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Response characteristics of the normal retino-cortical pathways as determined with simultaneous recordings of pattern visual evoked potentials and simple motor reaction times

Michelle McKerral [a,c], Franco Lepore [b], Pierre Lachapelle [b,c,*]

[a] *Centre de réadaptation Lucie-Bruneau, Programme d'intégration dans la communauté (PIC), 2275, Avenue Laurier Est, Montréal, QC, Canada H2H 2N8*

[b] *Groupe de recherche en neuropsychologie expérimentale (GRENE), Département de psychologie, Université de Montréal, C.P. 6128, succursale Centre-Ville, Montréal, QC, Canada H3C 3J7*

[c] *Department of Ophthalmology, McGill University-Montreal Children's Hospital Research Institute, 2300 Tupper Street, Montréal, QC, Canada H3H 1P3*

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Abstract

Purpose: In an attempt to explain the existing discrepancies regarding the relationship between electrophysiological and psychophysical measurements of visual transmission time we compared, in humans, the response characteristics of the normal retino-cortical pathways with simultaneously obtained pattern visual evoked potentials (PVEP) and simple motor reaction times (RT). *Methods:* PVEPs and manual RTs were recorded simultaneously using a reversing checkerboard with different spatial frequency and contrast combinations chosen to elicit responses favoring the magnocellular or parvocellular pathways. The amplitude and peak time of the P1 wave of the PVEP were compared to the mean RT. Other parameters of the RT, such as mode and standard deviation were also considered. *Results:* The RT is not modified in the same fashion as the peak time of the P1 wave of the PVEP, the peak time of the PVEP demonstrating a spatial frequency selectivity, while the RT does not. Further comparative analysis of the PVEP and RT shows that the RT is faster for stimuli of lower contrast and spatial frequency, while the PVEP amplitude is larger and its peak time shorter for higher contrast and spatial frequency stimuli. *Conclusions:* Our findings suggest that PVEP and RT measures recruit distinct physiological characteristics and appear to be differently modulated while travelling along the retino-cortical pathway. Our results also show the importance of obtaining electrophysiological and psychophysical measures concomitantly to insure elimination of combined inter-stimulus and inter-session variability.

Keywords: Contrast; Motor reaction time (RT); Pattern reversal visual evoked potential (PVEP); Retino-cortical processing; Spatial frequency

1. Introduction

In humans, the clinical assessment of the retino-cortical pathways is often based on the amplitude and peak time characteristics of the scalp-recorded pattern-reversal visual evoked potential (PVEP) (Chiappa, 1990; Regan, 1989; Halliday, McDonald, & Mushin, 1972) whose components are thought to mainly originate from prestriate and striate cortical areas (Ducati, Fava, & Motti, 1988; Maier, Dagnelie, Spekreijse, & van Dijk, 1987). The simple motor reaction time (RT), which is a method considered by some as an alternate means to measure the retino-cortical processing time has been shown to be, like the PVEP (Kubová, Kuba, Spekreijse, & Blakemore, 1995; Tobimatsu, Kurita-Tashima, Nakayama-Hiromatsu, & Kato, 1993; Musselwhite & Jeffreys, 1985), contrast- and spatial frequency-dependent (Felipe, Buades, & Artigas, 1993; Parker & Dutch, 1987).

Previous studies which compared the PVEP and RT suggested that their relationship varied depending on the stimulus parameters (Hartwell & Cowan, 1993;

* Corresponding author. Tel.: +1-514-9344400; fax: +1-514-9344331.

E-mail address: mdpl@musica.mcgill.ca (P. Lachapelle).

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Baedeker & Wolf, 1987; Musselwhite & Jeffreys, 1985). For example, while some studies revealed a linear relationship between the PVEP and RT over a specific range of contrasts (Hartwell & Cowan, 1993), others could only demonstrate a partial (McKerral, Lachapelle, & Benoit, 1992) or no correspondence at all (Hartwell & Cowan, 1993) between the two measures over a limited range of luminances or spatial frequencies respectively. Furthermore, most studies which compared PVEPs with RTs were performed without obtaining the two measures simultaneously and some used different stimuli to evoke the two responses.

