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Hemispheric Asymmetry in the Maturation of the Extrastriate Checkerboard Onset Evoked Potential

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Recently we have shown that the single positive deflection in the checkerboard onset evoked potential (EP) of young children of striate origin develops into a negative–positive complex. However, also an early positive peak becomes apparent in the checkerboard onset EP. To determine the origin and development of the activity underlying this early positive deflection we studied the checkerboard onset EPs in children of 9–16 years of age. It was found that for the children in this age group two different dipole sources are responsible for the activity underlying the pattern onset EP. One of the dipoles corresponds to the activity generated in the striate cortex, whereas a second dipole of extrastriate origin is responsible for the appearance of the early positive deflection. This extrastriate activity shows hemispheric asymmetry, i.e. the strength of the right hemispheric extrastriate source exceeds the strength of the left hemispheric source. These results are in accordance with histological studies of Conel (1939–1963) [*The postnatal development of the human cerebral cortex* (Vols 1–8). Cambridge, Mass.: Harvard Univ. Press] which show that the maturation of the extrastriate areas of the left hemisphere is delayed with respect to the right hemisphere.

Checkerboard onset EP   Equivalent dipole   Maturation   Extrastriate activity   Hemispheric asymmetry

INTRODUCTION

The pattern onset evoked potential (EP) does not obtain its characteristic positive–negative–positive complex with adult-like CI, CII and CIII peak-latencies before puberty (Spekreijse, 1978; De Vries-Khoe & Spekreijse, 1982; Spekreijse, 1983). In the first years of life the child checkerboard onset EP consists mainly of a single positive deflection (Spekreijse, 1978; De Vries-Khoe & Spekreijse, 1982), which has its origin in striate cortex (Ossenblok, Reits & Spekreijse, 1992). From the age of about 4 years on waveform changes of the pattern onset EP become apparent in the checkerboard onset EP, reflecting the growth of a negative peak (CII) which is preceded by an early positive peak (De Vries-Khoe & Spekreijse, 1982; Spekreijse, 1983; Apkarian, Reits & Spekreijse, 1984). It was shown by Ossenblok *et al.*

(1992) that the growth of the negative peak reflects changes in striate activity as a function of age. This paper deals with the origin and development of the activity underlying the early positive peak of the child checkerboard onset EP.

The analysis is based on the assumption that the sources of the VEP can be modelled by equivalent dipole sources, which have a fixed position and orientation while the source strength is varying. Using the spatial-temporal dipole model of De Munck (1990) we studied the origin and development of the activity underlying the early positive peak of the pattern onset EP for children of 9–16 years of age. Since local contrast favours the early positive peak of the pattern onset EP (Spekreijse, Van der Tweel & Zuidema, 1973) we used relatively large checkerboard elements, high modulation depths and large stimulus fields to increase the signal-to-noise ratio of the responses. Histological studies of Conel (1939–1963) have shown that the maturation of the extrastriate areas of the left hemisphere is delayed with respect to the right hemisphere. We, therefore, compared also the results of left and right half-field stimulation systematically for all subjects studied.

METHODS

Stimuli

Stimulation was by means of an electrostatic monochrome CRT (Hewlett Packard HP1321A) with a

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resolution of 256*256 pixels and a frame rate of 107.76 Hz. The CRT was driven by a digital display generator (Neuroscientific VENUS system). A/D acquisition rate was set to twice the frame rate (215.52 Hz) and was locked onto the frame rate of the CRT. The mean luminance of the CRT was 65 cd/m². All stimuli were presented in the left or right hemifield surrounded by a steady homogenous field of the same mean luminance, with a field size subtending to 4 or 8 deg. The modulation depth of the stimulus is chosen such that the retinal contrast is constant at, respectively, a level of 25.3% or 52.1%. The retinal contrast was kept constant by means of the point spread function for the light scattering in the eye (Vos, 1984). The checkerboard pattern was presented for 300 msec every 800 msec, without net variation in overall luminance level. In this way the responses evoked by the onset and offset of the checkerboard could be registered separately. The results presented were obtained for both left and right half-field stimulation with check sizes of 24′.

Recording

VEPs were recorded at 24 scalp electrodes. The electrodes were fixed in a grid, with an inter-electrode distance of about 4 cm, covering the occipital region of the head and the actual positions were measured afterwards. A reference electrode was placed at the frontal midline; the ground was located near the vertex. Three reference points are required to define the reference frame of the electrodes. For this we used the two external auditory meati and the vertex. By positioning the legs of a pair of compasses at the electrode location and at the three reference points the location of every electrode P_i is uniquely defined. In this way the best fitting sphere for the electrode positions on the head is found (De Munck, Vijn & Spekreijse, 1991).

The children were seated as comfortably as possible. The monitor was viewed binocularly from a distance of 86 cm. If necessary recording was interrupted by automatic artifact rejection or by an observer who monitored the child's behaviour. Fixation was established with a set of three LEDs of different colour. This fixation point was presented in the centre of the screen and the subject had to respond verbally to each random appearance of a particular colour. To hold the attention of the children in between the recordings a children's movie was presented.

