RESEARCH ARTICLES

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Saccade–vergence dynamics and interaction in children and in adults

Abstract Peak velocity, duration and accuracy of eye movements (saccade, vergence and combined saccade–vergence eye movements) were investigated in fourteen normal children (4.5 to 12 years of age) and ten normal adults (22 to 44 years of age). Horizontal movements from both eyes were recorded simultaneously by the oculometer, a photoelectric device. Peak velocity of all eye movements, saccades, and vergence (convergence and divergence), attains adult levels by the age of 4.5 years and there is no significant change over the age range studied (4.5 to 44 years). Vergence duration is longer only in young children (below 8 years of age). The reciprocal interaction between saccade and vergence during combined movements known in adults, i.e. acceleration of the vergence by the saccade (increase of velocity and decrease of duration) and deceleration of the saccade by the vergence (decrease of velocity and increase of duration) was found to be similar in children. The accuracy of eye movements is good on average for both saccades and vergence by the age of 4.5 years, and does not change with age; an exception is the variability of saccade amplitude, which is higher in children less than 8 years old. Taken together, the results indicate early maturation of brainstem structures controlling spatio-temporal aspects of saccades, vergence and their interaction.

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Introduction

Oculomotor behavior when looking at objects in three-dimensional space is controlled by the complex interaction of several oculomotor subsystems: saccades (in the horizontal or vertical direction or both), and vergence eye movements allowing the adjustment of the angle of the visual axes to the distance of the target. Most frequently we perform combined movements both in direction and in depth. In children, saccades are well studied while vergence and combined saccade–vergence movements are almost unexplored. The evaluation of eye movement parameters such as latency, accuracy, peak velocity and duration can provide information about cortical and subcortical control of eye movements. Yang et al. (2002) showed recently that the latencies for all three types of movements decrease with age and approach the adult values at the age of 10–12 years old. These findings support the notion that the cortical/central visual-motor pathways involved in the initiation of eye movements are not developed completely until 10 to 12 years of age, and this is compatible with several prior studies restricted to saccades (Fukushima et al. 2000; Munoz et al. 1998; Ogawa et al. 1998).

Prior investigations suggested dissociation in the development of latency and of peak velocity of saccades (Cohen and Ross 1978; Fukushima et al. 2000; Munoz et al. 1998). The peak velocity and duration of the saccades depend on the properties of the saccade burst generator located mainly at the paramedian pontine reticular formation (PPRF) in the brain stem (Hepp et al. 1989; Leigh and Zee 1999; Munoz et al. 1998). The PPRF receives the major descending input from the frontal eye field and the superior colliculus. Cohen and Henn (1972) found that the peak velocities of saccades vary little with age, suggesting that the brainstem areas, particularly the PPRF are fully developed by the age of 4 years. Furthermore, histological

examination of senescent brains has failed to identify neuronal degeneration in brainstem reticular formation (Brody and Vijayashankar 1977). Munoz et al. (1998) also reported that the peak velocity and duration of saccades were relatively constant for ages of 5 to 59 years, and amplitudes of these movements were also constant from the ages of 12 to 59 years. All these studies support the idea of early maturity and absence of degeneration of the saccade brainstem generator.

During the last two decades, neurons involved specifically in the control of vergence eye movements have been found in the mesencephalic reticular formation of monkeys (Judge and Cumming 1986; Mays 1984; Mays et al. 1986). Convergence and divergence burst neurons were found to discharge in relation to vergence velocity in a manner analogous to the saccade burst neurons that discharge in relation to saccade velocity. Tonic vergence neurons and phasic-tonic neurons have also been identified in the above studies. Thus, the neural organization of the vergence brainstem generators resembles that of the saccadic generators (Leigh and Zee 1999; Mays et al. 1986). To our knowledge, the development of vergence dynamics in humans is entirely unexplored. We attempt here to contribute to this issue by investigating the peak velocity and duration of vergence in children from the age of 4.5 to 12 years of age, and in adults.

Although saccade and vergence eye movements are considered to be produced by distinct brainstem neural subsystems, there is a degree of interaction between the two subsystems during the combined eye movements. The vergence movement is believed to be 'facilitated' (Zee et al. 1992) or 'enhanced' (Hung 1998) when it is combined with saccade in normal adults, e.g. vergence velocity is higher for combined movements; reciprocally saccades have been found to be slower when combined with vergence (Collewijn et al. 1995). Whether such interaction of saccade–vergence exists in young children is not yet known. Thus, the second goal of this study was to explore saccade–vergence interaction in children.

Methods

Subjects

Fourteen children and ten adults participated in the present experiment. The children's ages ranged from 4.5 to 12 years (seven female, seven male): six children of 4.5–6 years; four children of 7–8 years and four children of 10–12 years. The adult's ages ranged from 22 to 44 years (28.1±6.2, six female, four male). All children had normal vision and none of them wore spectacles. Adult subjects were all emmetropic (no refractive errors). No subjects showed visual, neurological, or psychiatric disorders or received medication. All subjects had normal motility and normal ocular alignment. Binocular vision was assessed with the TNO test of stereoacuity; all individual scores were normal, 60" of arc or better. The investigation adhered to the tenets of the Declaration of Helsinki and was approved by the institutional human experimentation committee of CPPRB, Saint Antoine Hospital, Paris. Informed consent was obtained from adults and children's parents after the nature of the procedure had been explained.

The experimental task was explained to the subjects and to children's parents before the experiments. Subjects were requested to move their eyes to the light-emitting diodes (LEDs) as soon as possible and as accurately as possible after appearance of the target, but not before. The subject's head was stabilized on a chin rest (for details see Yang et al. 2002).

Eye movement recording

A computer-controlled the visual stimulation was used; data collection was controlled by REX software (obtained online at http://www.tchain.com from Timothy C. Hain, Northwestern University Medical School, Chicago, IL, USA), which was developed for real-time experiments and run on a personal computer. Horizontal movements from both eyes were recorded simultaneously with a photoelectric device (Oculometer, Bouis, Karlsruhe, Germany; see Bach et al. 1983). The eye is homogeneously illuminated by infrared light that is produced by infrared LEDs within a measurement tube (located outside the visual field) and reflected into the eye of the subjects by means of an infrared mirror. The infrared picture of the subject's eye is reflected back into the tube and projected (using some appropriate optical lenses) onto the infrared-sensitive surface of a two-dimensional photodiode. From the outputs of this photodiode the gravity center of the infrared light falling onto its surface is computed by using analogue electronics in the horizontal as well as the vertical direction. Since different parts of the eye reflect the infrared light differently and in a circular-symmetric way (the white sclera reflects most, the iris less, the pupil nearly nothing), this center of gravity accurately represents the actual position of the center of the pupil. This system has a resolution of 1 to 5 minutes of arc and linear range of ±20°. There is no obstruction of the visual field with this recording system. The accuracy of this system is between 5 and 10 minutes of arc when subject's head is well restricted. Eye-position signals were digitized with a 12-bit analogue-to-digital converter and each channel was sampled at 500 Hz.

