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Author(s): Stephen J. Anderson, Ian E. Holliday, Krish D. Singh, Graham F. A. Harding
Source: *Proceedings: Biological Sciences*, Vol. 263, No. 1369 (Apr. 22, 1996), pp. 423-431
Published by: The Royal Society
Stable URL: http://www.jstor.org/stable/50724
Accessed: 04/09/2011 08:51

Localization and functional analysis of human cortical area V5 using magneto-encephalography

STEPHEN J. ANDERSON*, IAN E. HOLLIDAY, KRISH D. SINGH AND GRAHAM F. A. HARDING

Department of Vision Sciences, Aston University, Aston Triangle, Birmingham, B4 7ET, U.K.

SUMMARY

Using a multi-channel SQUID-based neuromagnetometer, we have determined the location, temporal dynamics and functional response properties of the human homologue of the primate cortical area V5 (MT). We provide evidence that area V5 in humans is located near the occipito-temporal border in a minor sulcus immediately below the superior temporal sulcus. This area is selective for low spatial frequencies ($\leqslant 4.0$ c/deg), responds to a wide range of temporal frequencies ($\leqslant 35$ Hz) and shows response saturation for stimulus contrasts greater than 10%. In addition, we find that this area is not responsive to purely chromatic patterns but is responsive to motion-contrast stimuli. Our results are consistent with the hypothesis that area V5 in humans represents a stage of processing within the magnocellular pathway. We discuss our results in relation to the widespread belief that area V5 in humans is specifically concerned with motion perception.

1. INTRODUCTION

Evidence for the existence of an area within the human visual cortex believed to be specialized for the analysis of motion has come from behavioural studies on brain-damaged patients (Zihl *et al.* 1983; Hess *et al.* 1989), and most recently from measurements of cortical activity using positron emission tomography (PET) (Zeki *et al.* 1991; Corbetta *et al.* 1991; Watson *et al.* 1993*a*) and functional magnetic resonance imaging (fMRI) (Tootell *et al.* 1995*a*). This area is located near the occipito-temporal border and is thought to be the human homologue of the primate cortical motion area V5 (MT) (Zeki 1974; Van Essen *et al.* 1981). Like the primate motion area, the area identified as human V5 is anatomically delineated by its heavy myelination and widespread callosal connections (Clarke & Miklossy 1990). Recent evidence suggests that human V5 responds to both real and illusory motion (Zeki *et al.* 1993; Tootell *et al.* 1995*b*).

Our aim in this study was to determine the location and functional properties of human V5 using magneto-encephalography (MEG). This is a completely non-invasive technique that measures magnetic fields arising from electrical brain activity, and as such is a direct measure of cortical neural activity (for a review, see Hamalainen *et al.* 1993). With MEG, extensive measurements can be completed on a single subject to obtain high signal-to-noise ratios, thus avoiding the need to average across subjects, which is vital given the variations evident in human sulcal patterns (Ono *et al.* 1990; Watson *et al.* 1993*b*). Our MEG system has a positional accuracy of less than 3 mm in each dimension and a temporal resolution limited by the data acquisition rate, which is typically 1 KHz. The high temporal resolution of MEG allows the sequence of activation of different cortical areas to be resolved. Unlike electro-encephalography (EEG), which also has millisecond resolution, the localization of the generating current sources of MEG responses is only weakly dependent on the conductivity profile of the head, and therefore fewer assumptions are required in the source localization algorithm.

While PET and fMRI have good spatial resolution, neither can provide information about the dynamics of neural activity as they have a temporal resolution of seconds to minutes. Furthermore, both PET and fMRI only provide an indirect measure of neural activity as both methods rely upon associated metabolic events within the brain for functional imaging. With fMRI, neural activity is reflected by changes in the relative concentrations of oxygenated and deoxygenated haemoglobin in the vicinity of the activity. Some authors have questioned the extent to which signal changes revealed by fMRI reflect neural activity or subject-movement artefacts (Hajnal *et al.* 1994). With PET, changes in regional cerebral blood flow, reflected by changes in the spatial distribution of intravenously administered positron emitting radioisotopes, are assumed to reflect changes in neural activity. Clearly, both PET and fMRI require independent validation with human experimental data.

* Correspondence address: Department of Psychology, Royal Holloway, University of London, Egham, Surrey, TW20 0EX, U.K.