Signals were amplified (Medelec 5000) and bandpass filtered between 1.5 and 70 Hz. The high cut-off frequency (70 Hz) was set by a low-pass fourth order Butterworth filter, which introduces a phase shift increasing the response latencies by about 7 msec. Peak-latencies estimated from the recordings in this paper should be corrected for this latency increase. The EEGs were sampled with a 215.52 Hz sample frequency, and on-line averaged with the CED 1401 system. The signal-to-noise ratio was estimated by means of the plus–minus averaging method (Schimmel, 1967). For the dipole analysis of the pattern onset EP a time window of 65.0–227.4 msec after pattern onset was chosen which includes the prominent maxima and minima of the responses.

Equivalent dipole analysis

Dipole sources give an adequate description of the scalp recorded potentials (De Munck, Van Dijk & Spekreijse, 1988a, b). To localize the dipoles the spatio-temporal dipole model of De Munck (1990) was used. In this model the problem of temporal overlapping source activity was solved by assuming *a priori* that the generators of the pattern onset EPs may be described by a fixed number of stationary dipoles, with time varying amplitudes. It is not known in advance how many dipoles are activated upon visual stimulation. Therefore a singular value decomposition (SVD) of the data is performed which provides us with an estimate of the minimal number of activated sources, by arguing that the number of significant principal components (PCs) equals the number of activated sources. The number of activated dipoles is chosen such that the lower limit of the residual, which depends solely on the number of significant PCs, reaches the noise level of the data. The starting locations of the dipoles used in the inverse calculation procedure are obtained by means of the moving dipole model. However, to be certain that the algorithm did not converge only to a local minimum different starting locations were tried, which all give the same solution. The dipoles are localized within the spherical three-shell model for the head, describing the brain surrounded by the skull and scalp (Ary, Klein & Fender, 1981), while no further constraints are placed on the volume searched. If the percentage of the recorded data variance not explained by the dipole solution reaches the lower limit of the residual the actual residual of the least square fit can be explained purely by noise. Note, however, that the actual residual obtained also may depend on model errors of the head and the sources. In this study the final solution of the inverse calculation is obtained if the difference between the actual residual obtained and the lower limit of the residual is minimal, which is reached if the partial derivative of the residual (see De Munck, 1990) is smaller as 10^{-5}.

Subjects

The results presented in this paper were obtained in 18 healthy children of 9–16 years of age recruited from employees of our institute. For all of these children the difference amplitude of the right and left hemifield responses is depicted. For comparison we also present the difference amplitude of nine adults, ranging from 21 to 47 years of age. For 13 of these children for whom the significant variance of the response sets evoked by both the right and left hemifield amounted to 80% of the total power of the responses or more also the results of the SVD are tabulated. Furthermore, for five of these children who are representative for the group, the results of the equivalent dipole analysis are depicted.

Presentation of results

The position and orientation of the dipoles are given with respect to the best fitting sphere (see Figs 2–4).
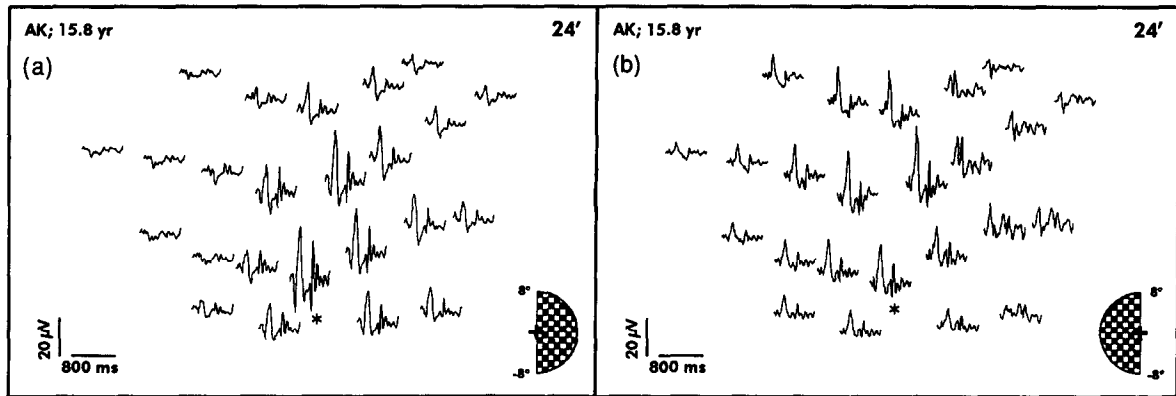
FIGURE 1. The visual evoked responses to the appearance of a 24' checkerboard in the central 8 deg of the right half-field (a) and of the left half-field (b). The responses are plotted according to a 2-dimensional projection of a spherical surface with horizontal and vertical distances of approx. 4 cm. The asterisk indicates the position of the inion, which is located at the midline of the head, approx. 2 cm above the bottom row of electrodes.

Transformation over the x- and z-axis gives the inion–ear co-ordinate system. In Table 1 the parameters of the dipoles are given with respect to this inion-ear system: the position parameters of the sources are given in the cartesian co-ordinates X, Y and Z and the orientation of the dipoles is given in the polar co-ordinates θ and ϕ. The radial orientation is given as θ, whereas ϕ yields the orientation in the tangential plane. The residual error (R.err) equals the difference between the actual residual obtained and the lower limit of the residual. Note, furthermore, that in the computations of the source strength relative values for the radii and conductivities of the concentric shells describing the volume conductor were used (Rush & Driscoll, 1968).

