Spatial frequency and hemispheric asymmetries in visual information processing

S. Saunoriūtė-Kerbelienė[1], P. J. Benson[2], O. Rukšėnas[1]

[1] Dept. of Biochemistry-Biophysics, Faculty of Natural Sciences, Vilnius University, LT-2009 Vilnius, Lithuania
[2] Lab Physiology, Oxford University, Oxford, UK

Verbal-visuospatial differences in hemispheric processing could be explained by variations in the processing of spatial frequencies of the sensory stimuli. The main aim of our research was to consider differences in spatial frequencies processing by the left and right hemispheres, using measurements of the visual evoked potentials (VEPs). Subjects were presented with three categories of low-pass filtered visual stimulus: upright faces, inverted faces, vegetables and fruits as control. VEPs were recorded from observers while they judged whether two sequentially presented images showed the same emotion, irrespective of identity, gender and spatial frequency content. Evoked potentials (P300) in the right hemisphere were insensitive to the spatial frequencies used for all categories of stimuli. Potentials recorded over the left hemisphere showed a significant lag (60–100 ms) for higher frequencies compared with the lower frequencies. Differences in the early evoked potentials for facial and non-facial stimuli were also recorded.

Key words: evoked potentials, face, facial expressions, hemispheric asymmetry, spatial frequency

INTRODUCTION

One of the characteristic features of the human brain is that its two hemispheres are functionally differentiated. Despite the accumulation of a great number of empirical reports based on research of controls [1–9] and patients with brain damage [10], the basic problem of the nature of hemispheric specialisation remains unsolved.

Several different dichotomies have been proposed as an explanation, such as verbal-visuospatial or analytic-holistic, but some authors argue that these are unsatisfactory, because they are mainly descriptive and not explanatory [7]. Moreover, the substantial literature from the study of hemispheric asymmetry provides conflicting results that cannot be accounted for by many of the existing theories. In particular, many proposed explanations neglect a body of experimental evidence suggesting that the pattern of cerebral asymmetry may change according to the perceptual characteristics of stimuli.

When discussing the relevance of theory to the classical verbal-visuospatial and analytic-holistic dichotomies, Sergent [8] argued that these might not represent any fundamental differences between the hemispheres. The so-called left hemisphere (LH)-verbal and the right hemisphere (RH)-visuospatial specialisation may emerge from a preferential sensitivity of the hemispheres to particular frequencies of the input, because verbal material requires a high level of sensory resolution for processing, whereas visuospatial stimuli usually do not.

Similar reasoning may explain the analytic-holistic dissociation. Efficient analytic operations require the extraction of details from the stimulus, whereas holistic processing is based on the general contour of the stimulus, leaving finer characteristics and details unrecognised [7].

Based on that, the following hypotheses have been made:

- Hemispheric differences in visuospatial processing may be related to spatial frequency channels identified in psychophysical experiments [11].
- Inverted facial images should decrease the amplitude of the related visual evoked potentials (VEPs) [12].
- Control stimuli (fruit, vegetables) should also alter responses in some way that may reflect cognitive categorisation different from facial processing.

- If the effects of the spatial frequency or hemispheric processing are robust, then alternative category of stimuli might also elicit important differences in VEPs.

METHODS

Participants

Two male observers (PJB and EK) and one female observer (SSK) participated voluntarily (mean age 33 yrs). All had normal or corrected to normal vision.

Material

Subjects were presented with three categories of visual stimulus: upright faces, inverted faces, vegetables (5 kinds) and fruits (6 kinds) as control.

Images of faces were taken from Ekman and Friesen [13]. Images of 6 males and 8 females displaying seven facial expressions (anger, disgust, fear, happiness, neutral, sadness and surprise) were used in the experiment. None of the faces wore glasses, beards, or moustaches.

Stimuli were created by low-pass filtering the original portraits with frequencies 0.5, 2 and 8 cycles/deg (cpd) (Fig. 1). Images were 239 x 360 pixels (11.4 x 17.1 degrees, when viewed at a distance of 57 cm). All stimuli were masked with an eliptical aperture to exclude external features (hair, ears, etc.).