Given the above discrepancies, the purpose of our study was to explain the existing differences between electrophysiological and psychophysical measurements of visual transmission time by comparing the contrast- and spatial frequency-dependence of the amplitude and peak time of the P1 wave of the PVEP with that of the simultaneously recorded simple motor RT in order to examine if they were similarly modulated. Our results, in showing that the RT and PVEP are differently influenced by the stimulus combinations used, would suggest that these two measures of retino-cortical processing are mediated distinctly along the visual pathways.

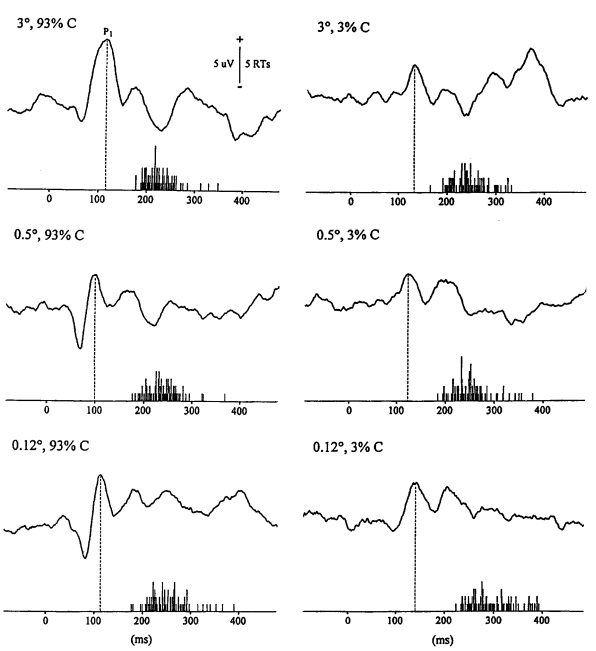

Fig. 1. Representative PVEP waves and RT histograms obtained from one subject (29 years old) for the three spatial frequencies tested at 93% (left column) and 3% (right column) contrast levels. A vertical line links the P1 wave of the PVEP to the abscissa in order to better appreciate the peak time shifts across stimulus conditions. °, degrees of visual angle; C, contrast. Stimulus onset occurs at time 0 ms. Vertical calibration: 5 μV (PVEP) or five reaction times.

2. Methods

2.1. Subjects and recording procedure

Simultaneous recordings of monocular full-field PVEPs and RTs were obtained from the preferred eye of seven normal subjects aged 12–32 years, all of whom had best corrected visual acuities of 20/20 or better. There was only one child subject and there were no PVEP or RT differences related to age. The research followed the tenets of the Declaration of Helsinki, informed consent was obtained from all subjects after the nature and possible consequences of the study had been fully explained, and the research was approved by the Institutional Review Board of the Montreal Children's Hospital.

PVEP and RT responses were evoked to the reversal of a checkerboard screen generated by a Grass model 10 visual pattern generator and displayed on a black and white monitor positioned 2.28 meters from the subjects. The stimulus field covered 12° horizontal by 9° vertical. The subjects, who were not dark-adapted prior to recordings, were instructed to fixate a small red dot placed in the center of the screen and ocular stability was verified visually by the experimenter. PVEPs and RTs were evoked to checks of 0.12, 0.5 and 3° of visual angle in size and 93 and 3% contrast levels, for a total of six stimulus conditions which were presented in random order, respectively. Stimulus luminance was held constant at 30 cd/m^2 across conditions. The interstimulus interval varied between one and two seconds (0.5–1 Hz reversal rate) in order to eliminate anticipatory RT responses (Roy, Lachapelle, Polomeno, Frigon, & Lepore, 1994).