RESULTS

The left part of Fig. 1 shows pattern EPs recorded at 24 scalp electrodes upon presentation of a pattern onset stimulus in the right half of the visual field. The responses are maximal at the midline of the head, above the inion. The wave form of the responses is characteristic for children of this age (Ossenblok et al., 1992) and consists mainly of a negative–positive complex. For stimulation with a left half-field, however, also an early positive peak, at about 100 msec, becomes apparent in the responses [Fig. 1(b)]. Note that this peak, which dominates at the contralateral recording site, is absent in the contralaterally recorded responses evoked by right half-field stimulation.

The equivalent dipoles

A SVD of the responses evoked by right half-field stimulation showed that the power of the first principal component (93.5%) accounts for the significant power of the responses within the time window chosen for the analysis. The variation in strength of the source is reflected by the component of the pattern onset EP [Fig. 2(a)]. Since the activity underlying this pattern onset EP can be described by a single source the shape of this component is, of course, similar to the time varying amplitude of the pattern onset EP. The corresponding dipole source is located near the midline of the

head, above the inion, with an orientation which is partly radial and partly tangential. The location of the equivalent dipole indicates an origin in the striate cortex (area 17). Since the residual error of the dipole fit amounts to 2.5% of the total power of the responses the actual residual obtained can be explained largely by noise.

A SVD of the responses evoked by left half-field stimulation showed that the accumulated power of the two major principal components, amounting respectively to 82.0 and 14.4%, accounts for the significant power of the response set. Thus, two dipoles are needed to account for the significant variance of the responses.
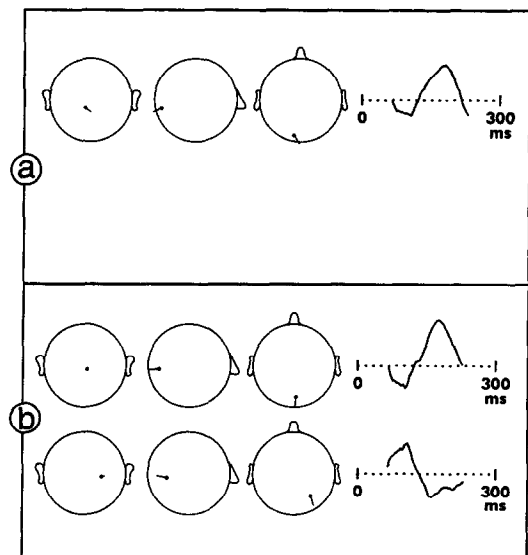

FIGURE 2. The locations and orientations of the sources are plotted in diagrams viewed from behind (left), from the right (middle) and from above (right). The location of the dipole source is referred to the best fitting sphere of the head whose outer limit is depicted. The length and direction of the arrow in each plane shows the strength and orientation of the dipole. In this figure the locations and orientations of the dipoles responsible for the responses shown in Fig. 1 are depicted. (a) The responses evoked by right half-field stimulation could be explained by a single source. (b) For left half-field stimulation two dipoles could be localized originating in the striate and extrastriate cortex. The shape of the components is shown for each dipole source. The components covered a time window that started at 65.0 msec after pattern onset and ended at 227.4 msec.
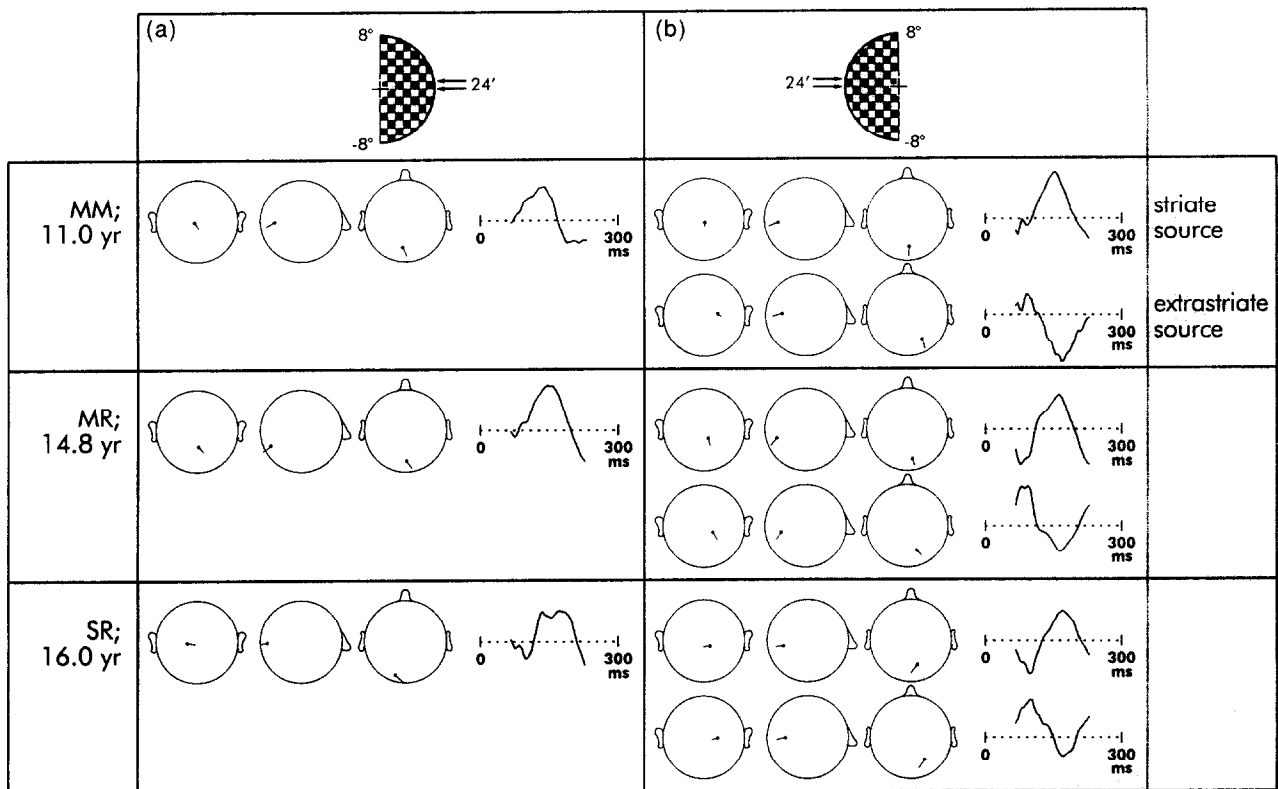
FIGURE 3. In this figure the parameters of the dipoles are depicted for three of the subjects studied, ranging from 11 to 16 years of age. The dipoles were activated by a 8 deg checkerboard with elements of 24′ for right and left half-field stimulation. The responses evoked by right half-field stimulation could be explained by a single source (a). For left half-field stimulation two dipoles could be localized (b) originating in the striate and extrastriate cortex. For further information on the presentation of the results see the legend of Fig. 2.

