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Magnetoencephalographic study of speed-dependent responses in apparent motion

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Abstract

Objectives: There have been only few studies of visually-evoked cortical responses to apparent motion as a function of stimulus speed. Most earlier findings on evoked peak magnitudes and latencies, utilizing various types of smooth and apparent motion stimuli, have demonstrated that greater spatial separation/speed resulted in enhanced peak magnitudes, decreasing onset latencies in individual extrastriate neurons and in shorter motor reaction times in subjects. However, some reports using partial-coverage magnetoencephalography stated that increasing the stimulus displacement actually triggered a substantial reduction of the evoked main peak latency while the magnitude showed no clear change.

Methods: To resolve the issue of the dependency of evoked responses on stimulus speed in apparent motion, we presented moving bar stimuli to 6 subjects at velocities within a 100 fold range and investigated the ensuing evoked visual cortical activity using a whole-cortex magnetoencephalograph. The magnitude and the latency of the first major evoked peak M1 was measured and compared for 6 discrete bar-stimuli displacements in all subjects.

Results: Our results showed clearly that the M1 peak response magnitudes increased in a nonlinear way with higher apparent speeds (larger displacements), in compliance with the logarithmic Fechner law. We observed also that the fluctuations of the mean evoked M1 peak latency (140 ± 10.6 ms) did not reach significance over the tested range of stimulus velocities.

Conclusions: These findings probably reflect global motion processing mechanisms which rely on nonlinear speed-dependent feedback connectivity between striate and extrastriate visual cortex areas. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Apparent motion; Magnetoencephalographic; First-order motion; Displacement; Response latency; Stroboscopic motion; Spatial integration

1. Introduction

The ability to identify correctly the path of motion for partially occluded objects (Johansson and Ahlstrom, 1998) is crucial for the survival of many biological species. Under certain conditions the visual system can detect spatiotemporally-discrete motion sequences or 'apparent motion' (Watanabe, 1998) in a similar way to smooth motion (Burr et al., 1986). However, single-step apparent motion stimuli can induce only transient movement responses, in contrast to sustained 'real' motion stimuli. Most theories explain the smooth perception of discrete apparent motion by the spatiotemporal properties of the early visual system (Fahle et al., 2001). Low-level visual memory mechanisms, which retain stimulus attributes and which are located probably beyond the primary visual cortex (Magnussen, 2000), may also play a role in discrete motion perception. In spite of the large number of well-designed studies on visual motion processing in general (see Palmer, 1999; Finley, 1982; Albright and Stoner, 1995 for reviews; Newsome et al., 1986), only a small number of reports have targeted systematically basic parameters of the visual cortical activity during apparent motion. Almost a century ago, Korte (1915) summarized 3 basic laws for simple two-point apparent motion linking the successful perception of movement to the functional relationships between 3 stimulus parameters: spatial separation versus luminance, repetition rate versus luminance and separation versus rate (Palmer, 1999). Since then, a number of studies have expanded our knowledge about the influence of apparent motion parameters like contrast, luminance, color, spatial separation, texture,

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eccentricity, stereopsis, background illumination, interstimulus time interval (Choudhury and Carvill, 1983; Cavanagh et al., 1989), stimulus onset asynchrony (SOA) (Boulton and Baker, 1993), stimulus orientation (Werkhoven et al., 1990) and even gender-related sensitivity to shape and distance (Shechter et al., 1991) on apparent motion perception. These experiments have been performed on the background of similar 'real' motion reports showing also the effects of motion stimulus coherence (Patzwahl and Zanker, 2000), motion duty cycle (Bach and Ullrich, 1994), spatial frequency (Korth et al., 2000), color (Derrington, 2000) and the subject's attention (Torriente et al., 1999), among others.

