



The development of hemispheric asymmetry in human motion VEPs

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Abstract

In six healthy adults we examined the sources underlying P1 and N2 of the motion VEP. For this purpose we acquired, in addition to the VEP, MRI images and patterns of regional cerebral blood flow with SPECT for three of the subjects. With the same motion stimulus we also examined the spatial distribution of N2 in children. In both adults and children left and right half-field responses were compared. It was found that N2 is generated by extrastriate activity and that motion stimuli are not equivalently processed in the two cerebral hemispheres. In adults, N2 dominates in one hemisphere irrespective of the visual half-field used for stimulation whereas children show an ipsilateral maximum for N2 upon half-field presentation. © 1999 Published by Elsevier Science Ltd. All rights reserved.

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1. Introduction

Motion onset evokes well defined VEP responses in humans. Major components are an early positivity around 130 ms (P1) and a negativity around 180 ms (N2) (Göpfert, Müller & Simon, 1990; Kubova, Kuba, Hubacek & Vit, 1990; Kuba & Kubova, 1992; Kubova & Kuba, 1992; Schlykova, Van Dijk & Ehrenstein, 1993; Bach & Ullrich, 1994). It has been suggested that N2 reflects the processing of visual motion and that P1 can be attributed to local pattern processing (Kuba & Kubova, 1992; Kubova, Kuba, Spekreijse & Blake-more, 1995; Bach & Ullrich, 1997).

Left and right hemispheres contribute asymmetrically to the motion onset VEP. Kubova et al. (1990) studied motion VEPs upon full-field stimulation in a group of

80 subjects and found that in 60% of subjects the maximum amplitude of N2 was found in the lead from the right hemisphere. A left-hemispheric predominance occurred less frequently (i.e. in 20% of subjects). The predominance of one hemisphere in the amplitudes measured with VEPs upon motion stimulation has also been reported in the visual half-field studies by Manning, Finlay and Fenelon (1988), and Patzwahl, Zanker and Altenmüller (1994). All these studies used however only a limited number of electrodes and therefore the precise location of the sources underlying N2 could not be determined.

The present study aims to determine the origin of the dipole sources underlying the motion VEP to left and right half-field stimulation. The scalp distributions of the VEP in adults in the two half-field conditions will be compared with those of children because it is known that motion sensitivity, measured psychophysically, develops asymmetrically in the left and right visual half-

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fields during childhood (Hollants-Gilhuijs, Ruijter & Spekreijse, 1998).

2. Methods

2.1. Subjects

Six adults ranging from 28 to 55 years of age (two females and four males), and 18 children ranging from 9 to 16 years of age (six girls and 12 boys; mean age: 12.7 years) participated in the experiments. All subjects were healthy volunteers with no history of neurologic disorders. Visual acuity, as assessed with the Landolt-C acuity chart, was normal or corrected-to-normal (between 4/5 and 1/1).

2.2. Stimulus

The stimulus consisted of a motion phase of 240 ms and a stationary phase of 1 s. A short duration of motion and a long interstimulus interval was chosen since such stimuli decrease motion adaptation effects and yield therefore the largest motion-specific evoked potentials (Kuba & Kubova, 1992; Schlykova et al., 1993; Bach & Ullrich, 1994). The stimulus was generated by means of a black-and-white monitor (Mitsubishi) driven by a digital stimulus generator (Venus 1020, Neuroscientific, USA) with a resolution of 256×256 pixels and a frame rate of 120 Hz. During the motion phase, seven dot patterns were successively presented, each for a duration of 34 ms. Each dot pattern contained randomly distributed dots of 4 arcmin. From pattern to pattern the dots were coherently displaced in an oblique direction (45° or 135°), resulting in a total displacement of 24 arcmin. Motion direction varied between motion intervals. The speed of movement was $1.6^\circ/\text{s}$ for 240 ms periods. The dots within the boundaries of the Landolt-C figures ($1.8 \times 1.8^\circ$) were displaced in a direction opposite to that of the dots of the surround (Fig. 1). This stimulus is the same as we used in another study on the detection of motion-defined forms (Hollants-Gilhuijs et al., 1998). To avoid that such detection could be done on the basis of blurring of the dots due to movement differences in the after image the dots inside and outside the figures moved in the same way but in opposite direction. The dots had a contrast of 95%, and a probability of 50% for black or white. At the viewing distance of 110 cm the stimulus field corresponded to a visual angle of $8.3 \times 8.3^\circ$.

In the stationary phase the last presented random dot pattern remained at a fixed position on the screen. Mean luminance of the screen was $40 \text{ cd}/\text{m}^2$, and there was no luminance change between the motion and the stationary phase.

2.3. Recording

In the experiments with adults, which shall be referred to as Experiment 1, VEPs were recorded at 31 scalp electrodes. The electrodes were placed on the occipital, temporal, and parietal cortices, and were fixed in a grid with an inter-electrode distance of about 3 cm. The lowest row of electrodes was positioned 1.5 cm below the inion.

In the experiments with children, Experiment 2, motion VEPs were recorded from five scalp electrodes placed on a horizontal line 4.5 cm above the inion with a 3 cm spacing between electrodes. These sites show the largest amplitudes in adults (Fig. 2, Experiment 1). Channel 3 was on the midline of the head, Channels 1–2 on the left hemisphere, and Channels 4–5 on the right hemisphere (Fig. 6). In both age groups the ground electrode was placed near the vertex, and the reference electrode at mid-frontal.

