Available online at www.sciencedirect.com
SCIENCE DIRECT®
Vision Research 46 (2006) 536–544
Vision Research
www.elsevier.com/locate/visres

Motion-onset VEPs reflect long maturation and early aging of visual motion-processing system

J. Langrová *, M. Kuba, J. Kremláček, Z. Kubová, F. Vít

Department of Pathophysiology, Charles University—Faculty of Medicine, Šimkova 870, 500 38 Hradec Králové, Czech Republic

Received 11 February 2005; received in revised form 10 June 2005

Abstract

Pattern-reversal and motion-onset visual evoked potentials (VEPs) were simultaneously tested in a group of 70 healthy subjects between the ages of 6–60 years to verify suspected differences in maturation and aging dynamics of the pattern and motion processing subsystems of the visual pathway. The motion-onset VEPs displayed dramatic configuration development and shortening of latencies up to 18 years of age (correl. coeff. -0.85; $p < 0.001$) and systematic prolongation from about 20 years of age (correl. coeff. 0.70; $p < 0.001$). This confirms long-lasting maturation of the magnocellular system and/or motion processing cortex and their early age related changes. Less significant changes of pattern-reversal VEPs in the tested age range can be interpreted as a sign of early maturation of the parvocellular system and its enhanced functional endurance in the elderly.

Keywords: Motion-onset VEPs; Magnocellular system; Dorsal stream; Maturation; Aging

1. Introduction

Visual perception represents the most important information input in human beings. The quality of visual perception changes substantially during human life with maturation during childhood and a significant decline in the elderly. The latter is currently of interest due to the increase of human average age. A great deal of this visual decline cannot be attributed to optical and retinal changes and must therefore be due to deficits of the central visual pathways (Spear, 1993). It is therefore important to have an objective tool for classification of the quality of visual perception, as well as a way to recognise both maturational problems in childhood (e.g., in developmental dyslexia) and physiological or pathological deterioration of visual perception and cognition in elderly. The methods for detecting vision defects (and their improvement) at the level of the eye (retinal disorders) are commonly available; however, there are not enough precise and objective tools for verification of visual information transmission in the primary and association areas of visual cortex. Commonly used visual evoked potentials (VEPs) do not cover the testing of all main qualities of visual sensation because only a limited spectrum of visual stimuli have so far been used. On the other hand, there are numerous attempts to evaluate visual perception via brain imaging techniques. But none of them, even the most progressive method of fMRI, provide sufficient time resolution to detect subtle delays in transmission and processing times. Furthermore, fMRI is not widely available to a large number of subjects.

We investigated age related changes in visual perception using new variants of VEPs. We extended the standard pattern-reversal VEPs (see the Standards of the International Society for Clinical Electrophysiology of Vision—Odom et al., 2004) through implementation of various kinds of motion-onset related VEPs that, according to their properties (see below), seem to

* Corresponding author. Tel.: +420 495816331.
E-mail address: langrovaJ@lfhk.cuni.cz (J. Langrová).

0042-6989/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2005.06.024

selectively test the magnocellular subsystem of the visual pathway and motion-processing visual cortex. Early studies of motion-related VEPs (e.g., Clarke, 1973; Dagnelie, 1986; De Vries, VanDijk, & Spekreijse, 1989; Göpfert, 1983) yielded inconsistent results. Later work has shown the importance of temporal frequency, contrast, motion duration and interstimulus interval, stimulus field size and electrode derivation on determining whether the most reliable motion-onset specific N2 peak (representing mainly magnocellular activity) dominates or some other components (positive peaks with shorter latency representing mainly activity of the parvocellular system/ventral stream) contaminate the motion-related VEPs (see Bach & Ullrich, 1994, 1997; Hoffmann, Unsöld, & Bach, 2001; Kuba & Kubová, 1992; Kuba, Toyonaga, & Kubová, 1992; Kubová, Kuba, Spekreijse, & Blakemore, 1995; Odom, De Smedt, Van Malderen, & Spileers, 1998–1999).

The scalp location of maximal motion-onset VEP amplitude also depends on the character of the motion stimulus. While linear motion mainly activates human MT analogues in the occipito-temporo-parietal cortex (the maximum is lateralised to the right hemisphere in the majority of subjects—see Kubová, Kuba, Hubáček, & Vít, 1990), radial motion (''expansion/contraction'') produces maximum responses in the centro-parietal cortex (Kremláček, Kuba, Kubová, & Chlubnová, 2004) (verified also by MEG studies—e.g., Holliday, Meese, & Barnes, 1998).

A special note should be addressed to the terminology used to describe the visual motion processing system. As claimed by Skottun and Skoyles (2004), it is not adequate to interpret prolonged motion-related VEPs as a ''magnocellular system deficit'' since it is not possible to directly differentiate from these studies the level (subcortical, primary cortical, and association cortex) of involvement of the motion processing system. Thus, we tried to respect this statement and considered our motion-onset VEPs findings as magnocellular system and/or dorsal stream areas related. We were also aware of the fact that our results obtained with motion stimuli did not necessarily represent all general properties of the magnocellular system.

2. Subjects and methods

2.1. Subjects

Our normative study was performed in a group of 70 healthy subjects (33 men, 37 women) between the ages of 6 and 60 years. All of them (or parents of minors) signed a written informed consent before the beginning of the examination that conformed to the Declaration of Helsinki. This group comprised seven subgroups of ages 6–10, 11–15, 16–20, 21–30, 31–40, 41–50, and 51–60 years with 10 subjects in each and about an equal proportion of both sexes. All subjects had a visual acuity 4/8 or better (with correction if needed). During the VEPs examination they sat in a sound shielded Faraday cage and were instructed to fixate on the marked centre of the stimulus field during each VEP recording. Correct fixation was monitored via CCD camera.