In our experiments, the design of the stimuli was based on the known physiological properties of magnocellular (M) neurons because we know from primate studies that area V5 receives its major input via the M pathway (Zeki & Shipp 1988; DeYoe & Van Essen 1988; Maunsell *et al.* 1990; Felleman & Van Essen 1991), which responds preferentially to high-velocity, achromatic stimuli of low spatial frequency (Merigan & Eskin 1986; Merigan & Maunsell 1990; Merigan *et al.* 1991). We show that rapidly drifting achromatic sinusoidal gratings of low spatial frequency evoke strong magnetic responses from both occipital and occipito-temporal cortical regions. Our results provide evidence that the extra-striate area we have identified using MEG is human V5.

2. METHODS

(*a*) *Stimuli*

The stimuli were generated using a VSG2/2 graphics board (Cambridge Research Systems) and displayed on an Eizo Flexscan T560i colour monitor at a non-interlaced frame rate of 100 Hz, with a resolution of 816 pixels by 589 lines. The monitor was positioned outside a magnetically shielded room (Vacuumschmeltze GmbH) and viewed from within at 3.2 m using two front-silvered mirrors, giving it an angular size of 4.2 deg vertical by 5.6 deg horizontal. All grating stimuli were spatially windowed with a two-dimensional Gaussian envelope ($\sigma = 1.5$ deg) and presented for 600 ms within a 4 deg square stimulus zone centred in the right visual field 2.5 deg along the horizontal meridian. This configuration confined the stimulus input to a single cortical hemisphere. The screen outside the stimulus zone was uniform and of the same mean luminance as the stimulus (40 cd m^{-2}). The stimulus presentation time included a 100 ms raised cosine-ramp onset from zero to maximum contrast, and 200 responses were averaged in synchrony with the start of this ramp. The inter-stimulus interval was 1 s. After 100 response sweeps, subjects were instructed to close their eyes and rest for one minute. To avoid recording an offset response, the recording time was limited to 500 ms.

(*b*) *Procedure*

Experiments were done on three adults, each with full visual fields and a binocular Snellen acuity of 6/6 or better. Viewing was binocular. One observer (JA) was mildly amblyopic (6/12) in the left eye. The observers were seated with their heads stabilized using a forehead rest and bite bar. Evoked responses were recorded in the magnetically shielded room using a 19-channel SQUID neuro-magnetometer, then amplified, bandpass filtered (0–30 Hz) and averaged on-line at a sampling rate of 1 KHz. The room illumination was low photopic. The channels resided in a liquid helium dewar and were distributed in a hexagonal planar array over a 17.5 cm diameter circular area. In addition, a vector magnetometer recorded fluctuations in the ambient magnetic field and was used for adaptive noise cancellation. For further details of this system, see Matlashov *et al.* (1995).

Preliminary experiments were done to establish the optimum dewar position for recording cortical evoked responses to motion stimuli. They were completed using a 0.5 c/deg luminance modulated sinusoid of 80% contrast and 8 Hz drift temporal frequency. Between each set of measurements, the dewar was systematically positioned over the surface of the skull using the *International 10–20 System* (Jasper 1958) of electrode placement as a reference guide. Evoked responses were evident with the dewar positioned over the midline at the back of each observer's head, and again over the right and left occipito-temporal regions of each observer. The highest signal-to-noise ratios were achieved with the dewar positioned over the left occipito-temporal region of each observer, and all the results reported below were obtained with the dewar fixed in that position.

(*c*) *Co-registration of* MEG *and* MRI *data*

Dipole source solutions were co-registered with magnetic resonance (MR) images of each subject's brain. The images were obtained, with each subject's bite bar in place, using a 1.5T Siemens magnetic resonance scanner with 1 mm × 1 mm × 1.5 mm voxel size. To co-register the MEG source solutions with the MR images, we used three anatomical markers (oil-filled capsules positioned over the nasion and left and right pre-auricular notches) and four extra reference markers on each subject's bite bar (1.5 × 4 mm oil-filled drill holes). The reference markers appeared as small white spots on the MR images. The position of each marker in relation to the sensors was determined using a Polhemus Isotrak system at the time of the experiment. This research followed the tenets of the Declaration of Helsinki and received Aston Ethical Committee approval.

3. RESULTS AND DISCUSSION

Figure 1*a* shows the evoked magnetic responses from subject IEH to the onset of a sinusoidal grating of 0.5 c/deg spatial frequency, 8 Hz drift rate and 80% contrast. The response traces were biphasic, their sign and amplitude dependent upon the position of the detectors relative to the underlying cortical activity. The averaged signal-to-noise ratio (figure 1*b*) had major peaks at 166 ms and 220 ms. This time course of activity was observed in all subjects. The responses were modelled as one or more independent dipolar current sources (Mosher *et al.* 1992; Supek & Aine 1993) fixed in position and orientation and with time-varying magnitude. Best-fit solutions were estimated using a nonlinear, least squares minimization procedure based on a homogeneous spherical head model (Cuffin & Cohen 1977). Our objective was to determine the number and location of cortical generators required to model the data at all latencies where the signal-to-noise ratio exceeded 3.0, namely the primary (150–180 ms) and secondary (215–223 ms) response phases (see figure 1).

