibers are formed when the granule cells mi-
 17 grate from the external granular layer (EGL) in-
 wards, causing this layer to get thinner with age. In
 19 their study of the histogenesis of the human cere-
 bellum, Rakic and Sidman (1970) and Lavezzi et
 21 al. (2006) found that the EGL is formed at ~10–11
 weeks after conception. The thickness decreases
 23 from 25 to 30 μ during the first 6 weeks of life. At 2
 months, the EGL starts looking thinner and be-
 25 tween 5 and 7 months of age the involution pro-
 cess increases. The layer is not visible at 12 months
 of age. Friede (1973) found a similar pattern al-
 27 though at a slightly younger age. Abraham et al.
 (2001) concluded that the EGL disappears be-
 29 tween 8 and 11 months of age. The MFs are im-
 mature in the newborn (Seress and Mrzljak, 2004).

31 In summary, it can be argued that the PF–PC
 33 connection (glomerulus) begins to function at
 1.5–2 months of age and has matured considera-
 35 bly at 5 months of age. The MFs follow the same
 course, but the CFs are connected to the PCs at
 birth.

37 *Cerebellar functioning during development*

41 An important function of cerebellum is to regulate
 sensory-motor coordination. Miall and Reckess
 43 (2002) stated that “one of the fundamental func-
 45 tions of the cerebellum is to act as a sensory pre-
 dictor” (p. 212). This is manifested, at least to
 47 some extent in adaptive learning (Ito, 2001). What
 is learnt is the dynamics, not the individual part, of
 a movement (Ito, 1993). The cerebellar pathways

1 create networks that serve sensory-motor func- 1
 tions. Most studies of cerebellar function reveal 3
 that predictive models have their site in loops that 3
 include the IO, PC, PF, MF units. However, if this 5
 neuro-anatomical basis is not developed, the cer- 5
 ebellar functioning is incomplete.

7 Two types of responses have been studied in in- 7
 fants that illustrate the development of cerebellar 7
 learning. The first one is the conditioned eye blink 9
 response. It develops gradually during the first 5 9
 months of life (Ivkovich et al., 1999; Klafin et al., 11
 2002). Little et al. (1984) measured the eye-blink 11
 response in infants aged 10, 20, and 30 days. For 13
 the first 10 days, no learning occurred, but it was 13
 observed for the 20- and 30-days groups. Klafin et 15
 al. (2002) found a dramatic increase in the re- 15
 sponse at 5 months of age that they relate to the 17
 maturation of the cerebellar circuits. The interpre- 17
 tation of this response is that the MF carries the 19
 conditioned stimulus information, and the CF the 19
 unconditioned one. Then, the learning of eye blink 21
 is explained by the long-term depression (LTD) at 21
 the PF synapse on the PC (Ekerot and Jörntell, 23
 2003). For this response, the PFs play an impor- 23
 tant role and the dramatic increase in learning at 25
 5 months of age is in agreement with the neurode- 25
 velopment of the PFs. 27

29 A second example of cerebellar learning is the 29
 vestibulo-ocular reflex. The vestibulo-cerebellar 29
 cortex receives several inputs: from MFs originat- 31
 ing in the labyrinths, from the vestibular nuclei, 31
 from CFs originating in the IO, and from MFs 33
 from the LGN and/or the SC. In the flocculo- 33
 nodular region, a translation of the degree of head 35
 motion relative to eye rotation is performed, so 35
 that the eye movements completely compensate 37
 the head movements. The VOR shows adaptable 37
 learning, and it has been suggested (Ito, 1993) that 39
 the glomerulus with the PF signal is a model for 39
 the desired eye trajectory resulting from the VOR. 41
 According to Blazquez et al. (2003), however, one 41
 might alternatively consider the important role of 43
 the brainstem structures. For rotations at frequen- 43
 cies of 0.2–0.5 Hz, the VOR does not function 45
 perfectly in neonates. The phase is, up to 1 month 45
 of age, not perfectly compensatory (Cioni, 1984; 47
 Weissman et al., 1989) and the eyes move too fast 47
 relative to the head. From then on, the VOR gain