2.2. Stimuli

The stimuli were generated using our own software on a 21″ Iiyama monitor with a 105 Hz frame frequency and a mean luminance of 17 cd/m^2 (Kremláček et al., 2004).

Our examination covered the following set of VEPs:

1. High contrast (96% according to Michelson's formula) checkerboard pattern-reversal (2 Hz reversal rate) VEPs recorded from O_Z derivation. Check sizes of 40′, 20′, and 10′ were used. Latencies and inter-peak amplitudes of the N–P–N potential complex around P100 peak were evaluated.
2. Two variants of moving visual stimuli were used. (a) Unidirectional linear motion—''translation'' ($v = 10$ deg/s) of isolated checks (check size 40′, check-to-check distances in both vertical and horizontal axis of 120′) with random order of the direction of motion (to reduce adaptation of direction-specific cortical neurones). (b) Radial motion—randomly changing expanding/contracting (centrifugal/centripetal) motion of a concentric pattern (rings) with decreasing spatial frequency (1–0.2 c/deg) toward the periphery of the visual field to account for cortical magnification and with increasing motion velocity (5–25 deg/s) towards the periphery to account for different motion sensitivities in the centre versus the periphery of the visual field (McKee & Nakayama, 1984; Orban, Kennedy, & Bullier, 1986). Thus, the temporal frequency of 5 c/s was kept constant over the whole stimulus field.

In both variants of the motion-onset VEPs a low contrast (10%) pattern was used for more selective activation of the magnocellular pathway (Kaplan & Shapley, 1986). The circular pattern (rings) for the radial motion had sinusoid modulation of luminance to eliminate high spatial frequencies. The same timing for both moving stimuli—200 ms moving phase with long (1 s) inter-stimulus interval (period of stationary structure between two motions) was used to avoid adaptation to motion (Bach & Ullrich, 1994; Kuba & Kubová, 1992). Besides full field (28° × 37°) stimuli, separate central 8° and peripheral stimuli (outside the masked central 20° of the visual field) were also used in the radial motion variant to verify differences in the related VEPs that may be used in diagnostics of pathological processes influencing central

versus peripheral parts of the visual field (e.g., in Glaucoma).

Parameters of the P–N–P potential complex around the dominant N2 motion-onset specific peak (specified as N160 or N170 in some papers) were statistically tested. All stimulus specifications are available on our website: http://www.lfhk.cuni.cz/elf.

2.3. Recordings

Our standard recordings include unipolar derivations (with an ear lobe reference) from the midline—O_Z, P_Z, C_Z, and F_Z and also lateral leads O_L and O_R (5 cm to the left and right from the O_Z position), since N2 motion-onset specific peak is mostly lateralised (irrespective of the dominant hemisphere) toward the temporo-occipital cortex. Six channels were selected on the basis of results from previous multi-channel recordings which are available on our web page (see above).

Forty single sweeps (440 ms epochs 20,000 times amplified in the frequency band of 0.1–45 Hz with sampling frequency of 500 Hz) were averaged and each condition was repeated at least twice to verify the reliability of the recorded parameters. Three variants of both monocular pattern-reversal VEPs and four variants of the motion-onset VEPs, three peak-latencies and two inter-peak amplitudes in six derivations (420 parameters) were statistically analysed within this study with the use of Statistica 6.1, USA (altogether 58,800 values = two repetitions in 70 subjects).

3. Results

Pattern-reversal results from the O_Z derivation are presented here since this derivation provided the largest potentials with the lowest variability. However, the motion-onset VEPs displayed distinct inter-individual differences in maximal amplitudes and shortest latency localisation because of their variable generation from occipital and medio-temporal and parietal association areas (see e.g., Holliday et al., 1998; Kremláček, Kuba, & Kubová, 1998; Schellart, Trindade, Reits, Verbunt, & Spekreijse, 2004). According to these circumstances, an "optimal" derivation was selected in each subject (the derivation with the shortest VEP latency and in case of non-significant latency differences it was the derivation with the largest VEP amplitude) for further statistical analysis of the motion-onset VEPs. In about 40% of subjects the optimal derivation was P_Z. Twenty five percent of the subjects displayed lateralisation of their motion-onset VEPs to the right occipital derivation (O_R) and 20% to the left hemisphere (O_L derivation). In only 15% of the subjects did the O_Z electrode represent the "optimal" derivation. Particular proportions differed slightly according to the variant of motion stimulation. The parietal derivation was optimal more frequently in case of the radial motion (compared to the "translation" motion, having maximum response typically in the lateral occipital derivations—see Kuba & Kubová, 1992).

Considering the inter-individual variability in the motion-onset VEPs topography decreased both the range of latency and amplitude, which improved their diagnostic utility (compare data for single derivations with the "optimal" derivation in Table 1B).

Table 1A presents the pattern-reversal P100 peak latencies and amplitudes calculated as the mean of inter-peak amplitudes between P100 and the preceding and subsequent negative peaks. Only with 10′ check size did the pattern-reversal VEPs display significant amplitude dependence on the visual acuity of subjects.

Pattern-reversal VEPs display much lower variability over the whole age span compared to motion-onset VEPs, which are shown in Table 1B as N2 peak latency and its mean inter-peak amplitude calculated from the P–N–P complex. In this table subjects are divided into two age-subgroups according to regression analysis results (see below). It includes data of all tested variants of the motion-onset VEPs from six original derivations and from the selected "optimal" one. Radial motion (full field stimulation) exhibited larger amplitudes than translation motion in both age-subgroups. The shift of maximal motion-onset responses from occipito-temporal to the parietal P_Z region when radial motion was used, is recognisable from the table in the full field and peripheral visual field conditions. In general, the more peripheral moving stimuli increased activation of the "higher" cortical areas up to C_Z, where the later P2 peak dominates (Hoffmann et al., 2001; Kremláček, Kuba, Chlubnová, & Kubová, 2004).