Figure 2 shows the ratio of residual error to signal noise for dipolar models of the primary response phase ($t = 150$–180 ms) shown in figure 1*a*. In figure 2 the minimum number of generators required to model the primary response phase is indicated when the residue/noise ratio is near 1.0 from 150–180 ms. The dashed curve shows the results of the model for a single current source, which is only adequate over the latency range 162–169 ms. Increasing the model order to two (solid curve) reduces the residue/noise ratio to approximately 1.0 over the whole latency range, indicating that the two-dipole model is an adequate description of the

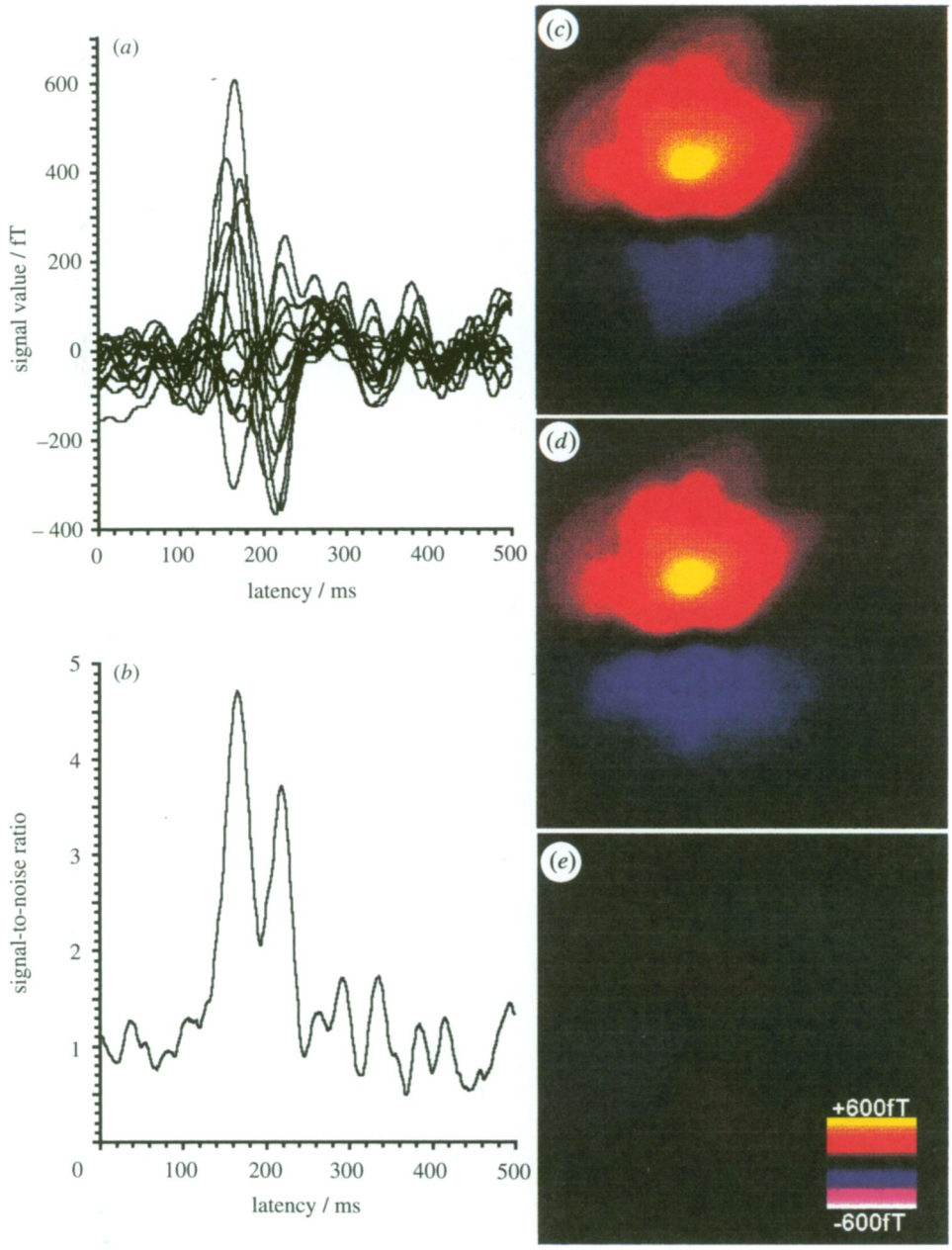

Figure 1. Magnetic evoked responses from observer IEH to the onset of a 0.5 c/deg luminance modulated sinusoid of 80% contrast and 8 Hz drift temporal frequency. (*a*) The evoked magnetic field as a function of time for 19 channels; each trace is the average of 200 individual trials. (*b*) The averaged signal-to-noise ratio as a function of time, with peaks at 166 ms and 220 ms. This ratio was calculated as $\Sigma_{i=1}^{19} Si(t)/\Sigma_{i=1}^{19} Ni$ where $Si(t)$ is the signal strength in the ith channel at a latency of t ms, and Ni is the standard deviation (σ) of the noise in the ith channel calculated using an anti-averaging procedure. (*c*) A pseudo-colour map of the magnetic field strength at $t = 166$ ms. Field magnitude is plotted with reference to the colour scale (inset in panel *e*): positive values indicate a magnetic field emerging from the head. (*d*) The predicted magnetic field at $t = 166$ ms from a two-dipole model fit to the data associated with the primary response phase ($t = 150$–180 ms). (See text and legend to figure 2 for model details.) (*e*) The residual field, calculated as the difference between the model and data at $t = 166$ ms.

data. The suitability of this modelling approach is illustrated in figure 1, where a pseudo-coloured map of the measured magnetic field at $t = 166$ ms (figure 1*c*) can be compared with the calculated field from the two-dipole model (figure 1*d*).

For each subject and for all experiments employing achromatic luminance modulated sinusoidal stimuli, a two-dipole model was required to describe the evoked responses associated with the primary response phase. One source was located in the occipital cortex, consistent with a V1 origin, and the details of this source are being investigated in a separate study (Fylan *et al.* 1995). The second source was located near the temporo-parieto-occipital junction and is characterized in detail below. Analysis of the secondary response phase ($t = 215$–223 ms) identified the same two dipoles, except that their orientation was reversed, indicating a reversal of current flow.