PVEPs were recorded with the active electrode placed at O_z and reference and ground clipped to each earlobe (Grass silver cup electrodes) (McKerral, Roy, Benoit, Lepore, & Lachapelle, 1997; McKerral, Lachapelle, Tremblay, Polomeno, Roy, Beneish, & Lepore, 1996). Electrode impedance was measured and kept below 5 kΩ (Grass electrode impedance meter, model EZM5). The PVEP signals (sweep duration: 600 ms; 100 ms pre-stimulus delay) were obtained within a 1–100 Hz bandwidth and amplified 50 000 ×. For RT measurements, the subjects were instructed to signal the reversal of the checkerboard stimulus by pressing a manual switch (with their preferred hand) which triggered the data acquisition (Computerscope-Enhanced Graphics Acquisition and Analysis: EGAA, RC Electronics, Goleta, CA). One hundred PVEP and RT measurements were recorded simultaneously in blocks of 50 (with a short break between the two blocks) for each stimulus condition. All data were recorded in a single recording session that lasted about one hour and a break was also given between each stimulus condition tested. Each PVEP tracing illustrated represents an average of 100

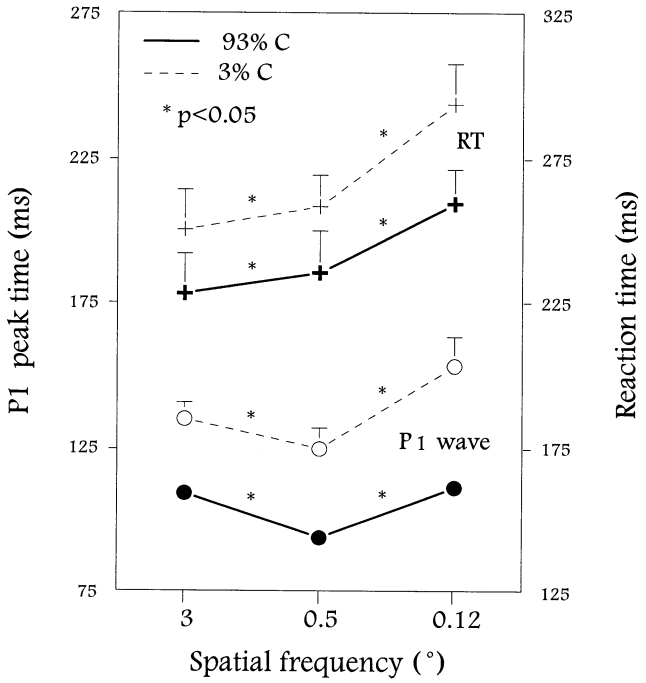

Fig. 2. Mean group peak time results (in ms + 1 S.D.) across spatial frequency for the P1 wave of the PVEP and for the RT at 93% (filled symbols, thick lines) and 3% (open symbols, thin lines) contrast levels. C, contrast. Error bars are smaller than the size of data points for P1 wave at 93% contrast. *, statistically significant differences across spatial frequency.

responses (Fig. 1). For the RT, the data were graphically reported in the form of post-stimulus time histograms (PSTH) containing 100 RTs, where each vertical bar represents one or more responses (Fig. 1).

2.2. Data analysis

The amplitude of the P1 wave of the PVEP (linked by vertical line to abscissa in Fig. 1) was measured in a peak-to-peak fashion (i.e. from the preceding trough to the P1 peak) and its peak time was measured from reversal onset (at 0 ms) to peak. For the RT, the individual measurements obtained for each stimulus condition were transferred to a spreadsheet (Quattro Pro, Borland International, Scotts Valley, CA) where responses faster than 140 ms or slower than 400 ms, which accounted for $< 3\%$ of the trials, were rejected on the grounds of anticipatory responses or responses due to inattention (Roy et al., 1994). The amplitude and peak time of the P1 component of the PVEP and the RT mean, mode and standard deviation parameters were compared in responses obtained to the stimulus conditions used. Statistical analyses were performed with repeated measures ANOVA and Student t-tests when applicable.

