

Development and learning of saccadic eye movements in 7- to 42-month-old children

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From birth, infants move their eyes to explore their environment, interact with it, and progressively develop a multitude of motor and cognitive abilities. The characteristics and development of oculomotor control in early childhood remain poorly understood today. Here, we examined reaction time and amplitude of saccadic eye movements in 93 7- to 42-month-old children while they oriented toward visual animated cartoon characters appearing at unpredictable locations on a computer screen over 140 trials. Results revealed that saccade performance is immature in children compared to a group of adults: Saccade reaction times were longer, and saccade amplitude relative to target location (10° eccentricity) was shorter. Results also indicated that performance is flexible in children. Although saccade reaction time decreased as age increased, suggesting developmental improvements in saccade control, saccade amplitude gradually improved over trials. Moreover, similar to adults, children were able to modify saccade amplitude based on the visual

error made in the previous trial. This second set of results suggests that short visual experience and/or rapid sensorimotor learning are functional in children and can also affect saccade performance.

Introduction

In everyday life, we move our eyes almost constantly, making three to four saccades per second without even noticing it. Saccades bring objects of interest onto the high-resolution fovea and allow the detailed visual processing that extrafoveal vision does not support. In the first years of life, eye movements represent the major means to collect information from the surroundings and actively learn from them (Aslin, 2007). They support the child during the important steps of development from the first look given to his or her

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parents to the learning of various motor, cognitive, emotional, and social skills, such as reaching and grabbing an object, responding to a smile, playing interactive games, crawling and walking, and reading the first words.

Surprisingly, basic aspects of saccadic eye movement control in infants and toddlers remain poorly understood. Most developmental studies focused on childhood from 4–5 years of age into adolescence (for review, see Luna, Velanova, & Geier, 2008). Others described saccade characteristics in infants mostly within the first 6 months of life (Aslin & Salapatek, 1975; Hainline, 1984; Regal, Ashmead, & Salapatek, 1983; Salapatek, Aslin, Simonson, & Pulos, 1980). One study tested inhibitory control in 18 children from 8 to 38 months of age (Scerif et al., 2005). There is thus a large paucity of oculomotor studies in the intervening period.

Two parameters are frequently analyzed in developmental studies: saccade reaction time and saccade amplitude (i.e., accuracy). The studies mentioned above showed that habitual saccadic hypometria that is very small in adults (saccades usually cover 90% of target eccentricity; Becker, 1989) is even more pronounced in children. Moreover, children are slow to initiate saccades. Saccade accuracy seems to be adult-like by 8 years of age, and reaction time continues to decrease into adolescence. These changes are often linked to maturational changes in brain anatomy and function (for reviews, see Johnson, 1994, 2001; Luna et al., 2008).

The goal of the present study was to fill the gap of knowledge on saccade control in early childhood by analyzing basic characteristics of reactive saccades to a 10° eccentric target in 93 children from 7 to 42 months of age. Based on the studies described above, we hypothesized that saccade reaction time would be longer and amplitude more hypometric in children compared to adults. Saccade reaction time should progressively decrease, and amplitude should progressively increase with age in the child group, probably related to concurrent developmental brain changes. An alternative hypothesis is that saccade improvements throughout childhood may be related to sensorimotor learning.

Oculomotor learning occurs in adults, a phenomenon known as saccadic adaptation. In response to the visual errors that result from inaccurate saccade landing positions, saccade amplitude changes to decrease future errors. Amplitude adjustments occur progressively over the course of repetitive errors (Pélissou, Alahyane, Panouillères, & Tilikete, 2010). Saccadic adaptation is classically induced in the laboratory by displacing the target during the saccade in midflight, leading to artificial targeting errors. The repetition of these displacements leads to progressive

changes in saccade amplitude so that after 100 trials, saccades land closer to the new target position. Such learning also occurs on a faster timescale after every saccade (Collins, 2014; Srimal, Diedrichsen, Ryklin, & Curtis, 2008). In this case, the amplitude of the current saccade changes to correct for the targeting error of the previous saccade. Whether such learning is functional in children and when it emerges during development is unknown. We hypothesized that it would be present in children but may be less precise than in adults, which may explain why their saccades are less accurate.

To disentangle the developmental versus learning hypotheses, we examined (a) how saccade parameters (reaction time, amplitude) changed with development by comparing children to adults and also by performing correlations with age within our child cohort and (b) how saccade performance progressed over the course of an experimental session of 140 trials (learning effects).

Methods

Participants

Children were recruited from four different day care centers in the Paris area. One hundred twenty-two families volunteered to participate in the study. Among them, seven children were immediately excluded because of their withdrawal at the beginning of the experiment or because they did not pass the initial calibration step (see “Setup and eye movement recordings”). In sum, 115 children between 5 and 42 months of age (mean \pm *SD* = 25.4 \pm 9.6 months, 57 females) were included in the study. A group of 26 adults (ages 20–31 years, mean = 25.5 \pm 3.6 years, 22 females) from the Paris Descartes University community was included for comparison. All experimental procedures were in accordance with the Declaration of Helsinki and were reviewed and approved by the local institutional ethics committees. Adult participants and parents of children gave informed and written consent after the purpose and procedures were fully explained. Adults had normal or corrected-to-normal vision (one wore glasses and two wore contact lenses), and no vision deficits were reported in the children (none of them wore glasses). Adults performed the experiment in the laboratory whereas children did it in the day care centers where we installed our setup and material in a dedicated room. The setup and installation were kept as similar as possible between the different sites. For the purpose of the present study, we kept only participants who performed the entire experiment of 140 trials (see “Data analysis”). We thus report here on