The residual error of the dipole fit amounts to 1.0% of the total power of the response set, thus indicating that the actual residual obtained can be explained by noise. One of these dipoles is located near the midline of the head [Fig. 2(b)] and the strength profile of this source corresponds closely to the striate component found for stimulation of the right half of the visual field. The second dipole is located at the contralateral side of the head and away from the inion. This indicates an origin in one of the extrastriate areas of the visual cortex. The component corresponding to this dipole has a biphasic wave form with a positive deflection at 105 msec. This component dominates the early positive peak of the pattern onset EP.

The same picture emerges for three other subjects studied (Fig. 3). The significant variance of the responses generated by right half-field stimulation could always be accounted for by the activity of a single source, whereas

TABLE 1. The parameters of the sources underlying the responses generated by right and left half-field stimulation with elements of 24′ for four of the subjects studied. The characters S and E indicate, respectively, a striate and extrastriate source. The cartesian co-ordinates X, Y, and Z are given in cm and the polar coordinates θ and ϕ in deg. The last column gives the residual error of the dipole fit

Right half-field stimulation							
	S/E	X	Y	Z	θ	ϕ	R.err
MM	$S/$	7.41	−0.55	3.60	60.6	30.6	0.8%
MR	$S/$	9.74	0.33	2.19	54.8	32.6	2.1%
AK	$S/$	9.78	−1.27	3.38	56.6	47.2	2.5%
SR	$S/$	9.80	−2.48	4.50	68.1	70.2	2.3%

Left half-field stimulation							
	S/E	X	Y	Z	Θ	ϕ	R.err
MM	$S/$	7.58	0.29	3.32	45.2	−6.8	1.3%
	$/E$	6.76	4.57	2.99	48.4	−8.8	
MR	$S/$	9.36	1.09	3.81	92.7	1.6	1.8%
	$/E$	8.49	2.03	4.36	101.1	6.2	
AK	$S/$	8.90	0.49	4.52	36.5	20.8	1.0%
	$/E$	7.14	3.63	4.39	22.5	−24.8	
SR	$S/$	7.40	1.60	3.43	58.2	−68.1	1.6%
	$/E$	6.94	3.56	4.62	72.1	−67.7	

the responses evoked by left half-field stimulation needed two dipole sources. The striate sources generated by both right and left half-field stimulation are located near the midline of the head, about 2–5 cm above the inion (Table 1). Note that the variation in strength of the striate sources generated by left half-field stimulation corresponds closely to the time profile of the striate response generated by right half-field stimulation. The extrastriate sources activated by left half-field stimulation are located contralaterally with a distance of about 2–5 cm from the midline of the head for all the subjects studied, whereas the orientation of the sources is partly radial and partly tangential (see Table 1). Their response profiles are quite similar for the three subjects studied with a peak-latency for the positive deflection around 100 msec followed by a negative deflection at about 160 msec, as shown before (Maier, Dagnelie, Spekreijse & Van Dijk, 1987; Ossenblok & Spekreijse, 1991).

Hemispheric asymmetry

Thus we have shown that a single dipole is activated upon right half-field stimulation, whereas for left half-field stimulation two dipoles are needed to explain the significant variance of the responses. However, the hemispheric asymmetry is not always that clear. The results of the SVD show that for most of the children studied a second extrastriate source also may contribute to the responses evoked by right hemifield stimulation (Table 2). Note, however, that the power of the principal component corresponding to the right hemispheric extrastriate source (%PC2) exceeds these values of the corresponding left hemispheric source. For

TABLE 2. The results of the SVD are listed for both the right (R) and left (L) hemifield for 13 of the children studied. The significant variance of the response sets (%SP) and the results of the SVD, obtained within the time window of analysis, are given as percentages of the total signal plus noise power. The power of the first and second principal component are denoted, respectively, as %PC1 and %PC2