The subjects were seated comfortably and viewed the visual field binocularly. The fixation point was a light emitting diode (LED) which was placed on the left or right edge of the stimulus field so that only one visual half field was stimulated at the time. During recording the room was dark. The subjects were instructed to

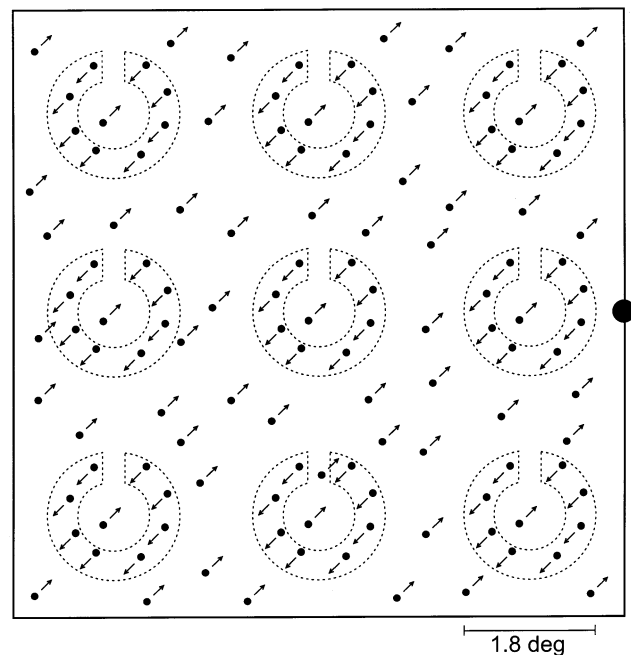


Fig. 1. Illustration of the stimulus appearing in the left half-field. The large dot on the right edge of the field indicates the fixation spot (a LED) and the dotted lines (absent in the stimulus) indicate the pre-determined borders of the 'C's'. Pixels within the border of the 'C' were coherently displaced in a direction opposite to that of the pixels of the background, along oblique radials (arrows). For clarity, the pixel size (i.e. the small dots) and the pixel displacement (i.e. the arrows) are depicted 1.5 times larger than in reality. Pixel probability was in reality 50% for black or white. For right half-field stimulation the fixation spot was placed on the left edge of the stimulus field.

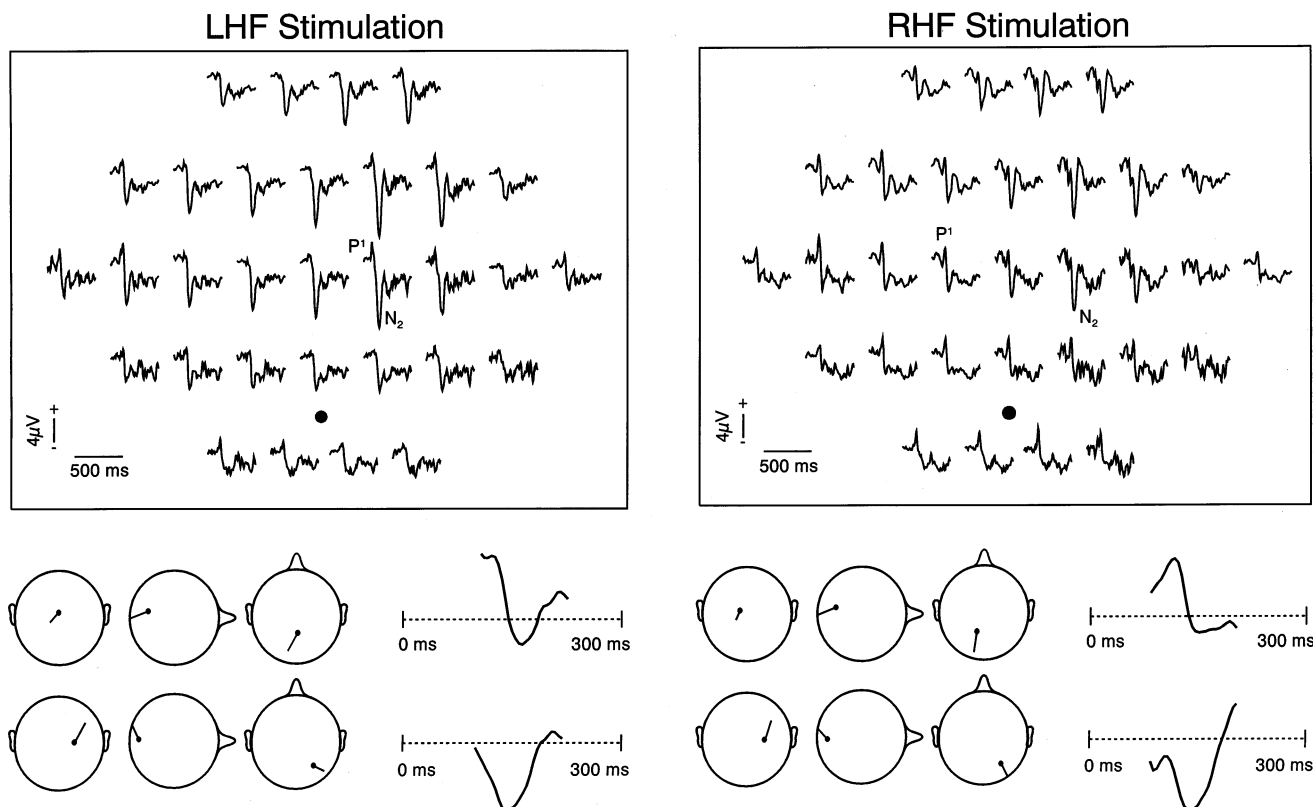


Fig. 2. The upper part of the figure shows the evoked potential waveforms in the first 500 ms post motion onset for respectively the left half field (LHF) and right half field (RHF) stimulation. The waveform is characterised by P1 and N2. The responses are plotted in a 2-dimensional projection of a spherical surface; the interelectrode distance was 3 cm. The dot indicates the position of the inion, which is located at the midline of the head, approximately 1.5 cm above the bottom row of electrodes. In both stimulus conditions the peak amplitude of N2 is maximal on the right hemisphere. In the lower part of the figure the positions and orientations of the dipole sources responsible for the upper part of the figure are plotted in schematic views of the head 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 through the back of the head. The length and direction of the line in each plane shows the strength and orientation of the dipole. The strength profile of each dipole covered a time window that started at 116 ms after motion onset and ended at 232 ms. For both the LHF and RHF stimulus two dipole sources were localised, one with a striate (P1) and the other with an extrastriate (N2) origin. Note that the extrastriate dipole has an origin in the right hemisphere irrespective whether left or right half field is stimulated. See also Fig. 5, label 1.

fixate at the LED and not to follow the motion with their eyes.