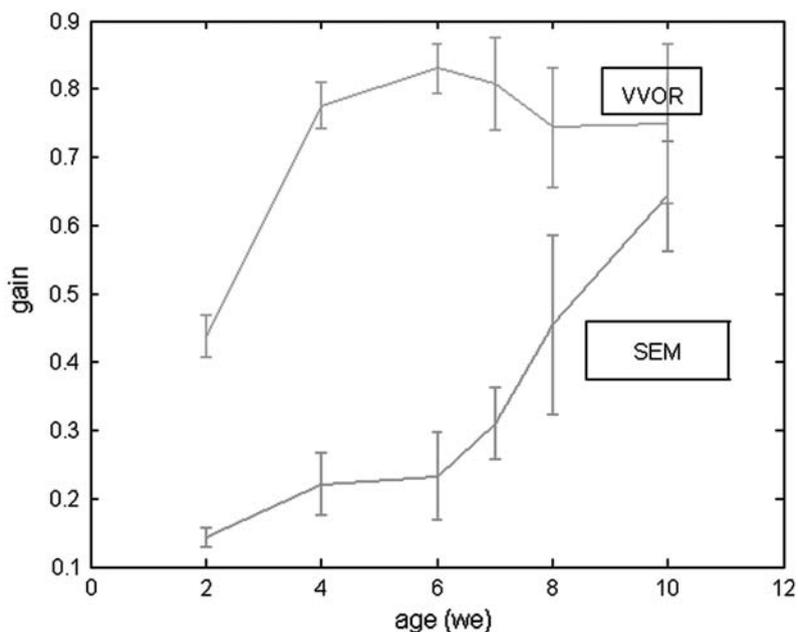


Fig. 8. Calculated gain for the smooth eye component in two situations: the tracking one when the object is moving (lower curve) and the vestibular one when the object is stationary (upper curve) as a function of age.

is close to 1.0 (Eviatar et al., 1974; Weissman et al., 1989; Finocchio et al., 1991). Rosander and von Hofsten (2000) showed that the gain is close to 1.0 at 8 weeks of age. In Fig. 8 the gains of the estimated SEM and VOR gain are shown. At 2 weeks of age the VOR gain is very low but it increases rapidly to 4–6 weeks of age. At 0.25 Hz the timing of the eye is ahead of the head with 25–75 ms at 2 weeks of age. The gain is around 0.45. From these data one can conclude that essential parts of the VOR loop have matured at 1–1.5 months of age. This is confusing considering that if there are no MF input (which is the main sensory input) and no PFs, the VOR should appear to be jerky and nonprecise, as the flocculus (Ito model) estimates the gain.

Taken together, the eyeblink response and the VOR develop in synchrony with the expanding PFs that constitute a critical part of the motor learning and predictive ability properties of the cerebellum. Maturation of these functions appears to take place in synchrony with neuronal growth and differentiation being established at 4 months of age.

Visual-vestibular interaction

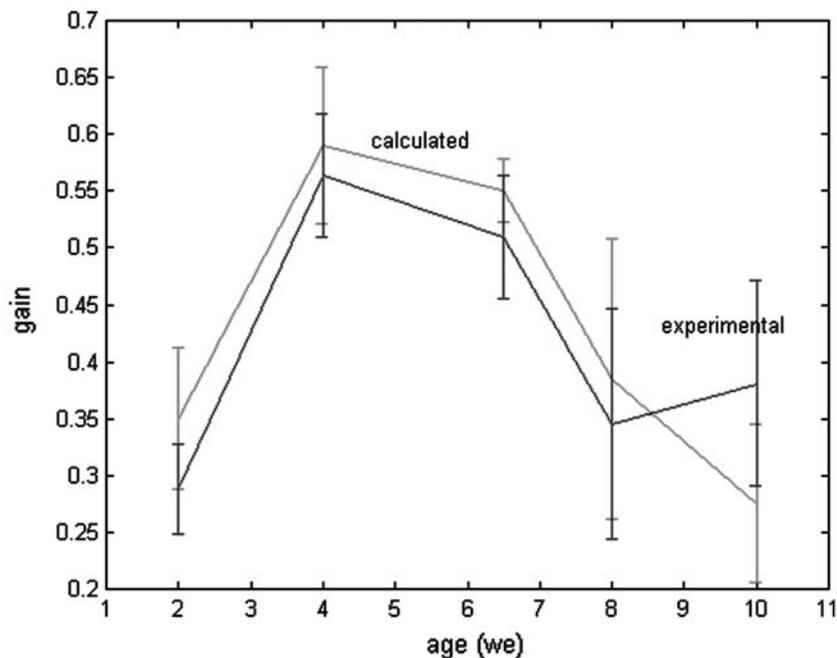
When a moving object is tracked with the head and eye, visual and vestibular information must be utilized in an optimal way. All brain areas that are involved in the production of SEMs are also receiving vestibular information and a great deal of the integration of vestibular and visual information takes place in the cerebral cortex (Fukushima, 2003a). In adults it is assumed that the areas of VN, flocculus, vermis, and the brainstem nuclei are reached by visual information of moving objects, as well as by vestibular information. Lesions in the flocculus area impair the ability to suppress vestibular signals in a visual-vestibular interaction situation (Zee et al., 1981). We have performed two studies on how the visual-vestibular interaction is challenged when the infant and the environment (the drum) rotate in synchrony during light conditions (VINHIB described above). In the first study (2000), suppression of the gain of VOR was observed from 3 weeks of age. The counter-rotation of the eyes were not fully compensatory, the mean phase between eye and chair being