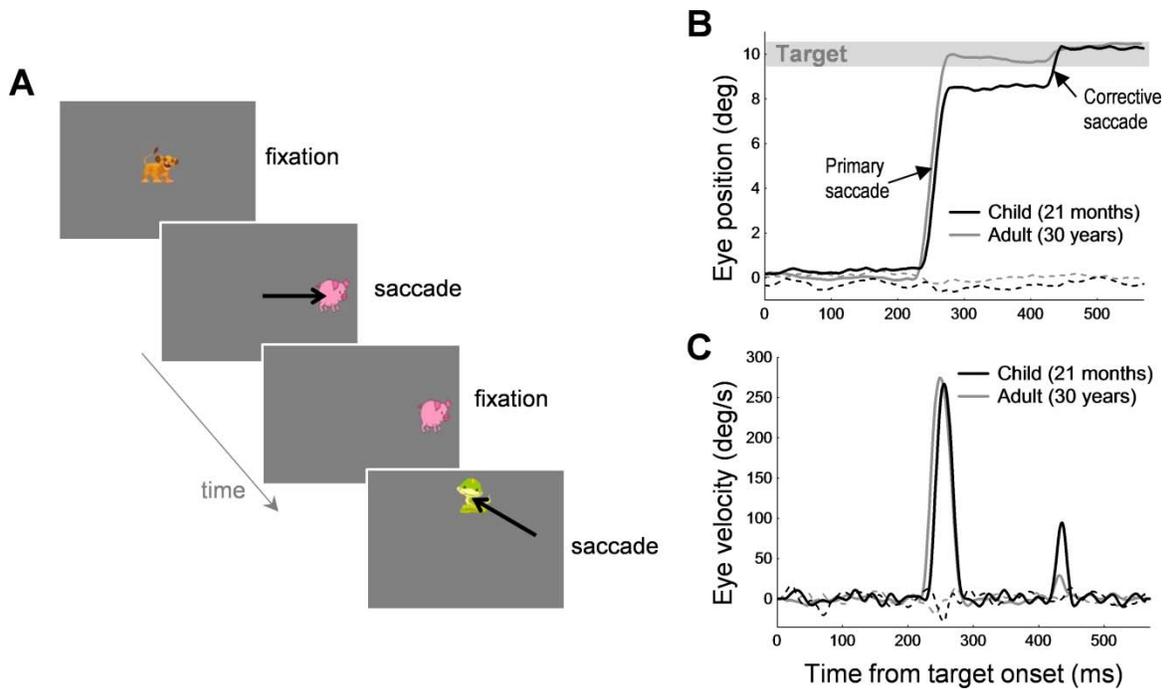


Figure 1. Task and stimuli. (A) Two example successive trials. Visual stimuli were $1^\circ \times 1^\circ$. (B) One example horizontal saccade and the corresponding velocity profile (C) in one child (black trace) and one adult (dark gray trace). Saccades started from center toward a visual target appearing on the right at 10° on the horizontal axis (see trial 1 in A). Solid (dashed) lines represent the horizontal (vertical) component of the saccades.

93 children (age range 7–42 months, mean \pm $SD = 27.6 \pm 8.6$ months, 40 females) and 26 adults.

Setup and eye movement recordings

Adult participants were seated in a chair in a darkened, quiet room, facing the center of a computer screen located 68 cm away, and children were seated on a caregiver's lap. The LCD monitor was 27×36 cm (HM240DT; Iiyama, Nagano, Japan) with a resolution of 800×600 pixels and a refresh rate of 160 Hz. Eye position was recorded using the remote Eyelink 1000 eye-tracking system (Desktop Mount, SR Research Ltd., Canada). Viewing was binocular, but only the right eye was digitized in both the vertical and horizontal axes at a sampling rate of 500 Hz and a spatial resolution of 0.05° . A small target sticker was placed on the volunteer's forehead allowing for correct eye position measurements across changes in head position.

Before the task, participants performed a calibration session in which they followed an animated cartoon character appearing sequentially and randomly at five positions over the entire screen (center, up, down, right, left). The maximal separation between the leftmost target and the rightmost target on the horizontal axis was 27° , and the maximal separation between the upper target and the lower target on the vertical axis was

19.1° . After calibration, the process was repeated to validate that the average error between fixation and target was $<1^\circ$ and that no loss of eye tracking occurred. There was no statistically significant difference in average calibration error between children ($0.63^\circ \pm 0.05^\circ$) and adults ($0.53^\circ \pm 0.04^\circ$), $t(117) = 1.04$, $p = 0.3$. Moreover, this calibration step ensured that subjects, in particular children, were able to orient their eyes to the different target positions and correctly fixate the targets. Calibration was repeated during the experiment when necessary.