Visual display

The visual display consisted of LEDs positioned on two isovergence circles: one at 20 cm from the subject, and the other at 150 cm. On the near circle three LEDs were used; one at the center and others at ±20°. The required mean vergence angle for fixating any of these three LEDs was 17°. On the far circle, five LEDs were placed: one at the center, two at ±10° (only for calibration) and two at ±20° (for both calibration and main task); fixation to any of these LEDs required a vergence angle of 2.3° (for a diagram of visual display, see Fig. 1).
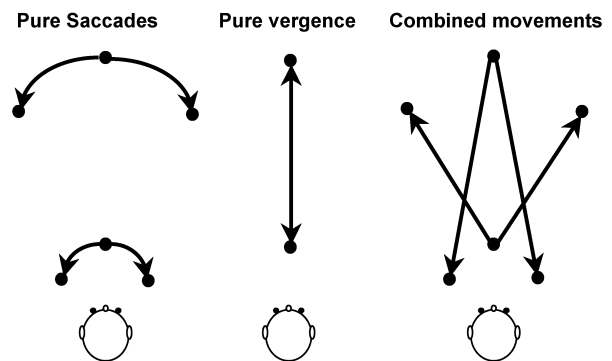
Fig. 1 Different types of elicited eye movements; horizontal saccades, pure convergence, or divergence along the median plane, and combined convergent or divergent movements

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Oculomotor procedure

The subject was seated in a dark room on an adapted chair with a head and chin support. Subjects viewed binocularly and faced the visual display of the LEDs, which was placed at eye level to avoid vertical eye movements.
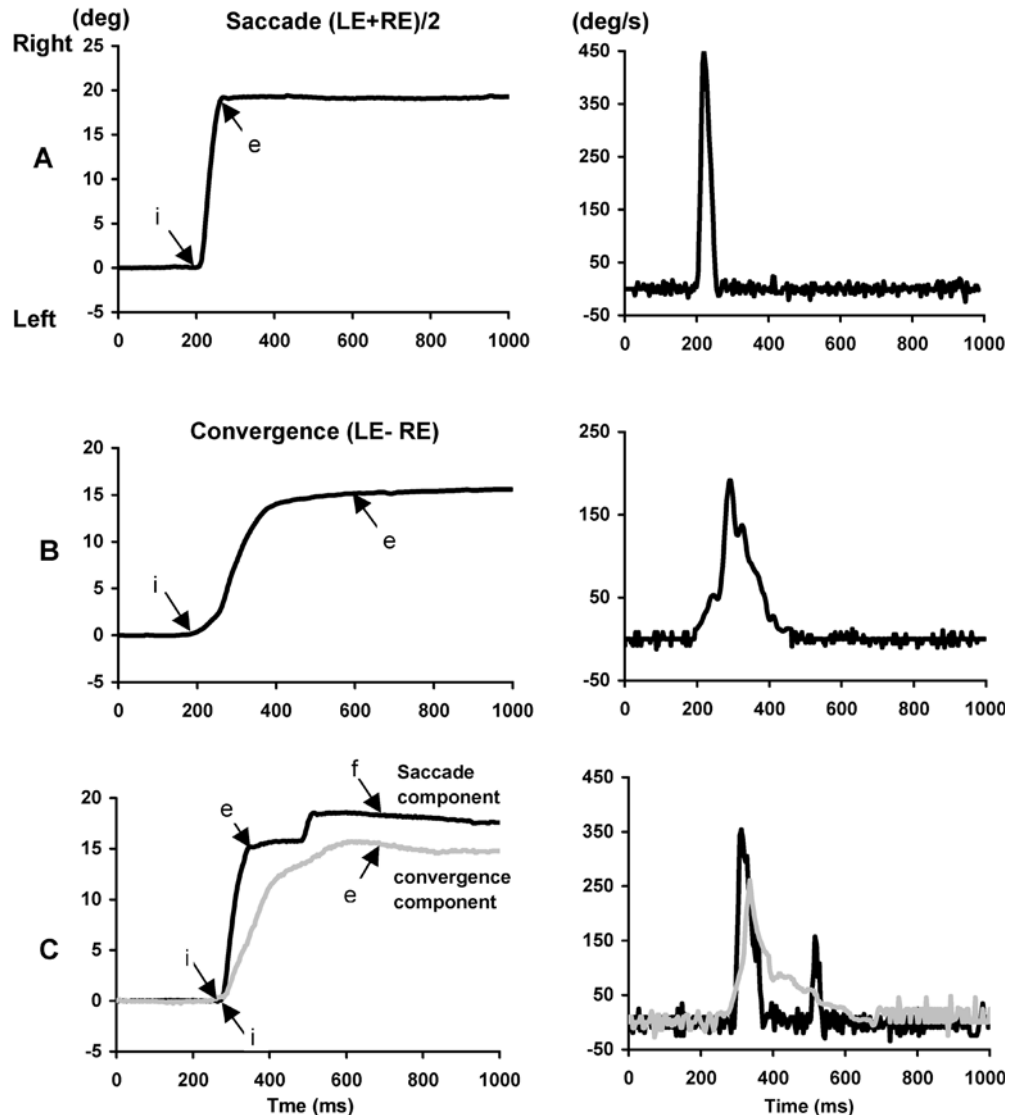
Calibration task

The subject made a sequence of saccades to an LED target jumping from zero to left or right ±10°, or ±20° at the far isovergence circle. During each of these trials, the target remained at each location for 2 s; this was sufficiently long to allow accurate and stable fixation. The calibration factors were extracted from these recordings (see Data Analysis).

Main oculomotor task: saccade–vergence combined movements

Each trial started by lighting a fixation LED at the center of one of the circles (far or near). After a 2.5-s fixation period the central LED was extinguished and a target LED appeared for 2 s. According to its location relative to the fixation LED, the target LED called either for a pure saccade (at far or at near), or for a pure vergence (convergence or divergence along the median plane), or for a combined (convergent or divergent) eye movement (Fig. 1). It should be noted that the use of the term pure movement describes more the requirement rather than the real behavior. It is known that saccades are almost always associated with small divergent disconjugacy, while during requirements of pure vergence along the median plane, vergence movements usually contain small saccade components (Collewijn et al. 1995; Zee et al. 1992). All target LEDs for saccades were at 20°. All targets along the median plane required a change in ocular vergence of 15°; combined movements required a lateral saccade of 20° and a vergence of 15°. In each block, the three types of eye movements were interleaved randomly. Each block contained 24 trials, i.e. four saccades at far, four saccades at near, four convergence, four divergence, four combined convergent movements and four combined divergent movements. For the large majority of the subjects (children or adults), four blocks were run, separated by a rest period of a few minutes; calibrations were repeated at the beginning of each block. For the youngest children, rest periods between blocks were longer; the child was seated on his or her parent's knee with the chin of the child resting on the chin rest of the recording apparatus.