3. Results

Representative PVEP waves and RT histograms obtained from one subject to stimuli differing in contrast and spatial frequency are shown at Fig. 1. The peak time of the P1 wave of the PVEP demonstrates a spatial frequency selectivity in that it is faster in response to the 0.5° stimuli compared to that measured at larger or smaller check sizes, and that irrespective of the contrast level used (93% contrast: 3° checks = 114.8 ms, 0.5° checks = 98.0 ms, 0.12° checks = 113.6 ms; 3% contrast: 3° checks = 134.0 ms, 0.5° checks = 125.6 ms, 0.12° checks = 138.8 ms). Conversely, the RT appears progressively delayed as the check size decreases (93% contrast: 3° checks = 229.3 ms, 0.5° checks = 242.0 ms, 0.12° checks = 255.1 ms; 3% contrast: 3° checks = 245.6 ms, 0.5° checks = 253.5 ms, 0.12° checks = 297.0 ms).

Group data analysis (Fig. 2) reveals that at both high and low contrast, the P1 wave demonstrates a statistically significant ($P < 0.05$) spatial frequency tuning where the shortest peak time is obtained with the 0.5° stimuli for all subjects. There is no such evidence of a spatial frequency selectivity for RT measurements. Rather, the latter demonstrate, at both contrast levels, a gradual and significant ($P < 0.05$) increase in timing with progressively smaller check sizes. Notwithstanding the above, it is important to note that a reduction in contrast from 93 to 3% significantly ($P < 0.05$) and similarly lengthens the timing of the PVEP P1 component and the RT evoked to all the check sizes used.

In view of the above results, which show that the PVEP and RT are differently modified by the stimulus conditions used, we sought to relate our observations to the selective response characteristics of the two parallel visual pathways in order to identify their respective contributions to the RT and to the PVEP. We thus tested the postulate proposed by Barlow and Levick (1969) that responses dominated by magnocellular (M) visual neurons would be: (1) of shorter latency because M cells are faster-responding; and (2) less variable since these neurons respond in a more transient fashion compared to the sustained parvocellular (P) cells. We postulated that stimuli of lower contrast and spatial frequency should primarily recruit M-pathway activity and thus yield a PVEP response of shorter peak time, and a RT distribution with a faster mean latency and a smaller standard deviation (i.e. less variation) than PVEP and RT measurements evoked to stimuli of higher contrast and spatial frequency which would recruit P-pathway activity.

Considering the physiological response characteristics of the M and P pathways (DeYoe & Van Essen, 1988; DeMonasterio & Gouras, 1975), the 3% contrast, 3° stimulus condition was considered as that recruiting a M-dominated response, while the 93% contrast, 0.12° one was chosen to mainly recruit a P-dominated re-

sponse. The PVEP and RT results obtained in response to these stimulating conditions are reported at Fig. 3(A–B), respectively. PVEP results (Fig. 3(A)) reveal that the amplitude of wave P1 is significantly ($P < 0.05$) larger and its peak time significantly ($P < 0.05$) shorter for the stimulus favoring a P pathway activation. For the RT (Fig. 3(B)), we compared the mode, mean and standard-deviation parameters. Results show that the mean RT is shorter, although not quite significantly in the M condition, and the mode occurs at a significantly ($P < 0.05$) faster time in the M compared to the P condition. Furthermore, the reaction time variability, as reflected with the standard-deviation, is significantly ($P < 0.05$) smaller in the M-recruiting stimulus condition.

4. Discussion

In this study, we have investigated the contrast and spatial frequency dependence of simultaneously recorded PVEPs and simple motor RTs. The originality of the present study not only lies in the fact that we concomitantly varied the contrast and spatial frequency of the stimulus, but also that PVEP and RT responses were recorded simultaneously. In contrast, previous reports which compared PVEP and RT responses did so with measures obtained separately (Musselwhite & Jeffreys, 1985). Similarly, those strictly interested with PVEP responses either obtained their data with a range of spatial frequencies and only one contrast level (e.g. high contrast) (Török, Meyer, & Wildberg, 1992; Kurita-Tashima, Tobimatsu, Nakayama-Hiromatsu, & Kato, 1991), or with a range of contrasts and only one check size (e.g. intermediate spatial frequency) (Previc, 1988).