Behavioral task

The experiment was programmed with Experimenter Builder (SR Research). Because we could not give any instruction to the young children and because they can easily be tired or bored, we developed an original protocol that included animated cartoon characters as stimuli to both stimulate children's interest and motivation and naturally induce automatic eye movements without instruction. Stimuli were $1^\circ \times 1^\circ$ colorful cartoon characters displayed on a medium gray background at unpredictable locations. Participants performed seven blocks of 20 trials with possible rests between blocks and new calibration if necessary. A novel stimulus was presented in every trial. Figure 1A shows an example of two successive trials. In the first

trial, a stimulus was presented at screen center. Once the participant successfully fixated the stimulus, it became animated (growing, shrinking, or spinning) and a sound (onomatopoeia, music note) was played. We then pressed the space bar of the keyboard to validate fixation and proceed to the trial. The current fixation stimulus disappeared while another target appeared at a location 10° away. The target was displayed until a saccade was detected. A saccade was detected when velocity and acceleration reached $30^\circ/\text{s}$ and $3000^\circ/\text{s}^2$, respectively. After 300 ms, the target became animated and a sound was played. The stimulus became the fixation point of the subsequent trial. The fixation point also served to perform the standard Eyelink calibration correction to ensure that measurements in each trial were sufficiently close to calibration values. In the case of a fixation measurement greater than 1° , calibration was automatically renewed. Over the course of a 20-trial block, the stimuli therefore performed a pseudo-random walk across the screen. Target eccentricity was always 10° , but there were 10 possible directions: right and left on the horizontal 0° axis, up and down at 15° from the horizontal axis (left and right hemifields), up and down at 30° from the horizontal axis (left and right hemifields). The entire experiment took 10 to 15 min. All the participants, including the youngest children, successfully looked at the stimuli without instruction.

Data analysis

Data were processed with Data Viewer (SR Research) and Microsoft Excel. Statistical analyses were performed with Statistica (Statsoft).

We collected in total 14,907 trials in our 115 5- to 42-month-old children and 3,640 trials in our 26 adults. Four children performed between 30 and 60 trials (ages 5–19 months, mean = 10.5 ± 6.2 months, all females), four between 61 and 80 trials (ages 7–28 months, mean = 17 ± 9 months, all females), six between 81 and 100 trials (ages 6–18 months, mean = 12.3 ± 4 months, four females), and eight between 101 and 120 trials (ages 8–33 months, mean = 20.9 ± 8.7 months, five females). Importantly, of the 115 children, 93 (thus a proportion of 81%) performed the whole experiment containing 140 trials. For the purpose of the study, we kept only these 93 children (7–42 months old, mean \pm $SD = 27.6 \pm 8.6$ months, 40 females).

We analyzed the first, or primary, saccade in response to target appearance in every trial. Saccade reaction time (SRT) was defined as the time interval (in milliseconds) between fixation point disappearance and saccade onset. Saccade amplitude was defined as the difference between saccade end and initial eye position. We discarded trials with blinks occurring during the saccade, SRT shorter than 50 ms or longer than 600 ms,

saccade amplitude shorter than 4° or longer than 16° , saccade direction outside an angle of 30° around target position, and outliers. Outliers were values that lied below ($Q1 - 2.3 \times IQR$) or above ($Q3 + 2.3 \times IQR$), $Q1$ and $Q3$ being the first and third quartiles, respectively, and IQR the interquartile range (Tukey box plot). The proportion of discarded trials for children and adults, respectively, was 5.8% and 3.8% for blinks, 6.4% and 9.8% for incorrect directions, 0.3% and 0.1% for $SRTs < 50$ ms, 0.6% and 0.2% for $SRTs > 600$ ms, 0.8% and 0.6% for amplitudes $< 4^\circ$, 0.3% and 0.1% for amplitudes $> 16^\circ$, 4.2% and 5.2% for outliers. Note that few other trials in children contained no saccade and were thus discarded (1.9%). Importantly, based on all these exclusion criteria, the proportion of valid trials was similar between children (mean \pm $SD = 80\% \pm 9\%$) and adults ($80\% \pm 8\%$, independent samples t test, $p = 0.95$). Each child contributed to 78–134 valid trials for a total of 10,429 valid trials. Each adult contributed to 90–132 trials for a total of 2,920 valid trials. This information is crucial because it indicates that our protocol was successful in collecting a large amount of data from young children in a short amount of time without instruction and with a very low attrition rate that was comparable to adults.

We also analyzed the second, or corrective, saccade that followed the primary saccade. Secondary saccades were deemed corrective when they were directed toward target position within an angle of $\pm 15^\circ$ and when they landed closer to target position than the preceding saccade (namely, the visual error between the end of the secondary saccade and target location was smaller than the visual error between the end of the primary saccade and target position). If the primary saccade was followed by multiple saccades, we only considered the first corrective saccade.

In a first set of statistical analyses, we examined developmental effects on primary saccade performance using the first 20-trial block only. We compared SRT and intraindividual variability in SRT and saccade amplitude and intraindividual variability in amplitude between children ($n = 93$) and adults ($n = 26$) using independent samples t tests. We also performed correlations between age and the different saccade parameters within the child group.

In a second set of analyses, we tested whether learning effects could occur across the seven 20-trial blocks of the experiment. Primary saccade performance was submitted to repeated-measures ANOVAs with Blocks of trials as a within-subject factor and Age group (adults vs. children) as a between-subjects factor. Significant effects were further examined with post hoc Tukey honestly significant difference (HSD) tests. The proportion of corrective saccades relative to the total amount of trials was also submitted to Blocks of trials \times Age group repeated-measures ANOVAs.