Fig. 2A–C Typical recordings of the three types of eye movements: **A** pure saccade, **B** pure convergence and **C** combined saccade–convergence movements. Traces on the *right* indicate the corresponding velocity profile of each type of eye movement. Note that for all movements, even for convergence examples, the peak velocity occurs early in the course of the movement and its value could be high. The saccade signal is obtained by averaging the position signal of the two eyes, (LE+RE)/2; the vergence signal is the difference between the two signals, LE−RE. *Arrows* indicate the initiation (*i*) of each movement, the end (*e*) of each movement, or the point for measuring the total amplitude of saccade and vergence component of combined movement (*f*)

Data analysis

Data analysis methods are similar to those described by Yang et al. (2002). Calibration factors for each eye were extracted from the saccades recorded in the calibration task; a linear function was used to fit the calibration data. From the two individual calibrated eye position signals we derived the vergence signal (left eye − right eye) and the conjugate signal [(left eye + right eye)/2]. The onset of a pure saccade or of the saccadic component of the combined movements was defined as the time when eye velocity exceeded 5% of saccadic peak velocity; the offset was when eye velocity dropped below 10 deg/s. The onset and the offset of the vergence signals (for pure vergence movement and for the vergence component of the combined movements) were defined as the time point when the vergence velocity exceeded or dropped below 5 deg/s. These criteria are standard and similar to those used by other authors (Takagi et al. 1995; Yang et al. 2002) The placement of the markers by the computer was verified by one of the investigators scrutinizing saccade and vergence components on the screen. Eye movements in the wrong direction, and movements contaminated by blinks were rejected. Although the latency of eye movements is not presented here, anticipatory eye movements with latencies shorter than 80 ms or eye movements with latencies longer than 1000 ms, indicating a loss of attention, were also excluded from the analysis. Using such criteria 6% of the trials were rejected for all subjects except for the youngest children (4.5–6 years old), for whom the rejection rate was higher (20%).

For all types of eye movements, we measured the peak velocity, the duration (the time between the initiation, i, and end, e, of eye movements; see examples in Fig. 2), and the gain of the response (movement amplitude/target amplitude, for saccade components calculated from the amplitude of first saccades); for saccade components of combined movements the total amplitude was indicated by f in Fig. 2C, corresponding to the end of the vergence components. Analysis of variance (ANOVA) was used to evaluate differences between types of eye movements (e.g. saccade versus vergence) within each group of subjects. To account for differences in the distributions between children and adults, at least for some parameters, the non-parametric Kruskal-Wallis test was performed.

Results

Pure eye movements requirement

Figure 3A,B presents the distribution of peak velocity and of duration of pure eye movements—saccades, convergence and divergence—for children and adults. For peak velocity and for all three types of pure eye movements, distributions were similar for children and adults. Figure 3C shows the mean of peak velocities; the values (means ±SD) for saccades were 427±93 and 421±91 deg/s in children and in adults, respectively. For convergence, the respective values were 219±74 and 228±105 deg/s, and for divergence, 160±58 and 180±62 deg/s. There was no significant difference in the peak velocity between children and adults for any of the three types of eye movements (in all cases $P>0.05$, Kruskal-Wallis test). For the duration, the distributions of saccades were narrow, but those of convergence or divergence were wider; this was the case for both children and adults. Figure 3D shows the mean durations. The values for saccades were 86±29 and 84±25 ms in children and in adults, respectively; for convergence, the respective values were 365±100 and 312 ±69 ms, and for divergence, 547±107 and 513±58 ms. There was no significant difference in duration between

Fig. 3A–D Distribution of peak velocities (**A**) and of duration (**B**), and group means of peak velocity (**C**) and duration (**D**) for saccades, convergence and divergence in children and in adults. *Vertical lines* in **C,D** indicate the standard deviations
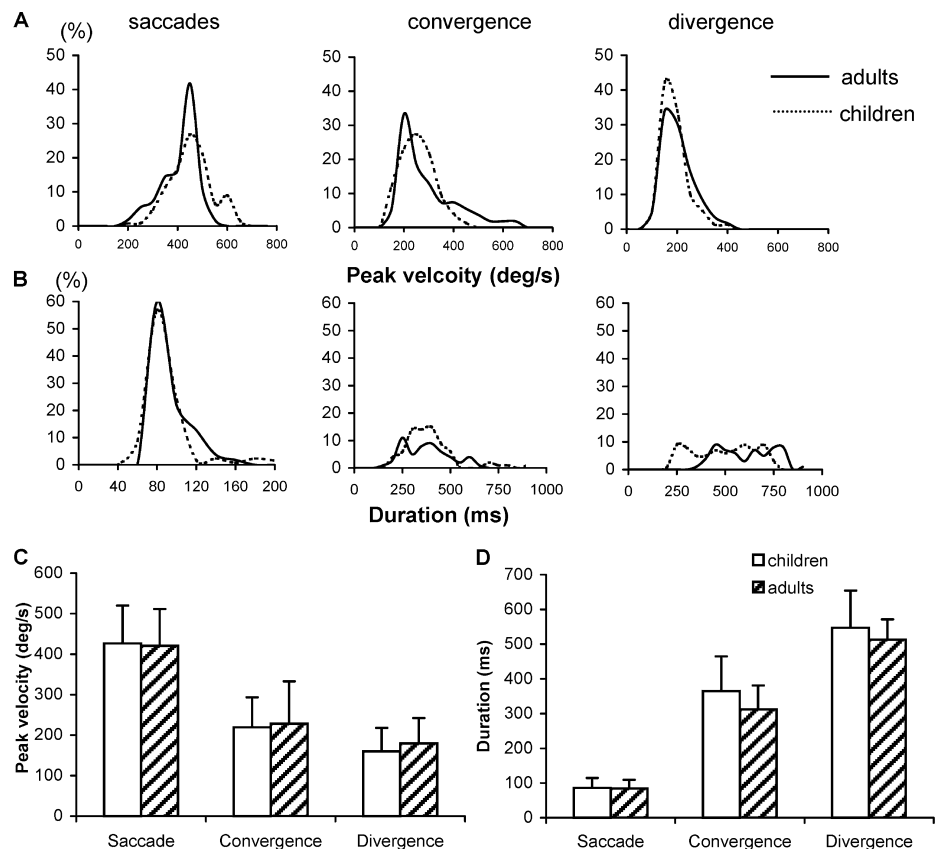
children and adults for any type of pure eye movement ($P>0.05$)

For both children and adults, the peak velocity of saccades was the highest among the three types of eye movements (ANOVA, $P<0.01$). Furthermore, planned comparisons showed higher peak velocity for convergence than divergence for both children and adults ($P<0.05$). Consistent with the velocity data, the duration of saccades was shortest among these three types of eye movements for both children and adults ($P<0.01$); the convergence showed shorter duration than divergence ($P<0.01$).

Combined eye movements

Figure 4A,B presents the distribution of peak velocity and of duration of combined eye movements for the group of children and for the group of adults. As for pure movements, the distributions are similar for children and adults, and durations of convergence or divergence components showed distributions that deviated from normal. Figure 4C presents the mean peak velocities for saccade and vergence components of combined movements: for combined convergent movements, the mean