The extrastriate dipole source solution was co-registered with surface-rendered and coronal MR

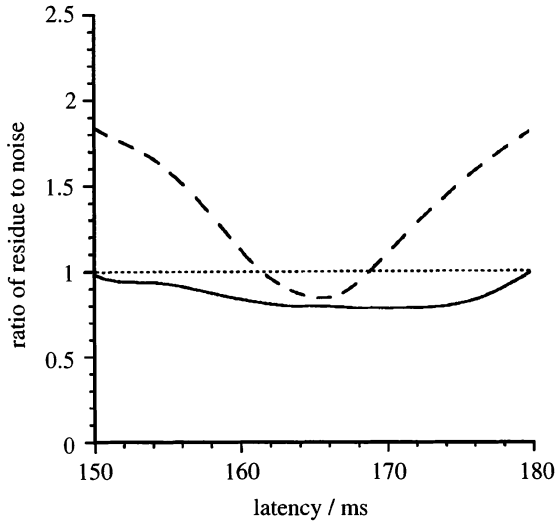

Figure 2. The ratio of residual error to signal noise for dipolar models of the primary response phase (t = 150–180 ms) shown in figure 1*a*. Responses were modelled as one or more independent dipolar current sources fixed in position and orientation and with time-varying magnitude, with best-fit solutons estimated using a nonlinear, least squares minimization procedure based on a homogeneous spherical head model. Signal noise was calculated as $\Sigma_{i=1}^{19} Ni$. A residue/noise ratio near 1.0 indicates an adequate fit. The dashed curve shows the results for a single dipole model; the solid curve shows the results for a two-dipole model.

images of subject IEH (figure 3*a*), JA (figure 3*b*) and AE (figure 3*c*). In each image the source solution is delineated by a red ellipse, which is the 95 % confidence region for the location of the source determined using Monte-Carlo analysis (Press *et al.* 1989). The confidence ellipsoid is located near the occipito-temporal border inferior to the superior temporal sulcus (STS, solid yellow line) in each subject. From the surface-rendered images it can be seen that in subjects IEH and JA the source solution is near the start of the ascending limb of the STS, a feature absent in AE. Intersubject anatomical variations are also evident in the coronal images. In two subjects (IEH and JA) the STS curves superiorly with increasing depth (figure 3*a*, *b*), and the source solution lies deep within a minor sulcus immediately inferior to it. In subject AE the STS curves inferiorly with increasing depth, and the confidence region for the source solution overlaps the STS and the minor sulcus beneath it (figure 3*c*). The variations evident in each individuals' sulcal patterns are within normal bounds (Ono *et al.* 1990; Watson *et al.* 1993*b*). The most parsimonious interpretation of the data for all subjects is that the evoked magnetic responses arise from within a visual area located near the occipito-temporal border in a minor sulcus immediately below the STS. That the delineated regions are the same functional area is supported by the similarity of the response characteristics of this area for subjects IEH and AE (see figure 4). Both PET (Zeki *et al.* 1991) and fMRI studies (Tootell *et al.* 1995*a*) have concluded that this region of the human brain is the homologue of the primate cortical area V5 (MT), and we refer to this region as human V5.