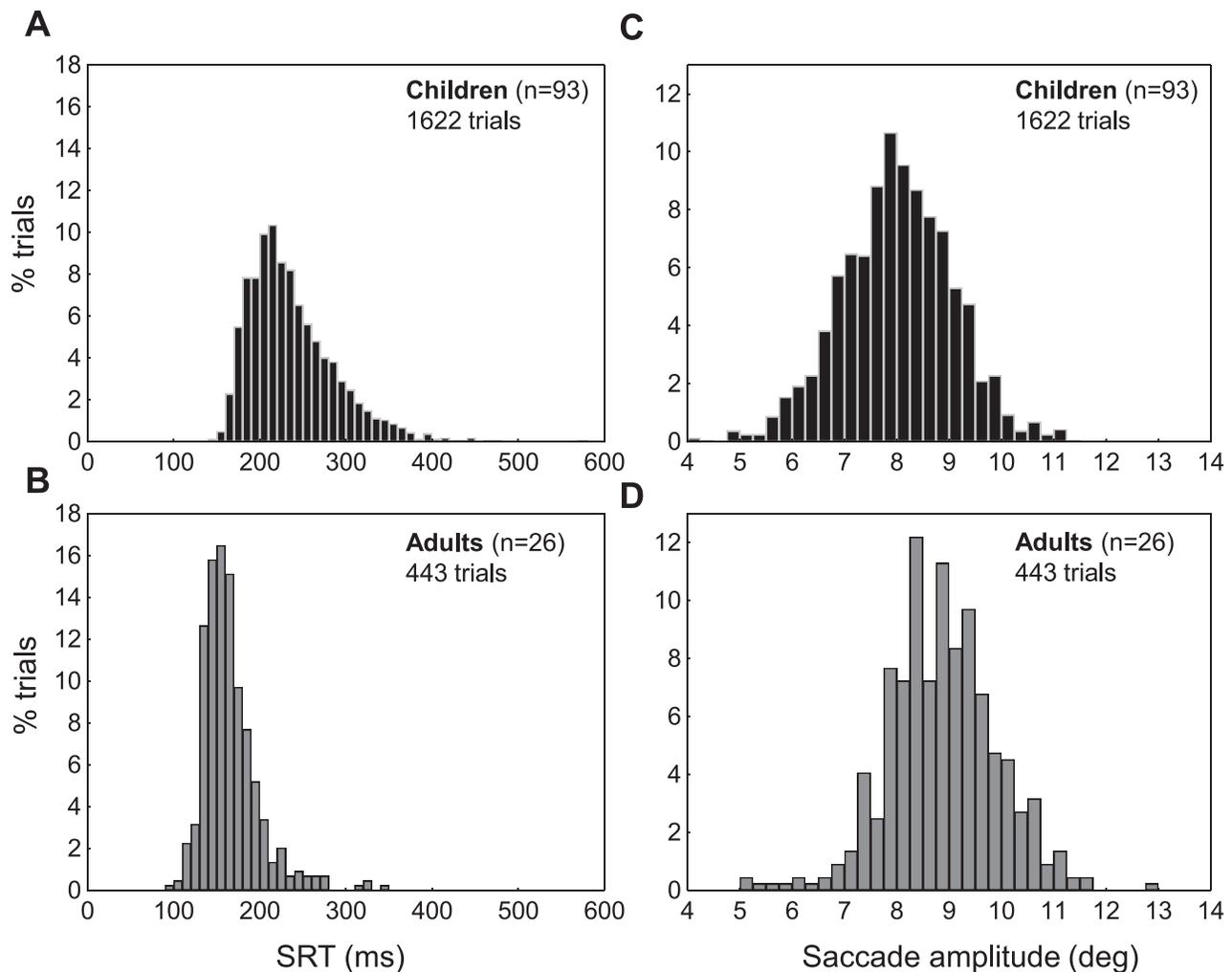


Figure 2. Distribution of SRT (A, B) and saccade amplitude (C, D) in children and adults in the first block of 20 trials. (A, B) Bars represent 10-ms bins. (C, D) Bars represent 0.25° bins.

We pooled all saccade directions as differences depending on saccade directions were not the purpose of our study, and there were too few trials per direction. Note that we did not find any significant effect of gender for any of the analyses ($F_s < 1$ or close to 1). Significance was set at $\alpha = 0.05$.

Results

Developmental effects on saccade performance

Figure 1B and C depict an individual trial recorded from one 21-month-old child and one 30-year-old adult when a target appeared at 10° to the right. Eye movement traces are comparable. A notable difference however is that the child's primary saccade was shorter than the adult's. The child then made a second, corrective, saccade to acquire the peripheral target.

Figure 2 shows SRT and amplitude distributions for all saccades in the first 20-trial block in the child group and the adult group. Age strongly influenced the distribution of SRT (Figure 2A, B). Compared to adults, the distribution was broader in children and included longer SRT. In children, the majority of saccades were initiated from 160 ms to 320 ms after target appearance whereas in adults most SRTs ranged from 100 ms to 230 ms. The distribution of saccade amplitude also varied with age although to a lesser extent. Indeed, compared to adults (Figure 2D), children showed a larger proportion of saccades between 5.5° and 8° in amplitude (Figure 2C), shifting thus the peak of the distribution toward smaller amplitudes. All these developmental trends were confirmed statistically in the following analyses.