values were 359±97 and 388±128 deg/s for saccade components in children and in adults, respectively, and for convergence components, 253±108 and 267±80 deg/s. For combined divergent movements, the mean values for saccade components in children and in adults were, respectively, 309±87 and 295±66 deg/s, and for the divergence component, 220±88 and 234±106 deg/s. The Kruskal-Wallis test showed no significant difference of peak velocity between children and adults for any components of combined movements (all comparisons fail significance, $P>0.05$). Figure 4D presents the duration of combined eye movements in children and in adults. For combined convergent movements, the mean values were 108±17 and 113±40 ms for saccade components in children and in adults, respectively, and for convergence components, 338±126 and 292±85 ms. For combined divergent movements, the mean values were 114±39 and 126±34 ms for saccade components in children and in adults, respectively, and for divergence components, 487 ±122 and 420±71 ms. As for pure vergence, durations of vergence components of combined movements tended to be slightly longer in children but there was no statistically significant difference between the group of children and the group of adults (all comparisons fail significance,
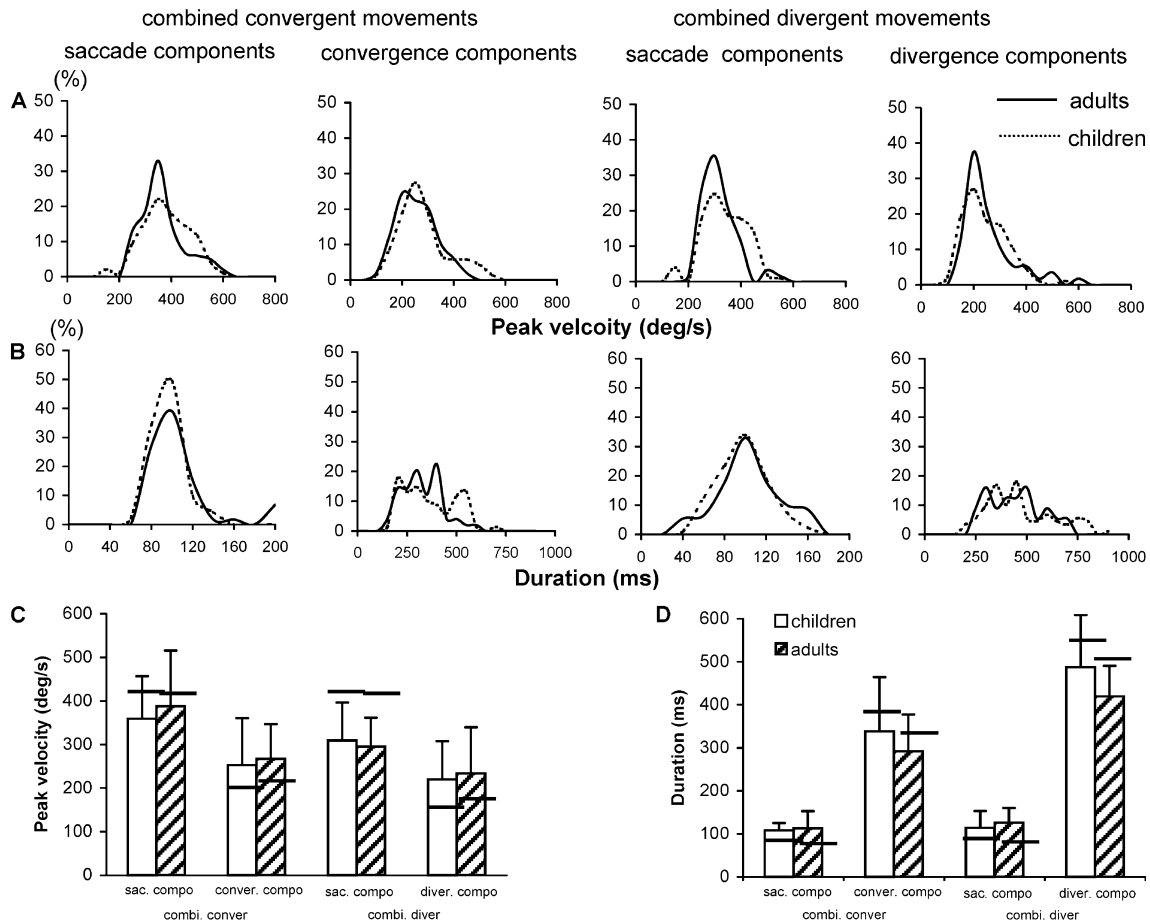
Fig. 4A–D Distribution of peak velocities (**A**) and of duration (**B**), and group means of peak velocity (**C**) and of duration (**D**) for combined movements in children and in adults. *Bold horizontal lines* over the bars in **C,D** indicate the corresponding values of pure eye movements reported from Fig. 3; *vertical lines* indicate the standard deviations

$P>0.05$). Thus, overall duration and peak velocity data were not significantly different between adults and children. Nevertheless, the tendency for the longer vergence duration will be further explored (see Developmental Aspects section).

Saccade–vergence interaction

In Fig. 4 information on saccade–vergence interaction can be extracted by comparing the bar values with the values shown by the horizontal lines (corresponding to pure movements from Fig. 3). In agreement with prior studies in adults (Collewijn et al. 1995), vergence components, convergence or divergence, showed higher peak velocity than that of corresponding pure vergence (significant at $P<0.05$). A similar significant increase of velocity of vergence components (convergence or divergence) relative to the velocity of pure vergence is observed for children (significant at $P<0.05$). Consistently, the duration of all vergence components was shorter than that of pure vergence for adults and for children (all comparisons are significant at $P<0.05$). Thus, vergence acceleration by the saccades during combined movements was similar for children and for adults.

The difference of the peak velocity between pure saccades and saccade components during combined movements was also statistically significant: pure saccades show higher peak velocity than saccade components for adults ($P<0.001$), and for children ($P<0.001$). Consistently, the duration of pure saccades was shorter than that of saccade components of combined movements, for adults ($P<0.05$), and for children ($P<0.05$). Further comparisons showed higher peak velocity for saccade components of combined convergent movements than for saccade components of combined divergent movements for both children ($P<0.01$) and adults ($P<0.01$). Consistently, duration of saccade components of combined convergent movements was significantly shorter than that of saccade components of combined divergent movements for children ($P<0.05$), and for adults ($P<0.01$).

