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Peripheral and central delay in processing high spatial frequencies: reaction time and VEP latency studies

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Abstract

Visually evoked potentials (VEP) and reaction time (RT) were recorded under stimulation with sinusoidal gratings. Grating spatial frequency (SF) was 0.5, 5 or 12 cd and grating contrast was varied. Consistent with previous findings, both VEP latency and RT increased with the increase of grating SF and with the decrease of grating contrast. It was found, in addition, that RT and VEP latency increased by approximately the same amount when SF increased from 0.5 to 5 cd, thus suggesting that the main source of the RT delay at 5 cd in comparison with RT at 0.5 cd is of peripheral origin. However, in comparison with the data at 0.5 and 5 cd, RT at 12 cd increased much more than VEP latency. We conclude that the RT delay at high SF involves a substantial central component in addition to the peripheral delay. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Reaction time (RT) to grating stimuli is prolonged when grating spatial frequency (SF) is increased (Breitmeyer, 1975; Vassilev & Mitov, 1976; Lupp, Hauske & Wolf, 1976; Felipe, Buades & Artigas, 1993; Bonnet, Thomas & Fagerholm, 1996). Similarly, visually evoked potentials (VEP) are delayed on increasing grating SF (Parker & Salzen, 1977; Jones & Keck, 1978; Vassilev & Strashimirov, 1979). These findings have been interpreted as evidence of slower processing of high SF signals in comparison with low SF signals. Models of perceptual phenomena such as perception of form (Mitov, 1982; Watt, 1987; Parker, Fraser & Lishman, 1988) or global precedence (Hughes, Nozawa & Kitterle, 1996) are based on this inference. The nature of the delay is, however, a matter of debate (Parker & Salzen, 1977; Vassilev & Strashimirov, 1979; Musselwhite & Jeffreys, 1985; Vassilev & Stomonyakov, 1987).

An important piece of information concerning the origin of this delay could be obtained by comparing RT and VEP data. RT comprises components of peripheral sensory and motor origin as well as components of

central origin (Welford, 1980). In most RT experiments cited above care has been taken to ensure constancy of the motor RT component. If the latency of the early VEP waves reflects mainly the peripheral sensory processing and conduction time, any change in the difference between RT and VEP latency would mainly depend on changes in the central processing time. Thus, the comparison of RT and VEP latency would help to determine whether delay is taking place at peripheral sensory level or at central level. Surprisingly, no systematic comparison of RT and VEP latency exists. Musselwhite & Jeffreys (1985) and Strasburger, Scheidler & Rentschler (1988) were probably the only ones to point out that, with increasing grating SF, RT increases at a higher rate than VEP latency. Since Musselwhite and Jeffreys found no VEP delay with gratings of the same suprathreshold contrast level, their data suggest that, when contrast sensitivity reduction at high SF is compensated for, the RT increase at high SF is due entirely to a central delay. However, the lack of VEP delay with gratings of the same suprathreshold level was not confirmed (Vassilev & Stomonyakov, 1987).

We re-examined the relationship between RT and VEP latency because of its importance for the correct application of the data on the temporal order of processing of low and high SFs in models of perceptual

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phenomena such as global precedence (Hughes, 1986; Hughes, Nozawa & Kitterle, 1996). Some of the results obtained are, however, of interest concerning the question of peripheral or central origin of RT delay at high SFs, and are the subject of the present paper.

2. Methods

2.1. Stimulation

Vertical sine-wave gratings were generated on the screen of an X-Y display Tektronix 608 with white phosphor (P4) by electronics designed in our laboratory (Manahilov, 1995). The frame rate was 200 Hz and the mean luminance was 30 cd/m². The subjects fixated a small black mark (x) at the screen centre. A back-illuminated transparency of 30 × 30° of arc surrounded the screen. It approached the screen in luminance and hue. Viewing was binocular, with natural pupils, from a distance of 114 cm, at which the screen subtended 5.5/3.9° of visual angle at the eyes. A forehead- and chin-rest minimised head movements. The display and the subject were in a sound- and electrically-shielded chamber, where the only light sources were the display and its surround.

Stimulus SF was 0.5, 5, or 12 cd and its contrast ranged from 2.5 to 50%. Contrast was measured in percent as $m = 100 \times (L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$. Stimulus duration was 100 ms.