Averaging of the EEG signals was triggered at the transition between the stationary and moving phase of the stimulus. 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 thus increasing the response latencies by about 7 ms. The sweeps were sampled at 215 Hz and online averaged with a CED 1401 system.

For each half-field stimulation 80–120 averages were obtained in four to six recording sessions in each subject. To obtain an estimate of the noise level, every second sweep was subtracted from the previous one which yields the plus–minus average. The significant power was calculated as the difference between the variance of the average response and the variance of the plus–minus average divided by the sum of the two.

2.4. Experiment 1: source localisation in adults on the basis of VEP, MRI, and SPECT

We localized the sources underlying the prominent peaks in the motion VEP (i.e. P1 and N2) in the time window from 116 to 232 ms post motion onset. For this purpose we used the spatio-temporal dipole model of De Munck (1989) which solves the problem of temporal overlapping source activity by assuming that the generators of the motion VEP can be modelled by stationary dipole sources with a fixed position and orientation in the head and with time varying strength. The minimum number of dipoles that are needed to account for the significant variances of the motion VEP within the chosen time window, is estimated from a singular value decomposition (SVD) of the data. The number of activated dipoles is chosen such that the lower limit for the residual, which depends solely on the number of significant principal components, reaches the noise level of

the data. The source localization procedure is described in detail in De Munck (1989, 1990). The dipoles were localized within a spherical three-shell model of the head. This model describes the brain surrounded by the skull and scalp (Ary, Klein & Fender, 1981).

To identify the precise anatomical location of the dipoles, the positions of the dipoles were projected onto MRI images of the subject. This was done for three subjects. For this purpose the heads were digitized with the Isotrack II tracking system (Polhemus Incorporated, Vermont, USA). The first part of the digitized points coincided with the electrode positions and the rest of the points were regularly distributed over the part of the head having bone right below it. In total, the digitized head consisted of about 220 points. During the digitization the subjects had their head fixated using a bite board. A sphere was fitted through the digitized points and the electrode positions, and the dipoles were first computed with respect to this sphere. Chamfer matching (Van Herk & Kooy, 1994) was used to register the MRI and digitized points. Since the dipoles are determined with respect to the digitized points, the same transformation determines the desired projection of the dipoles onto the MRI image.

In three subjects, SPECT recordings (Single Photon Emission Computed Tomography, Strichman Medical Equipment, Inc., Medfield, MA, USA) were performed in addition to the VEP measurements and MRI registration. The SPECT images provide information about the location of activated brain regions during visual motion stimulation, and were used in the mathematical inverse calculation procedure (i.e. dipole source localization). The radioactive probe used in the SPECT experiments was ^{99m}Tc -HMPAO, which is known to distribute in the brain as a function of regional cerebral blood flow (Woods, Hegeman, Zubal, Krystal, Koster, Smith et al., 1991). Whole brain SPECT images, starting from the orbito-meatal line, were obtained twice for each subject. We applied a split-dose technique using repeated injections of ^{99m}Tc -HMPAO (Ebmeijer, Dougall, Austin, Murray, Curran, O'Carroll et al., 1991). The first series of SPECT images was recorded in the baseline condition while the subject watched the stationary random dot pattern. The second series was obtained in the activated condition with the same subject watching the motion stimulus. The two series of SPECT images were acquired immediately after one another. The subject remained in the scanner during the whole procedure with the head fixated with respect to the SPECT apparatus using a bite board. Thus, negligible motion of the head occurred between the rest and the activated state allowing a direct pixel-to-pixel subtraction of the SPECT images in the two conditions. The difference image yields information about the brain regions that are involved in the processing of the motion stimulus.

2.5. Experiment 2: motion VEPs in children

The lateralization of N2 was studied in children. A comparison was made for the amplitude distribution of N2 across the scalp for left half-field and right half-field stimulation. In order to compare data from different subjects, the response of each subject was normalized to the maximal amplitude across channels (Fig. 6). Amplitude measurement was done to the plus–minus average. A repeated measure analysis of variance was used to test for differences in amplitude and latency values across channels and between left and right half-field stimulation.

3. Results

3.1. Presentation of the results of Experiment 1 (Figs. 2–5)

The position and orientation of the dipole sources are given with respect to the best fitting sphere through the head (Figs. 2 and 4). The best fitting sphere through the head is calculated from the position of the electrodes with respect to landmarks on the head. Therefore, the position of the best fitting sphere through the head may vary amongst subjects. In order to compare

Fig. 3. SPECT image, recorded +4 cm above and parallel to the orbito-meatal line, showing peak metabolic activity in the left striate and right tempo-parietal regions of the visual cortex (yellow areas indicated by arrows). The image is obtained by pixel-to-pixel subtraction of the SPECT image acquired during the baseline condition from the SPECT image obtained during the visual activation condition (onset of motion in the right visual half-field).

