A principal component analysis of multifocal pattern reversal VEP

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Multifocal visual evoked potentials (mfVEP) were recorded with three channels from 31 control subjects. A principal component analysis was applied to all local responses. The first principal component reversed polarity above and below the horizontal meridian and across the vertical meridian in the case of the lateral channel. In addition, the first principal components of the responses around the vertical meridian were reversed in polarity compared to those around the horizontal meridian, consistent with the region near the vertical meridian lying outside the calcarine fissure. A model was proposed that allowed for the construction of a coronal section of V1 based on the distribution of the first principal component. This approach provides a means of deriving a V1 component from mfVEP recordings with only three recording channels.

Keywords: multifocal VEP, principal component analysis, cortical source, V1

1. Introduction

The visual evoked potential (VEP), a measure of neural activity in the visual cortex, is widely used because it has a high temporal resolution and often a high signal-to-noise ratio (Regan & Spekreijse, 1986). However, the VEP has very poor spatial resolution because it is a mixture of signals from various cell types and multiple regions, each of which can have a response with a different time course. Some signals even have similar waveforms but reversed polarities. For example, because of the anatomy of V1 inside the calcarine fissure, a response from the upper visual field has a polarity that is reversed compared to a response from the lower visual field (Halliday & Michael, 1970; Jeffrey & Axford, 1972; Michael & Halliday, 1971). Recovering the sources of the VEP is complicated by large inter-subject variability in waveforms due to the variability in cortical folding among individuals. To circumvent the problem of poor spatial resolution, two methods, the cortical source localization technique (da Silva & Spekreijse, 1991; Maier, Dagnoile, Spekreijse, & van Dijk, 1987; Srebro, 1985) and the multifocal VEP (mfVEP) technique (Baseler, Sutter, Klein, & Carney, 1994) have been proposed.

As typically employed, the cortical source localization technique requires a simultaneous recording of VEP signals with multiple electrodes. This technique allows for the extraction of VEP components, each of which can be modeled as originating from an equivalent dipole, which may be located within either the striate cortex or the extra-striate areas (Maier et al., 1987; Ossenblok & Spekreijse, 1991; Srebro, 1985). Because the inter-subject variability mainly comes from the variability in cortical folding, the inter-subject variability of the waveform of an isolated VEP component is smaller than that of the waveform of the VEP (Maier et al., 1987). However, two problems make it difficult to apply this technique to the VEP. First, to obtain responses with relatively large signal-to-noise ratios required for the analysis, a relatively large stimulus is needed. This stimulus produces a response that is heterogeneous. Second, the cortical localization technique requires a head conductivity model. Obtaining an adequate model that considers the anatomy of an individual subject is difficult, although this has been attempted based upon individual MRIs (Bonovas, Kyriacou, & Sahalos, 2001; Haueisen et al., 2002). Towle, Cakmur, Cao, Briggell, and Parmegiani (1995) pointed out that a dipole could be mislocated because of the discrepancy between the spherical volume model used to calculate dipole and the non-spherical shape of the human head. Researches also found the non-homogeneous nature of skull and brain can alter the location of dipoles (He & Musha, 1989; Skrandies & Lehmann, 1982). In addition to these problems, the need for many recording channels makes the implementation of this technique relatively challenging.

The mfVEP technique offers a different approach to the spatial resolution problem. With this technique, developed by Sutter (1991), many local stimuli are presented simultaneously and the pattern of the stimulus is modulated with mutually independent pseudo-random sequences. Each local response can be derived by a cross-correlation between the record and the sequence that modulates the pattern of the stimulus. Because each response comes from a small retinal region, it reduces the size of regions contributing to the VEP response and thus reduces the complexity of the VEP. Further, although each local response may contain striate (V1) and extra-striate
components, the mfVEP appears to contain a relatively smaller extrastriate contribution than does the conventional large-field VEP (Fortune & Hood, 2003; see Hood & Greenstein, 2003, for a review of the mfVEP technique).