The latency of the peak occipital and human V5 evoked responses decreased at the same rate with increasing stimulus contrast. For a contrast of 80 %, the latency of the peak occipital response was 150 ms, preceding the peak V5 response by 16–20 ms. This time course of activity is in agreement with electroencephalographic (Probst *et al.* 1993) and transcranial magnetic stimulation (Choi *et al.* 1995) studies employing random-dot kinematograms to investigate motion processing in human vision. It is possible that the V5 response we have identified reflects a forward projection of information from the occipital source, as the V5 source was only active after the occipital source was active, and the two sources maintained a constant temporal relation over a wide range of stimulus contrasts. However, other studies provide evidence for a more direct motion pathway in humans, with information flowing from the LGN to V5, bypassing the striate cortex (Beckers & Homberg 1992; Barbur *et al.* 1993; Beckers & Zeki 1995). Moreover, geniculo-prestriate input to human V5 is deemed sufficient for both the directional discrimination and conscious awareness of a moving target (Barbur *et al.* 1993). Beckers & Zeki (1995) conclude that some visual motion signals reach V5 by this pathway in about 30 ms. In our studies with MEG, we found no evidence for early human V5 responses reflecting rapid geniculo-prestriate input, perhaps because it yields responses too small to be detected with current MEG techniques. Another possible route for visual signals to reach V5 is via the superior colliculus and LGN. It remains an open question as to which anatomical projection gave rise to the responses we measured in V5.

We determined the response characteristics of human V5 in subjects IEH and AE by examining the variation in magnitude of the fitted equivalent current dipoles as a function of grating contrast, spatial frequency and drift temporal frequency. Our results show that this area exhibits response saturation for stimulus contrasts greater than 10 % (figure 4*a*), is selective for spatial frequencies $\leqslant$ 4.0 c/deg (figure 4*b*) and is responsive to a wide range of temporal frequencies (0–35 Hz) (figure 4*c*).

A total of three further experimental observations were made: (i) human V5 is responsive to motion-contrast stimuli (where responses were averaged in synchrony to the onset of a 1.5 deg square patch of random-dot leftward motion contained within a 4 deg square field of constant random-dot rightward motion); (ii) following 30 min of dark adaptation, human V5 is responsive at scotopic light levels to drifting achromatic sinusoids of 0.5 c/deg spatial frequency, 8 Hz temporal frequency and 80 % contrast; and (iii) human V5 is not responsive to stationary chromatic (red–green) sinusoidal gratings of 1.0 c/deg spatial frequency, isoluminant by standard flicker-photometry criteria.

These results are consistent with the hypothesis that the cortical area we have identified resides within the M pathway, in that: (i) M-cell responses in the primate retina tend to saturate above 10–15 % contrast, whereas parvocellular (P) responses show no evidence of saturation up to at least 60 % contrast (Kaplan *et al.*