Four emmetropic right-handed observers ranging in age from 19 to 28 years participated in all experiments. Their handedness was evaluated by the Edinburgh Inventory (Oldfield, 1971, Appendix II). For all subjects, the laterality quotient was above 85.7. All subjects, except one, who was also an author (MM), were naive as to the aim of the study. All subjects were given training in RT experiments.

2.2. VEP recording

Stimuli of a given combination of SF and contrast were presented in a block. The interstimulus interval was randomly varied within the range of 700–1400 ms. Blocks of different SFs and contrast were presented in random sequences.

As far as VEPs to stimuli of varying contrast were to be recorded, including near-threshold contrast, we were interested in techniques enhancing the signal-to-noise ratio. Hjorth (1975) has shown that the Laplacian analysis increases the signal-to-noise ratio, is independent of the reference electrode, and, by sensing the local curvature of the potential field, attenuates the contribution from remote generators. The advantage of Laplacian analysis has been recently demonstrated by Manahilov, Riemslog & Spekreijse

(1992). In order to apply Laplacian analysis VEPs were recorded from Oz and two other points placed 4 cm to the left and to the right of Oz. The reference electrode was positioned on the left mastoid and an Fp electrode served as a ground. The signal was amplified, band-pass filtered (0.5–70 Hz) and fed into a microcomputer at a sampling interval of 2.48 ms. Sweeps started 62 ms before grating onset and lasted for 632 ms. Traces with artefacts were automatically discarded. The three-point Laplacian was calculated off-line as twice the potential at Oz minus the sum of the potentials at the lateral electrodes (Flanagan & Harding, 1986). At each combination of SF and contrast, 20–100 sweeps were recorded in a daily session. The number of sweeps depended on the signal-to-noise level expected from pilot experiments. This ensured obtaining Laplacians with an early negative wave exceeding the pre-stimulus fluctuations at least by a factor of three. With each subject, the responses obtained in two to six daily sessions, depending on stimulus parameters, were averaged for final processing.

2.3. RT measurement

While the stimuli were the same as those used in the VEP recording, their presentation was different due to the requirements of the RT experiments. In order to reduce time uncertainty effects on RT, as well as the variability in subject's readiness to respond, each trial was started by the subject. He (she) pressed a key by the left hand. This produced a click and 800 ms later a grating might appear with a probability of 0.5. The subjects were instructed to respond as soon as possible to the grating onset by pressing another key on a separate keyboard by the right hand. Following a practice period, RT was measured in seven daily sessions. Each daily session consisted of three blocks of trials. Within a block, the grating SF was fixed, 0.5, 5 or 12 cd, while grating contrast varied randomly from trial to trial taking any one of eight pre-determined values within the 2.5–50% range. A block was automatically terminated when the grating was presented ten times at each contrast level. The serial position of blocks was counterbalanced across different days. RT was measured by a microcomputer with an accuracy of 1 ms. The false positive responses were less than 2% of the total trials. The subjects responded to all stimuli of the contrast of 7% or higher but might happen to miss stimuli at contrast levels below 7%, particularly at 12 cd, (those could also be responses with RTs longer than 1 s, the maximum time interval programmed for RT recording).

The RT and VEP daily sessions were alternated.

2.4. Contrast thresholds measurement

Contrast thresholds were measured using a two-interval forced choice method, combined with the staircase procedure described by Stomonyakov & Vassilev (1996).

3. Results

An example of the VEPs is shown in Fig. 1. Only traces from -50 to $+300$ ms are shown because of the lack of any significant later potential modulation. Negativity is downward and positivity is upward. The three groups of traces were recorded at 0.5, 5, and 12 cd at