Visual evoked potentials (VEPs) were recorded using right and left mastoid references and eight scalp electrodes at standard EEG recording locations: Oz, FCz, CP3, CP4, P7, P8, T7, T8 (10–20 system; Fig. 2 [14]). The EEG was amplified using an isolated amplifier (Contact Precision Instruments, London, UK). Data were acquired via a Metrabyte DAS-1800HC analogue-to-digital card (Keithley Metrabyte, Tauton, MA, USA) in a standard PC. Software control was via Scan 4.0 ('Acquire' package Neurosoft, USA) which calibrated, acquired and saved the EEG activity to disk. The 'Edit' software extracted and sorted continuous EEG into stimulus-related epochs identified by trigger codes sent from the stimulus presentation software from a separate PC.

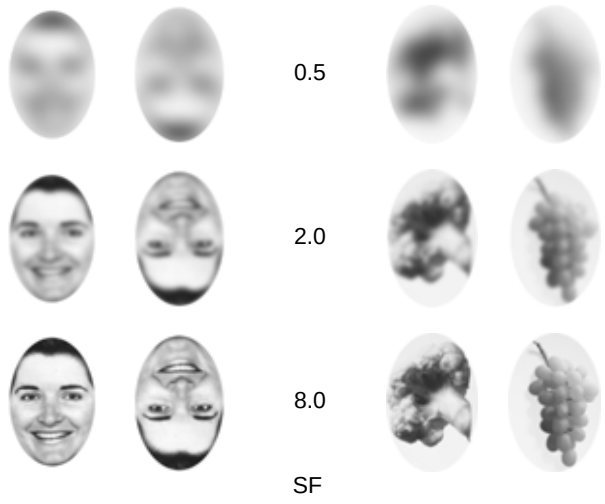

Fig. 1. Examples of facial expressions and food images used as stimuli. SF – spatial frequency

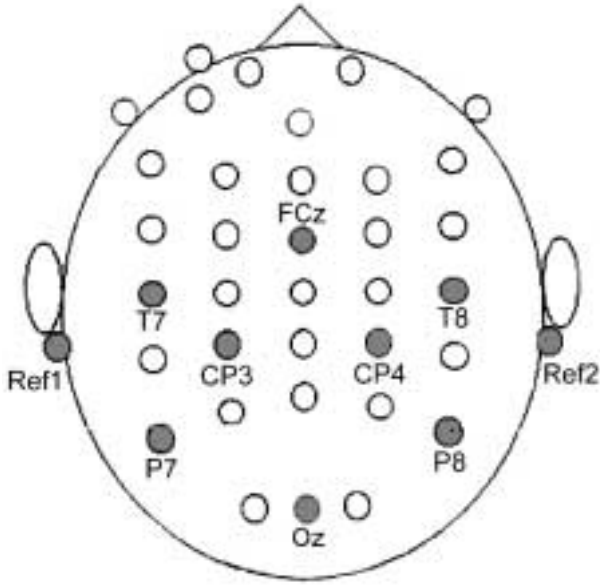

Fig. 2. Schematic view of the 8-channel electrode array [14]. Recording sites highlighted in grey

Trials containing artefacts were rejected and the remaining data were filtered (0.3–50 Hz bandpass) before averaging per stimulus condition (visual field – VF; spatial frequency – SF). Each evoked related potentials (ERP) that consisted of a pre–stimulus baseline (–150–0 ms) and post-stimulus VEP (0–800 ms). Analysis of facial expression will not be presented here, therefore the discussion will be restricted to the stimulus conditions mentioned.

Procedure

Subjects were required to fixate a small point (0.25° in diameter) at the center of the display. The distance between the subject and the screen was 57 cm. Before starting up images, the subject heard a 350 Hz-tone lasting 150 ms. After an initial 2000 ms delay, an unfiltered target image was presented centrally for 50 ms. After 750 ms, a filtered probe image was presented for 50 ms 3° laterally into either the left or right visual field. Subjects were instructed to respond as quickly and accurately as possible – to push an indicated key, if the facial expressions

were the same or different. The next trial followed the subject's response. The inter-trial interval was 1000 ms. Use of different keys for the same and for different responses was counterbalanced. Presentation of stimuli (expression, visual field, spatial frequency) was fully randomised. Fifty to 100 practice trials were given. In addition, observers EK and SSK were shown stimuli lasting 200 ms in order to evaluate the effect of the availability of high SF presented for the normal period of 50 ms. Stimuli were fully randomised, and then selected in blocks of ~120 trials to minimise fatigue. A total of presented trials was 6750 (mean, 2233/observer).