AGE	FIELD	%SP	%PC1	%PC2
9.6	R	96.6	94.7	3.1
	L	90.8	80.3	16.4
10.6	R	96.6	89.9	7.2
	L	93.7	67.7	25.7
11.0	R	90.0	87.3	7.7
	L	92.7	69.7	27.1
11.1	R	90.5	65.6	26.3
	L	91.5	55.3	40.1
11.2	R	93.7	90.6	4.3
	L	97.2	82.7	13.7
11.8	R	84.8	82.9	13.6
	L	88.9	66.1	26.0
12.6	R	94.3	82.6	12.1
	L	88.3	72.8	24.6
12.7	R	94.5	80.1	13.5
	L	93.1	76.2	16.6
12.8	R	96.2	71.2	27.4
	L	96.5	65.7	31.3
13.5	R	98.1	64.4	34.2
	L	92.5	52.7	40.2
14.8	R	95.6	92.2	4.8
	L	94.7	80.5	16.3
15.8	R	95.1	93.5	3.9
	L	96.4	82.0	14.4
16.0	R	94.2	91.9	4.6
	L	92.4	76.7	17.4

instance, for the subject of 11.1 years old (KL), the results of the SVD show that two dipoles are needed to account for the significant variance of the responses
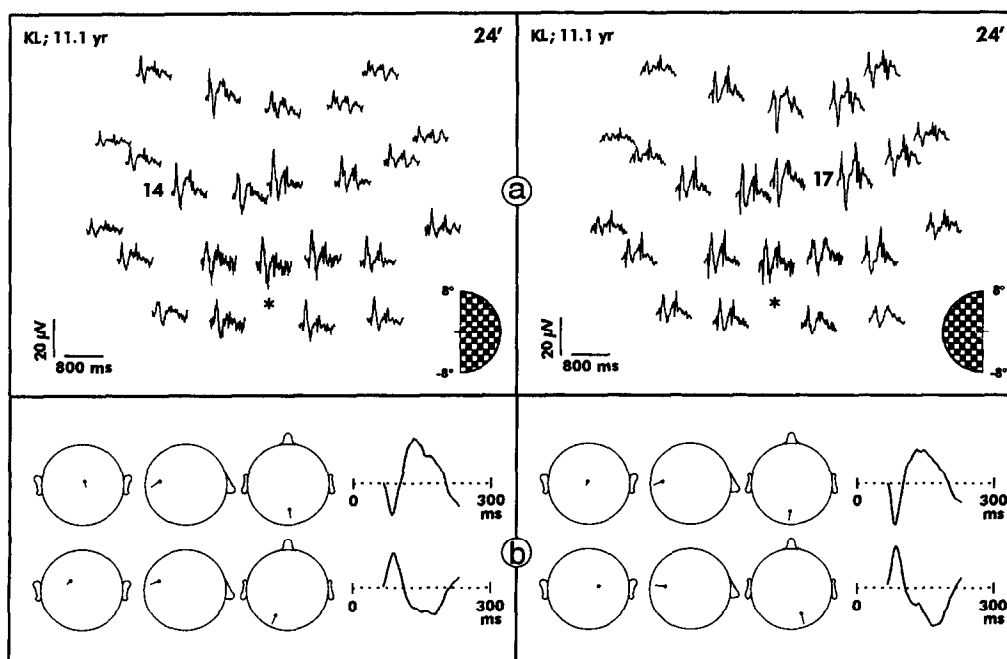

FIGURE 4. The results obtained for subject KL are presented. Stimulation and the presentation of results is the same as described in the legends of Figs 1 and 2. The response evoked by right half-field stimulation and recorded at the electrode site 14 and the response evoked by left half-field stimulation and recorded at electrode site 17 are marked with the respective numbers. Note that the mean strength of the extrastriate component generated by left half-field stimulation exceeds that of the extrastriate component generated by right half-field stimulation.
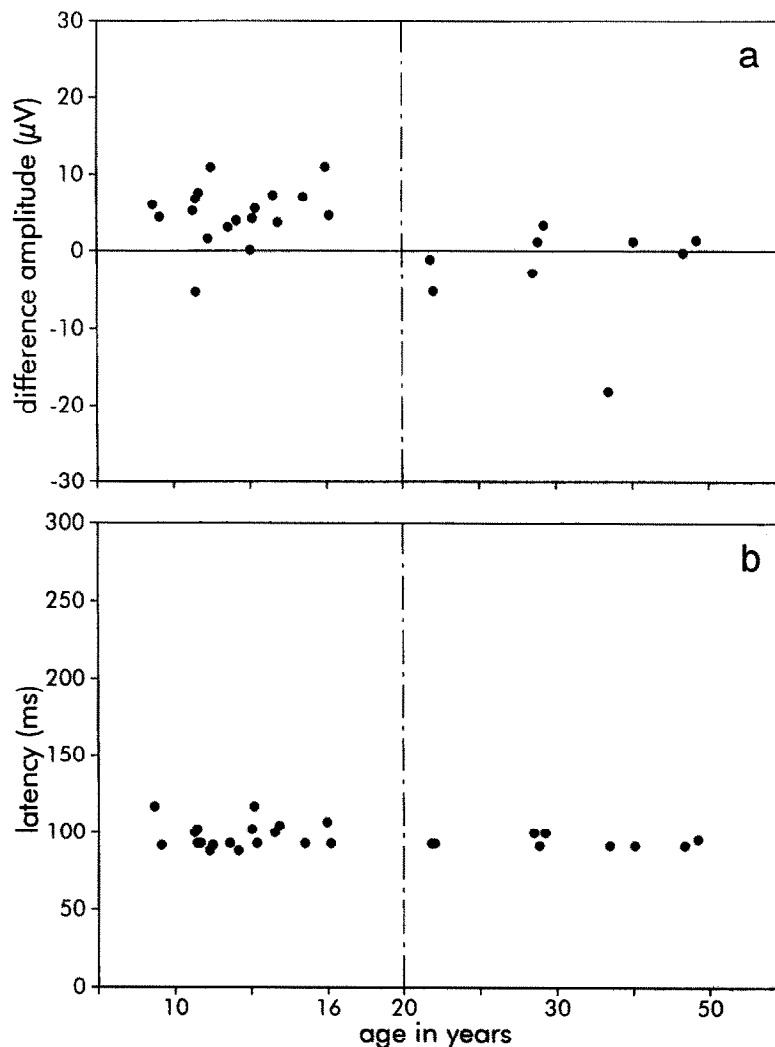
FIGURE 5. (a) The difference amplitude is depicted for 18 subjects younger than 20 years of age and for 9 adult-subjects (>20 years) vs a logarithmic age scale. The vertical striped-dotted line separates the data points of both age groups. The difference potential was obtained by subtracting the left hemispheric response, recorded at electrode derivation 14, from the right hemispheric response recorded at electrode derivation 17 [see Fig. 4(a)]. Subsequently the amplitude of the difference potential was obtained at the peak-latencies depicted in the bottom half of the figure. (b) The peak-latencies depicted vs the logarithmic age scale. These peak-latencies were measured at the incidence of the maximal amplitude of the first positive peak of the checkerboard onset EP.