LHF Stimulation

RHF Stimulation

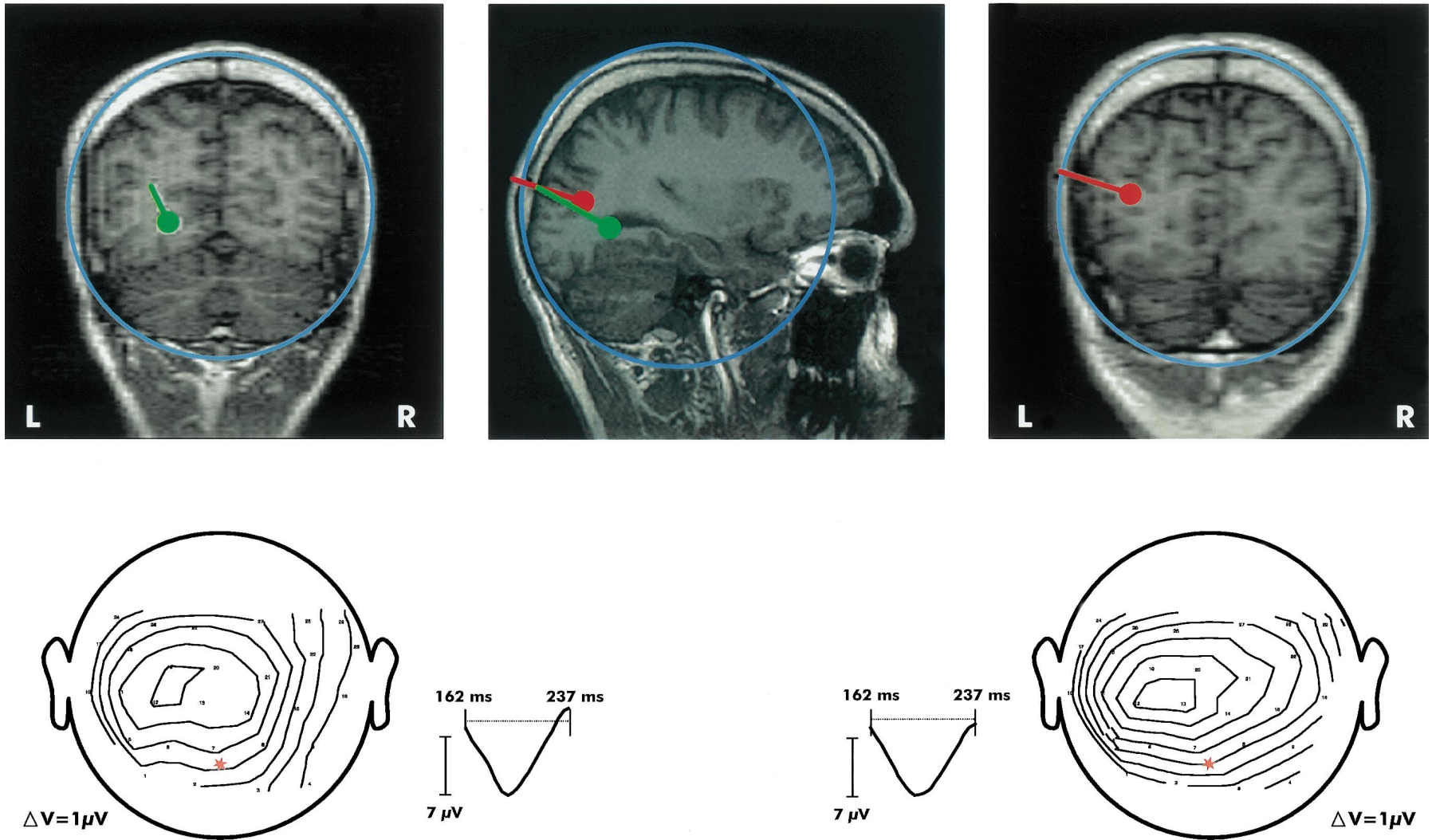


Fig. 4. The upper part of the figure shows the extrastriate source activated by motion onset stimulation of either the left half-field (LHF) or right half-field (RHF). The position of the dipole is calculated with respect to the best fitting sphere (shown in blue) and is projected onto a MRI image of the same subject. The dipole upon LHF stimulation is shown in green (coronal MRI image on the left), and the dipole upon RHF stimulation is shown in red (coronal MRI image on the right). In both conditions the dipole is located in the occipital-temporal-parietal area of the left hemisphere, 2–3 cm from the midline of the head, and 4–5 cm above the inion (see also Fig. 5, label 2). The lower part of the figure shows the equipotential maps derived for LHF or RHF stimulation. The maps were taken at 194 ms after motion onset (where strength of the extrastriate dipole was maximal). The numbers in the equipotential maps indicate the positions of the electrodes, and the asterix (red) indicates the position of the inion. The equipotential maps (in steps of $1 \mu V$) show that activity is maximal on the left hemisphere. The VEP recorded on the left hemisphere from the electrode with maximal amplitude is shown as well in the time window from 162 to 237 ms post motion onset.