RESULTS

Several interesting properties of the stimulus-evoked potentials were evident. In general, we found that VEPs recorded over CP3 and CP4 had the greatest amplitude. Averaged VEPs at Oz were flat. At FCz, potentials were larger but very similar in shape to the CP3/4. In addition to these midline channels, the lateralised sources showed notable waves of early (0–250 ms) and later (250–700 ms) activity.

Spatial Frequency

For stimuli lasting 50 ms, VEPs from observer PJB indicated that the left visual field-right hemisphere (LVF-RH) processed low-pass images filtered at 0.5, 2 and 8 cpd with equal efficiency (Fig. 3). Stimuli received in the right visual field-left hemisphere (RVF-LH) showed a different response: a related potential to images blurred at 0.5 cpd peaked on average 130 ms before the potential to stimuli filtered at 8 cpd. The amplitude of these potentials was similar (average, 16.7 ± 5.7 μV). The VEP due to 2 cpd filtering was rather different, having a less distinguished peak and a lag of 57 ms.

Comparison of SSK's (50 ms) data of the upright face condition in the right visual field-left hemisphere (RVF-LH) with the 50 ms data for PJB (Fig. 3) shows that SSK's responses were distinguished not by significant latency differences due to filtering of stimuli, but instead by a larger positive vertex to 0.5 cpd filtered images at each site (identified as the P300) (Fig. 4). The differences between these and images blurred at 2 and 8 cpd were at CP3 = 14.5 μV, P7 = 9 μV and T7 = 12.9 μV. The average aligned vertex peak latency difference between the upright faces filtered at 0.5 cpd and 2/8 cpd was ~37 ms. Responses for stimuli blurred at 2 and 8 cpd were highly correlated ($r \geq 0.97$). For this observer brief stimulus presentations (50 ms) may have reduced the availability of higher frequencies in the images [15–16]; the lower frequency in-

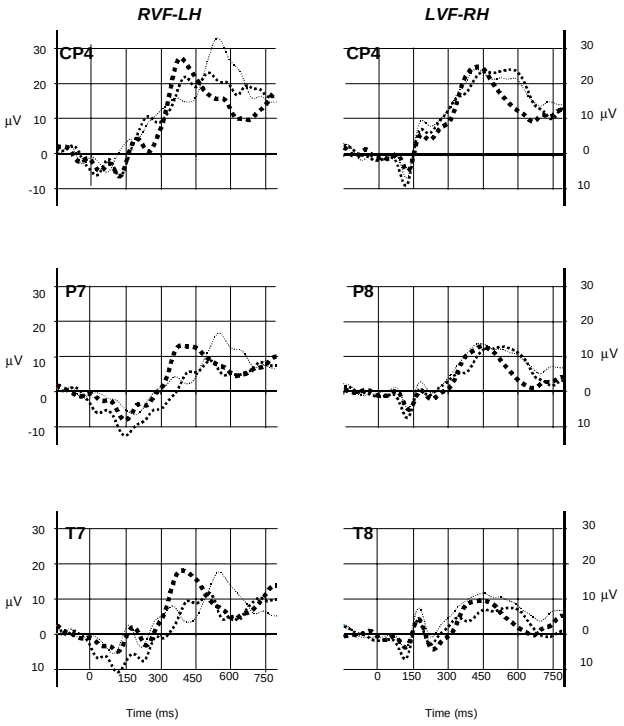

Fig. 3. VEPs from observer PJB for upright faces stimuli presented for 50 ms. LVF-RH– left visual field – right hemisphere; RVF-LH – right visual field – left hemisphere. Visual evoked potentials recording locations: CP3/4 – central parietal; P7/8 – parietal, T7/8 – temporal. Upright faces filtered at 0.5 cpd – ▪▪▪▪ ; 2 cpd – ···· ; 8 cpd – ·····

formation was always available during presentation 50 ms. Each VEP observed in the LVF-RH was highly similar ($r \geq 0.92$) and represented an equally efficient processing of all stimuli in this hemisphere.