evoked by either half-field [Fig. 4(a)]. One of the dipoles has a striate origin, whereas a second dipole is located at the contralateral hemisphere [Fig. 4(b)]. Like for the other subjects studied the location and strength profile of the striate sources are quite alike for either half-field. The dipoles located contralaterally represent extrastriate sources. Note that in accordance with the results of the SVD the mean strength of the extrastriate right hemispheric source exceeds that of the left one.

Since the activity of the extrastriate source dominates the early positive peak of the pattern onset EP the hemispheric asymmetry can also be obtained by subtracting the left hemispheric response recorded at electrode 14 from the right hemispheric response recorded at electrode 17, since at these electrode sites the early positive peak of the responses is maximal [see Fig. 4(a)]. Figure 5(a) shows that the peak-amplitude of the difference potential is positive for 17 of the 18 children studied, whereas for adults (>20 years) the sign of the difference amplitude alternates around zero. A positive

difference amplitude means that the right hemispheric response exceeds the left hemispheric response, while the difference amplitude in μVs is an indication for the strength differences of the extrastriate sources. The difference amplitudes of the group of children studied and of the adult group differ significantly from each other (Mann–Whitney test, $p < 0.001$), while the mean value of the difference amplitudes of children differs significantly from zero ($p = 0.001$). For children the mean value of the peak-latencies amounts to 98.1 ± 2 msec, whereas the peak-latency of extrastriate activity found in adults amounts to a mean value of 94.2 ± 1.1 msec [Fig. 5(b)]. So they do not differ significantly.