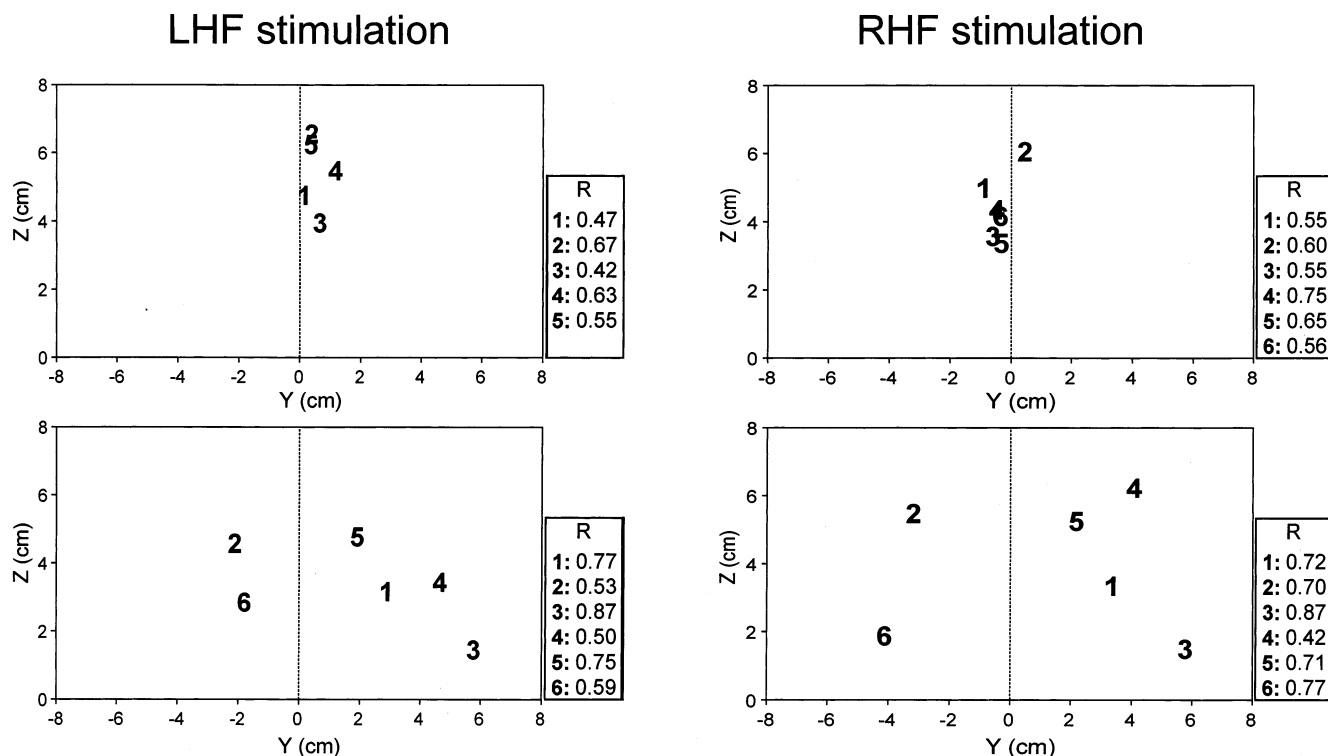


Fig. 5. The position parameters of the dipoles generated by left half-field (LHF) or right half-field (RHF) stimulation. The positions of the sources of the six subjects are numbered 1–6. The *striate sources* are shown in the upper part of the figure, and the *extrastriate sources* in the lower part. The cartesian co-ordinates Y and Z are given in cm and indicate horizontal and vertical distances from theinion, respectively. The spherical co-ordinate R , which can vary between 0 (mid of the best fitting sphere) and 1, represents the eccentricity of the dipole source. For Subjects 1, 3, 4 and 5, the extrastriate source originates in the right hemisphere regardless whether left or right half-field stimulation was used. For Subjects 2 and 6, extrastriate activity was lateralised in the left hemisphere. The striate sources were always in the contralateral hemisphere except for RHF stimulation of Subject 2.

the position parameters of dipole sources between subjects, position parameters of dipoles are given with respect to the inion-ear co-ordinate system (Fig. 5) in which the origin is located half-way between both ears (De Munck, 1989, 1990). The positive x -axis is running backwards through the inion, the positive y -axis runs through the right external auditory mati, and the positive z -axis runs upwards.

3.2. Results of Experiment 1

The waveform of the motion VEP in adults is characterized by the dominance of a positive-negative (P1-N2) deflection with peak latencies between 130 and 150 ms, and 160 and 200 ms, respectively. The waveform of the motion VEP was identical to those obtained in other studies (Göpfert et al., 1990; Kubova et al., 1990; Kuba & Kubova, 1992; Kubova & Kuba, 1992; Schlykowa et al., 1993; Bach & Ullrich, 1994; Kubova et al., 1995).

The upper part of Fig. 2 shows the responses of Subject 1 at the 31 scalp electrodes for left half-field and right half-field stimulation. The significant power of the response was 96.1% upon left half-field stimulation, and 95.5% upon right half-field stimulation. The

figure shows that when the motion stimulus is presented in the left visual half-field N2 gives the largest amplitudes for extrastriate channels on the right hemisphere. When the same visual stimulus is presented in the right visual half-field the same right-hemispheric extrastriate channels show the largest peak amplitudes. Since the scalp distribution of N2 differs from that of P1, for left or right half-field stimulation, the cortical origin of P1 and N2 must be different. A SVD indeed showed that at least two sources are needed to explain the signal.

The source localization analysis revealed that P1 and N2 are generated by different dipole sources. The loci of peak activity during motion stimulation were obtained with the use of SPECT (Fig. 3). The loci were transformed into spherical co-ordinates and were used as starting values to solve the source localization problem. The position, orientation and the time varying amplitudes of the dipoles are shown in the lower part of Fig. 2, for both left half-field and right half-field stimulation. One of the dipoles, in both the left and right half-field stimulus condition, is located close to the midline of the head in the occipital cortex. The position of this dipole in the contralateral hemisphere indicates a striate origin, and its strength profile overlaps with P1.

The other dipole is located more laterally with respect to the position of the striate source. Its position suggests an extrastriate origin, and its strength profile overlaps with N2. Note that the extrastriate dipole evoked by either left half-field or right half-field stimulation originates in the subject's *right hemisphere* whereas the striate dipole originates in the hemisphere contralateral to the stimulated visual half field. The orientation of both the striate and extrastriate sources was partly tangential and partly radial. The residual error of the dipole fit was 1.9% for left half-field stimulation and 2.8% for right half-field stimulation.

Lateralization of extrastriate activity was consistent amongst the subjects studied. In two of the six subjects extrastriate activity was however lateralized to the *left hemisphere*. In these cases the extrastriate source was located in the occipital-temporal-parietal region of the left hemisphere regardless of the use of left or right half-field stimulation (Fig. 4).