The data for SSK's LVF-RH stimuli lasting 200 ms showed a slight difference for stimuli filtered at 0.5 cpd (Fig. 5). At P8 an earlier peak response (92 ms) was the largest in amplitude (–3.3 μV); at T8, VEP was lower in amplitude but similar in latency (–2.9 μV, 90 ms); at CP4, the effect was also present but less significant (–2.8 μV, 98 ms). Stimuli presented to the RVF-LH produced rather different VEPs and were more in line with the data from observer PJB. At each LH site an earlier peak (by 114 ms) was seen for stimuli blurred at 0.5 cpd, as compared with images filtered at 2 and 8 cpd. The responses to images filtered at 2 and 8 cpd were inseparable (Pearson, $r \geq 0.97$).

The 200 ms stimulus data for observer EK (Fig. 6) demonstrated that the amplitude and latency of responses to upright faces at CP4 was dependent on filtering frequency: increasing filtering frequency caused reduction of amplitude and latency: at 0.5 cpd was 11.4 μV, 516 ms, at 2 cpd was 12 μV, 654 ms and 8 cpd was 6 μV, 604 ms. In the RVF-LH condition, each electrode site showed a larger and earlier VEP to images blurred at 0.5 cpd and

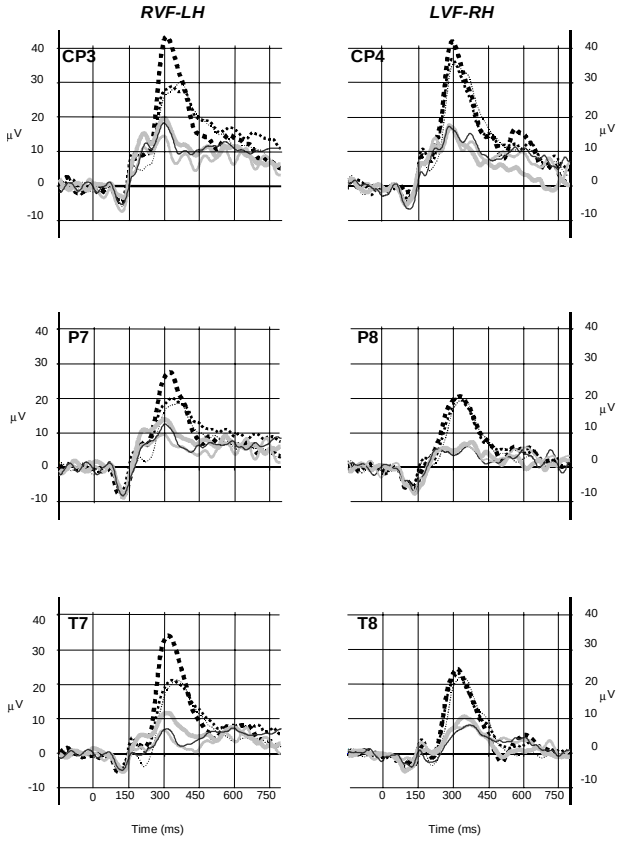

Fig. 4. VEPs from observer SSK for upright and inverted faces stimuli presented for 50ms. LVF-RH– left visual field – right hemisphere; RVF-LH – right visual field – left hemisphere. Visual evoked potentials recording locations: CP3/4 – central parietal; P7/8 – parietal, T7/8 – temporal. Upright faces filtered at 0.5 cpd – ▪▪▪▪ ; 2 cpd – ▪▪▪▪ ; 8 cpd – ·····. Inverted faces filtered at 0.5 cpd – ▬ ; 2 cpd – ▬ ; 8 cpd – ▬