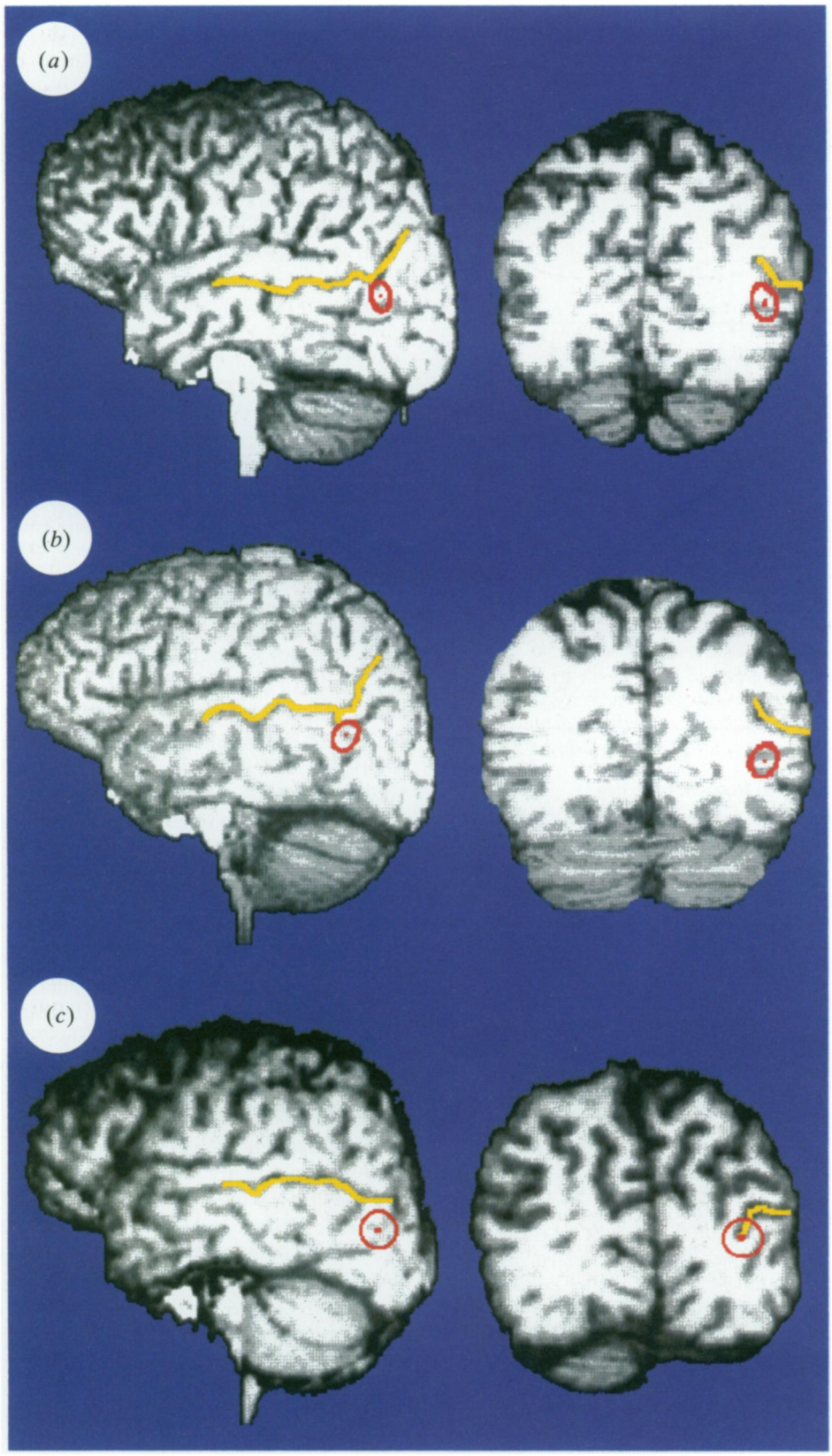

Figure 3. The extrastriate current dipole source solution to the evoked responses measured using a 0.5 c/deg sinusoid of 80 % contrast and 8 Hz drift rate, co-registered with surface-rendered and coronal magnetic resonance images for subjects (*a*) IEH (male, aged 39 years), (*b*) JA (female, aged 27 years) and (*c*) AE (female, aged 32 years). In each image the source solution is shown as a 95 % confidence ellipsoid estimated by Monte-Carlo analysis (Press *et al.* 1989). The solid yellow line in each image serves to highlight the superior temporal sulcus (STS). The activated cortical area is located near the occipito-temporal border in a minor sulcus immediately below the STS in all subjects. The Talairach coordinates of this area for subject IEH are $x = -32$, $y = -75$, $z = +6$, for subject JA are $x = -39$, $y = -61$, $z = -2$ and for subject AE are $x = -30$, $y = -74$, $z = +1$ (reported in millimetres according to the conventions of the Talairach & Tournoux (1988) stereotactic atlas).