The position of the striate and extrastriate dipole sources for the six subjects are shown in Fig. 5. Both left half-field and right half-field stimulation yielded motion VEPs with a significant power above 90% for each subject. The striate dipole sources (upper part of Fig. 5) are located near the midline of the head, in the contralateral hemisphere, 3–7 cm above the inion. The extrastriate sources (lower part of Fig. 5) have a location 2–6 cm from the midline of the head. The residual errors of the dipole fits were between 0.4 and 4.3% of the total power of the individual responses. Note that

in four subjects (labels 1, 3, 4, and 5) extrastriate activity originates in the right hemisphere regardless whether left or right half-field stimulation was used. In two subjects (labels 2 and 6) extrastriate activity was lateralized in the left hemisphere. One female and one male showed a left-hemispheric dominance, and the other female and three males showed a right-hemispheric dominance.

3.3. Results of Experiment 2

N2 was prominent in the motion VEP of children, and had a peak latency between 165 and 203 ms. Normalized amplitudes of N2 were averaged over subjects and are plotted in Fig. 6 as a function of electrode position. It is clear from the figure that the normalized amplitudes are maximal at the ipsilateral recording sites, for both the left and right half-field stimulus condition. In the left half-field stimulation condition the group's mean amplitude on Channel 2 was $-6.7 \mu\text{V}$ (S.D. = $3.9 \mu\text{V}$). In the right half-field stimulation condition the group's mean amplitude on Channel 4 was $-6.4 \mu\text{V}$ (S.D. = $3.2 \mu\text{V}$).

It appeared that upon left half-field stimulation mean amplitudes at Channels 1 and 2 on the left hemisphere were significantly larger ($P < 0.005$) than the mean at Channel 5 (right hemisphere). Right half-field stimulation, on the other hand, yielded mean amplitudes on Channels 4 and 5 on the right hemisphere that were significantly larger ($P < 0.005$) than the mean at Chan-

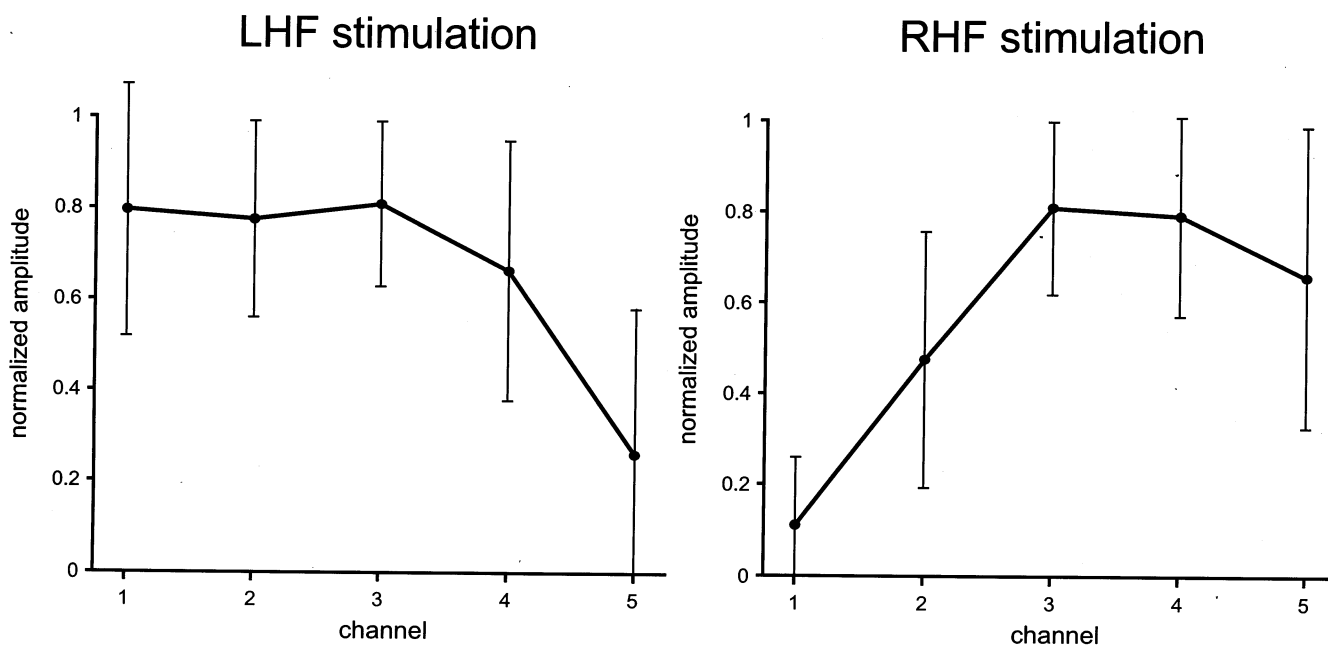


Fig. 6. Peak amplitudes of N2 for left half-field (LHF) and right half-field (RHF) stimulation, respectively. Amplitude measurement was done to the plus minus average. The amplitudes were normalised to the maximal amplitude and plotted as a function of electrode channel with Electrode 3 on the midline. Vertical bars indicate standard deviation. Maximal peak amplitude is found at the ipsilateral recording sites in either stimulus condition.