Although these studies have exploited a large variety of visual stimuli (Zanker, 1994a,b), bars (Westheimer, 1998) are interesting as apparent motion stimuli due to their closer resemblance to natural objects than gratings or random dot clusters, especially when there is no ambiguity in the visual system for the motion correspondence problem. Despite the drawbacks concerning their spatial frequency spectrum, single bars have been shown to invoke a better neuronal synchronization than multiple bars in extrastriate cells with different preferences for motion direction (Kreiter and Singer, 1996). Visual area MT neurons prefer narrow bars (Lagae et al., 1993) less than 1° in width (Felleman and Kaas, 1984), while gratings may be inappropriate for the analysis of local motion mechanisms in striate neurons (Orban et al., 1987).

Many studies have demonstrated contradicting findings and as a result, it is still difficult to summarize the influence even of some most basic apparent motion parameters like spatial displacement and apparent speed on the latency and strength of the evoked responses (Gallichio and Andreassi, 1982; Andreassi et al., 1973; Szirtes et al., 1988; Ebersole and Galambos, 1973).

There are several latency (and corresponding amplitude) measures, which can be determined experimentally in stimulus response studies. One of them is the cellular onset latency, also called the response latency, which is extracted from histograms of individual neuronal spike trains. Another type of latency is the experimental subject's motor reaction time after detecting a stimulus. On the other hand, typical evoked latency measurements of synchronized neural activity in many electroencephalographic (EEG) and magnetoencephalographic (MEG) studies are realized by searching for the peak latency (Novak et al., 1992) since it is the most reliable evoked latency measure. The peak latency avoids the subjective thresholding inherent in the evoked onset latency measure (the point backwards from the peak, where the signal reaches an amplitude threshold; Ritter et al., 1988) and has the advantage of achieving a higher signal-to-noise ratio.

Reported values for the peak latency of the first major evoked response to motion have included 156 ms for grating stimuli using MEG (Uusitalo et al., 1997), 150–200 ms for random dot stimuli using EEG (Hoffmann et al., 1999) and 150–180 ms for low-contrast ring stimuli, expanding and reversing at a constant speed of 2.4°/s, using a combination of MEG and fMRI (Ahlfors et al., 1999). While these motion studies were not designed specifically to survey the peak latency as a function of the stimulus velocity, latencies of evoked peaks in checkerboard experiments were not significantly influenced by the displacement of the visual stimulus (Parry-Jones and Fenwick, 1979; Wu et al., 1992). Furthermore, Nakamura and Ohtsuka (1999) demonstrated that moving random dot patterns exhibit a constant motion-related peak latency of about 150 ms for 5 stimulus velocities between 5°/s and 25°/s.

A few earlier reports have indicated that the strength of the evoked responses was influenced by the degree of spatial displacement or speed. Using EEG recordings, MacKay and Rietveld (1968) demonstrated that doubling the speed of a moving bar stimulus on an oscilloscope screen increased the magnitude of the evoked cortical potentials. In a study comparing visual evoked potentials (VEP) and electroretinograms (ERG), Bach and Hoffmann (2000) showed an increase in the evoked N2 peak amplitudes as motion speed of contracting 'dartboards' varied from 4.7°/s to 36.2°/s, while the corresponding peak latencies changed little at about 160 ms. Furthermore, several EEG studies using checkerboard pattern displacements (Wu et al., 1992; Parry-Jones and Fenwick, 1979) have also established a relationship between the degree of their spatial shifts and the strength of the evoked potentials. In their checkerboard study, Wu et al. (1992) demonstrated that when the pattern displacements increased from 0.09° to 4.4°, the amplitudes of evoked peaks N1, P1 and N2 showed a significant increase, especially for smaller check sizes. In contrast to these findings, previous reports by Kaneoke et al. (1997, 1998) have asserted that evoked peak latencies decreased substantially from 182 to 72 ms as bar-stimuli displacements (and the apparent motion speed) were increased. These experiments employed horizontally moving bar stimuli and partial sensor coverage MEG measurements. Although peak response amplitudes were not discussed in these reports, when inspecting the presented data (Fig. 2 in Kaneoke et al., 1998), we could not detect any immediate relationship between the peak response magnitudes and the degree of displacement. In another study on evoked ERG and VEP responses to moving vertical stripes with velocities from 0.25°/s to 200°/s, Korth et al. (2000) found that while the amplitudes of the so called N200 peaks exhibited a maximum at about 18°/s, the peak latencies decreased from about 300 ms down to about 170–180 ms with declining stripe pattern speed (with clear dependence on spatial frequency and subject).