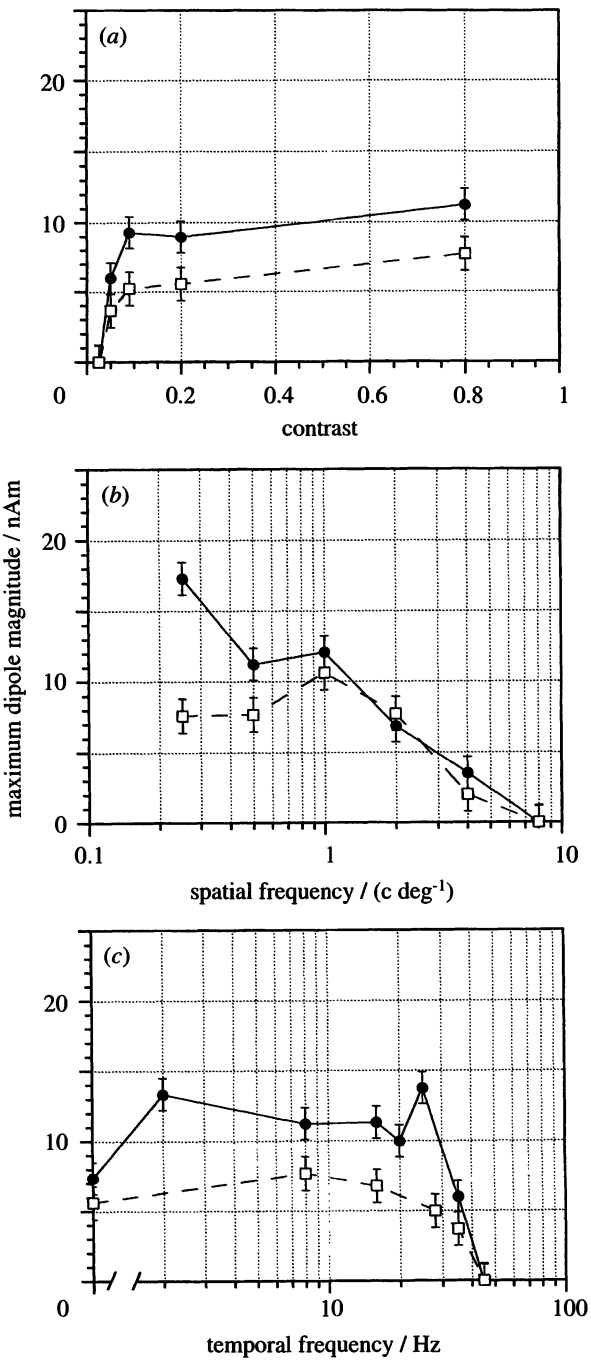

Figure 4. Current dipole magnitude (nAm) of the extrastriate source solution to magnetic responses evoked by: (*a*) 0.5 c/deg sinusoids drifting at 8 Hz, with contrasts of 2.5–80%; (*b*) 80% contrast sinusoids drifting at 8 Hz, with spatial frequencies of 0.25–8.0 c/deg; and (*c*) 80% contrast sinusoids of 0.5 c/deg, with drift temporal frequencies of 0–45 Hz. The solid symbols are for observer IEH and the open symbols are for observer AE. Standard deviations were calculated from the average noise level. For each fit, the dipole magnitude represents the strength of activation of a single cortical area and is directly correlated with the size of the active neuronal population (Lu & Williamson 1991). Each stimulus type evoked bi-phasic response traces of the type shown in figure 1 *a*, which were best fit with a two-dipole model source solution (see legend to figure 2 for model details). In each case the model identified one striate and one extrastriate current source, the latter being the same as that shown in figure 3, which we identify as the human homologue of the primate cortical motion area V5.

1991); (ii) M-cells are preferentially responsive to drifting, low spatial frequency targets (see §1); (iii) cells in area V5 of primates carry information about local motion contrast (Born & Tootell 1992); (iv) the M pathway is responsive at scotopic light levels (Purpura *et al.* 1988, 1990), though there is no clear evidence that it dominates vision at low light levels (see Lennie & Fairchild 1994); and (v) no responses were evoked by isoluminant chromatic stimuli, consistent with evidence that the P pathway alone is responsible for conveying colour information (for a review see Lennie 1993).

4. GENERAL DISCUSSION

Using MEG we have confirmed that human V5 is located near the occipito-temporal border in a minor sulcus immediately below the superior temporal sulcus, in agreement with recent PET (Zeki *et al.* 1991; Watson *et al.* 1993*b*) and fMRI (Tootell *et al.* 1995*a*) studies. By systematic variation of the stimulus parameters, we were able to determine the spatio-temporal frequency characteristics and contrast response properties of this area. We find that human V5 is selective for low spatial frequencies ($\leqslant$ 4.0 c/deg), responds to a wide range of temporal frequencies ($\leqslant$ 35 Hz) and shows response saturation for stimulus contrasts greater than 10%, consistent with the hypothesis that this area receives its major input via the M pathway.