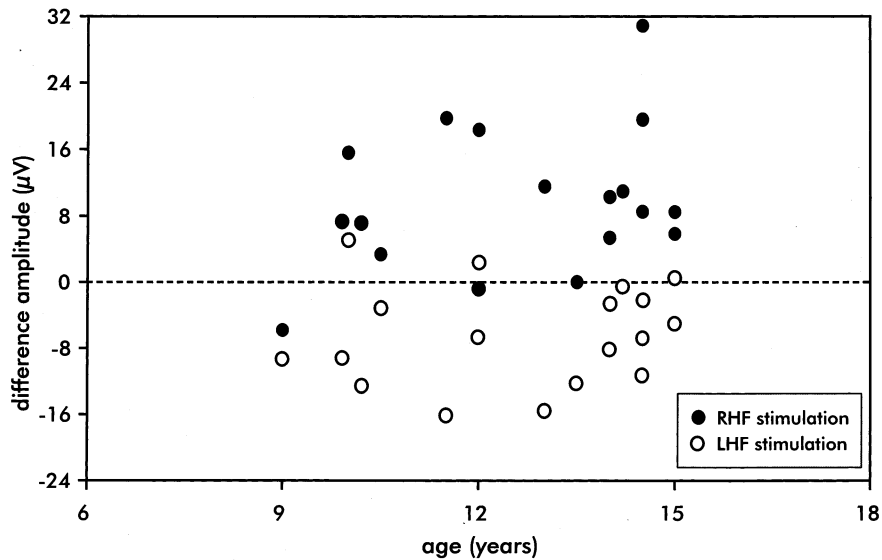


Fig. 7. Difference amplitude of N2 as a function of age in the child group. The difference amplitude was obtained for each child by subtracting the sum of peak amplitudes of N2 recorded on the right hemisphere (i.e. Channels 4 and 5) from the sum of peak amplitudes of N2 recorded on the left hemisphere (i.e. Channels 1 and 2).

nel 1 (left hemisphere). A comparison of left and right half-field responses revealed no differences in peak amplitudes of N2 between the two stimulus conditions, neither were there significant latency differences.

The child data is individually treated in Fig. 7. The peak amplitude of N2 recorded at the right hemisphere (i.e. the sum of the amplitudes recorded at Channels 4 and 5) is for each child subtracted from the peak amplitude of N2 recorded at the left hemisphere (i.e. the sum of the amplitudes recorded at Channels 1 and 2). Fig. 7 shows that for nearly all children this difference amplitude is positive for the right half-field stimulus condition, and negative for the left half-field condition. This means that in nearly all children in the right half-field stimulus condition the amplitude on the right hemisphere exceeds the amplitude on the left hemisphere, and that in the left half-field condition the amplitude on the left hemisphere exceeds the amplitude on the right hemisphere. Because the amplitude of N2 has a negative sign, the difference amplitude is positive in the right half-field stimulus condition and negative in the left-half field stimulus condition. The difference amplitude of N2 in girls was in the same range as that in boys, for both right half-field stimulation and left half-field stimulation.

4. Discussion

The present study was focused on the hemispheric projection of visual motion information in the left versus right visual half-fields. With dipole source analysis we have estimated the hemispheric origin of the

brain regions underlying the human motion VEP. We have shown that an extrastriate source is active. This extrastriate dipole is located in the occipital-temporal-parietal region (Fig. 4). In agreement with other source localization studies (Probst, Plendl, Paulus, Wist & Scherg, 1993; Anderson, Holliday, Singh & Harding, 1996) this extrastriate dipole is responsible for the N2 component of the motion VEP (Fig. 2). Schlykova et al. (1993) have shown that it is unlikely that N2 is caused by eye movement. We have furthermore confirmed that activity from the striate cortex constitutes P1 of the motion VEP (Maier, Dagnelie, Spekrijse & Van Dijk, 1987), and that this striate dipole originates in the hemisphere contralateral to the stimulated visual half-field, as in agreement with the classic notion of retinotopic organization within the striate cortex (Holmes, 1945); (Figs. 2 and 5).

The difference in retinotopic organization of the striate and extrastriate sources underlying the motion VEP (Figs. 2 and 5) supports the view of a functional segregation between P1 and N2 (Kuba & Kubova, 1992; Kubova et al., 1995), and may result from parallel inputs into the striate cortex and motion area MT-V5 (Barbur, Ruddock & Waterfield, 1980; Blythe, Kennard & Ruddock, 1987; Barbur, Watson, Frackowiak & Zeki, 1993; Ffytche, Guy & Zeki, 1995).

4.1. Left versus right-field motion VEPs in adults

In adults the hemispheric origin of extrastriate activity was independent of the visual half-field in which the motion stimulus was presented. In four adults (labels 1, 3, 4, and 5) the extrastriate dipole originated in the

right hemisphere regardless of whether left or right half-field stimulation was used (Fig. 5). In two other adults (labels 2 and 6) the *left hemisphere* dominated. There is some variability in the position parameters of the extrastriate dipoles evoked by left or right half-field stimulation in the same subject. This variability may be due to source localization errors that are caused by contamination of the data with noise (Lehnertz, Lütkenhöner, Hoke & Pantev, 1989). The variability in dipole parameters amongst subjects may be due to the properties of the volume conductor model (Ary et al., 1981; Peters & De Munck, 1990; Van Dijk & Spekreijse, 1990), and to the inter-subject variability in anatomy of visual areas (Brindley, 1972; Stensaas, Eddington & Dobbelle, 1974; Watson, Myers, Frackowiak, Hanjal, Woods, Mazziotta et al., 1993). A source localization may also be responsible for the right-hemispheric location in one subject of the striate dipole upon right half-field stimulation (Fig. 5, label 2). Based on the anatomy of the visual pathway (Holmes, 1945) the left striate cortex is the most realistic location for this source. The deviation from the left striate cortex is however only a few millimetres with respect to theinion nasion midline. MRI images have shown that this line may overlap one of the hemispheres (no MRI scans of Subject 2 were available).

For three subjects from our study of whom SPECT data were available we calculated from the SPECT images the percentage of increase in radioactivity in the extrastriate motion area. Homologous regions in the left hemisphere and right hemisphere were analysed. The values obtained upon right half-field stimulation are listed in Table 1. Table 1 shows that for two subjects (e.g. labels 1 and 3) the highest increase in radioactivity was observed in the motion area in the right hemisphere, and for label 6 in the motion area in the left hemisphere. This is in agreement with the location of the extrastriate dipole observed in these subjects (Fig. 5).