A t test for independent samples revealed indeed that children were slower than adults to respond to stimulus appearance, $t(117) = 9.33$, $p < 0.001$ (Figure 3A). Standard deviation of SRT indicated that children were

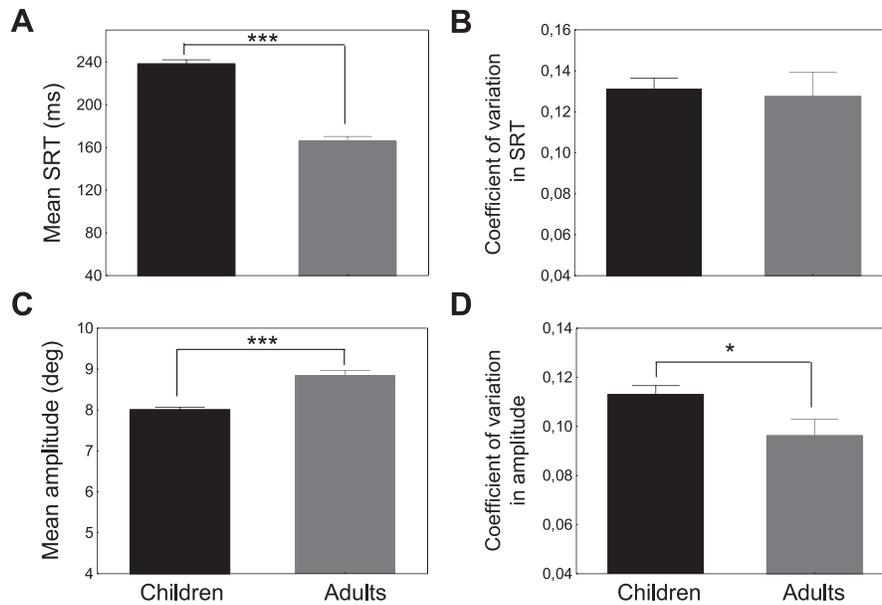


Figure 3. Saccade performance in the first block of 20 trials. (A) SRT. (B) Intraindividual variability in reaction time (see text for details). (C) Saccade amplitude. (D) Intraindividual variability in amplitude. * $p < 0.05$, *** $p < 0.001$, others: nonsignificant. Error bars represent standard errors of means.

more variable than adults, $t(117) = 3.06$, $p < 0.005$. However, because standard deviation often scales with the mean, we used instead the coefficient of variation in reaction time (cvSRT) as an index of intraindividual variability to avoid this confound (McIntosh, Kovacevic, & Itier, 2008). The cvSRT, calculated as the standard deviation divided by the mean reaction time, was similar between children and adults, $t(117) = 0.3$, $p = 0.766$ (Figure 3B).

In children, the amplitude of the first saccade was shorter, $t(117) = -6.46$, $p < 0.001$, and more variable, $t(117) = 2.34$, $p < 0.05$, compared to adults (Figure 3C, D). Children seemed to compensate for this hypometria by making more corrective saccades than adults ($44\% \pm 2.3\%$ vs. $29\% \pm 3.6\%$; Figure 5D, block B1), a difference that was statistically significant, $t(117) =$

3.18 , $p < 0.005$. Note that the percentage of corrective saccades in adults here is in agreement with past studies in adults for a 10° target eccentricity (Weber & Daroff, 1972).

Next, we examined whether saccade performance changed within our child sample (7–42 months old). Figure 4 presents SRT and amplitude as a function of age. SRT gradually decreased with age ($r = -0.541$, $p < 0.001$; Figure 4A), suggesting that children's saccades are initiated faster as they grow up. Amplitude did not change significantly with age ($r = 0.141$, $p = 0.177$; Figure 4B). There was a marginally significant tendency for within-subject variability in amplitude to decrease with age ($r = -0.199$, $p = 0.06$). The proportion of corrective saccades was not significantly correlated with age ($r = -0.137$, $p = 0.191$).

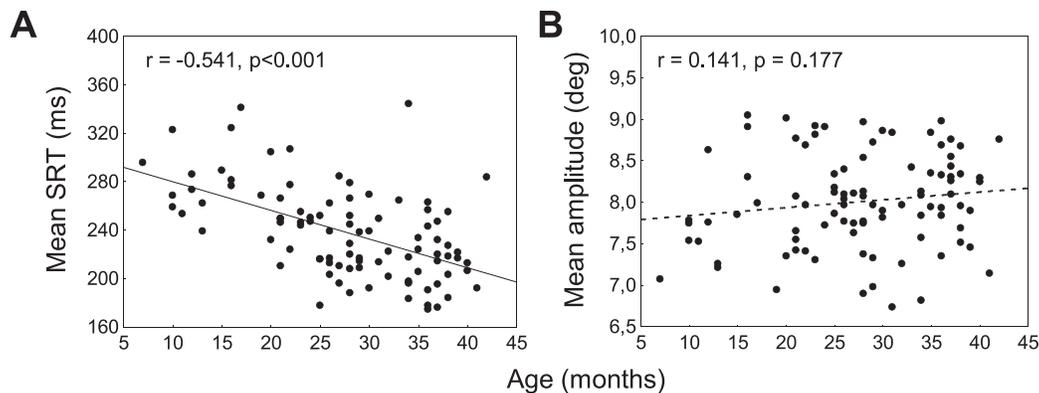


Figure 4. Correlation analyses between saccade performance (reaction time; A), saccade amplitude (B), and age across all children participants ($n = 93$). The full line indicates a significant correlation with age; the dashed line indicates a nonsignificant correlation with age.