The perceptual role of area V5 remains uncertain, though the role most usually ascribed to it is the analysis of motion, a conclusion based largely on physiological studies showing a preponderance of direction-selective cells in area V5. Our results indicate that human V5 responds not only to moving patterns but also to the onset of stationary patterns (figure 4*c*). However, this does not preclude it from being a motion centre as there is good psychophysical evidence that velocity extraction in human vision involves a weighted comparison of lowpass and bandpass temporal filters (Smith & Edgar 1994). It may be the case that the evoked magnetic responses from human V5 reflect the envelope of activity of these filters.

From psychophysical studies we know that the human motion system is responsive to drifting (8 Hz) gratings with spatial frequencies as high as 35 c/deg (Anderson & Burr 1989). Assuming that human V5 is the centre for the analysis of motion, it is surprising therefore that we were unable to record a response from this area to spatial frequencies higher than about 4 c/deg (figure 4*b*). There are at least two possible explanations for this. First, the motion acuity limit determined psychophysically may reflect the activity of a relatively small number of neurons (Newsome *et al.* 1989), too few to be recorded with MEG (Hamalainen *et al.* 1993). However, this seems an unlikely explanation for the weak responses obtained with high contrast sinusoids having spatial frequencies near the peak of the sensitivity function for direction discrimination, namely 3 c/deg (Watson & Turano 1995). Alternatively, high spatial frequency motion information may be conveyed by the P pathway, as suggested by both

physiological (Merigan *et al.* 1991) and psychophysical (Galvin 1994; Anderson *et al.* 1995) studies. Presumably at some stage of analysis the information carried by each pathway is combined to produce a unified motion percept. This is consistent with various reports showing that the M and P pathways converge early in the cortex, thereby contributing jointly to many visual tasks (for reviews, see DeYoe & Van Essen 1988; Zeki & Shipp 1988; Felleman & Van Essen 1991; Merigan & Maunsell 1993).

(*a*) *The role of the M pathway*

Merigan *et al.* (1991) have demonstrated that two important tasks of the primate motion system, direction and speed discrimination, can be accomplished in the absence of the M pathway (achieved by ibotenic acid injections in the magnocellular layers of the macaque LGN), suggesting that the P pathway can sustain motion perception. Striking as this conclusion is, it is consistent with physiological evidence that, along the dimensions of spatial frequency and temporal frequency, M and P cells have largely overlapping ranges of sensitivity (Derrington & Lennie 1984; Spear *et al.* 1994). The contribution of each pathway to motion perception in the intact animal remains uncertain, but it is possible that the M pathway plays little or no role in motion perception. The fact remains that the properties of M-cells revealed by physiological studies on monkeys, and those of human V5 reported in this study, may reflect a variety of perceptual functions other than motion perception.

Given the evidence that the parietal pathway in primate cortex depends largely on M-cell contributions, Merigan & Maunsell (1993) suggest that, rather than being specialized for motion perception, M-pathway function may be related to the general nature of parietal lobe processing. For example, Lennie (1993) has suggested that the M pathway may underlie attentional processes rather than motion processing per se, arguing that this pathway could provide the signal that allows the rapid detection of objects in the peripheral visual field prior to foveation. Support for this view comes from the fact that area V5 projects to parietal association areas (Ungerleider & Desimone 1986) involved with visual attention (Corbetta *et al.* 1993), that V5 lesions disrupt eye movements (Yamasaki & Wurtz 1991), and that the distribution of M ganglion cells is concentrated in the peripheral retina in humans (Dacey 1993, 1994).

If area V5 was involved in the detection of moving objects in the peripheral field, one could argue that an important signal for V5 would be the motion of an object relative to its background. This is consistent with Born & Tootell's (1992) report that interband cells in primate area V5 carry information about local motion contrast, information that could be used to detect motion boundaries. Using MEG, we can confirm that motion-contrast patterns do evoke strong responses from human V5.

With MEG we were unable to elicit any evoked responses from human V5 to isoluminant red-green sinusoidal gratings, a finding consistent with physiological reports that cells in area V5 are not colour-selective (Zeki 1974). However, using PET, ffytche *et al.* (1995) have demonstrated that the motion of green stimuli relative to a red background increase cerebral blood flow in human V5, and concluded that this area can use motion-defined signals based on chromatic information alone. ffytche *et al.* go on to suggest that human V5 can use motion-defined information derived from any source. Together with the evidence discussed above, these findings provide strong support for the hypothesis that a major function of human V5 is the rapid detection of objects moving relative to their background.

We thank Neville Drasdo, Fiona Fylan and Gareth Barnes for helpful discussions throughout the course of this work. This work was made possible by grants from Fight For Sight, Institute of Ophthalmology, London, the European Commission and a Wellcome Travel Grant to I.E.H.

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