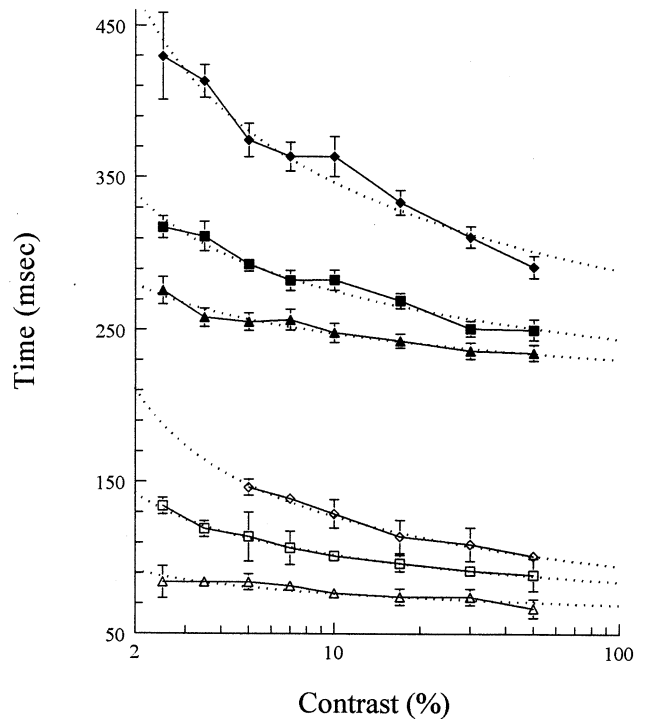


Fig. 2. Reaction time and peak latency of the early VEP wave as functions of grating contrast at three SFs: 0.5 cd, triangles; 5 cd, squares; and 12 cd, diamonds. Open symbols—VEP latencies, filled symbols—RTs. Vertical bars—95% confidence intervals of the means ($S.E. \times t_{0.05}$). If no vertical bar is present, the confidence interval is smaller than the symbol. Dashed lines—Pieron's power functions ($a + bm^{-n}$, where m is grating contrast) fitted to the experimental data. Subject MT.

various contrast levels. Note that the voltage scale is not the same with all records. The largest VEPs were recorded at 5 cd and VEP amplitude was lower at both 0.5 and 12 cd. Dashed lines across the traces connect the peaks of the early negative wave, the latency of which was the first reliably measured VEP latency.

The dependencies of VEP latency and RT on grating contrast at the three SFs are illustrated in Fig. 2. Vertical bars represent the 95% confidence intervals of the means ($S.E. \times t_{0.05}$). The lower three graphs are for the VEP-latency/grating-contrast functions. As expected, VEP latency was longer at higher SFs and lower grating contrast. In agreement with earlier findings (Musselwhite & Jeffreys, 1985; Vassilev, Stomonyakov & Manahilov, 1994), grating contrast affected more the latency of the response to the high-SF grating, 12 cd in this case, than the latencies at 0.5 and 5 cd.

The upper three graphs in Fig. 2 demonstrate the dependence of RT on grating contrast and SF. In common with VEP latency, RT was shortest at 0.5 cd and longest at 12 cd at any contrast level. In line with the findings of Musselwhite & Jeffreys (1985), the RT functions were as a rule steeper than the VEP functions for the same SF and contrast range (this property is