One set of individual VEPs with typical characteristics (about average amplitudes and latencies) for all stimuli is presented in Fig. 1. In this subject there is a motion-specific N2 peak dominating in all types of motion-onset VEPs. This was not the case in some of the youngest children, where the first positive peak may be

Table 1A
Latencies and amplitudes (median and 25–75 percentiles) of the pattern-reversal VEPs

Derivation	R40′		R20′		R10′	
	L (ms)	A (μV)	L (ms)	A (μV)	L (ms)	A (μV)
O_Z	111 (108–114)	12.8 (8.8–18.0)	114 (110–117)	12.9 (8.3–17.2)	121 (116–127)	10.0 (5.8–15.2)

Table 1B
Latencies and amplitudes (median and 25–75 percentiles) of all tested motion-onset VEPs in two age related subgroups

Derivation	Translation motion		Radial motion		Radial motion c8°		Radial motion m20°	
	L (ms)	*A* (μV)	*L* (ms)	*A* (μV)	*L* (ms)	*A* (μV)	*L* (ms)	*A* (μV)]
Age 6–18								
O_Z	184 (168–224)	6.1 (4.1–8.4)	190 (170–240)	8.4 (6.4–12.0)	194 (176–240)	6.5 (4.7–8.4)	182 (154–268)	6.4 (5.3–8.9)
O_L	182 (172–224)	6.4 (4.9–9.0)	188 (172–234)	8.7 (6.8–12.1)	198 (180–244)	7.0 (5.3–9.9)	186 (162–268)	6.9 (4.9–9.2)
O_R	180 (170–214)	6.5 (5.0–8.4)	190 (168–240)	8.9 (6.4–11.2)	192 (177–240)	7.5 (5.4–10.3)	187 (154–271)	6.4 (4.5–9.4)
P_Z	168 (156–228)	7.5 (5.9–9.4)	179 (158–225)	10.1 (8.3–12.1)	184 (166–234)	7.6 (5.5–9.4)	175 (152–253)	8.0 (6.2–10.8)
Optimal	170 (158–212)	8.2 (6.5–11.1)	180 (160–222)	11.7 (9.5–13.4)	184 (168–238)	8.5 (5.9–11.0)	184 (152–266)	9.1 (7.0–11.3)
Age 19–60								
O_Z	176 (168–184)	4.8 (3.4–6.6)	172 (164–180)	9.1 (6.7–12.0)	176 (170–186)	7.0 (5.0–8.7)	172 (162–184)	7.1 (5.3–9.3)
O_L	176 (168–186)	4.9 (3.6–6.4)	172 (164–180)	9.2 (7.5–12.2)	176 (170–186)	7.4 (5.4–9.1)	172 (164–184)	7.7 (5.8–9.6)
O_R	176 (168–184)	5.5 (3.8–7.7)	168 (162–178)	9.8 (6.9–13.4)	172 (168–184)	8.0 (6.1–11.2)	172 (162–182)	7.2 (5.1–9.4)
P_Z	170 (164–180)	6.3 (4.9–8.6)	166 (158–176)	10.9 (8.0–13.4)	172 (162–178)	7.6 (6.0–10.0)	170 (160–181)	9.3 (7.3–12.0)
Optimal	170 (163–175)	6.7 (5.4–9.4)	164 (156–172)	12.4 (9.5–15.8)	170 (163–176)	8.9 (7.4–12.2)	169 (159–176)	9.3 (7.2–13.1)

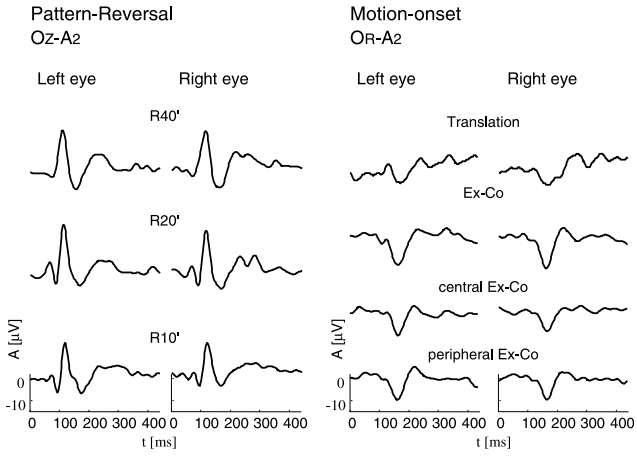

Fig. 1. Set of VEPs examined in all subjects—typical individual recordings. R40′, R20′, and R10′—pattern-reversal VEPs with 40′, 20′, and 10′ check sizes. Translation—VEPs to linear motion (“translation”) 10 deg/s. Ex-Co—Expansion/Contraction (radial motion), full field stimulus. Central Ex-Co—Expansion/Contraction in the central 8° of the stimulus field. Peripheral Ex-Co—Expansion/Contraction in periphery of the stimulus field, central 20° masked.