Slotnick, Klein, Carney, Sutter, and Dastmalchi (1999) combined the mfVEP technique with dipole analysis to locate the sources of the mfVEP. They extracted the dominant dipole from the multifocal VEP using a source localization technique and demonstrated that it had the characteristics expected of a potential generated in the calcarine fissure. In particular, it reversed polarity between the upper and lower visual fields as first shown by Jeffreys and Axford (1972) for the conventional VEP. In addition, orientation of the dominant dipole changed continuously around the horizontal meridian of the visual field as expected on anatomical grounds. They argued that the dominant component of the multifocal VEP originated from V1 because their dominant component accounted for most of total variance in the signal. Similarly, Tabuchi, Yokoyama, Shimagawa, Shiraki, Nagasaka, and Miki (2002) found that the equivalent dipole of multifocal visual evoked magnetic field was located at V1. (A number of studies have shown that the cortical source of the early portion of the traditional VEP is at V1. For a review, see Di Russo, Martinez, Sereno, Pitalis, & Hillyard, 2002.)

Here we take a different approach. Like the Slotnick et al. (1999) study, our goal was to isolate from mfVEP recordings a V1 component with a high signal-to-noise ratio. However, we make use of principal component analysis (PCA) rather than a source localization technique. With PCA, there is no need to assume a model of head conductivity, and three channels of recording are sufficient. The principal component analysis has been used for analyzing conventional VEPs. For example, Gutwitz, Zemon, Victor, and Knight (1986) studied the principal components of steady-state contrast reversal VEP. First, they found that two major principal components (or mechanisms) were sufficient to account for most of variance in the data, and, second, that the locations of the cortical sources of the principal components were independent of the parameters such as reversal frequency, checker size and area of the stimulus, while the dynamics (waveforms) of the principal components were related to the stimulation parameters. Their findings indicate that a set of consistent principal components can be derived under different conditions.

The basic assumption behind the approach here is that a component response has the same time course (waveform) across the entire visual field. Under this assumption, the local VEP waveform variation results from the cortical convolutions, the relative contributions from the V1 and the extrastriate regions, and the spatial distributions of different local generators (e.g., the magnocellular and parvocellular pathways). Therefore, the common principal components can be derived from all the local responses of the mfVEP with one PCA. Both Baseler and Sutter (1997) and James (2003) showed that the mfVEP waveforms could be approximated by two common principal components, thus suggesting that mfVEP responses consist of a small number of independent components. However, it is important to note that the PCA will decompose the VEPs into principal components that are orthogonal to each other. Because there is no basis for physiological VEP components being orthogonal to each other, the principal components need not be physiologically meaningful. The purpose of this study is to ask whether the mfVEP possesses a physiological meaningful principal component; our results suggest that the answer is yes.

2. Methods

2.1 Spatial display

The mfVEPs were obtained using a dartboard pattern shown in Figure 1A, a standard option (Dart Board 60 With Patterns) of the VERIS software (EDI, San Mateo, CA). The diameter of the display subtended 44.5°. There are 60 sectors in this display, and each sector contains 16 checks, 8 black and 8 white. The radii of the rings are 1.2°, 2.6°, 5.8°, 9.8°, 14.9°, and 22.2° of visual angle. The sectors and the checks are scaled to be of approximately equal effectiveness based on cortical magnification factors (Baseler et al., 1994; Horton & Hoyt, 1991a).

2.2 Subjects and recording

The data were obtained from 31 subjects with normal vision; all were enrolled for other studies (Hood et al., 2000). The average age was 36 years ± 13. Informed consent was obtained from all subjects before their participation. Procedures adhered to the tenets of the Declaration of Helsinki, and the protocol was approved by the committee of the Institutional Board of Research Associates of Columbia University.

For both eyes of each subject, a multifocal VEP was recorded for 14 min. The electrodes were placed on the inion (reference) and 4 cm above the inion (active) with a forehead electrode as the ground (Figure 1B). Additional active electrodes were placed 4 cm lateral to the midline. The midline active electrode and the two lateral active electrodes, all referenced to the inion electrode, provided three recording channels: the midline, the left, and the right channels in Figure 1B. The positions of the active electrodes were chosen for optimizing mfVEP recordings as well as based on anatomical considerations (Hood, Zhang, Hong, & Chen, 2002). PCA was performed on data of all three channels. Here, the data for two channels are presented. The first is the midline channel and the second the lateral channel (Figure 1B). The lateral channel data was derived by subtracting the records of the right channel from those of the left channel. These two channels were presented because they are commonly used in VEP recording, and the data from them convey the most information about the sources of the VEP components.
Figure 1. A. The 60-sector pattern reversal display for the multifocal visual evoked potential (mfVEP). B. The electrode placements for the electrodes showing the midline channel and the derived lateral channel. C. The average mfVEP responses for the right eyes of 31 normal subjects recorded with the midline channel. D. The average responses recorded with the lateral channel, which is derived by subtracting the right channel recording from the left channel recording. The cyan and magenta responses illustrate two distinctive waveforms in the mfVEP.