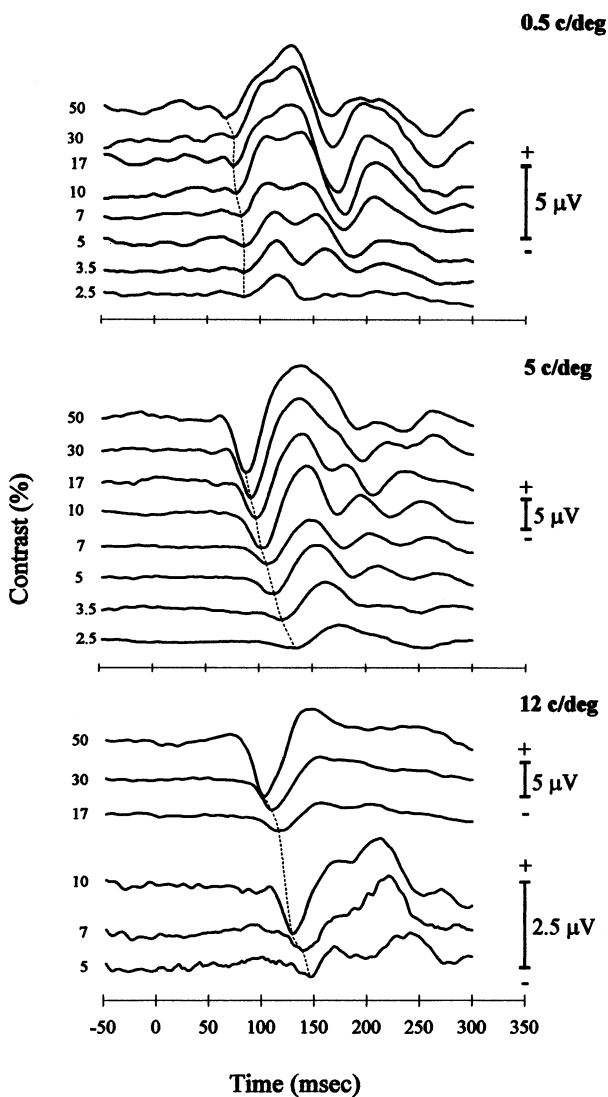


Fig. 1. Onset VEPs at three SFs: 0.5 (upper panel), 5 (middle panel) and 12 (lower panel) cd and various grating contrast levels. Grating contrast is shown on the left of each trace. Dashed lines connect the peaks of the early negative wave, the latency of which was measured. Different voltage scales are used in order to ensure visibility of the relevant waves. Subject MT.

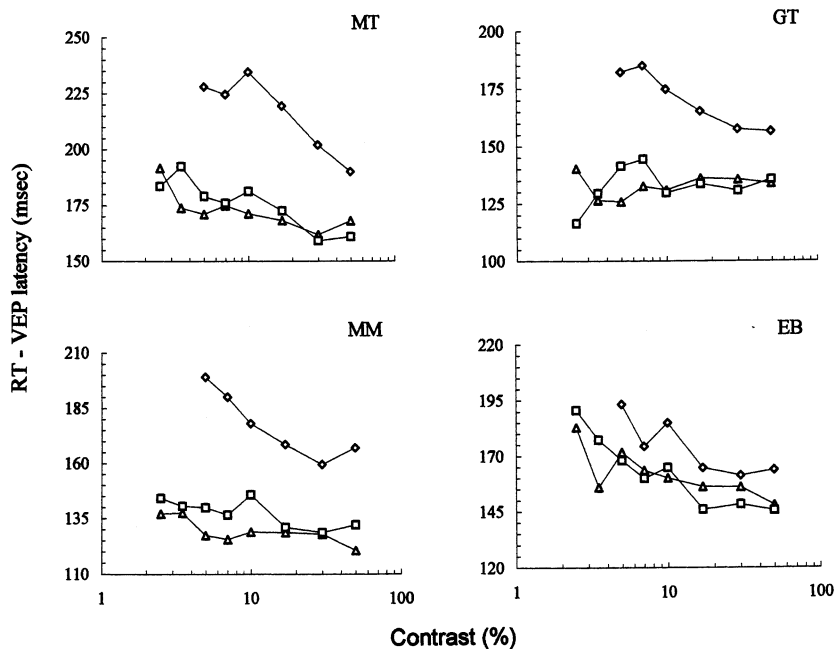


Fig. 3. The difference between RT and VEP latency ('relative RT delay') as a function of grating contrast at three SFs: 0.5 cd, triangles; 5 cd, squares; and 12 cd, diamonds. Data of all four subjects.

also evident from Fig. 3, where the differences between RT and VEP latency, obtained with all subjects, are presented as functions of grating contrast). The dashed curves in Fig. 2 are power functions of RT and VEP latency versus grating contrast, fitted to the experimental data according to Pierson's Law (with contrast substituting for stimulus intensity). Fitting was performed according to the least-squares method. Within the 95% confidence interval, most experimental points lie on these curves. A corollary RT finding is the confirmation of a previously reported (Harwerth & Levi, 1978; Felipe, Buades & Artigas, 1993) deviation of some experimental points from a single power function. With three of our four subjects RT at 5 cd was significantly longer than the predicted level at grating contrast of 10% (two subjects) or 7% (one subject). Similar deviations were also found with two subjects at 12 cd and contrast of 10%. These points tended to form a plateau with the closest points of lower contrast in the RT/contrast curves. Such a plateau has been reported by Harwerth & Levi (1978) and Felipe, Buades & Artigas (1993) in the same contrast range.