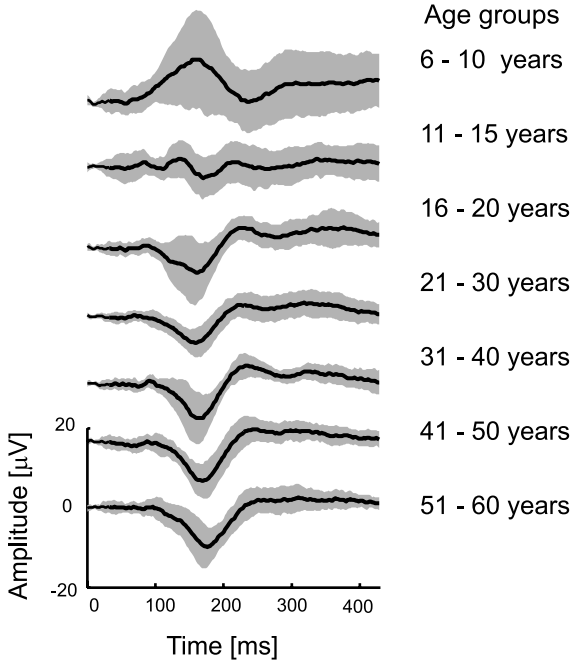

Fig. 2. Grand averages of the motion-onset VEPs to full-field radial motion for seven age groups are displayed together with point-vice computed standard deviation. The resulting curves represent average of monocular VEPs from the “optimal” derivation (see Section 3).

larger (mainly in “translation” of isolated checks), most probably due to prevailing activity of the parvocellular system—compare the shapes of the grand averages of the motion-onset VEPs for single age subgroups in Fig. 2 showing a decrease of the first positivity up to about 15 years.

The dependence of VEP parameters on the age of subjects was evaluated using correlation coefficients (and their significance values)—see Table 2A (pattern-reversal VEPs) and Table 2B (motion-onset VEPs).

In Fig. 3, the associations between individual latencies and amplitudes and the age of the subjects are depicted. Pattern-reversal P100 latencies for the 40′ check size and its average inter-peak amplitudes from the O_Z derivation are presented as well as the corresponding radial motion—onset VEPs parameters from the selected “optimal” derivation. Regression analysis of the dependence of these parameters on the age of the subjects was performed. Solid lines represent regression curves and dashed lines show the 95% borders of the predicted normal values. It is evident that pattern-reversal VEP latencies display the weakest dependence on age ($r = 0.18$). Pattern-reversal VEP amplitudes show a significant reduction from childhood towards the elderly ($r = -0.49$ for the check size 40′; $p < 0.001$).

Table 2B and Fig. 3 show that the most age-sensitive VEP parameter is the N2 latency of the radial motion-onset VEPs. This latency undergoes distinct shortening

Table 2A
Age dependence of pattern-reversal VEPs parameters

Age (years)	R40′				R20′				R10′			
	L (ms)		*A* (μV)		*L* (ms)		*A* (μV)		*L* (ms)		*A* (μV)	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
6–60	0.18	*	−0.49	***	0.23	**	−0.52	***	0.27	**	−0.60	***

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table 2B
Age dependence of motion-onset VEPs parameters

Age (years)	Translation motion				Radial motion				Radial motion c8°				Radial motion m20°			
	L (ms)		*A* (μV)		*L* (ms)		*A* (μV)		*L* (ms)		*A* (μV)		*L* (ms)		*A* (μV)	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
6–60	−0.16	n.s.	−0.31	**	−0.30	***	0.05	n.s.	−0.32	***	0.05	n.s.	−0.33	***	0.07	n.s.
⩾19	0.57	***	−0.30	**	0.66	***	−0.14	n.s.	0.63	***	−0.05	n.s.	0.70	***	−0.13	n.s.
<19	−0.69	***	−0.34	**	−0.85	***	−0.09	n.s.	−0.83	***	−0.10	n.s.	−0.82	***	0.20	n.s.