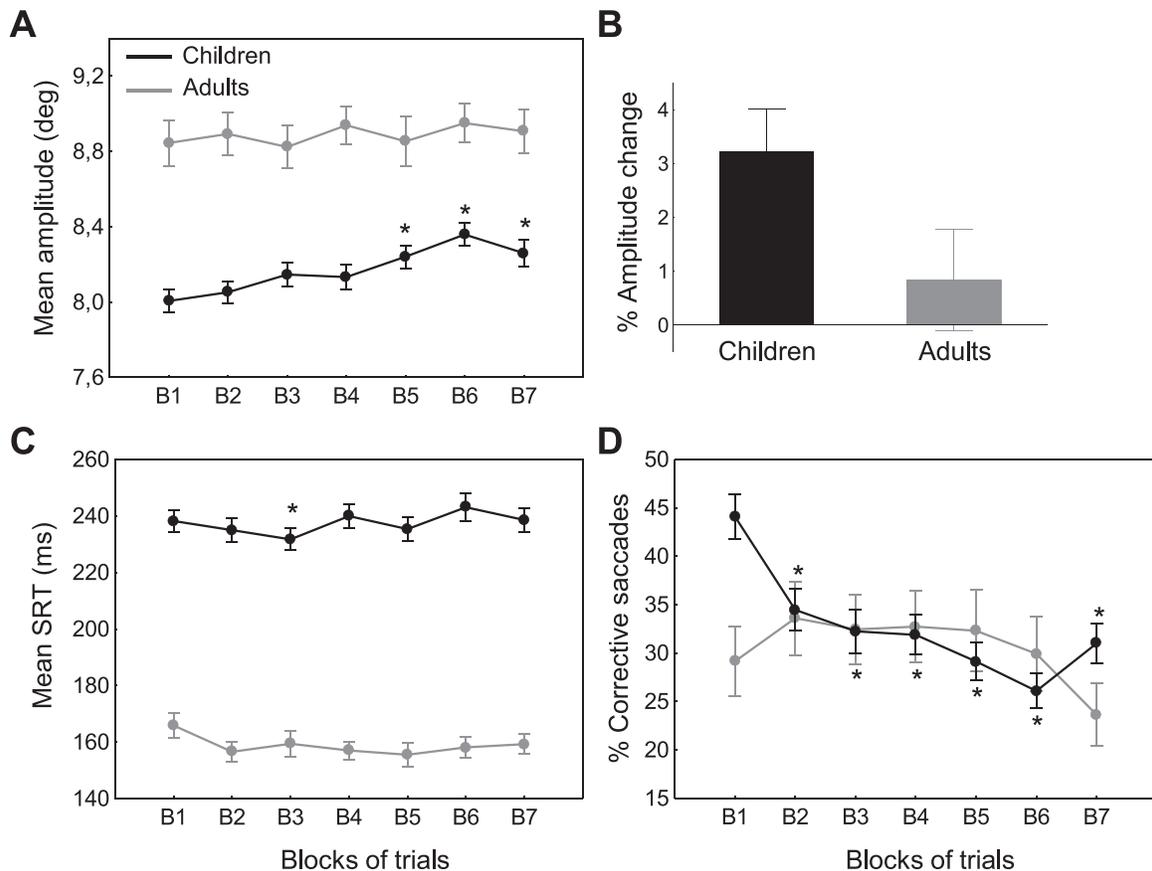


Figure 5. Saccade performance across the seven blocks of 20 trials B1 to B7. (A) Saccade amplitude. (B) Percentage amplitude change in amplitude calculated as follows: $([\text{mean amplitude in B7} - \text{mean amplitude in B1}] / \text{mean amplitude in B1}) \times 100$. Note that contrary to children, the amplitude change in adults ($0.837\% \pm 0.94\%$) was not significantly different from zero, $t(25) = 0.891$, $p = 0.381$. (C) SRT. (D) Proportion of corrective saccades. Asterisks in A, C, and D illustrate significant differences compared to the block B1 that were observed in children (post hoc Tukey HSD tests). Note that the percentage of corrective saccades was significantly different between children and adults for the blocks B1 and B7 (D) but not depicted here (see text). Error bars represent standard errors of means.

Learning effects on saccade performance

We investigated whether saccade characteristics in children could also progress across the seven blocks of trials, which would suggest some learning effects independent of development. Note that the number of scorable trials (see Methods) was similar between the two age groups (80%), precluding any effect of number of trials on the results. Trial effects were analyzed by repeated measures ANOVAs with Blocks of trials as a within-subject factor and Age group as a between-subjects factor.

Changes in saccade performance across blocks of trials

Unexpectedly in children, saccade amplitude gradually increased across blocks of trials whereas it was stable in adults (Figure 5A). A repeated-measures ANOVA showed a significant interaction between the factors Blocks of trials and Age group, $F(6, 702) = 2.54$,

$p < 0.05$. Post hoc Tukey HSD tests indicated that, in children, saccade amplitude was larger in Blocks 5–7 than in Block 1 ($ps < 0.001$).

This improvement in saccade amplitude was not obtained at the expense of reaction time because SRT did not consistently change over the course of the experiment (Figure 5C; post hoc Tukey tests, $ps > 0.3$ between Block 1 and all the subsequent blocks except Block 3, $p < 0.05$).¹ No block effects were found for intraindividual variability in amplitude or in SRT (all $ps > 0.12$).