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(A) \Rightarrow (U)_{M \times N} (w)_{N \times N} (v)_{N \times N}
\]

\[
\begin{pmatrix}
  r_{11} & r_{12} & \ldots & r_{1N} \\
  r_{21} & r_{22} & \ldots & r_{2N} \\
  \vdots & \vdots & \ddots & \vdots \\
  r_{M1} & r_{M2} & \ldots & r_{MN}
\end{pmatrix}
\begin{pmatrix}
  pc_{11} & pc_{12} & \ldots & pc_{1N} \\
  pc_{21} & pc_{22} & \ldots & pc_{2N} \\
  \vdots & \vdots & \ddots & \vdots \\
  pc_{M1} & pc_{M2} & \ldots & pc_{MN}
\end{pmatrix}
\begin{pmatrix}
  w_{11} & 0 & \ldots & 0 \\
  0 & w_{22} & \ldots & 0 \\
  \vdots & \vdots & \ddots & \vdots \\
  0 & 0 & \ldots & w_{NN}
\end{pmatrix}
\begin{pmatrix}
  c_{11} & c_{12} & \ldots & c_{1N} \\
  c_{21} & c_{22} & \ldots & c_{2N} \\
  \vdots & \vdots & \ddots & \vdots \\
  c_{N1} & c_{N2} & \ldots & c_{NN}
\end{pmatrix}
\]

\[
(1)
\]

\[
\begin{pmatrix}
  r_{11} & r_{12} & \ldots & r_{1N} \\
  r_{21} & r_{22} & \ldots & r_{2N} \\
  \vdots & \vdots & \ddots & \vdots \\
  r_{M1} & r_{M2} & \ldots & r_{MN}
\end{pmatrix}
\begin{pmatrix}
  pc_{11} & pc_{12} & \ldots & pc_{1L} \\
  pc_{21} & pc_{22} & \ldots & pc_{2L} \\
  \vdots & \vdots & \ddots & \vdots \\
  pc_{M1} & pc_{M2} & \ldots & pc_{ML}
\end{pmatrix}
\begin{pmatrix}
  w_{11} & 0 & \ldots & 0 \\
  0 & w_{22} & \ldots & 0 \\
  \vdots & \vdots & \ddots & \vdots \\
  0 & 0 & \ldots & w_{LL}
\end{pmatrix}
\begin{pmatrix}
  c_{11} & c_{12} & \ldots & c_{1N} \\
  c_{21} & c_{22} & \ldots & c_{2N} \\
  \vdots & \vdots & \ddots & \vdots \\
  c_{L1} & c_{L2} & \ldots & c_{LN}
\end{pmatrix}
\]

\[
(2)
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\[
\begin{pmatrix}
  r_{11} & r_{12} & \ldots & r_{1N} \\
  r_{21} & r_{22} & \ldots & r_{2N} \\
  \vdots & \vdots & \ddots & \vdots \\
  r_{M1} & r_{M2} & \ldots & r_{MN}
\end{pmatrix}
\begin{pmatrix}
  pc_{11} & pc_{12} & \ldots & pc_{1L} \\
  pc_{21} & pc_{22} & \ldots & pc_{2L} \\
  \vdots & \vdots & \ddots & \vdots \\
  pc_{M1} & pc_{M2} & \ldots & pc_{ML}
\end{pmatrix}
\begin{pmatrix}
  w_{11} & 0 & \ldots & 0 \\
  0 & w_{22} & \ldots & 0 \\
  \vdots & \vdots & \ddots & \vdots \\
  0 & 0 & \ldots & w_{LL}
\end{pmatrix}
\begin{pmatrix}
  c_{11} & c_{12} & \ldots & c_{1N} \\
  c_{21} & c_{22} & \ldots & c_{2N} \\
  \vdots & \vdots & \ddots & \vdots \\
  c_{L1} & c_{L2} & \ldots & c_{LN}
\end{pmatrix}
\]

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(3)
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Consistent with earlier work (e.g., Baseler & Sutter, 1997), the low- and high-frequency cutoffs of the amplifiers were set at 100 and 3 Hz (1/2 amplitude; Grass Instruments preamplifier P511J, Quincy, MA). The 100 Hz cutoff does not affect the waveform, although the 3 Hz cutoff will make some of the responses slightly shorter in latency and slightly less sustained as compared to the setting of 1 Hz recommended for the conventional VEP (Harding, Odom, Spileers, & Spekreijse, 1996).