** $p < 0.01$.
*** $p < 0.001$.

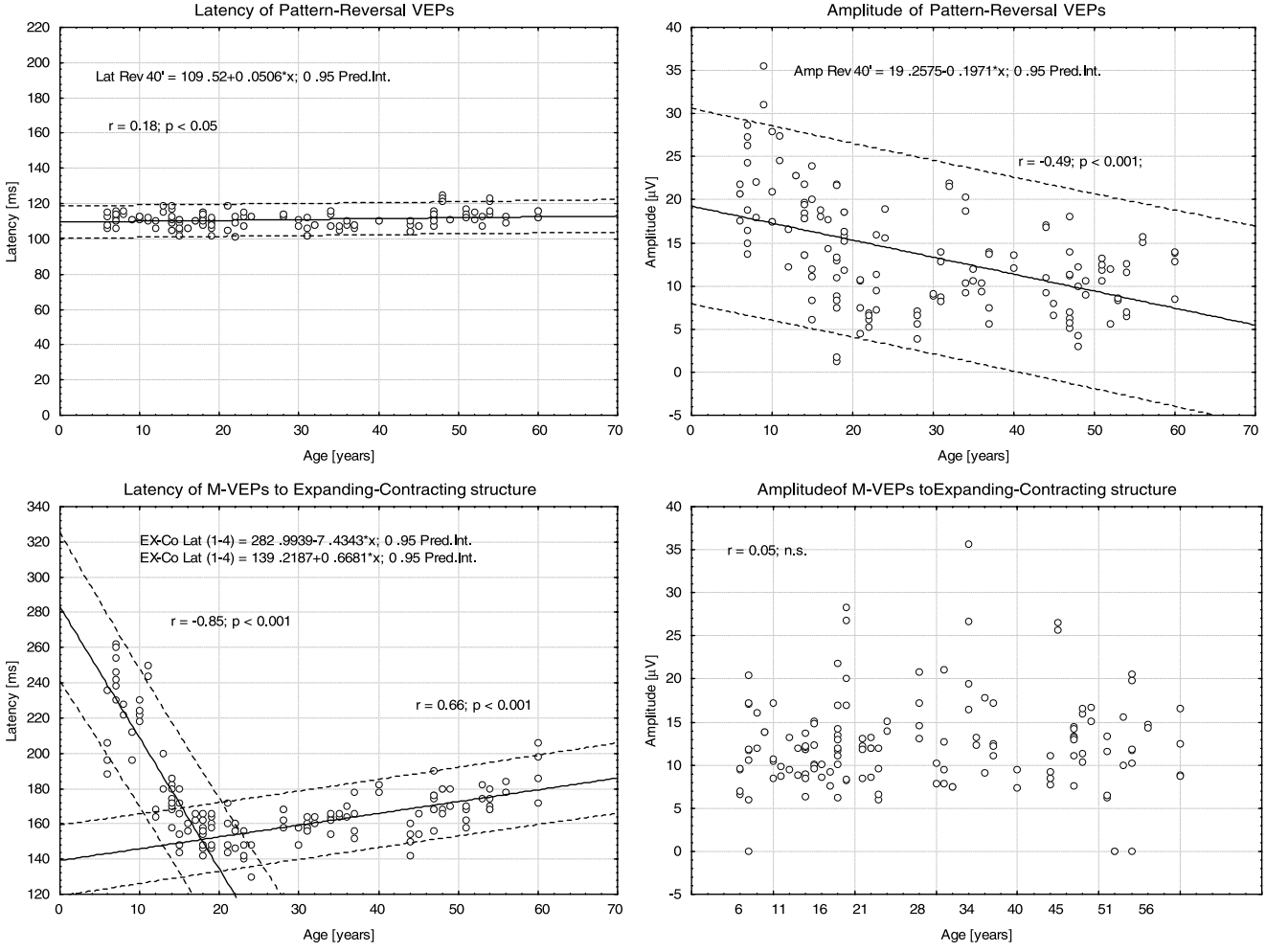

Fig. 3. Pattern-reversal (40′) and motion-onset VEPs (expansion/contraction) latency and amplitude dependence on age of subjects Solid lines—regression curves, dashed lines—95% borders of redicted interval of normal values Correlation coefficients, their significance and regression curve formula are specified. (Note to the motion-onset VEPs latencies: although the two linear regression curves are depicted in the whole calculated range of ages, their validity (for both younger and older subgroup) is limited by the intersection point at age of about 18 years.)

up to the age of 18 years ($r = -0.85$; $p < 0.001$) and then it systematically prolongs ($r = 0.66$; $p < 0.001$). The two linear regressions used here described in the best way the age dependence (compared to other tested regression fits by continuous polynomial functions of the second and third order). For the analysis the entire group was split into two intervals—from 6 to 18 and from 19 to 60 years, with respect to the highest correlations achieved in the resulting subgroups. Motion-onset VEP amplitudes did not display any significant changes throughout the tested age span.

The pattern-reversal VEPs for the three check sizes (40′, 20′ and 10′) did not differ significantly in their age dependence. All of them exhibited a significant decrease of amplitudes towards the elderly and a much lower latency dependence on the age of subjects (the highest correlation was 0.27) compared to the motion-onset VEPs.

Fig. 4 demonstrates latency differences among all motion-onset VEPs (linear motion, full field radial motion, central radial motion, and peripheral radial motion). The comparison is based on data taken from the "optimal" derivation. In all cases there was a relatively similar age-related distribution of latencies. The lowest variability (the narrowest 95% interval of predicted values) and the shortest latencies were achieved to full field radial motion stimuli. The longest latencies in childhood were found in the VEPs to the peripheral radial motion—they displayed the most distinct shortening during maturation and a significant prolongation beginning from about 20 years of age. This kind of VEPs thus seems to be the most sensitive in detecting functional changes in the elderly. The shortest latencies in childhood were produced by linear motion, which might indicate that the more complex radial motion represents a more difficult task for the non-mature magnocellular