These observations are further consolidated by examining the mean velocity (amplitude/duration) for saccades and saccade components of combined movements. For pure saccades mean velocities were 202 ± 37 and 209 ± 21 deg/s in children and in adults, respectively; for saccade components of combined convergent movements, the corresponding values were 144 ± 37 and 148 ± 27 deg/s, and for saccade components of combined divergent movements, 119 ± 28 and 117 ± 16 deg/s. These differences between saccade and saccade components are statistically significant for both children ($P<0.01$) and adults ($P<0.01$). Thus, saccades were slowed by vergence, particularly when combined with divergence, similarly in children and adults
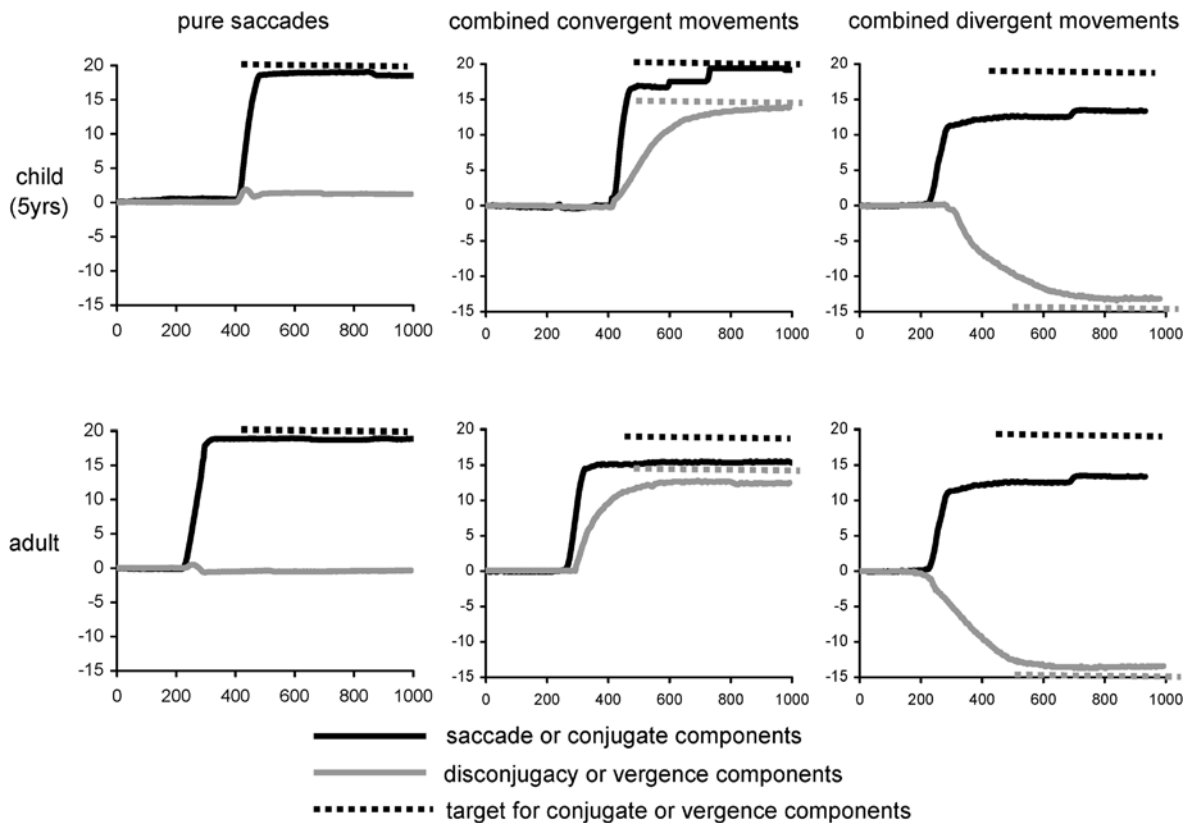
Fig. 5 Examples of pure saccades and of combined movements for a child of 5 years of age and for an adult. The saccade or the conjugate component trace is the average of the two eyes; the disconjugacy or vergence component is the difference between two eyes. *Dotted lines* indicate the location of the target; for combined movements target eccentricity and target depth are shown

Accuracy of eye movements

Figure 5 shows examples of saccades with their disconjugacy, and the two components of the combined convergent or divergent eye movements together with the corresponding location of the target in direction and in depth. Saccades were accurate while saccade components of combined movements can be less accurate. During combined movements the saccade signal had a staircase form with several corrective saccades occurring over the total period of the movement, especially for the youngest children. Quantitative data are shown in Fig. 6

Figure 6A,B presents the distribution of gain of pure eye movements and of combined movements for children and adults. All distributions were similar for children and adults. The group mean gains for saccades, convergence and divergence were, respectively, 0.87±0.16, 0.94±0.09

and 0.91±0.11 in children, and 0.88±0.09, 0.94±0.13 and 0.91±0.12 in adults (see Fig. 6C). All the values are close to unity, indicating good accuracy of all these movements. There was no significant difference of the mean gain between children and adults for these pure eye movements ($P>0.05$).

When combined with vergence, the mean gains of saccade components of combined convergent movements and combined divergent movements wer, respectively, 0.78±0.20 and 0.68±0.16 in children, and 0.80±0.15 and 0.74±0.10 in adults (see Fig. 6D). The gain for saccade components decreased significantly relative to pure saccades for both children ($P<0.01$) and adults ($P<0.05$). Moreover, the gain of saccade components was more diminished for combined divergent movements than for combined convergent movements, again for both children ($P<0.01$) and adults ($P<0.05$). Note, however, that the
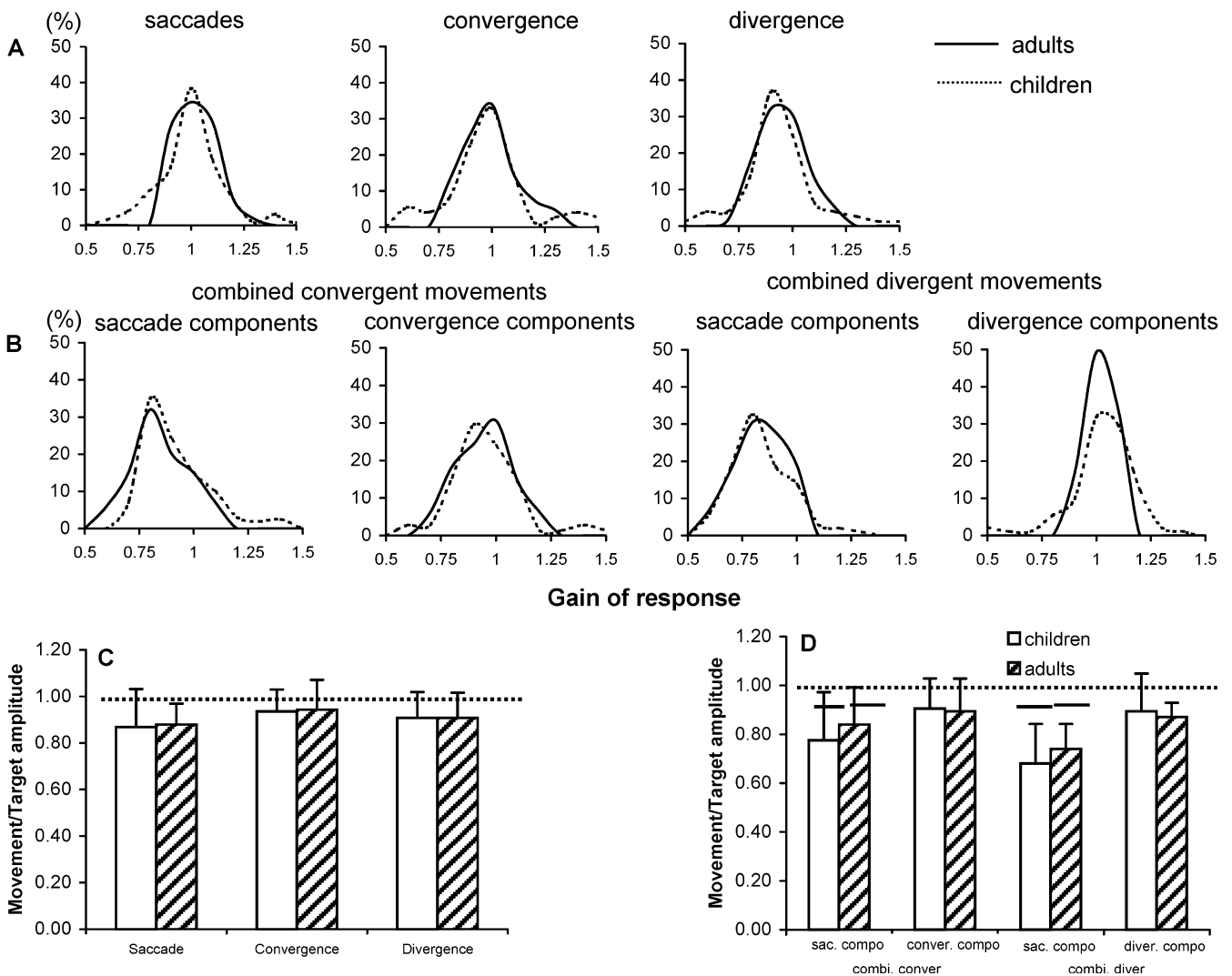
Fig. 6A–D Distribution of the gain for pure eye movements (**A**) and for combined movements (**B**), and group means of gain for pure eye movements (**C**) and for combined movements (**D**) in children and in adults. *Bold horizontal lines* over the bars in **D** indicate corresponding gain values of pure saccades reported from **C** (*sac. compo* saccade components, *conver. compo* convergence compo-

nents, *diver. compo* divergence components, *combi. conver* combined convergent movements, *combi. diver* combined divergent movements). *Dotted horizontal lines* indicate a gain of 1, which corresponds to a perfectly accurate eye movement (eye movement amplitude = target excursion amplitude); *vertical lines* indicate the standard deviations

final gain of the saccade components measured after the corrective saccades, coinciding with the end of the vergence signal (see Figs. 5 and 6D *horizontal lines*, and Methods section) was almost identical to that of pure saccades.