2.3 Deriving local VEPs

On every frame change, each of the 60 sectors either reverses contrast or remains unchanged, according to a mutually orthogonal m-sequence. The cross-correlation between the m-sequence that modulates the pattern reversal events of one location and the continuous record yields the pattern reversal VEP of that location (Baseler et al., 1994).

2.4 The SVD algorithm

PCA is implemented with the singular value decomposition algorithm (SVD). SVD methods are based on the following theorem of linear algebra, whose proof is beyond our scope. Any \( M \times N \) matrix \( A \) can be decomposed into a product of an \( M \times N \) column-orthogonal matrix \( U \), an \( N \times N \) diagonal matrix \( W \) with positive or zero elements (the singular values) and an \( N \times N \) orthogonal matrix \( V \) (Equation 1).

\[
V = \sum_{ii} W_i^2 / \sum_{ii} W_i
\]

In this study, \( w_i \) is used as the estimation of the average amplitude of the \( i \)th PC. To represent the relative amplitude of each PC, the waveform of a PC is multiplied by the corresponding \( w_i \) value. In other words, a PC presented in this work is actually the original PC multiplied by its \( w_i \) value.

3. Results

3.1 The results of PCA

The average mfVEPs for 31 normal subjects are shown in Figure 1C and 1D. In each plot, there are 60 responses, each of which corresponds to a stimulus sector. For example, the response enclosed in a red sector in Figure 1C is the response associated with the stimulus sector marked with a red sector in Figure 1A. Notice that the responses are not plotted at the actual centers of the stimulus sectors shown in Figure 1A. This is a common practice in mfVEP studies because plotting responses at the actual locations will cause overlap for the central responses. The responses in all figures are shown with positive potentials in the upward direction. However, the polarity of these responses is actually reversed compared to the conventional VEP, due to the way the VERIS software derives the second-order kernel. The mfVEP responses differ in waveform and amplitude between the midline (Figure 1C) and lateral (Figure 1D) channels. In addition, there are at least two different waveforms (the cyan and magenta traces in Figure 1C & 1D), indicating the involvement of more than one source in the generation of the mfVEP.

Among the principal components extracted from the mfVEP responses for each subject, the first three were significant. Figure 2A shows the average waveforms of the three PCs for the normal subjects. In each case, the PCs were extracted from the 31 individual recordings and then the 31 PCs were averaged. Note that PC1 is similar to the full-field pattern reversal VEP in that it has a trough and a peak resembling the N75 and the P100 component of the conventional VEP (Fortune & Hood, 2003).

The visual field distribution of the PCs is presented as a dot plot (Figure 2B) where the area of a dot represents the absolute value of the coefficient of the PC for a stimulus sector. A red dot indicates that for that sector, the PC in the response has a waveform as shown in Figure 2A. A blue dot indicates that the PC has a waveform reversed in polarity. For the midline channel, the PC1 is relatively smaller along both the vertical meridian and the angular arm below the horizontal meridian. The visual field distribution of PC1 (row 1, left column in Figure 2B) shows a polarity reversal between the upper and lower visual field. In addition, there is a polarity reversal between the responses along the vertical meridian and the responses along the horizon-
tal meridian. For the lateral recording channel, the PC1 tends to be relatively larger in regions where they were relatively smaller for the midline channel. The visual field distribution of PC1 (row 1, right column in Figure 2B) shows a polarity reversal between the left and the right visual fields. Note that PC1 captures the major feature of the mfVEP: the polarity reversal that occurs between the upper to the lower visual fields and the waveform difference between the responses along the vertical meridian compared to the other responses (Figure 1C). PC2 shows a polarity reversal from the upper field to the lower field for the midline channel but no consistent pattern for the lateral channel (row 2, Figure 2B). Finally, PC3 (row 3, Figure 2B) shows a suggestion of an upper to lower field and center-periphery polarity reversal. But, PC3 is small and will not be analyzed further.