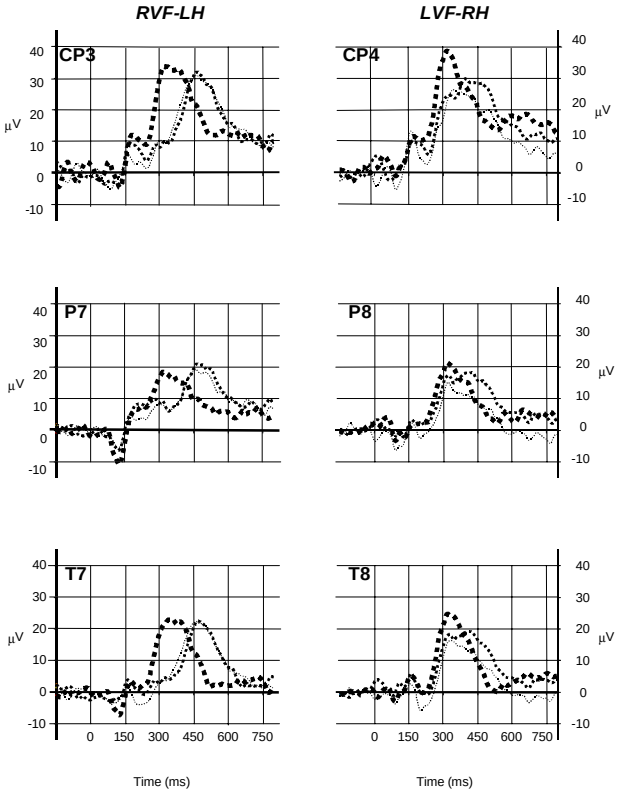

Fig. 5. VEPs from observer SSK for upright faces stimuli presented for 200 ms. LVF-RH– left visual field – right hemisphere; RVF-LH – right visual field – left hemisphere. Visual evoked potentials recording locations: CP3/4 – central parietal; P7/8 – parietal, T7/8 – temporal. Upright faces filtered at 0.5 cpd – ▪▪▪▪ ; 2 cpd – ▪▪▪▪ ; 8 cpd – ·····

this activity is part of later response. On average, the differences were 6.5 ± 1.1 μV and 71.3 ± ± 28.7 ms. For the latter time period, VEPs elicited by stimuli filtered at 2 cpd did not show the expected characteristic vertex.

Upright and Inverted Faces

The comparison between VEP responses to upright and inverted faces for observer SSK is shown in Fig. 4. The P300 responses to inverted faces were considerably diminished as compared to the upright faces. (The earlier VEP – approximately 0–250 ms – were closely matched in shape.) The response to inverted faces filtered at 0.5 cpd was also of a slightly higher amplitude (19.8 μV) than for images blurred at 2 cpd (14.6 μV) and 8 cpd (18.3 μV); the difference between inverted faces filtered at 0.5 cpd and stimuli blurred at 2 cpd was greatest (4 μV) in the RVF-LH at electrodes P7 and T7. The relative difference in the amplitude for the upright and inverted faces filtered 0.5 cpd in the RVF-LH was similar at CP3 (23.6 μV) and T7 (22.4 μV). The responses to inverted faces for LVF-RH presentations were very similar ($r \geq 0.82$). In summary, there was very little evidence for a significant influence of SF in the RVF-LH conveyed by filtered inverted facial expressions. However, the main difference was in the amplitude of the VEP to stimuli filtered at 0.5 cpd at P7 and T7; this may be an effect of stimulus exposure duration that similarly may have affected the processing of upright images.

Stimulus Category

Data for observer SSK using the fruit/vegetable category stimuli presented for 50 ms are shown in Fig. 7. Stimuli blurred at 0.5 and 2/8 cpd presented in the RVF-LH revealed different sensitivities as was the case for upright facial images described above (responses of images filtered at 2 and 8 cpd were highly correlated, $r \geq 0.95$). The mean latency difference was 60 ± 7 ms. Responses of the LVF-RH condition showed no clear latency differences in visual processing of 0.5, 2 or 8 cpd filtered images ($r \geq 0.83$). This was an important finding, because it demonstrates clearly that the lateralization of the