By contrast, the gain of vergence showed no changes when combined with saccades. The values of convergence and divergence components were 0.91±0.12 and 0.89±0.15 in children, and, 0.89±0.13 and 0.87±0.06 in adults (see Fig. 6D), respectively. There was no significant difference between pure convergence and convergence components nor between pure divergence and divergence components, for adults ($P>0.05$) or children ($P>0.05$).

Developmental aspects

We performed further analysis within the group of children to seek possible changes throughout childhood. We regrouped the 14 children into three subgroups, 4.5–6 years of age ($n=6$), 7–8 years of age ($n=4$), and 10–12 years of age ($n=4$). Figure 7A–D shows peak velocity,

Fig. 7A–D Developmental aspects of peak velocity (**A**), duration (**B**), gain (**C**) and variability of gain (**D**). Data represent values obtained for pure saccade and combined saccade–convergence movements (*left panels*), and pure vergence and vergence components (*right panels*) in children grouped by age (*4y* 4.5–6 years old, *8y* 7–8 years old, *10y* 10–12 years old) and in adults
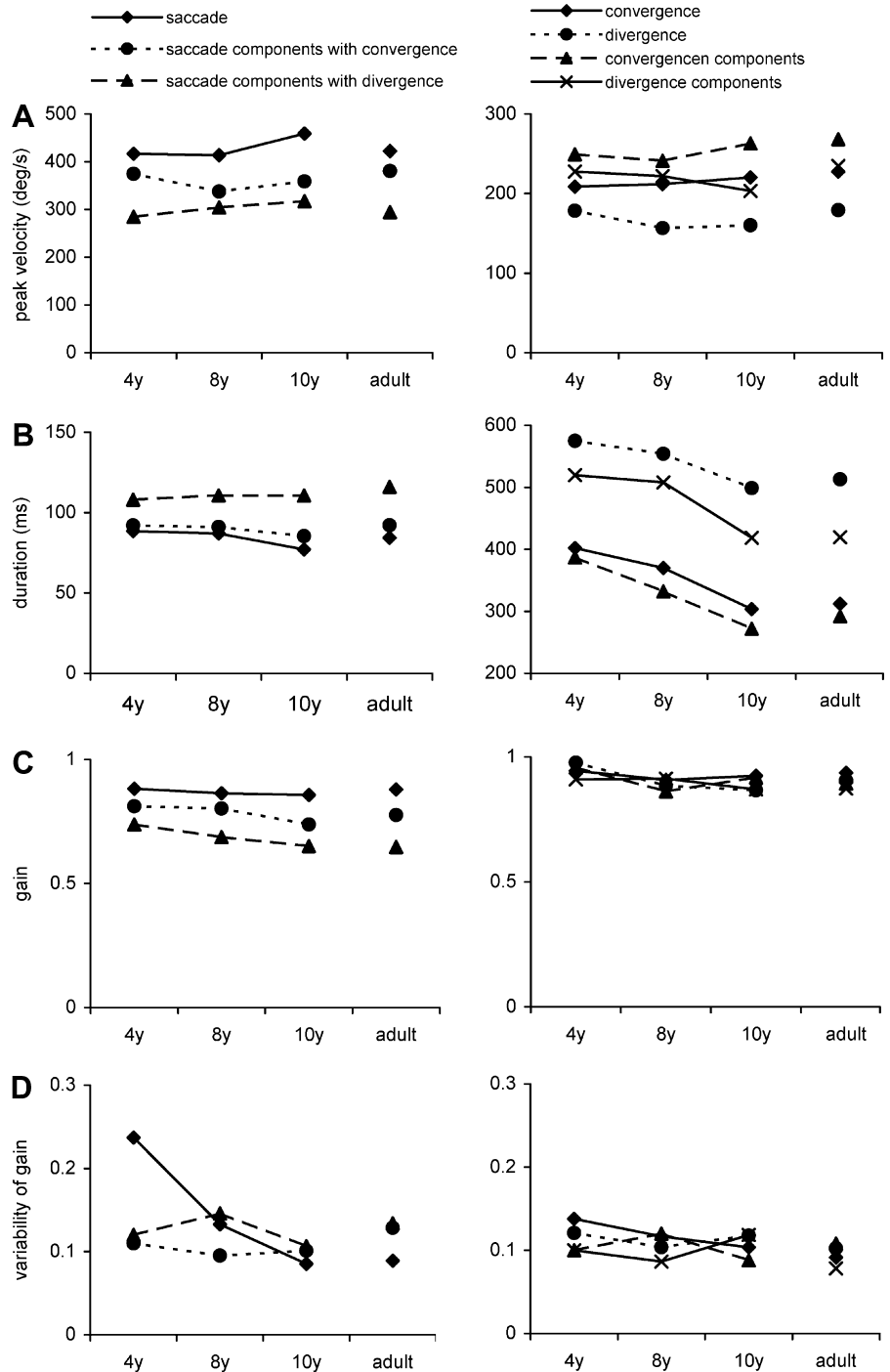
duration, gain and its variability for the different subgroups of children. Only the mean duration of vergence and of vergence components (Fig. 7B *right*), and the variability of saccade gain (Fig. 7D *left*) changed significantly in the different subgroups of children. The values for children 4.5–6 years and 7–8 years were significantly higher than those of older children (10–12 years) or of adults (all comparisons are significant at $P<0.05$). There are no developmental changes for any other parameter ($P>0.05$).