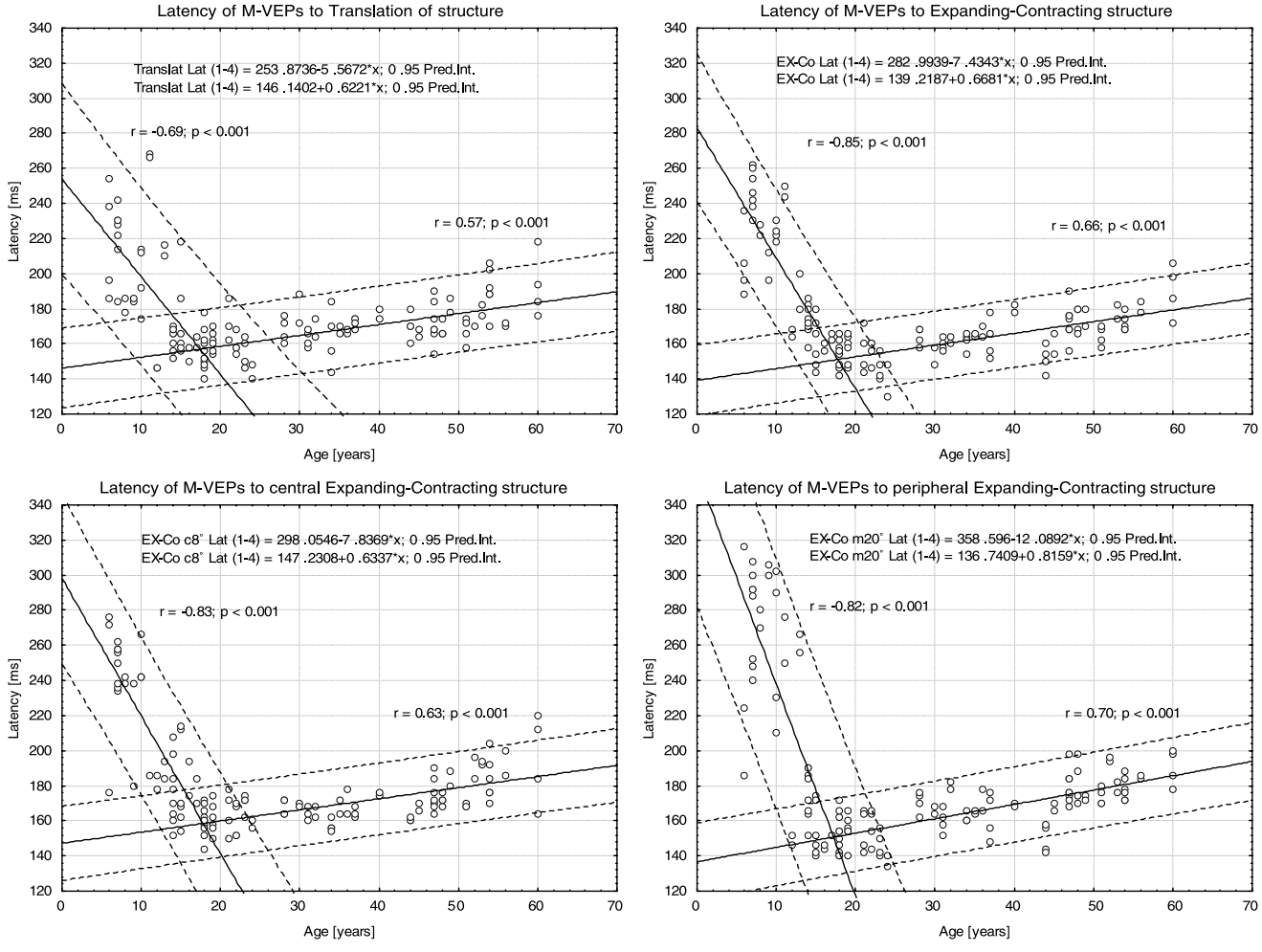

Fig. 4. Comparison of latency dependence on age in four variants of motion-onset VEPs (translation of structure, expanding-contracting structure—full field, expanding-contracting structure—central stimuli, and expanding-contracting structure—peripheral stimuli) Correlation coefficients, their significance and regression curve formula are specified. Although the two linear regression curves are depicted in the whole calculated range of ages (in each presented example of latency age dependence), their validity (for both younger and older subgroup) is limited by the intersection point at age of about 18 years.

system and it could serve as a sensitive criterion of maturation completion.

We were also interested in gender related differences in VEPs parameters for our group of subjects. The genders did not differ systematically in latencies, both in pattern-reversal and in motion-onset VEPs, but, women exhibited larger amplitudes in pattern-reversal VEPs.

4. Discussion

Since the age dependent pattern-reversal and motion-onset VEPs parameter profiles differ, it can be interpreted as further evidence, in additional to contrast sensitivity studies by Bach and Ullrich, 1997; Kubová et al., 1995 and adaptation experiments of Hoffmann et al., 2001 of a different origin of these VEPs (likely parvocellular system/ventral stream areas and magnocellular system/dorsal stream areas).

On the basis of our results we conclude the following:

- VEPs parameters can be used for the testing of visual pathway maturation and aging.
- Maturation of the magnocellular system/dorsal stream of the visual pathway as indexed by the latencies of motion-onset VEPs is completed only at the age of about 18 years.
- Magnocellular system/dorsal stream displays earlier signs of functional changes with age compared to the parvocellular system/ventral stream.
- The most sensitive stimulus for the detection of age related changes in the function of the visual pathway is radial motion of sinusoidally modulated low contrast structure in the periphery of the visual field.
- It is necessary to use specific, age-related norms in the examination of the motion-onset VEPs.

The existing literature concerning VEP testing of the aging visual pathway is so far oriented mainly towards standard pattern stimuli. Most frequently the conclusion has been that its maturation (according to VEP latency values for black-white stimuli) is completed at about the age of 6 years (e.g., Mitchell & Neville, 2004; Tomoda, Tobimatsu, & Mitsudome, 1999) and that the visual pathway shows little age related change from young adulthood to middle age (20–60 years). However, it has also been reported that ''maturation of the visual cortex continues until puberty and even later'' (Brecelj, Strucl, Zidar, & Tekavic-Pompe, 2002). Prolonged maturation and/or earlier aging was found in some studies using chromatic pattern stimuli (Crognale, 2002; Fiorentini, Porciatti, Morrone, & Burr, 1996). Although an increase in the mean amplitudes of the early components of the primary VEPs in groups of older subjects was described (Dustman & Shearer, 1987), it is difficult to use amplitude parameters for the investigation of individuals, since VEP amplitudes generally show a large interindividual variability.

The longer development of the visual motion processing system observed in this study (compared to the pattern processing system) confirms our previous results in control groups for dyslexic and amblyopic children (6–11 years old) in whom there is also substantial delay of the magnocellular system/dorsal stream maturation in comparison to the maturation of the parvocellular system/ventral stream (Kubová, Kuba, Peregrin, & Nováková, 1995; Kubová, Kuba, Juran, & Blakemore, 1996). As noted by Mitchell and Neville (2004), the longer developmental time course of the dorsal stream might be related to the hypothesised greater plasticity of this system as compared to the ventral stream. However, it is far beyond the scope of this article to discuss also large ''non-electrophysiological'' literature related to differential maturation of magno- and parvocellular systems.

The systematic prolongation of motion-onset VEP latencies beginning in early adulthood may be a good indicator of individual biological aging. It might be dependent on the suspected higher sensitivity of the magnocellular pathway (neurones) and the association cortical areas to possible degeneration processes due to speculated ischemic, toxic, peroxidation factors etc. (Kilic, 2003). Thus, the large differences in N2 peak latencies (from 160 to 200 ms) reported in literature may not be attributable only to different parameters of motion stimuli but also to differences in the age of subjects.