Our results show that at both high and low contrast levels, the peak time of the P1 wave of the PVEP demonstrates a spatial frequency selectivity at 0.5°, while the RT does not exhibit a similar spatial frequency tuning, its timing increasing as the size of the checks decreases, and that irrespective of contrast. Our results are in line with previous studies which showed a spatial frequency selectivity for the peak time of the P1 wave obtained at high contrast (Kurita-Tashima et al., 1991; Rimmer et al., 1989; Musselwhite & Jeffreys, 1985), as well as with studies which demonstrated a gradual lengthening of manual response times with increasing spatial frequency (Felipe et al., 1993; Parker & Dutch, 1987). However, these are separate studies in different subjects and do not allow a completely accurate inter-technique comparison of retino-cortical timing measurements.

Advantages to the simultaneous recording of electrophysiological and psychophysical techniques reside firstly in minimizing variability. In a previous study, we showed that the mean motor RT coefficient of variability was 1.6–1.7 times greater than that of the PVEP, which was a similar value as that obtained with other reaction time modalities and measurement approaches (McKerral et al., 1992). The same study also demonstrated that the mean motor RT coefficient of variability could vary from 5.7 to 11.7% depending on the stimulating conditions used. The above indicates that the RT is a reproducible and robust measure, but that when comparing it with electrophysiological data, it should be obtained in identical conditions to minimize inter-session variability. Second, since parameters (e.g.

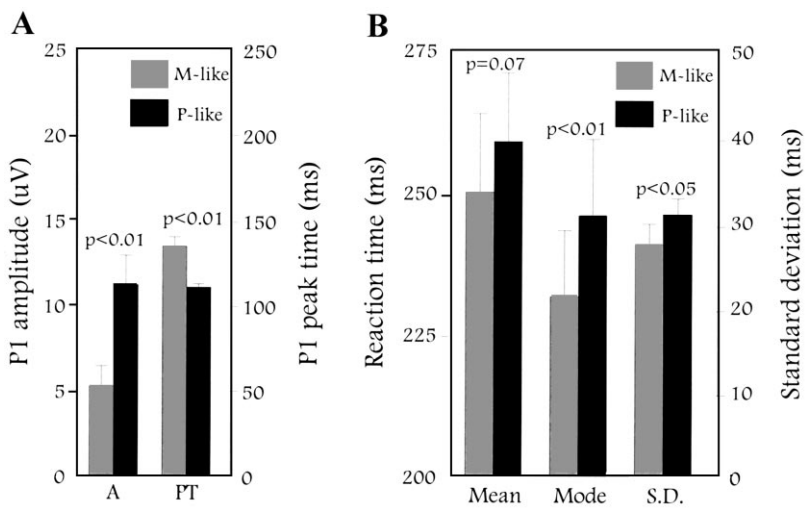

Fig. 3. (A) Mean group PVEP amplitude (in μV + 1 S.D.; left ordinate) and peak time (in ms + 1 S.D.; right ordinate) results for component P1 obtained to the M-like (3° checks, 3% contrast; hatched bars) and P-like (0.12° checks, 93% contrast; black bars) stimulus conditions. A, amplitude; PT, peak time. (B) Mean group RT mean and mode (in ms + 1 S.D.; left ordinate) and standard deviation (in ms + 1 S.D.; right ordinate) data for the M-like (3° checks, 3% contrast; hatched bars) and P-like (0.12° checks, 93% contrast; black bars) stimulus conditions. S.D., standard deviation.

low contrast) that render more difficult an accurate detection of the stimulus increase the variability of the RT as well as that of the PVEP, their simultaneous recording will also reduce undue variability.

The fact, however, that the RT does not exhibit a spatial frequency selectivity similar to that seen with the major component of the PVEP (i.e. P1), even when both measures are obtained simultaneously, indicates that the PVEP and RT are either relayed by different components of the retino-cortical pathways or modulated by different aspects of the stimulus. Both methods of evaluating retino-cortical processing can be broken down into the following three steps, namely: (1) perceptual integration time; (2) transmission time; and (3) delay in response process. However, the RT differs from the PVEP in that this psychophysical method also includes a motor component. It is, nonetheless, unlikely that the discrepancy between these two measures is due to the latter, since it is assumed that it adds a constant to the perceptual latency, given that there is no change in the task across stimulus conditions (Ejima & Ohtani, 1987).