Saccade amplitude in the child sample increased by 3.33% between the first and last blocks of trials (Figure 5B), which was significantly greater than zero, $t(92) = 4.23$, $p < 0.001$, but did not correlate with age ($r = -0.185$, $p = 0.076$). Among the 93 children, 25 showed a significant increase in amplitude with increases ranging from 7.5% to 25% (independent t tests between Block 1 and Block 7, $ps < 0.05$), and 24 children showed an increase in amplitude ranging from 2.5% to 7.3%. The

others showed a lower increase in amplitude or no increase. Importantly, the children who experienced greater improvement in saccade amplitude across the course of the experiment were those who made more hypometric saccades at the beginning of the experiment as revealed by the significant correlation between percentage of amplitude change and saccade amplitude in the first block ($r = -0.302$, $p < 0.005$).

Although primary saccade amplitude increased across trials in children, the frequency of corrective saccades decreased (Figure 5D). A repeated-measures ANOVA showed a significant interaction between the factors Blocks of trials and Age group, $F(6, 702) = 6.15$, $p < 0.001$. Post hoc Tukey tests indicated that the proportion of corrective saccades in Block 1 in children was significantly higher than in Blocks 2–7 ($ps < 0.001$). Moreover, except the first block of trials in which children made more corrective saccades than adults ($p < 0.05$) as already seen in the paragraph above, there were no differences between the two groups for the subsequent blocks ($ps > 0.93$).

Trial-by-trial changes in saccade amplitude

To characterize trial-by-trial learning, we calculated the retinal offset between primary saccade end point and target position. Positive offsets correspond to undershoots and negative offsets to overshoots. We also calculated the amplitude change as the difference between amplitude in a given trial with the amplitude in the trial just preceding it. Positive values indicate an amplitude increase from one trial to the next, negative values a decrease. We then examined the correlation between the amplitude change in a given trial (t) and the retinal offset on the previous trial ($t - 1$). Some amount of correlation is expected because the previous saccade amplitude contributes to the measure in both previous and current trials. What is of interest here are potential differences between the two groups. In the adult sample, as expected, there was a correlation between previous retinal offset and current amplitude change, replicating previous work (Collins, 2014). The correlation was positive, meaning that a positive retinal offset (undershoot) led to a positive amplitude change (increase). The correlation coefficient, although small, was significantly different from zero, $r = 0.18$, 95% confidence interval (CI) [0.04, 0.27], $p < 0.01$. The correlation was also significant in the child sample, $r = 0.18$, CI [0.13, 0.23], $p < 0.001$. The slope of the correlation is an index of the extent to which retinal offsets are compensated for in the next trial. On average, adults and children compensated equally: 0.14° , CI [0.016, 0.19], $p < 0.025$, and 0.14° , CI [0.10, 0.18], $p < 0.001$, respectively ($p > 0.45$). In sum, these results suggest that learning mechanisms are operational in children and seem to be as accurate as in adults.

Discussion

Developmental effects

Our results indicate that there are two markers of saccade control in young children: long SRT and hypometric (i.e., shorter) saccades, which may be related to immature brain saccade circuitry and anatomy. Saccade generation is subserved by an extended brain network that includes cortical eye fields, the superior colliculus, the basal ganglia, the thalamus, and the cerebellum (Johnston & Everling, 2008; Leigh & Zee, 2006; McDowell, Dyckman, Austin, & Clemenz, 2008; Pierrot-Deseilligny, Rivaud, Gaymard, & Agid, 1991). Our results suggest that the developmental improvement in SRT across toddlerhood may be related to increased function of cortical areas involved in saccade planning and preparation as may be predicted from studies that used event-related potentials in 6- and 12-month-old children (Csibra, Tucker, & Johnson, 1998; Csibra, Tucker, Volein, & Johnson, 2000) and functional neuroimaging in children over 8 years old (Alahyane, Brien, Coe, Stroman, & Munoz, 2014). Both SRT and functional development through this period of life may be supported by concurrent increase in brain white matter volumes (Matsuzawa et al., 2001; Pfefferbaum et al., 1994) that likely reflects myelination of axons (Barkovich, Kjos, Jackson, & Norman, 1988; Nakagawa et al., 1998). This latter process likely speeds up information processing times within the saccade cortical network but also between cortical and subcortical areas.

It is not excluded that differences in SRT and amplitude between children and adults may be due to differences in disparity processing when fixating from one target to another. However, the spatial characteristics² of our setup make any influence of vergence eye movements on saccadic parameters very unlikely.

The 7- to 42-month-olds also showed shorter and more variable saccade amplitude compared to adults. These behavioral patterns in young children resemble those of patients (Golla et al., 2008; Panouillères et al., 2013; Straube, Deubel, Ditterich, & Eggert, 2001) and monkeys (Barash et al., 1999; Takagi, Zee, & Tamargo, 1998) with lesions to the cerebellum, in particular the medio-posterior part. The medio-posterior cerebellum, or oculomotor vermis, plays a key role in visually guided saccade accuracy by stopping the saccade when the eyes reach the desired position (Pélisson, Goffart, & Guillaume, 2003). Our results are therefore compatible with suboptimal cerebellar function in young children (Mall et al., 2005).

Perhaps the less intuitive result at first glance is the similar cvSRT we found between children and adults. Trial-by-trial intraindividual variability in reaction

times is thought to be an index of attention selection, cognitive control, and motivation (Bellgrove, Hester, & Garavan, 2004; Garrett, MacDonald, & Craik, 2012; West, Murphy, Armilio, Craik, & Stuss, 2002). It is higher in children (age >6 years) than adults (Williams, Hultsch, Strauss, Hunter, & Tannock, 2005) and in tasks that require higher cognitive resources than less demanding tasks in preadolescents (Wu et al., 2011). Here, saccades were externally triggered by visual stimuli appearing suddenly on the screen at unpredictable locations. These saccades are thus reactive or automatic, requiring minimal effort or cognitive control. Moreover, we presented a novel stimulus at every trial to keep children's interest and motivation constant across the entire experiment.