The point of main interest in the present work was the comparison of RT with VEP latency measured at the peak of the early negative wave in the Laplacian record. Fig. 3 represents the RT minus VEP latency values (named 'relative RT delay' here) obtained with all subjects at 0.5, 5 and 12 cd as functions of grating contrast. The feature that is immediately seen is that the relative RT delay was almost the same at 0.5 and 5 cd but was much larger at 12 cd. It was of the order of 116–192 ms at 0.5 and 5 cd, depending on the subject

and grating contrast and between 157 and 234 ms at 12 cd. The relative RT delay decreased on increasing grating contrast. The steepest decline on increasing grating contrast was observed at 12 cd.

We also calculated the relative RT delay from published data of Musselwhite & Jeffreys (1985) who recorded both RT and VEP (the so-called CI, which is an early wave) at 1, 4, and 10 cd as a function of grating contrast. The relative RT delay in their experiments turned out to be a little bit larger at 4 cd than at 1 cd and much larger at 10 cd. Thus, relationships similar to those in Fig. 3 are also present with a slightly different SF-set and VEP recording technique. Unfortunately, Musselwhite and Jeffreys obtained comparable RT and VEP data with one subject only.

4. Discussion

Like RT, VEP is a complex phenomenon and simultaneous electrical activity from both striate and extrastriate origin contribute to its early waves (Maier, Dagnelie, Spekrijse & van Dijk, 1987). This complexity renders difficult the interpretation of the functional significance of its latency and hence of the relative RT delay. We assume here that the latency of the early VEP waves recorded in the present experiments corresponded to the onset of striate cortex activity. Our assumption is based on the following. The early wave of the VEP to sinusoidal gratings has been interpreted as a surface negative wave originating in striate cortex (Parker, Salzen & Lishman, 1982). Like Parker et al.,

we observed in a control experiment, the data of which are not illustrated here, polarity inversion of the early wave in the monopolar VEPs from the left and right electrodes when the stimulus position was changed from the left to the right visual field. At the same time, the largest early wave was recorded from Oz and the Laplacian was not affected by stimulus position. Source derivation (Flanagan & Harding, 1986; Manahilov, Riemslog & Spekreijse, 1992) and pattern adaptation (Manahilov, Riemslog & Spekreijse, 1992) experiments suggest that the generator of the early negative wave in the Laplacian record, centred at Oz, is located in the striate cortex. The latency of this wave is comparable to the latency of the negative wave recorded by us when stimulus spatial dimensions and contrast are taken into account. Furthermore, in the present experiments, the asymptotic peak latency level of the earliest detectable negative wave was between 67 and 79 ms at 0.5 cd with our four subjects, i. e. close to the latency of the early negative wave in human flash VEP, the source of which has been estimated by Kraut, Arezzo & Vaughan (1985) to be located in layer 4C of V1, the recipient layer of the primary visual cortex (see also Regan, 1989). We assume, therefore, that the peak latency of the early negative wave, measured by us, is nearly equal to the time necessary for the neural signals, triggered by grating onset, to reach the primary visual cortex. If this is the case, the relative RT delay (Fig. 3) is a sum of the other RT components: the central component for signal detection, decision and organisation of the motor response as well as the peripheral motor component, i.e. the time necessary for the conduction of motor commands and response execution. Insofar as there were no differences in the motor task across the stimuli, we also assume that the average peripheral motor time is constant across stimulus SF and contrast. Hence, the results presented in Fig. 3 show that the central RT component was almost the same at 0.5 and 5 cd and longer by 20–70 ms at 12 cd. In other words, a significant additional central delay at 12 cd occurred before the execution of the motor response.

As it can be seen from Fig. 3, the relative RT delay was longer at low than at high grating contrast (with the only exception at 0.5 and 5 cd with Subject GT). The contrast effect was particularly strong at 12 cd. It is therefore tempting to suggest that the longer central RT delay at 12 cd is a contrast effect. We have in mind both the reduced contrast sensitivity at this SF and the physical modulation transfer function (MTF) of the display monitor (Morgan & Watt, 1982). Monitor MTF might reduce grating contrast, particularly at 12 cd. If the effect were purely due to monitor MTF, we should be able to obtain identical curves at all three SFs simply by shifting the uppermost curve to the left. Such a manipulation would be effective with the data of one subject only, EB. Estimates of monitor MTF,

performed after Morgan & Watt (1982), indicated a contrast reduction of about 8% at 12 cd for the testing distance of 114 cm. The corresponding shift of the 12 cd curve along the abscissa would not eliminate its difference from the other curves for any subject. We also measured contrast sensitivity of all subjects at each SF (Table 1), and redrew our Fig. 3 with suprathreshold contrast levels instead of nominal contrast on the abscissa. The results were essentially the same: the relative RT delays grouped together at 0.5 and 5 cd and were higher at 12 cd. Factors other than monitor MTF and subjects' contrast sensitivity might be responsible for the additional RT delay at high SF.