One could hypothesize that the PVEP (as represented with the P1 wave) and the RT recruit contributions from specific but different portions of the visual neural population. The P1 wave of the PVEP was, at one time, suggested to reflect a response to motion (i.e. M pathway) due to the apparent lateral movement that a checkerboard produces while reversing (Spekreijse, Dagnelie, Maier, & Regan, 1985). However, other authors demonstrated a major contribution of the central retina to the P1 wave of the PVEP (Kubová, Kuba, Juran, & Blakemore, 1996; Sokol, 1976), that is the retinal region which comprises the highest number and density of neurons projecting to the P pathway (Van Essen & DeYoe, 1995; Dowling, 1987; Stone, 1983). Furthermore, in a previous study where we investigated hemiretinal contributions to the timing of the PVEP, we also obtained results suggesting that the P1 wave originates from the central retina (McKerral et al., 1997). Consequently the present findings, in showing that the P1 wave is highly dependent on contrast, along with those described above, are in line with the results of a recent study which suggested that the P1 wave of the PVEP would be produced by the contrast reversal of the black and white checkerboard (Kubová et al., 1995), and thus suggest that the P1 wave would reflect specific activation of the pattern processing system (i.e. P pathway).

As for the RT task, it requires, contrary to the PVEP, a conscious detection of the stimulus in order for a response to be produced. Furthermore, during the recording sessions, some subjects reported a subjective impression that the stimulus was moving, suggesting that the RT could have been triggered by the perception of movement of the stimulus. Consequently, it could be argued that with our experimental procedure where the subjects had to respond to the reversal of a checkerboard screen, neurons involved in the detection of motion (i.e. M pathway) contributed more to the RT than to the PVEP (as represented with the P1 wave), the latter being more closely linked to the pattern processing system (i.e. P pathway) (Kubová et al., 1995). Thus, the distinct tuning curves which characterise the PVEP and RT responses (Fig. 2) could ultimately reflect the physiological differences between the M and P pathways which contribute to these two measures. The faster portions of the RT tuning curve (i.e. those corresponding to lower spatial frequencies) would reflect M pathway activation, while the spatial tuning curve of the P1 wave of the PVEP would primarily reflect P pathway activity.

The present study also tested the hypothesis proposed by Barlow and Levick (1969) which stipulated that responses modulated by the M pathway would be of shorter latency and less variable, since M cells respond faster and more transiently than P cells. Our results support the above hypothesis. The mean and mode of RT distributions (i.e. visual latency) are shorter for stimuli of lower contrast and spatial frequency. Similar findings favoring a sustained/transient dichotomy have also been demonstrated using flicker detection (Kelly & Burbeck, 1987). Furthermore, the standard-deviation (i.e. variability) was smaller for the M-recruiting stimulus. Using hetero- and homochromatic stimuli, Schwartz (1992) reached a similar conclusion in showing shorter latencies and more tightly clustered RT distributions in stimulus conditions associated with the achromatic (i.e. M) than with the chromatic (i.e. P) system. These findings suggest that the stimulus combinations used in our study, to produce simple motor RT histograms, appear to have favored responses from the M or P pathways. Thus, provided that appropriate stimuli are utilized, our results clearly indicate that the RT technique represents a reliable alternative (to PVEP recording) to investigate separately the function of the parallel visual pathways.

In conclusion, we have shown that the PVEP and RT responses are differently mediated by the retino-cortical pathways and consequently can be of help in further characterizing anomalies of visual function (McKerral, Polomeno, Lepore, & Lachapelle, 1999). Our results also show the importance of obtaining electrophysiological and psychophysical measures concomitantly to insure elimination of combined inter-stimulus and inter-session variability. The simultaneous use of these techniques, when assessing patients afflicted with disorders of the retino-cortical pathways, whether developmental (e.g. amblyopia) or acquired (e.g. traumatic brain injury), is thus indicated in order to refine our diagnostic ability with functional testing.

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