It might appear as a contradiction that we confirmed significant changes of the motion-onset VEPs towards the elderly and simultaneously we designated them as a sensitive tool for recognition of some pathological processes in the aging visual system. However, we believe that a method capable of recognising even slow functional deteriorations might also be sensitive enough to detect the first pathological manifestations—like an early involvement of the magnocellular system in Glaucoma (Kubová, Kuba, Svěrák, & Hrochová, 1996; Willis & Anderson, 2000). Although it is necessary to take into consideration their age related changes, the motion-onset VEPs can detect some pathologies better than the pattern-reversal VEPs that are less sensitive to both aging and magnocellular system involvement (Kubová & Kuba, 1992; Korth, Kohl, Martus, & Sembritzki, 2000).

In our opinion (in agreement e.g., with Skrandies, Jedynak, & Kleiser, 1998), the results of some papers reporting different findings concerning the developmental processes within the visual motion processing system seem to be influenced through use of inappropriate stimuli (pattern and motion parameters, timing of stimuli, etc.—see the description of important parameters in Introduction) for activation of the magnocellular pathway and the dorsal stream (e.g., De Vries et al., 1989;

Gordon & McCulloch, 1999) leading to formation of mixed pattern and motion related components. Classification is especially difficult during childhood when characteristics of motion-related VEPs undergo significant changes.

Although the motion-specific N2 peak cannot be attributed as a fully "isolated" motion response (according to Hoffmann et al., 2001 it represents at least partially also a pattern-related activity), we believe that thanks to our "tuned" stimulus parameters respecting properties of the magnocellular system and motion processing cortex, its motion specificity is quite high. This is supported by the fact that its age related changes differ significantly from changes of the pattern related parameters (pattern-reversal VEPs).

Besides pre-existing electrophysiological studies of developmental disorders like dyslexia (Demb, Boynton, & Heeger, 1998; Kuba, Szanyi, Gayer, Kremláček, & Kubová, 2001; Kubová et al., 1995; Schulte-Korne, Bartling, Deimel, & Remschmidt, 2004), still more detailed insight into maturation processes of the magnocellular system/dorsal stream in childhood could be achieved with optimised motion stimuli.

We believe that the main contribution of this study to an objective description of aged related changes in visual perception has been done through application of the specified new variant of motion-onset related VEPs. The relevancy of our results is supported by some psychophysical studies that report a long maturation and/or an early decrease of visual system sensitivity to motion stimuli during aging (e.g., Benedek, Benedek, Keri, & Janaky, 2003; Fischer & Hartnegg, 2002; Gilmore, Wenk, Naylor, & Stuve, 1992).

Acknowledgments

This study was supported by Grant Agency of the Czech Republic (Grant No. 309/02/1134) and by Grant Agency of the Czech Ministry of Health (Grant No. NR 8421-4/2005).

References

Bach, M., & Ullrich, D. (1994). Motion adaptation governs the shape of motion-evoked cortical potentials. *Vision Research, 34*, 1541–1547.

Bach, M., & Ullrich, D. (1997). Contrast dependency of motion-onset and pattern-reversal VEPs: Interaction of stimulus type, recording site and response component. *Vision Research, 37*, 1845–1849.

Benedek, G., Benedek, K., Keri, S., & Janaky, M. (2003). The scotopic low-frequency spatial contrast sensitivity develops in children between the ages of 5 and 14 years. *Neuroscience Letters, 345*, 161–164.

Brecelj, J., Strucl, M., Zidar, I., & Tekavic-Pompe, M. (2002). Pattern ERG and VEP maturation in schoolchildren. *Clinical Neurophysiology, 113*, 1764–1770.

Clarke, P. G. H. (1973). Visual evoked potentials to changes in the motion of a pattern field. *Experimental Brain Research, 18*, 145–155.

Crognale, M. A. (2002). Development, maturation, and ageing of chromatic visual pathways: VEP results. *Journal of Vision, 2*, 438–450.

Dagnelie, G., 1986. Pattern and motion processing in primate visual cortex. Thesis. University of Amsterdam.

Demb, J. B., Boynton, G. M., & Heeger, D. J. (1998). Functional magnetic resonance imaging of early visual pathways in dyslexia. *Journal of Neurosciences, 18*, 6939–6951.

De Vries, M., VanDijk, B., & Spekreijse, H. (1989). Motion onset-offset VEPs in children. *Electroencephalography clinical Neurophysiology, 74*, 81–87.

Dustman, R. E., & Shearer, D. E. (1987). Electrophysiological evidence for central inhibitory deficits in old age. *Clinical Neurophysiology, 39*(Suppl.), 408–412.

Fiorentini, A., Porciatti, V., Morrone, M. C., & Burr, D. C. (1996). Visual ageing: Unspecific decline of the responses to luminance and colour. *Vision Research, 36*, 3557–3566.

Fischer, B., & Hartnegg, K. (2002). Age effects in dynamic vision based on orientation identification. *Experimental Brain Research, 143*, 120–125.

Gilmore, G. C., Wenk, H. E., Naylor, L. A., & Stuve, T. A. (1992). Motion perception and aging. *Psychology and Aging, 7*, 654–660.

Göpfert, E. (1983). Visual evoked potentials in pattern motion. *Zeitschrift für EEG-EMG, 14*, 47–51.

Gordon, G. E., & McCulloch, D. L. (1999). A VEP investigation of parallel visual pathway development in primary school age children. *Documenta Ophthalmologica, 99*, 1–10.

Hoffmann, M. B., Unsöld, A. S., & Bach, M. (2001). Directional tuning of human motion adaptation as reflected by the motion VEP. *Vision Research, 40*, 2187–2194.