DISCUSSION

The equivalent dipoles

The striate sources activated by left and right half-field stimulation are located both near the midline of the head, above the inion (see Figs 2–4) and the time profiles
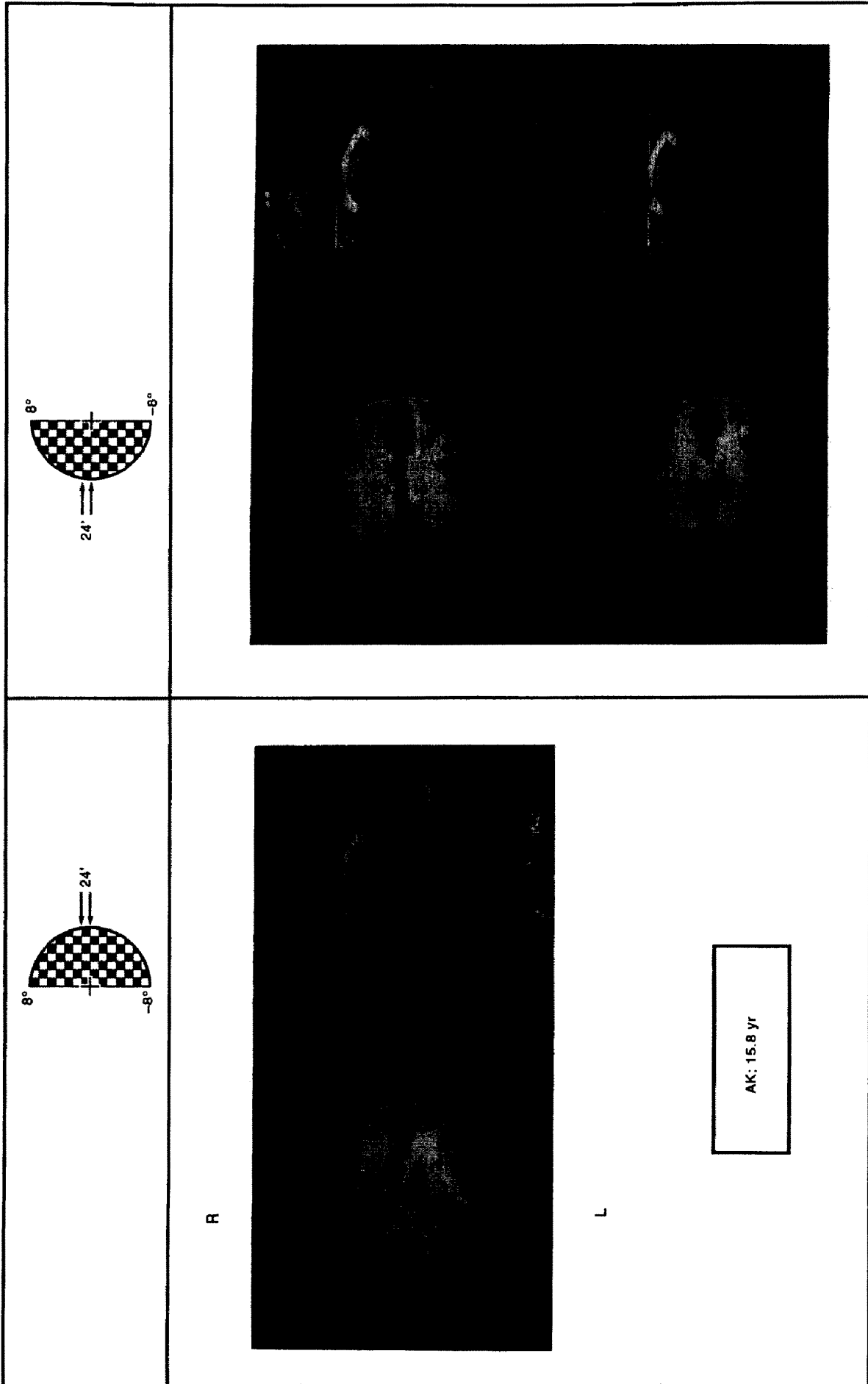
FIGURE 6. The MRI-scans of one of the subjects studied (AK) were reconstructed such that a three-dimensional picture emerges of the head, with markers placed at the auditory meati. Since in this reconstruction also the inion can be seen the best fitting sphere could be drawn with respect to the inion-ear system. The upper part of the horizontal section shows the right (R) hemisphere, the bottom part the left (L) hemisphere. The positions of the sources, indicated by white circles, are given with respect to this best fitting sphere for right (a) and left (b) half-field stimulation. In the horizontal section also the orientation, indicated by the white line, is depicted. In the vertical section of the MRI-scan the position of the dipole and the intersecting line in the horizontal plane is shown. Note that the best fitting sphere, shown in the horizontal section, fits the back of the head quite well.

of the corresponding components look very much alike. The variation in strength of the extrastriate sources is reflected in a positive–negative wave which dominates the early positive peak of the pattern onset EP. The waveforms of the extrastriate components of the different subjects studied look very much alike. Thus, waveform changes as a function of age due to changes at the neuronal level, as reported for the striate component (Ossenblok et al., 1992), are not apparent for the extrastriate component. Note that the strength profile of the extrastriate source and its contralateral origin is identical to the CI component of the adult response (Maier et al., 1987), which has an origin in area 18 of the visual cortex (Ossenblok & Spekreijse, 1991). Therefore the extrastriate source found in the child checkerboard onset EP has probably also an origin in area 18.

Figure 3 shows, however, that the parameters of the dipoles vary amongst the subjects studied. This may be due to source localization errors (Ary et al., 1981; Stok, 1987; Van Dijk & Spekreijse, 1990) although a large part of the variability could be due to anatomical variation of the visual cortex (Brindley, 1972; Stensaas, Eddington & Dobelle, 1974; Steinmetz, Fürst & Meyer, 1989). For one of the subjects studied (AK) the positions of the sources are depicted with respect to the anatomical structures of the visual cortex, as shown in the MRI-scans of Fig. 6. Note first that all three sources lay within the grey matter of the cortex, representing brain tissue. The horizontal section of the MRI-scans shows that the striate dipoles are located about 1 cm anteriorly and approximately mirror symmetric with respect to the medial plane for right and left half-field stimulation, although the left hemispheric source is more eccentric. Thus the position of these sources is in accordance with the geometry of the primary visual cortex (Stensaas et al., 1974). The position of the striate sources in the vertical direction also falls well within the anatomic variation of the striate cortex, since this part of the cortex is located near the occiput, 3–4 cm above the inion, with an absolute variation in reference to the inion of 4 cm (Steinmetz et al., 1989). The distance from the medial plane of the source activated by left half-field stimulation, which is indicated as an extrastriate source (see Fig. 1), is about 4 cm as in adults (Ossenblok & Spekreijse, 1991). The MRI images show, furthermore, that none of the sources are hidden within one of the sulci of the visual cortex, thus accounting for the predominant radial orientation of the dipoles. These results, therefore, provide further evidence (1) for the predominant radial orientation of the striate sources underlying the child checkerboard onset EP (see also Ossenblok et al., 1992) and (2) for an area 18 origin of the extrastriate sources underlying the child checkerboard onset EP, since the sources originating in area 19 of the adult visual cortex are orientated tangentially (Ossenblok & Spekreijse, 1991).