In Figure 3, the black traces represent the recorded mfVEP, and the red traces represent the VEPs reconstructed with PC1 and PC2 using Equation 3. This comparison shows that the first two PCs account for most of the variance in VEP waveform for both channels. On average, PC1 accounts for $61 \pm 9\%$, the first two PCs account for $81.6 \pm 10\%$, and the first three PCs account for $86.5 \pm 9\%$ of the variance in the signal window (from 45 ms to 150 ms). This represents good agreement, especially when
one considers that these are small responses with relatively large contributions from noise.

The variance that can be accounted for with the first two PCs, or the goodness of fit, varies among subjects. The results from three subjects, representing the 10, 50, and 90 percentile in the ranks of the goodness of fit between PC1 and PC2 and the recorded data, are shown in Figure 4, Figure 5, and Figure 6. PC1 and PC2 account for 91% (subject FB), 84% (SG), and 63% (LC) of the variance in the mfVEP for the three subjects, respectively. Both the waveforms (Figure 4) and the visual field distributions (Figure 5) of these two PCs are similar for these subjects.

Figure 4 shows the recorded responses and the responses reconstructed from the addition of PC1 and PC2. It appears that the goodness of fit is mainly determined by the magnitude of the random noise in the records as the recorded data (black), and the reconstructed responses (red) are similar for all three subjects.

3.2 The latency variation across the visual field

Because a PC has a fixed latency, latency variations in the VEP responses across the visual field present a potential problem for the PCA approach. In fact, latency differences in the mfVEP responses do exist. We observed a consistent latency difference between the nasal and the temporal mfVEP responses (Hood & Zhang, 2000). In addition, Baseler and Sutter (1997) also showed that the latency of the mfVEP varies with increasing eccentricity of the stimulus. However, these latency differences are small and tend to be variable. Figure 7 shows the averaged mfVEPs from Figure 1C and 1D with the PC1 component superimposed. The agreement is good. Figure 8 shows four responses from Figure 1C along the horizontal meridian. As expected, the response to the peripheral nasal stimulus (yellow) is faster than that to the peripheral temporal stimulus (blue) (Hood and Zhang, 2000). However, the latency differences in the mfVEP are subtle. Therefore, the variations in latency across the visual field contribute relatively little to the over-
Figure 6. The mfVEP responses of the right eyes of the three subjects. The black traces represent the recorded responses and the red ones the linear combinations of the first two PCs.

all variance. Slotnick et al. (1999) also showed that the result of cortical source localization could be improved by combining responses from the same eccentricity. By doing so, they also ignored the temporal-nasal latency differences. Although the latency differences are relatively trivial here, other conditions (e.g., use of stimuli differing in contrast) might produce larger latency differences and thus invalidate the PCA approach.

3.3 A model of V1 based on the distribution of PC1

Assuming that PC1 is generated in V1, the spatial distribution of PC1 in V1 can be predicted with a model. This model takes as its input the visual field distribution of PC1, as measured with the midline and lateral channels, and produces a coronal section of the cortex with the visual field locations of each of the angular sectors indicated. The model has two assumptions. First, it assumes that the source of PC1 can be represented as a dipole located in V1. Assuming that this dipole is oriented perpendicular to the surface of the cortex, the amplitude of the scalp VEP recorded with the midline channel is proportional to \( \cos(\alpha) \), where \( \alpha \) is the angle between the dipole (an arrow in Figure 9A) and the axis of the midline channel (Jeffreys & Axford, 1972). Because the axis of the lateral channel is approximately perpendicular to the midline channel, the amplitude of scalp VEP recorded with the lateral channel is proportional to \( \sin(\alpha) \). (If the dipole of VEP source is oriented at an angle other than perpendicular to the surface of cortex, then the predictions of the model will have an identical shape but will be rotated by that angle.) Figure 9A shows two examples, one for the case where the midline and lateral channel recordings are positive (left panel) and one for the case where the midline channel is negative and the lateral channel positive (right panel). The red dashed arrows show the magnitude of PC1 as recorded from the midline and lateral channels. By assumption 1, the solid red arrow indicates the direction of the dipole. For the second assumption, the visual field is divided into 12 angular sectors of equal area (left column in Figure 9B). We assume that these equally sized angular sectors in the visual field are represented in V1 with equal areas (right column in Figure 9B) and that each hemifield (the left or the right hemifield) is continuously located within the contra-lateral hemisphere. This assumption embodies the generally accepted view of V1 (Horton et al., 1991a; Wandell, 1999). Figure 9C (lower two rows) shows the average PC1 amplitude for both channels for each of the 6 sectors from the left visual field. The central 12 locations, within the central 2.6° (radius), were not included in these averages so that each angular sector had the same number of responses. The upper row in Figure 9C shows the resulting dipole orientations for each of the 6 sectors of the left hemifield. By assumption 2, these vectors should be perpendicular to the surface of V1. Figure 9D shows the predicted bend of the cortex with the center of each sector indicated. Note that this reconstruction algorithm is sensitive to local variation in cor
tical folding because each such variation causes an angle distortion, and these distortions will accumulate. Therefore, the algorithm will not work well for data from individual subjects. It does, however, work well for average data because local distortions are canceled out. Consistent with the known anatomy, the model shows V1 both within the calcarine fissure and on the medial surface. Note that the horizontal meridian is not at the bend of the calcarine as expected from the smaller responses along the angular arm below the vertical meridian (Hood & Greenstein 2003).