The analysis of the relative RT delay within the framework of subjects' contrast sensitivity might be, however, misleading. It is well known that RT sharply increases at near-threshold levels and, at these levels, the correspondence between RT and other measures of relative perceptual delay breaks down probably because of subjects' uncertainty about the stimulus presence (Roufs, 1974). RT and VEP latency are parallel functions when stimulus intensity is at least 0.6 log units above threshold while the RT-VEP latency difference increases at lower intensity levels much like the RT increase (Krauskopf, 1973). In view of these data, our findings of a larger relative RT delay at 12 cd might be considered due to subjects' uncertainty. This factor seemed to be of importance at low contrast, up to 7%, where misses of the grating of the highest threshold, the 12 cd grating, were observed during the RT experiments (5 and 2.1% missed at 5 and 7% contrast, respectively, averaged across subjects) and it might play a role at somewhat higher contrast levels. However, the difference in the relative RT delay with stimuli of different SFs was not merely a result of differences in contrast sensitivity. It was also present when the relative RT delay was plotted against relative grating contrast, i. e. against contrast in threshold units (not shown because of similarity with Fig. 3). The relative RT delay was larger at 12 cd than at 0.5 and 5 cd even at the highest contrast levels which in the present experiments reached 30–50 times the threshold contrast, i.e. far above the uncertainty range. Note that the relative RT delay

Table 1
Threshold contrast and its 95% confidence interval at 0.5, 5, and 12 cd

Stimulus SF (cd)	Subjects			
	MT	MM	GT	EB
0.5	1.17 ± 0.1	0.96 ± 0.07	0.70 ± 0.06	1.01 ± 0.09
5	0.64 ± 0.1	0.81 ± 0.05	0.53 ± 0.09	0.78 ± 0.08
12	1.52 ± 0.06	1.03 ± 0.07	1.36 ± 0.06	1.62 ± 0.05

Data of all four subjects.

reached asymptotic levels for all SFs with most subjects. We conclude that the larger relative RT delay at 12 cd and high contrast, reported here, reflects SF specific slower central signal processing at high SFs. The slower processing at high SFs is probably cortical or takes place after the cortical activation in view of the data of striate-cortex localisation of the generator of the wave used in the calculation of the relative RT delay.

Considering brain activation as a momentary process and measuring the so-called central delay is a simplification. We accepted it in order to be able to carry out the above analysis. It should however be taken into account that the peak latency of the early negative wave is in fact an overestimate of the peripheral sensory time. This error is not the same at all SFs because of differences in the amplitude and time course of the waves. The records presented in Fig. 1 suggest a larger error at 5 cd than at 0.5 cd. As a result, the central processing time would be underestimated to a larger degree at 5 cd than at 0.5 cd. We assume, therefore, that a slightly longer central processing time at 5 cd than at 0.5 cd is a more reasonable inference than the equality suggested by the data in Fig. 3. We attempted measuring the latency of the onset of the early negative wave in order to solve this problem. For obvious reasons such a latency is difficult to measure. Where possible, we measured the onset latency and compared it with the RT. The relative RT delay obtained in such a way was slightly longer at 5 than at 0.5 cd, thus confirming the above conclusion. On the other hand, RT-VEP latency difference (Fig. 3) was so large at 12 cd that the above analysis does not concern the inference of a slower central processing at 12 cd in comparison with 0.5 and 5 cd. Our previous findings (Vassilev, Manahilov & Mitov, 1983) of a longer delay of the late VEP waves in comparison with the early VEP waves when grating SF is increased are compatible with such an inference. It follows then that, in addition to their longer peripheral sensory time, the high-SF signals are processed at a slower rate by the brain than low- and medium-SF signals.

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