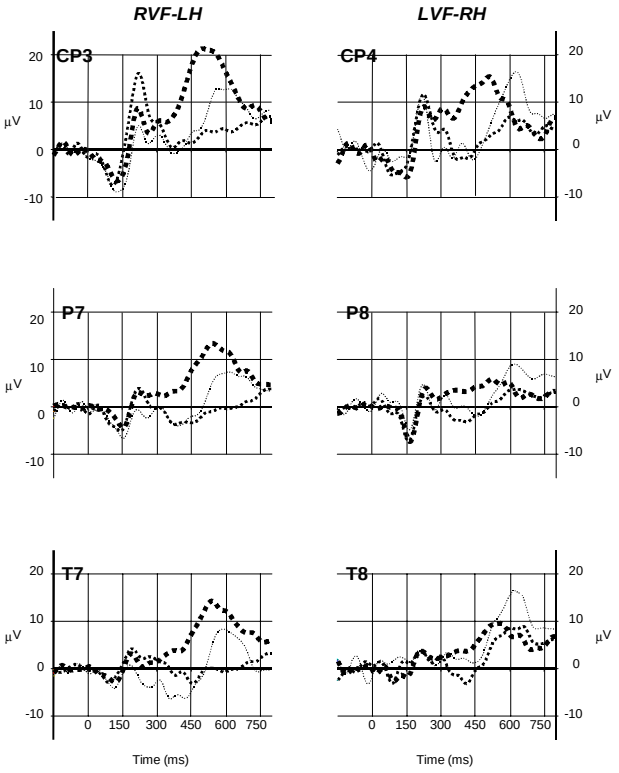

Fig. 6. VEPs from observer EK for upright faces stimuli presented for 200 ms. LVF-RH– left visual field – right hemisphere; RVF-LH – right visual field – left hemisphere. Visual evoked potentials recording locations: CP3/4 – central parietal; P7/8 – parietal, T7/8 – temporal. Upright faces filtered at 0.5 cpd – ▪▪▪▪ ; 2 cpd – ▪▪▪▪ ; 8 cpd – .....

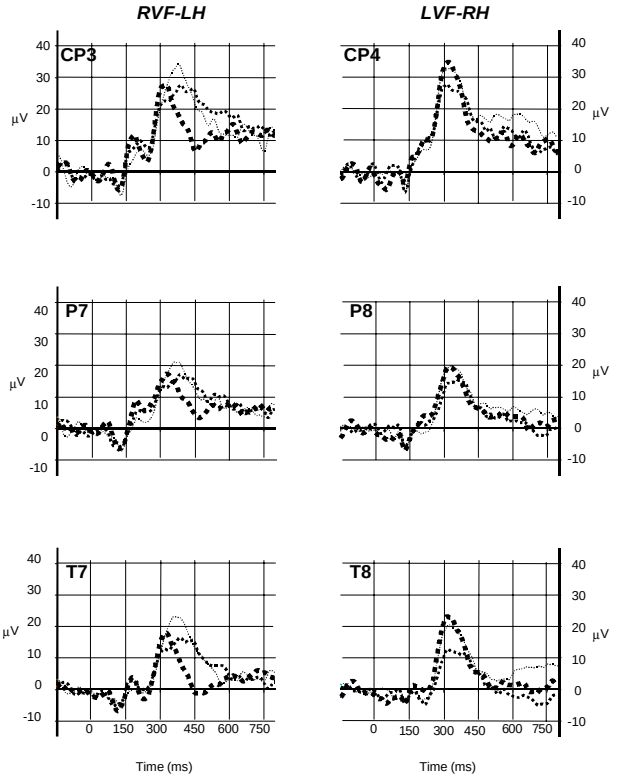

Fig. 7. VEPs form observer SSK for food category stimuli presented for 50 ms. LVF-RH– left visual field – right hemisphere; RVF-LH – right visual field – left hemisphere. Visual evoked potentials recording locations: CP3/4 – central parietal; P7/8 – parietal, T7/8 – temporal. Food category stimuli filtered at 0.5 cpd – ▪▪▪▪ ; 2 cpd – ▪▪▪▪ ; 8 cpd – .....

SF processing for lower spatial scales was not restricted to facial image carriers.