Figure 10 shows the orientations of the dipoles of PC1 for all the local responses. The angle of the dipole was determined with the same procedure as shown in Figure 9. In particular, the length of a line was determined using the amplitudes of PC1 of both midline and lateral channels. Because the amplitude of a local response should be similar for any given eccentricity, the length of a line largely reflects the orientation of the dipole. Notice that for each angular arm, the orientation of dipoles appears to change gradually and orderly with increasing eccentricity.

4. Discussion

The evidence here argues that PC1 of the mfVEP represents a source or sources, or more likely the major source(s), generated in V1. Basically, there are two general lines of reasoning that support this conclusion.

First, the mfVEP is likely to be dominated by V1 activity (Slotnick et al., 1999; Fortune & Hood, 2003). Therefore, because PC1 accounts for the maximum variance in the data, it is likely that PC1 consists mainly of a V1 response. However, this does not preclude the possibility that PC1 also includes an extrastriate contribution. In fact, because V1 and V2 are located close to each other in the brain, they will have a similar scalp distribution. Thus, it is very likely that the traditional PCA, which analyzes the responses to a single stimulus from many electrodes, will not yield a PC1 that represents a pure V1 component. For this reason, it has been argued that one cannot assume that a PC is associated with a single V1 source (Kavanagh, Darcey, & Fender, 1976; Lamothe & Stroink, 1991; Maier et al., 1987; Ossenblok & Spekreijse, 1991; Van Rotterdam, 1970). On the other hand, the PCA of the mfVEP dictates that PC1 accounts for the maximum variance in the distribution of responses across the field, in addition to the temporal (waveform) and the spatial (scalp distribution) domains as is traditionally for PCA. If the PC1 were to include an extrastriate component, it would have to be correlated with the V1 (striate) component in the visual field distribution domains or otherwise it would not increase the variance that is accounted for by PC1. This implies that the visual field distribution of this additional component should be similar to that of the V1 component. This is very difficult, if not impossible, to accomplish because the visual field distribution of the VEP is determined by the anatomical structure of the source and V1 has a unique folding structure that is not shared with other visual areas.
Figure 9. A schematic for deriving the model of a coronal section of V1. A. The method for determining the orientation of a dipole. Each circle indicates the location of an electrode. \( \alpha \) is the angle between a dipole and the midline channel. \( \cos(\alpha) \) is obtained from the coefficient from the midline channel and \( \sin(\alpha) \) the coefficient from the lateral channel. B. At left is the visual stimulus of the mfVEP. At right is a diagram of flattened visual cortex. A color indicates either an angular area in the visual field or an area in the visual cortex that receives the projections from the corresponding visual area. C. The first row is V1 cortex flattened with the orientation of the dipole for each angular area shown. The second and third rows show the average coefficient for the midline channel and the lateral channel. The area of a dot represents the absolute value of the average PC1 coefficient, and the color represents the sign. The angle of a dipole is calculated as the arctan (lateral channel value/midline channel value). D. The reconstructed coronal section of the left and the right calcarine fissures based on the PC1 coefficients shown in the first row of Figure 2B. For both C and D, the range of the eccentricity is from 2.6\(^\circ\) to 22.2\(^\circ\).
Therefore, the unique structure of V1 makes it possible for PCA of the mfVEP to extract a purer V1 component than can be extracted from the responses to one stimulus recorded with many electrodes. It is worth noting in this context that the PCA approach described here will not be able to localize components outside of V1 because these regions do not show the unique structure of V1.