Maturation of extrastriate activity

Striate activity dominates the checkerboard onset EP of the youngest children (Ossenblok et al., 1992),

whereas extrastriate activity starts to contribute later in life. While the maturation of striate activity is reflected in the growth of the negative peak (CII) of the pattern onset EP, extrastriate activity dominates the early positive peak at about 100 msec. Thus not the ingrowth of the negative peak (CII) is responsible for the appearance of this early positive peak, as was suggested by Spekreijse (1983) and Apkarian et al. (1984), but the contribution of area 18 activity to the pattern onset EP. Note, furthermore, that area 19 activity recorded in adults (Ossenblok & Spekreijse, 1991) is absent in the child checkerboard onset EP. The regional development of activity underlying the child checkerboard onset EP is in accordance with the regional development of myelination patterns as shown by Conel (1939–1963), Yakovlev and Lecours (1967) and Holland, Haas, Norman, Zawadzki and Newton (1986). The primary visual cortex is the first to become myelinated at the age of about 7 years, therefore, probably, upon visual stimulation area 17 activity is the first to appear in the pattern onset EP (Ossenblok et al., 1992). The myelination of the secondary visual areas can continue to late puberty (area 18) or even beyond the second decade of life (area 19) (Conel, 1939–1963; Yakovlev & Lecours, 1967). Progress in myelination involves both the contribution of regional activity to the VEP and a decrease in peak-latency (McDonald, 1977; Halliday, McDonald & Mushin, 1977). Note, however, that the peak-latencies of the extrastriate components found in children do not change significantly as a function of age, although the variability is much larger than for the adult subjects [see Fig. 5(b)].

Thus the activity generated in area 18 of the visual cortex still develops at the age of 16 years while area 19 activity does not yet become apparent in the surface potential. According to the delayed development of area 18 activity in the child checkerboard onset EP these subjects may show impaired perception of spatial relations [see e.g. recent studies of Von der Heydt and Peterhans (1989) and Peterhans and Von der Heydt (1989)], although children at the age of 16 years and younger show good visual performance. Note, however, that even the acuity of these children has not reached adult levels yet (De Vries-Khoe & Spekreijse, 1982), thus indicating that visual performance may still develop. Perception experiments in relation with electrophysiological results may provide a clue to answer the question to what visual deficits the absence of extrastriate activity in the pattern onset EP may lead.

Hemispheric asymmetry

We have shown that extrastriate activity underlying the child checkerboard onset EP shows hemispheric asymmetry. This asymmetry varies amongst subjects, probably because of the large variation in the state of development between the subjects in the age group studied, although also the dominance of one of the hemispheres, as described by Stensaas et al. (1974), may affect the variance of the hemispheric asymmetry values. For some of the subjects a single dipole accounts for the

significant variance of the responses evoked by right half-field stimulation, whereas for other, even younger, subjects two dipoles are needed to describe the significant variance of the responses evoked by either right or left half-field stimulation (see Figs 2–4). However, for many of the children studied something in between occurs: for these children two dipoles are needed to describe the significant variance of the left hemifield responses, while a second although weak extrastriate source may also contribute to the right hemifield responses (see Table 2). Note, furthermore, that the results of the SVD provide further evidence for extrastriate hemispheric asymmetry.

A systematic comparison of the strength of the extrastriate sources activated by right and left half-field stimulation is not always possible, because of the constraints placed on the solution of the dipole source localization problem. Since, however, the early positive peak of the pattern onset EP is dominated by extrastriate activity the difference amplitude of this peak may provide an indication for the hemispheric asymmetry of this activity. It was shown that the mean value of the difference amplitude recorded in children from 9 to 16 years is significantly larger than zero, thus reflecting extrastriate hemispheric asymmetry. This hemispheric asymmetry is in accordance with histological studies of Conel (1939–1963) who showed that the axons of the pyramidal neurons in the extrastriate areas of the right hemisphere myelinate faster than in the left hemisphere. Since this hemispheric asymmetry can be estimated easily by subtracting the maximal pattern onset EPs generated by, respectively, right and left half-field stimulation, it may provide a relative estimate of the maturation of the extrastriate checkerboard onset EP. For adults (>20 years) the difference amplitude does not differ significantly from zero [see Fig. 5(a)]. Moreover, the alteration of the sign of the strength difference around zero for the adult subjects is in accordance with the arbitrarily distributed left or right hemispheric dominance as shown by Stensaas et al. (1974). Thus the hemispheric asymmetry reflected in the pattern onset EP seems to disappear for subjects older than 20 years, which should imply that from 20 years on the myolegenetic cycle is complete for both hemispheres, at least up till area 18.

Apkarian, Reits and Spekreijse (1983) used the difference amplitude of CI in diagnosing albinism. However, they never reported systematic CI magnitude differences between both hemispheres. Note, however, that the asymmetry between the left and right eye topography, which is specific for albinos, remains apparent even when CI shows hemispheric amplitude differences. Thus the results of the study of Apkarian et al. (1983) are not contradictory to the present ones. Moreover, Apkarian and Spekreijse (1986) showed that the detection rate of diagnosing albinism decreases sharply for children younger than 6 years of age. This is in accordance with our results, since the early positive peak of the pattern onset EP of young children is still immature

(De Vries-Khoe & Spekreijse, 1982), while striate activity, which dominates the responses of children of this age, is distributed symmetrically with respect to the midline of the head (Ossenblok et al., 1992).

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