1 ~140°. The VCR was not suppressed for the age
 3 period studied. On the contrary, it increased up to
 5 18 weeks of age. In the experiment, the stimulus
 7 was a small happy face on a striped background.
 9 The second experiment was similar to the first one
 11 but the background was white. SEMs, saccades,
 13 and gaze were compared for three conditions:
 15 SEM, VVOR, and VINHIB. If no eye movements
 17 are observed during the last condition, this would
 19 imply a perfect inhibition of the VOR. Similarly, a
 21 perfect inhibition of the VCR means that no head
 23 movements are observed. Some smooth compensa-
 25 tory eye movements were observed in the
 27 VINHIB condition from the youngest age level
 29 at 2 weeks to the oldest at 16 weeks showing that
 31 VOR was never completely suppressed. The gain
 33 was constant up to 10 weeks of age and diminished
 35 thereafter. The VCR was small until 10 weeks of
 37 age when head mobility increased substantially.
 39 The saccades were directed so that the eye move-
 41 ment gain was decreased, contrary to the VVOR
 43 and SEM conditions where the saccades increased
 45 the gain.

1 When the SEM and VVOR vectors for smooth
 3 eye position are added, the “theoretical curve” in
 5 Fig. 9 is obtained. It fits well with the “experi-
 7 mental” curve, the SEM gain in the VINHIB case.
 9 This result indicates that the neural processing for
 11 the inhibition of VOR is related to the VOR and
 13 SEM processing, supporting the notion of a com-
 15 mon neural site like the flocculus. In VINHIB it
 17 seems easier to inhibit the vestibular induced eye
 19 movements if the background is neutral, and with-
 21 out texture of stripes.

23 *Development and predictive models*

25 Oculomotor control and regulation, as all motor
 27 control, is realized through predictive models.
 29 Such models provide a desired, predicted external
 31 state (the moving object) and how internal factors
 33 (delays in muscle activation) shall be regulated in
 35 order to fulfil that desired state. The goal of eye
 37 tracking is to stabilize gaze on the object of inter-
 39 est, and gaze position is based on eye, head, and
 41
 43
 45



47 Fig. 9. Gains of SEM in the VINHIB situation (“experimental”), together with vector sums of SEMs in the object tracking and VVOR situations (“theoretical”) as a function of age.

1 body movements. SEMs begin to contribute to
 3 tracking from 6 weeks of age and attain an adult-
 5 like function at around 12–16 weeks of age. Head
 7 movements are never predictive in this age period
 9 but the eye movements compensate for the lagging
 11 head so that gaze is predictive.