Fig. 8A,B Examples of the signals and velocity traces of convergence and divergence eye movements for a child of 5 years of age (**A**) and for an adult (**B**). Two examples of vergence traces are shown in the *left panels*, and the corresponding velocity traces in the *right panels* (*PV* peak velocity)
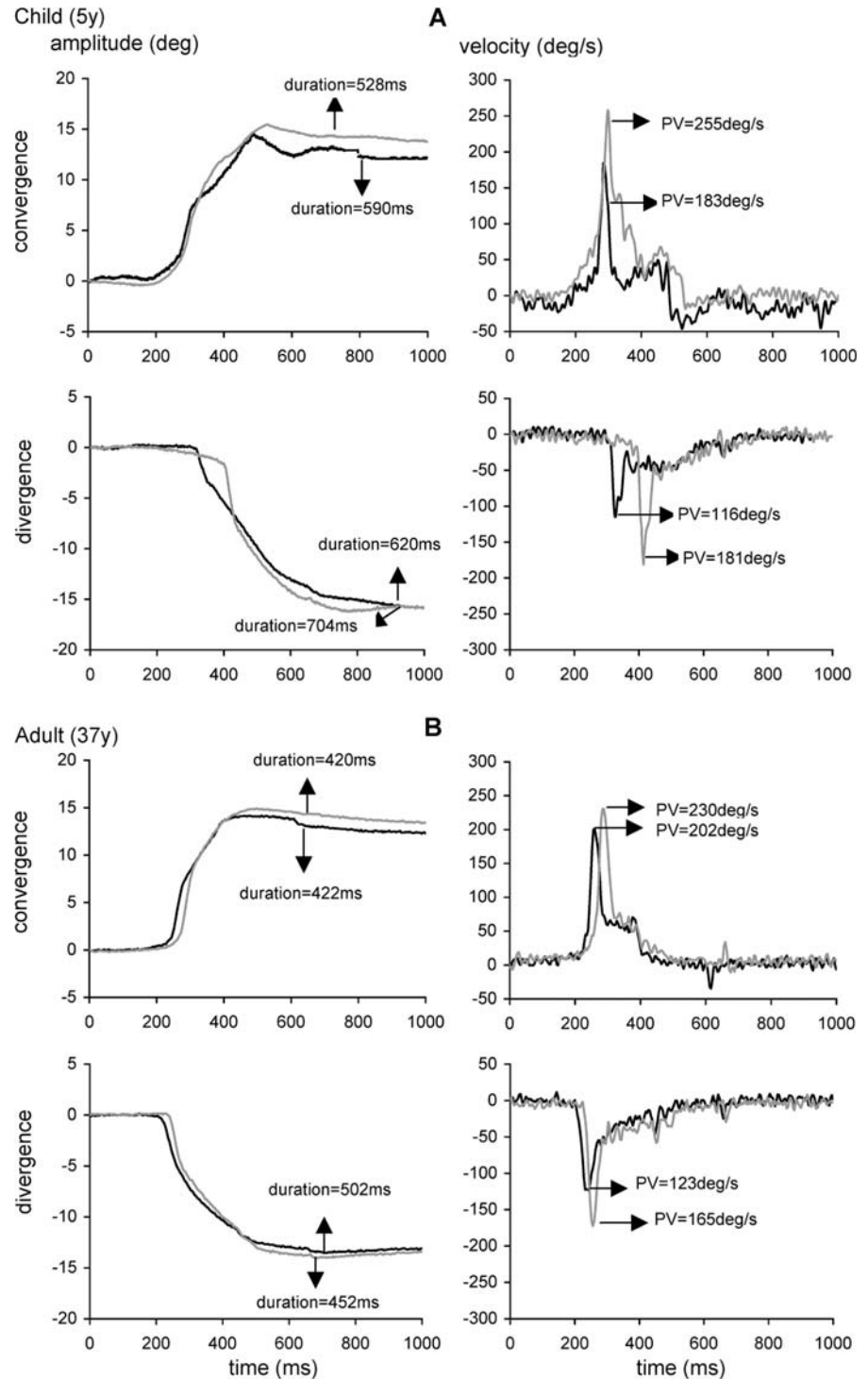
Discussion

Velocity and duration of saccades and vergence development

Peak velocity and duration of saccades showed no significant difference between children and adults. This is consistent with the studies of Munoz et al. (1998) and Fukushima et al. (2000), and suggests that the brainstem circuitry controlling the peak velocity and duration of saccades develops completely before the age of 4.5 years. The new result in this study is that vergence velocity and duration are also not different between the group of all children and adults. Further analysis within the group of children revealed significant developmental change only

for the duration of vergence movements (pure or combined), which is longer in young children. This may appear paradoxical as no similar developmental change was observed for peak velocity. Note that, in the case of vergence movements, the peak velocity is an instantaneous parameter while the duration is long because the execution of vergence is under visual feedback control. Examples of vergence position traces and their velocity are presented in Fig. 8; they show similar peak velocity of convergence in a child (255 and 183 deg/s) and in an adult (230 and 202 deg/s), but differences in the duration, being 528 and 590 ms in the child while being 420 and 422 ms in the adult. Similar differences are found in the examples of divergence. Peak velocities are similar in children and adults but total durations for divergence are longer for

Fig. 9A–D Examples of position and velocity traces of convergence (*dark lines*, the difference between the signals of the two eye, LE−RE) for a child of 5 years old (**A,B**) and for an adult (**C,D**). *Gray lines* show the saccadic intrusions and their velocity, obtained by averaging the signal of the two eyes, (LE +RE)/2. In **A,C** the vergence peak velocity occurred simultaneously with a saccade component; in **B,D** the vergence peak velocity occurred after the saccadic intrusion component. Vergence velocities are similar in all cases
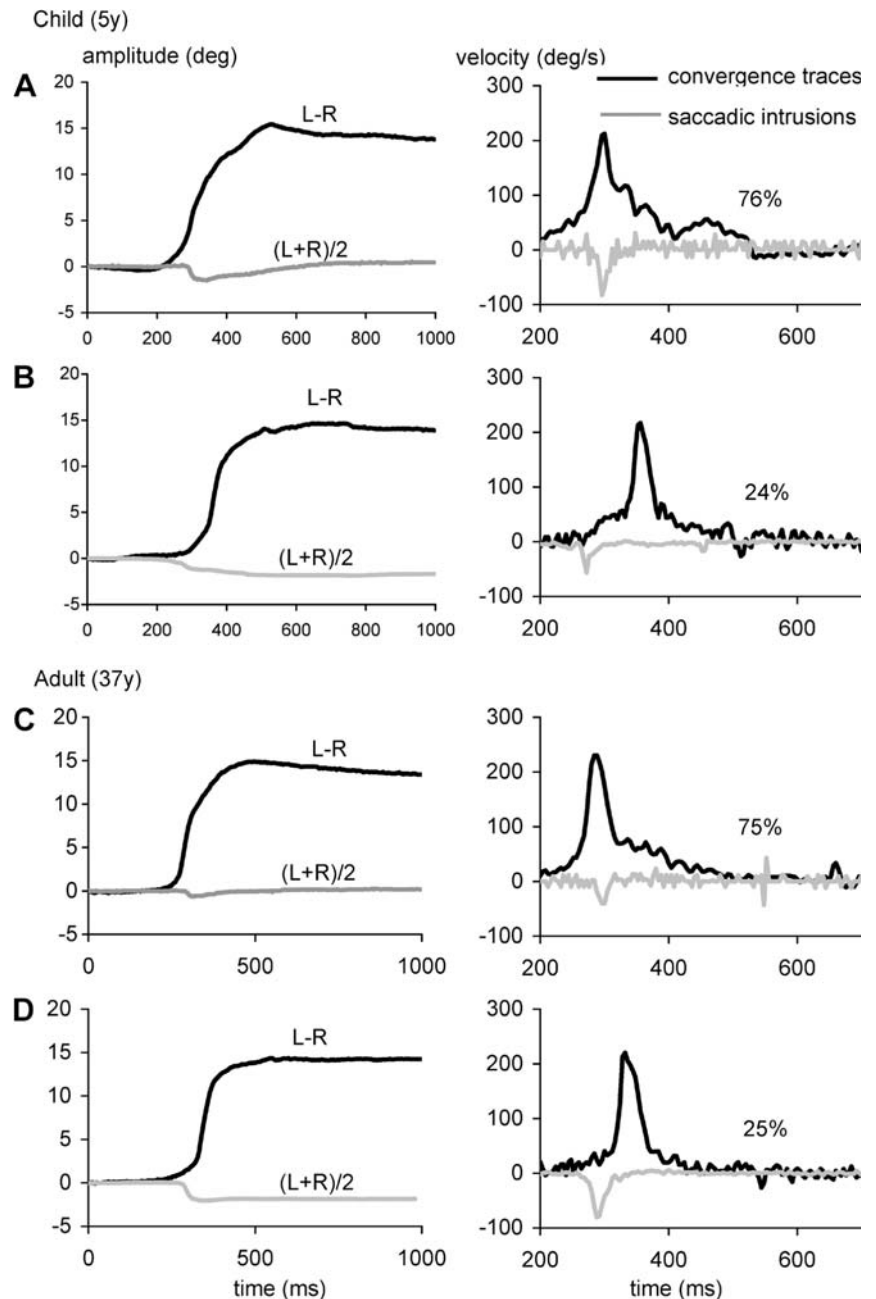
children. To understand this issue better, we considered the possibility that peak velocity of vergence for the younger children was somehow related to small saccade intrusive components.