Early (0–250 ms) VEP Component

A general difference in the early components could be characterised by negative (N120) and positive (P160) vertices. The P160 amplitude to upright facial stimuli was greatest in the LVF-RH, in order of decreasing magnitude CP4 > T8 > P8. Inverted faces caused no consistent P160 except over temporal areas recorded at T8. Responses to food category stimuli generated LVF-RH responses that also lacked a specific P160 component. In the RVF-LH, the early VEP components were fairly consistent, particularly for observers SSK and EK. Upright facial stimuli presented for 200 ms generated VEPs of greater amplitude than did stimuli lasting for 50 ms. For food category stimuli, the early VEP components were the clearest in the case of RVF-LH. Comparison of SSK's data for upright faces and food (left columns, Figs. 4 and 7) indicate that food category specific responses were characterised by 3 vertices that were related temporally and between the electrodes. At T7, the VEP was defined by N130 and P180; at P7 by P70, N130 and P200; at CP3 by P70, N130 and P190 (for stimuli blurred at 0.5 cpd) and P215 (for images filtered at 2 and 8 cpd). At CP3, a difference due to SF was also present in the early components, with images filtered at 2 and 8 cpd lagging by 25 ms behind the stimulus blurred at 0.5 cpd.

DISCUSSION

This experiment has demonstrated differences in spatial frequency processing by the left and right hemispheres, using measurements of the visual evoked potentials. Upright and inverted facial expressions, vegetables and fruit images were used as a vehicle for the transmission of frequency-specific information in a task-form that requires cognitive processing.

Spatial Frequency

The experiment showed that for stimuli lasting 50 ms (PJB, SSK) and 200 ms (EK, SSK) that the LVF-RH processed low-pass images filtered at 0.5, 2 and 8 cpd with equal efficiency as indicated by VEPs (Figs. 3, 5 and 6). Responses to stimuli filtered at

0.5 cpd were slightly more transient than the VEPs to higher SFs (PJB) (Fig. 3). Stimuli presented to the RVF-LH produced rather different VEPs. A significant latency difference was present for each filter value. Upright faces filtered at 0.5 cpd elicited potentials of 114–130 ms before did upright stimuli filtered at 8 cpd, although the amplitude of these potentials was similar. For stimuli lasting 50 ms, VEPs from observer SSK were distinguished not by particularly significant latency differences due to filtering, but by a larger positive vertex (P300) to 0.5 cpd filtered images at each site (Fig. 4).

A very similar effect was noticed in the analysis of inverted faces. Responses to inverted faces filtered at 0.5 cpd were also of a slightly greater amplitude than to images blurred at 2 and 8 cpd. But there was very little evidence for a significant influence of SF in the RVF-LH. The main difference between upright and inverted faces was in the amplitude of VEP to the stimuli filtered at 0.5 cpd with the electrodes placed at P7 and T7. Also, the amplitude for inverted faces was lower than for upright expressions at all SFs (Fig. 4). A similar upright/inverted difference was reported by Jeffrey [12].

This effect for upright and inverted faces might be evoked by brief stimulus presentation (50 ms). Some studies of Breitmeyer [15] and Tolhurst [16] showed that temporal properties of the two types of spatial frequency analysers differ. Low-spatial frequency channels have short latencies and short integration time, whereas high-spatial frequency channels respond slowly and have a long integration time. This means that at very brief exposure duration only low frequencies may be available.

The food category response demonstrated very clearly that the lateralization of SF processing for lower spatial scales was independent of facial image carriers. Stimuli of this category, filtered at 0.5 and 2/8 cpd and presented in the RVF-LH, revealed latency differences as was in the case of upright faces (Fig. 7). The P300 amplitude for food stimuli was less than for upright faces. There are two possible reasons for this. First, faces are known to be a more complex object and are also more socially important (expression, sex, name/identity, age). Most types of food do not possess as many high frequency features as faces do. These stimuli may have been affected less by the filtering, as was indicated by the different lag time for higher frequency images (difference for upright faces equals 136 ms, for food 60 ms). Second, fruit and vegetables are not polarised in the way that faces are. That is faces are considered mainly as 'upright' objects, while images of food have no particularly important orientation that helps to identify it as such.