13 Predictive models are the result of a learning
 15 process. One part is to create neural models of the
 17 motor system in the body (Glickstein, 1993; Miall
 19 et al., 1993), another to learn the dynamics of
 21 movements (Ito, 1993). There is much evidence
 23 that cerebellum is the neural site for such models.
 25 They assume an adult functioning cerebellum with
 27 the PFs, PCs, and CF as key structures, in which
 29 LTD is formed and modified by CF error signals
 31 (Kawato, 1999; Ito, 2001). Ito (1993) discusses
 33 how parallel processing, not looping, functions for
 35 cerebro-cerebellar connections. Feed-forward or
 37 inverse control of actions in cerebellum is parallel
 39 to feedback control in the cerebral cortex (Ito,
 41 1993). In their discussion of trans-cerebellar loops,
 43 Altman and Bayer (1997) suggested two types of
 45 loops regulating motor activity: a reactive one that
 47 includes error-correcting and negative feedback and a proactive one that has to do with error-avoiding and feedback. Both the upper proactive and the lower reactive loops originate in the deep nuclei. The reactive or lower one is phylogenetically older and has vestibular and spinal input: the cerebello-rubro-olivocerebellar loop. Hilbert and Caston (2000) discussed these models recently in connection with the motor learning in the Lurcher mice. The loops are regulatory and not part of executive function. The reactive regulatory task is to compensate for consequences of ongoing or previous actions. This is realized by feedback. The second type, the proactive one (cerebello-thalamo-cortico-ponto-cerebellar), is to make adjustments in preparation for actions. Recent research on the cerebro-cerebellar loops indicate that the closed loops between sensorimotor cerebral areas and the cerebellum are matched by closed loops with frontal, cingulate, parahippocampal, and occipitotemporal prestriate areas (Miall, 1998). The cerebellar projections to the prefrontal cortex, via thalamus, influence non-motor activities, as planning and spatial working memory utilizes information from

the dorsal visual stream (Middleton and Strick, 2001).

The gain of the SP improves dramatically between 2 and 4 months of age, in synchrony with the maturation of PFs, and with the expansion of the visual pathways from the visual area to the MT+ area. However, even though the gain is insufficient at 2 months, the timing is predictive. How can visual tracking of a moving object be predictive at 2 months of age when the PFs in cerebellum are still immature? This means that some other process gives predictive eye movements, as for example a corresponding proactive loop that includes area 8 (FEF). Keeler (1990) has discussed a dynamic system for cerebellar functioning where prediction is established in the cerebral cortex.

Recently, Manto (2006) discussed the cerebello-cortical interactions. Some neurons in the deep cerebellar nuclei project to the IO, and loops are thus formed for cerebellar learning and tuning of temporal patterns. In the young infant (<1 month) such a system may function as a reactive loop, the “Phylogenetic old loop” in Kawato’s model (1999). One possibility is that there are alternative systems; error-based brainstem (SC) loops (REF) or the more versatile nucleo-olivary pathways suggested by Bengtsson and Hesslow (2006). During the maturation of granule cells and MFs, a proactive loop may be formed that involves visual and vestibular information. Especially, a connection between the cerebellar and the cortical areas, that is MT+ and FEF, is established at ~4 months of age. At this age, behavior data have been presented showing that the visual tracking system is almost at the adult level (high gain and very small lag), with a smart coupling between head and eye movements. It is also possible that the LTD in cerebellum is utilized for tracking over occluders. That ability, built on prediction and an ability to represent object motion, is established at 17–20 weeks of age (von Hofsten et al., 2007). Finally, at this age, visually guided catching of moving objects is established in infants constituting one of the important purposes of visual tracking. This will challenge the perception–action loop demanding learning to establish cerebellar internal models.

1 **Abbreviations**

3 CF climbing fiber
 5 ERP evoked response potential
 5 FEF frontal eye field
 IO inferior olive
 7 LGN lateral geniculate nucleus
 LTD long term depression
 9 LTP long term potentiation
 MFs mossy fibers
 11 MT median temporal area
 PFs parallel fibers
 13 PC purkinje cell
 SC superior colliculus
 15 SEM smooth eye movements
 SP smooth pursuit
 17 V1 primary visual area, v17
 V2, V3 visual areas v18 and v19, respec-
 19 tively
 VCR vestibulo-colic reflex
 21 VINHIB vestibular inhibition
 VOR vestibular ocular reflex
 23 VVOR visual vestibular ocular reflex

27 **Uncited reference**

29 Buttner and Waespe (1984).

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