Holliday, I. E., Meese, T. S., & Barnes, G. R. (1998). Evoked magnetic fields to optic flow stimuli are largest for expansion. *Perception, 27*(Suppl.), 17.

Kaplan, E., & Shapley, R. M. (1986). The primate retina contains two types of ganglion cells, with high and low contrast sensitivity. *Proceedings of the National Academy of Sciences of the United States of America, 83*, 2755–2757.

Kilic, D. (2003). The effects of ageing and sulfur dioxide inhalation exposure on visual-evoked potentials, antioxidant enzyme systems, and lipid-peroxidation levels of the brain and eye. *Neurotoxicology and teratology, 25*, 587–598.

Korth, M., Kohl, S., Martus, P., & Sembritzki, T. (2000). Motion-evoked pattern visual evoked potentials in glaucoma. *Journal of Glaucoma, 9*, 376–387.

Kremláček, J., Kuba, M., & Kubová, Z. (1998). Electrophysiological manifestation of first-order motion perception. *Perception, 27*(Suppl.), 192–193.

Kremláček, J., Kuba, M., Chlubnová, J., & Kubová, Z. (2004). Effect of stimulus localisation on motion-onset VEP. *Vision Research, 44*, 2989–3000.

Kremláček, J., Kuba, M., Kubová, Z., & Chlubnová, J. (2004). Motion-onset VEPs to translating, radial, rotating and spiral stimuli. *Documenta Ophthalmologica, 109*, 169–175.

Kuba, M., & Kubová, Z. (1992). Visual evoked potentials specific for motion-onset. *Documenta Ophthalmologica, 80*, 83–89.

Kuba, M., Toyonaga, N., & Kubová, Z. (1992). Motion-reversal visual evoked responses. *Physiological Research, 41*, 369–373.

Kuba, M., Szanyi, J., Gayer, D., Kremláček, J., & Kubová, Z. (2001). Electrophysiological testing of dyslexia. *Acta Medica (Hradec Králové), 44*, 131–134.

Kubová, Z., Kuba, M., Hubáček, J., & Vít, F. (1990). Properties of visual evoked potentials to onset of movement on a television screen. *Documenta Ophthalmologica, 75*, 67–72.

Kubová, Z., & Kuba, M. (1992). Clinical application of motion-onset visual evoked-potentials. *Documenta Ophthalmologica, 81*, 209–218.

Kubová, Z., Kuba, M., Spekreijse, H., & Blakemore, C. (1995). Contrast dependence of of motion-onset and pattern-reversal evoked potentials. *Vision Research, 35*, 197–205.

Kubová, Z., Kuba, M., Peregrin, J., & Nováková, V. (1995). Visual evoked potential evidence for magnocellular system deficit in dyslexia. *Physiological Research, 44*, 87–89.

Kubová, Z., Kuba, M., Juran, J., & Blakemore, C. (1996). Is the motion system relatively spared in amblyopia. Evidence from cortical evoked responses. *Vision Research, 36*, 181–190.

Kubová, Z., Kuba, M., Svěrák, J., & Hrochová, J. (1996). Motion-onset visual evoked potentials improve the diagnosis of glaucoma. *Documenta Ophthalmologica, 92*, 211–221.

McKee, S. P., & Nakayama, K. (1984). The detection of motion in the peripheral visual field. *Vision Research, 24*, 25–32.

Mitchell, T. V., & Neville, H. J. (2004). Asynchronies in the development of electrophysiological responses to motion and color. *Journal of Cognitive Neuroscience, 16*, 1363–1374.

Odom, J. V., De Smedt, E., Van Malderen, L., & Spileers, W. (1998–1999). Visually evoked potentials evoked by moving unidimensional noise stimuli: effects of contrast, spatial frequency, active electrode location, reference electrode location, and stimulus type. *Documenta Ophthalmologica, 95*, 315–333.

Odom, J. V., Bach, M., Barber, C., Brigell, M., Marmor, M. F, & Tormene, A. P. (2004). Visual Evoked Potentials Standard2004. *Documenta Ophthalmologica, 108*, 115–123.

Orban, G. A., Kennedy, H., & Bullier, J. (1986). Velocity sensitivity and direction selectivity of neurons in areas V1 and V2 of the monkey: influence of eccentricity. *Journal of Neurophysiology, 56*, 462–480.

Schellart, N. A., Trindade, M. J., Reits, D., Verbunt, J. P., & Spekreijse, H. (2004). Temporal and spatial congruence of components of motion-onset evoked responses investigated by whole-head magneto-electroencephalography. *Vision Research, 44*, 119–134.

Schulte-Korne, G., Bartling, J., Deimel, W., & Remschmidt, H. (2004). Motion-onset VEPs in dyslexia. Evidence for visual perceptual deficit. *Neuroreport, 15*, 1075–1078.

Skottun, B. C., & Skoyles, J. R. (2004). Some remarks on the use of motion VEPs to assess magnocellular sensitivity(Letters to the Editor). *Clinical Neurophysiology, 115*, 2834–2836.

Skrandies, W., Jedynak, A., & Kleiser, R. (1998). Scalp distribution components of brain activity evoked by visual motion stimuli. *Experimental Brain Research, 122*, 62–70.

Spear, P. D. (1993). Neural bases of visual deficits during aging. *Vision Research, 33*, 2589–2609.

Tomoda, Y., Tobimatsu, S., & Mitsudome, A. (1999). Visual evoked potentials in school children: a comparative study of transient and steady-state methods with pattern reversal and flash stimulation. *Clinical Neurophysiology, 110*, 97–102.

Willis, A., & Anderson, S. J. (2000). Effects of glaucoma and aging on photopic and scotopic motion perception. *Investigative Ophthalmology and Visual Sciences, 41*, 325–335.