Brain imaging studies with positron emission tomography (PET) often show that visual stimulation with motion induces bilateral (i.e. in both hemispheres) foci

of activation in extrastriate area V5-MT (Zeki, Watson, Lueck, Friston, Kennard & Frackowiak, 1991; Watson et al., 1993; Cheng, Fujita, Kanno, Miura & Tanaka, 1995) instead of in the unilateral focus as we report for Subjects 3 and 6, and the bilateral asymmetric activation for Subject 1. The bilateral foci may however result from the averaging of the individual PET measurements of the subjects involved. Averaging may mask the hemispheric predominance in individual subjects. Therefore, the PET findings of bilateral extrastriate source activity are not necessarily contradictory to our reports of unilateral or asymmetric activity.

Tootell, Reppas, Kwong, Malach, Born, Brady et al. (1995) used functional Magnetic Resonance Imaging and studied activation of human MT in single subjects. In agreement with our results Tootell et al. (1995) showed for a single subject that motion area MT/V5 in the left hemisphere was activated upon either ipsilateral or contralateral half-field stimulation.

The reason is unclear why in some adults the motion VEP is lateralized to the left hemisphere, and in others to the right hemisphere. It is not related to handedness. Kubova et al. (1990) describe on the basis of a population study in 80 subjects that the right-side preference does not correlate with handedness. Andreassi and Juszcak (1982) found some gender differences in hemispheric activation by apparent motion stimuli in adults. In female subjects the right hemisphere showed larger amplitudes than the left hemisphere recordings for stimuli presented centrally, whereas males showed no hemispheric amplitude differences. Their results are not in agreement with our findings. We found a hemispheric lateralization in all subjects, and a left-hemispheric or right-hemispheric dominance was found to be present in males as well as in females.

The motion area in the dominant hemisphere receives upon motion stimulation input from both the ipsilateral (Tootell et al., 1995) and contralateral visual field (Van Essen, Newsome & Bixby, 1982; Tootell et al., 1995). Cells have been localized in the extrastriate motion area MT/V5 which respond to motion in the ipsilateral visual field. The receptive fields of these cells extend in humans more than 20° into the ipsilateral visual field (Tootell et al., 1995). The extrastriate motion area contains furthermore a complete representation of the contralateral visual hemi-field (Van Essen et al., 1982). Thus, the missing hemispheric lateralization switch in adults when the left visual half-field is stimulated instead of the right one is in agreement with the retinotopy of the cortical motion area in humans. In this respect retinotopy of MT/V5 is different from that of lower visual cortical areas. Activation of visual areas, area 17, 18, or 19, occurs strictly in the hemisphere contralateral to the hemi-field that is stimulated (Maier et al., 1987; Ossenblok & Spekreijse, 1991).

Table 1
Activation of extrastriate motion area^a

Subject	Motion area in l-hemi % increase in activity	Motion area in r-hemi % increase in activity
1	10.5	24.5
3	0.3	11.2
6	13.1	0.8

^a SPECT measurements obtained upon right half-field stimulation. The brain regions varied in size between 520 and 750 mm². Values denote the increase in radioactive counts during the stimulated condition with respect to the baseline condition (%), l-hemi and r-hemi indicate left-hemisphere and right-hemisphere, respectively.

It can be questioned whether our half-field stimulus is appropriate to study differences between left-hemispheric and right-hemispheric processing of visual motion information. Desimone and Gross (1979) describe that the temporal cortex of the macaque does not respect the vertical meridian. There is an overlap across the vertical meridian as large as 10–14° in the temporal cortex. If this animal model is extrapolated to the human subjects from the present study (Experiment 1) it will imply that with the stimulus we used, with the fixation spot on the edge of a stimulus field of 8°, areas MT should be activated in both hemispheres. As we show in Figs. 2–5 bilateral activation was not the case in our study. One hemisphere dominated the motion onset VEP. It thus seems that there is a discrepancy between the present data in humans (Experiment 1), and the animal data (Desimone & Gross, 1979). It could be possible that there is some weak MT activity in the other non-dominant hemisphere in the subjects from the present study, but source localization showed that the strength of this source does not contribute significantly to the VEP. Note, furthermore, that our results of asymmetric activation of the left and right hemispheres are in agreement with the hemispheric dominance reported in other motion VEP studies in humans in which the peripheral or the central visual field was stimulated (Kubova et al., 1990). Further study is necessary to elaborate on differences between left-hemispheric and right-hemispheric processing of visual motion information in humans. It is recommended in such studies to place the fixation spot about 15° separated from the stimulated half-field in order to rule out bilateral activation of MT/V5.

4.2. Left versus right-field motion VEPs in children

When children watch the same visual half-field motion stimulus as adults, N2 shows a maximum on the ipsilateral hemisphere, regardless of whether left or right half-field stimulation was used (Figs. 6 and 7). Upon left half-field stimulation the amplitude of N2 was maximal on the left hemisphere, and upon right half-field stimulation on the right. Thus, the hemispheric predominance of extrastriate activity observed in adults (see Experiment 1) was absent in children. Instead, the ipsilateral hemisphere dominates in children's motion VEP. Thus, the lateralization switch when the left visual half-field is stimulated in stead of the right half-field is present in children but is absent in adults. This suggests that the maturation of cortical mechanisms involved in the processing of visual motion is not completed before late puberty. Note, however, that although the cortical distribution of visual half-field motion VEPs in children differs from that in adults, peak latencies of N2 in children were in the same range as those observed in adults. In this respect

our findings differ from those of Kubova, Kuba, Peregryn and Novakova (1996) who found longer N2 latencies in children (mean age of 10 years) than in adults.

We have shown previously that motion sensitivity measured *psychophysically* differs for children's left and right visual half-fields (Hollants-Gilhuijs et al., 1998). It is therefore surprising that the *electrophysiological* data obtained in the same age group in the present study (see Experiment 2) does not reflect a visual half-field asymmetry. Even so surprising is the notion that adults do not show a visual half-field preference in psychophysical motion experiments (Hollants-Gilhuijs et al., 1998) whereas their VEP data (present study, Experiment 1) reveals that visual motion information is not equally processed in the two hemispheres. The explanation of this observation is still unknown.

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