Vergence velocity and saccade intrusions

As mentioned in Methods section, saccade components occur naturally during vergence even when a pure vergence movement is required (Collewijn et al. 1995, 1997). On the other hand, it is known that saccades are accompanied by transient vergence, mostly divergence (Zee et al. 1992). The question raised here is to what extent vergence velocity is increased by the transient, saccade-induced vergence. To examine this, we estimated the percentage of trials in which vergence peak velocity occurred simultaneously with a saccadic component, and the percentage in which vergence peak velocity occurred independently, without saccade component. The percentages of cases with saccadic component were 75±24 and 74±18% for convergence in children and in adults, respectively. Thus, in the majority of cases, vergence peak velocity occurred together with a saccade intrusive component, at a similar rate for children and adults. Within the group of children, the percentages were also very stable over the different age groups (76±18% for children of 4.5–6 years, 70±12% for children of 7–8 years, and 78±20% for children of 10–12 years). There was no significant difference in the peak velocity between trials for which convergence peak velocity occurred together with a saccade intrusion and trials without such saccades. On average, values were 205±49 and 190±43 deg/s in children, and 230±80 and 213±53 deg/s in adults, for cases with and without saccade intrusion (all comparisons fail significance, $P>0.05$). Figure 9 shows examples of convergence, together with the conjugate signal, indicating the occurrence of small saccade intrusions despite the fact that the target did not call for a saccade because it was placed along the median plane. The saccade intrusion occurs either at the onset of the convergence or later during the vergence. Vergence velocities are similar. This is the case for both adults and children, and also for divergence movements (not presented here). Thus, this analysis confirms that peak velocity of vergence is as rapid in children as in adults. Saccade transients do not significantly influence vergence peak velocity. Note that such a possibility was considered by Zee et al. (1992); our results show no significant contribution of saccadic intrusions to vergence velocity. Our observation of high vergence velocity that occurs independent of saccades and lasts less than 100 ms (see Fig. 9B,D) could be considered as evidence that the vergence itself is like saccades in opposite directions for the two eyes; this was suggested initially by Enright (1984) and later by Zhou and King (1997). However, it is still an open question and requires specific electrophysiological studies. Returning to the point of velocity versus duration differences, given all these considerations about the vergence peak velocity one must attribute the discrepancy between peak velocity and duration of vergence for the youngest children to differential activation of brainstem subcircuitry controlling the duration; eye movement peak velocity is related to the discharge of phasic velocity cells of the eye movement generators, while duration depends on both phasic and tonic cell activity. Perhaps the tonic and the phasic-tonic cells of the vergence generator, located in the mesencephalic reticular formation (Mays et al. 1986), maturate more slowly in humans than the phasic cells. Alternatively, longer vergence duration in the youngest children could be due to delay in visual processing of depth signals, particularly disparity processing; note that vergence execution, unlike saccades, is partly controlled in a closed loop by visual feedback (Leigh and Zee, 1999), and any delay of visual processing would lengthen the execution of this movement. Furthermore, models of the vergence system (Hung et al. 1986; Semmlow et al. 1986) have suggested the existence of a fast programmed part of the vergence and a slower, visually driven part. Perhaps, the distinction between vergence peak velocity and vergence duration in the youngest children we observed can be understood in the context of such a dual mode of vergence control that could be more manifest in the youngest children.

Finally, unlike the large variability in latency for all eye movements in children that was reported in a prior study (Yang et al. 2002), in the present study the variability of the peak velocity and of duration was similar for all age groups (data not presented).

To summarize, the results indicate that saccade and vergence brainstem generators are mature by the age of 4.5 years, and this contrasts with the slower maturation of the components, probably cortical, that control oculomotor latencies.

Saccade–vergence interaction

Relative to pure movements, the peak velocity of the saccade for combined movements decreased and that of vergence increased for all four age-groups studied. The duration data showed a complementary picture, i.e. duration of vergence component decreased while that of saccade component increased. Our results in adults are in agreement with several other reports (Chaturvedi and Gisbergen 1998; Collewijn et al. 1995, 1997; Erkelens et al. 1989; Hung 1998). The important new finding here is that children showed the same pattern of saccade–vergence reciprocal interaction by the age of 4.5 years. Thus, the interactivity between the otherwise distinct, brain-stem circuitry of saccades and of vergence, is also developed by the age of 4.5 years.

Spatial aspects—accuracy of movements

The accuracy of movements was good, as shown by the gain measure that approached unity for almost all types of

movements, in both children and adults. This indicates that the average spatial performance of the saccade and vergence generators attained adult levels also by the age of 4.5 years. For combined movements, the gain of the primary saccade was remarkably less than 1, while the gain of the vergence component did not change (close to unity). When the accuracy of the conjugate component was estimated at the end of the vergence, i.e. after corrective saccades were made, the total gain was also almost 1 (see Fig. 6D, *bold horizontal lines*). This aspect of our results, namely the existence of multiple saccadic components in the combined movements is compatible with the observations of Collewijn et al. (1997) for the segmented nature of binocular gaze shifts in adults; our study extends this observation to children. The only developmental difference that could be assessed was a larger variability in the amplitude of saccades.

In conclusion, this study shows for the first time that peak velocity and duration is similar for children and adults, not only for saccades but also for vergence (convergence and divergence). The reciprocal interaction between saccade and vergence during combined movements, i.e. acceleration of vergence by the saccade (increase of velocity and decrease of duration) and deceleration of the saccade by vergence (decrease of velocity and increase of duration) is also similar for children and adults. Finally, the average accuracy is good for all movements (about 90% of target amplitude) and is similar for children and adults. The only parameters that showed developmental changes are the duration of vergence (pure or combined), which is longer in children below 8 years, and the variability of saccade accuracy, which is higher for young children. We conclude that the brainstem structures controlling saccade and vergence dynamics and their interaction maturate early in life (by the age of 4.5 years of age). The data contrast to prior studies dealing with long latencies showing progressive development.

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