Learning effects

Despite this apparent immaturity in SRT and saccade amplitude in children, our results also suggest that learning mechanisms are functional in these children. Indeed, although saccade control improves through toddlerhood, which is probably related to development of brain saccade circuitry (see above), saccade amplitude gradually increases over trials, suggesting that visual experience and/or rapid sensorimotor learning can also affect saccade performance independently of brain or peripheral systems development. This gradual increase in saccade amplitude over trials while SRT remains stable strongly resembles saccadic adaptation, a form of motor learning (Herman, Blangero, Madelain, Khan, & Harwood, 2013; Pélisson et al., 2010). Saccadic adaptation has been observed after eye muscle paresis (Abel, Schmidt, Dell'Osso, & Daroff, 1978) or environmental perturbations in laboratory settings (McLaughlin, 1967). Saccade adaptation is functional in late childhood and adolescence (Doré-Mazars, Vergilino-Perez, Lemoine, & Bucci, 2011; Salman et al., 2006), and the present results suggest that it may also be functional in early childhood. Our experimental paradigm did not, however, introduce artificial targeting errors by displacing the target during the saccade as is usually the case in adaptation experiments. We examined instead another classic marker of saccadic adaptation, trial-by-trial adaptation. Contrary to our initial hypothesis, our results clearly showed comparable trial-by-trial learning abilities between adults and children. Such similar learning effects predict the differential pattern we observed over the course of the entire experiment: Children undershoot more than adults, so in every trial they compensate for a small portion of their error, but over the course of several trials, amplitude tends to increase. Because the average retinal offset in adults is

closer to zero, with the same learning rate there should not be an overall change in amplitude over the course of several trials.

The visual target, which was a novel cartoon character at every trial, may have been rewarding for the child. Thus, motivation and/or reward may have also led to the improvement in saccade performance, a hypothesis that was proposed by Madelain, Paeye, and Wallman (2011) to explain saccade adaptation in adults.

Children consistently make hypometric saccades

Overall, our results show that young children generate hypometric saccades compared to adults, but they are capable of increasing accuracy over successive trials thanks to existing plasticity mechanisms. One question that remains, however, is that if children have the same learning rate as adults based on our analyses on trial-by-trial adaptation, then why do their saccades remain hypometric? One possibility would be that targets were cartoon characters that did not need to be foveated. Smaller saccades were sufficient for children to get the information they needed about the characters (for example their identity). This hypothesis somewhat resembles the “lazy strategy” hypothesis proposed by Kapoula and Robinson (1986) to explain the frequent 10% undershoot in adults. Another possibility would be that, similarly to adults, saccade hypometria is a deliberate strategy by the oculomotor system to minimize total saccadic flight time (Harris, 1995) and minimize time to initiate any corrective saccades as it would be from the same brain hemisphere (Robinson, 1973). Although these two strategy assumptions are plausible, another reason would simply be that the fovea is not fully functional in the first years of life. Histological and optical coherence tomography studies revealed that the fovea progressively develops after birth to be adult-like by 15 to 18 months old (Dubis et al., 2012; Hendrickson, 1992; Hendrickson & Yuodelis, 1984) but continues to mature until 4–5 years of age (Hendrickson, 1992). However, if foveal maturation were the only reason for saccade inaccuracy in young children compared to adults, then the youngest would be the most inaccurate and saccade amplitude would change with age, which we did not see here (Figure 4B). Moreover, children were able to sometimes generate saccades with amplitudes >9° (see Figure 2C). Of course, these three hypotheses are not mutually exclusive. In other words, it may be possible that saccades are hypometric in children by strategy as in adults, but their hypometria may be more pronounced because of immature central or peripheral neural systems.

Conclusion

Our behavioral results highlight a dichotomy between changes in oculomotor performance that are related to development and those that are related to learning and visual experience. Despite saccade inaccuracy in early childhood, sensorimotor plasticity mechanisms are in place and functional and brought into play when necessary. Improvement in saccade amplitude with visual experience or/and learning suggests that caution should be taken in future studies that use saccade end points to assess cognitive development (for example, face processing). Saccade landing positions may indeed change over the course of the experiment.

Keywords: eye movement, saccade, development, learning, infants

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Footnotes

¹ Note that we also analyzed saccade peak velocity as an indicator of fatigue by performing a repeated-measures ANOVA with Blocks of trials as a within-subject factor and Age group as a between-subjects factor. Peak velocity was lower in children ($308^\circ/\text{s} \pm 4^\circ/\text{s}$) than adults ($333^\circ/\text{s} \pm 8^\circ/\text{s}$) as expected, $F(1, 117) = 9.08$, $p < 0.005$, but it did not change across trials, $F(6, 702) = 1.62$, $p = 0.141$. This analysis suggests thus that fatigue did not affect the results.

² We calculated that the difference in vergence angle between a target at the center of the screen and a target at the very edge of the screen (at a distance of 15°) was only one third of a degree, but in our setup, the maximal distance from screen center was lower (11.8°),

suggesting that the difference in vergence angle was negligible.

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