P300 or Later VEP Component

The hemispheric differences in VEPs due to spatial frequency filtering were manifested as changes in the latency of the P300. This was true for the upright faces and food stimuli. LVF-RH P300 latency was unchanged for all SFs.

The amplitude and latency of the P300 is often associated with reaction time and accuracy [17]. The latency of the P300 may place an upper limit on categorisation (*e.g.* same or different expressions) or stimulus evaluation time. Contrary to the suggestion that P300 latency increases with task difficulty [18], it has been shown here that RVF-LH P300 latency is due to the hemispheric asymmetry for SF.

Early VEP Component and Related Studies

A general difference in the early components could be characterised by negative (N120) and positive (P160) vertices. In the LVF-RH, the P160 amplitude to upright facial stimuli was greatest at CP4. The P160 response to inverted faces was present only at T8. Jeffrey [12] also found a similar VEP to facial stimuli, which was largest over Cz in his experiments. In, general, the vertex positive peak (VPP) of face had a latency of 170 ms in his experiment. In our experiment, the average latency of similar upright face VPP was 160 ms. The tasks in our and Jeffrey's [12] experiment were very different, therefore the difference is not surprising.

The food category stimuli generated more stimulus-specific responses in the RVF-LH. The shape of these VEPs differed somewhat from VEPs elicited by the upright and inverted faces. Jeffrey [12] noted that VEPs to non-face stimuli were similar in shape, but smaller in amplitude.

Summary

There are two issues that we cannot address here. First, a small number of electrodes were used. Three symmetric pairs were used to compare the effects of lateralised stimuli. A larger electrode array would allow better localisation of the sources of lateralised sensitivity. Electrodes placed at CP3/4, P7/8 and T7/8 indicated that the effects of low-pass filtering were detectable over quite large areas of the occipitoparietal and temporoparietal cortices.

Second, some quite obvious individual differences were apparent in the data. Observers SSK and PJB had more experience of the matching task than did observer EK (see Figs. 3, 4, 5 and 6). It is reasonable to suggest that some of the differences in EK's VEPs (see Fig. 6) could be due to task and stimulus familiarity. Nevertheless, EK's data showed

evidence for shifts in VEPs (RVF-LH) latency due to 0.5 and 8.0 cpd filtering. Some differences might be explained by observer's gender, however, a larger subject pool will be required to verify this.

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S. Saunoriūtė-Kerbelienė, P. J. Benson, O. Rukšėnas

ERDVINIAI DAŽNIAI IR PUSRUTULIŲ ASIMETRIJA REGIMOSIOS INFORMACIJOS APDOROJIMO PROCESE

S a n t r a u k a

Verbalinės-regimosios informacijos apdorojimo pusrutuliuose skirtumus būtų galima paaiškinti sensorinių stimulų erdvinių dažnių variacijomis. Mūsų eksperimento tikslas – remiantis regimųjų sukeltinių potencialų matavimais išnagrinėti galvos smegenų pusrutulių skirtumus erdvinių dažnių apdorojimo požiūriu. Eksperimente buvo naudojami žemų erdvinių dažnių vaizdai: septynios emocijas išreiškiančios normalios ir invertuotos orientacijos veido išraiškos, daržovės ir vaisiai kaip kontrolė. Tiriamojo užduotis – kiek galima greičiau ir tiksliau atpažinti dvi paeiliui rodomas veido išraiškas nepriklausomai nuo veidų individualumo, lyties ir erdvinių dažnių. Nuo kairiojo smegenų pusrutulio užregistruoti regimieji sukeltiniai potencialai parodė reikšmingus latencijos skirtumus: atsakai į žemesnių erdvinių dažnių stimulus buvo registruojami anksčiau (60–100 ms) nei į aukštesnių erdvinių dažnių vaizdus. Registruojant P300 sukeltinius potencialus dešiniajame smegenų pusrutulyje, gauta, kad vaizdų filtravimas skirtingais erdviniais dažniais neturi įtakos vaizdų atpažinimui. Lyginant ankstyvuosius sukeltinius potencialus į vaizdus – veidus ir ne-veidus gauti patikimi amplitudžių skirtumai.