The second line of reasoning supporting the conclusion that PC1 is a V1 component is based on the anatomical knowledge. Both qualitatively and quantitatively (the model), the amplitudes and polarity of PC1 agree with what is known about the anatomy of the V1. Anatomically, the upper and lower visual fields project to the lower and upper banks of calcarine fissure, respectively. Figure 11 from Horton and Hoyt (1991b) shows a coronal section of the left occipital cortex with the boundaries of the upper and lower fields indicated for V1 and V2. A signal from V1 should reverse its polarity between the upper and the lower visual fields when the electrodes are placed above and below the calcarine fissure, as in the case of the midline channel. As can be seen in Figure 2B, row 1, the visual field distribution of PC1 reverses its sign across the upper and lower field for the midline channel, in agreement with the cortical anatomy. In addition, because both the left and the right hemifields are represented in the contralateral sides of the cortex, a signal from V1 recorded from the lateral channel should be reversed in polarity between the left and the right visual fields. Again, PC1’s behavior is consistent with a signal generated in V1.

The calcarine cortex is folded with the upper and lower banks of the calcarine fissure receiving projections from the lower and upper visual fields, respectively. At the folding line, V1 passes through a point that is oriented vertically with respect to the upper and lower banks of the calcarine cortex. In addition, both the superior and inferior portions of V1 bend toward the medial surface of the occipital lobe, and the upper and the lower vertical meridian of the visual fields project to these regions as shown in Figure 11. Consequently, a signal from V1 oriented perpendicular to the surface of the cortex should be smaller at both the horizontal and vertical meridians when recorded with a vertically oriented (midline) channel, but relatively larger when recorded from the horizontal channel. As can be seen in Figure 2B, row 1, PC1 fulfills these expectations. PC1 is smaller for the midline channel and much larger for the lateral channel at these two areas.

Notice that the horizontal meridian in our model of calcarine fissure shown in Figure 9D is not at the folding line or the floor of the calcarine fissure. Also, the lower lip of the calcarine fissure extends to medial surface more than does the upper lip. The latter finding is consistent with Figure 11 and an observation made by Polyak (1957), who wrote that the striate cortex is found to extend to “... a varying extent upon the free medial surface in a zone along both sides of the fissure, usually less along the upper or cuneal than along the lower or lingual lip.” Assuming that the upper and lower fields are represented by the same amount of striate cortex, Polyak’s statement is consistent with our model that indicates, on average, that the horizontal meridian is inferior to the fold in the calcarine. The only published study we could find that directly states this to be the case is not an anatomical study but a magnetic electroencephalogram (MEG) study (Aine et al., 1996).

For the purpose of the model, the foveal responses were not included. Notice that PC1 for the central four responses is relatively small for both channels (Figure 2B). This observation is consistent with the known functional anatomy of V1. The central four responses are coming from the central 1.2°. This region is represented on the pole of the occipital cortex in many individuals (Brindley, 1972; Rademacher, Caviness, Steinmetz, & Galaburda, 1993). For the region of V1 on the pole, the dipole will be...
oriented approximately orthogonal to both recording channels and, thus, the responses recorded from this region should be relatively small (the center four lines in Figure 10).

PC2 accounts for most of the VEP waveforms that cannot be accounted for by PC1. The left column of Figure 2B, row 2, shows that the amplitude of PC2 varies relatively little with changes in the angular region of the stimulus. Perhaps PC2 is distributed in a small area of cortex and therefore is not subjected to cortical folding. On the other hand, the visual processes of this component may have a poor spatial resolution, not distinguishing the vertical from the horizontal meridian. In any case, it is not clear whether PC2 has its source(s) in extrastriate cortex or in some combination of striate and extrastriate cortex.

Although in theory the response from V1 can be any linear combination of the PCs, the agreement between the visual field distribution of PC1 and V1 anatomy, on the one hand, and the poor agreement between the visual field distribution of PC2 and V1 anatomy, on the other hand, make it unlikely that the V1 component includes substantial contributions from other PCs. In any case, we believe that PC1 of the multifocal VEP is a relatively pure V1 component and can be used to study the visual processing in V1.

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**References**