To help resolve these controversial issues, at first we have examined and compared the basic influences of various apparent motion and flash stimulus parameters on the corresponding peak cortical magnetic field responses in an earlier, preliminary MEG study on 3 subjects (Bakardjian et al., 1998), employing first-order (Lu and Sperling, 2001; Smith et al., 1998) bar stimuli. The purpose of our present experiments was to investigate more systematically the effect of changing apparent motion velocity (spatial displacement during a fixed time interval) on the transient evoked cortical responses in humans. The main goal was to extend our previous findings in a series of experiments and to address the question of the influence of apparent speed of moving stimuli on visual cortex activity. The experimental recording equipment that we used relied on the MEG technique (see Hamalainen et al., 1993 for review; Ahlfors et al., 1999 for an example with visual motion stimuli). Since the skull is transparent to magnetic fields but not to electric fields, this allowed us to track weak evoked responses from more concentrated brain regions compared to the EEG technique (Malmivuo et al., 1997).

2. Materials and methods

2.1. Subjects

Six healthy subjects, 5 male and one female, aged 23–38 (29 ± 6) years, gave their informed consent to participate in this study. Four of the subjects had normal visual acuity and two had corrected myopes, all of them with normal binocular and color vision. Three of the subjects were naive and 3 were proficient (authors) concerning the details of the experiments. All participants were properly instructed before the sessions. At the beginning of each sitting, subjects were sufficiently exposed to motion stimuli for training and allowed at least a 10 min dark adaptation period under ambient lighting conditions in the shielded room.

2.2. Data acquisition

An OMEGA-64 whole-cortex biomagnetometer system (CTF Systems Inc., Vancouver, Canada) was used to conduct the MEG experiments. The system was equipped with a quasi-regular grid of 64 DC-SQUID (super-conducting quantum interference device) sensors with an average inter-channel spacing of approximately 4.5 cm. The sensor grid consisted of first order axial gradiometer magnetic flux transformers with a 2 cm diameter and 5 cm baseline, which measured the radial component of the magnetic field (Endo et al., 1999). A proprietary 'higher order gradiometer formation' technique (CTF Systems Inc.) was applied for adaptive external noise cancellation, which was capable of suppressing the external noise level down to a 4–7 fT rms/$\sqrt{}$Hz level (Vrba, 1996). Subjects were sitting in a dimly illuminated magnetically shielded room, in which illuminance was maintained below 10 lux. Trials were recorded from -200 to $+500$ ms relative to stimulus onset, at a sampling rate of 625 Hz with no real-time filtering. For precise head positioning 3 external indicator coils were placed on the skull (left ear, right ear, nasion). Subjects were asked to minimize head movements and the head position in 3D space was registered and compared before and after each recording. Since the MEG sensor grid extended over the whole head, eye-movement control was based on anterior sensor readings and contaminated single trials were rejected.

2.3. Motion stimuli and experimental protocol

The image presentation device for this study was a liquid crystal display (LCD) projector SHARP XV-SV1 with 800×600 pixels resolution and a refresh rate of 60 Hz, which ensured sufficient flicker fusion. Viewing was binocular in a sitting posture under the MEG sensors, at a distance of 1.5 m from screen center to nasion. Due to the third-order-gradiometer, external-noise-cancellation capabilities of our biomagnetometer it was possible to make the MEG recordings with the LCD projector placed just outside the shielded room (more than 2 m from the sensors) while the door was open as shown in Fig. 1 (Takeda et al., 1996). The apparent motion stimuli in our experiments were rear-projected on the left side of a $29° \times 22°$ (retinal degree arc) semi-transparent anti-reflection screen in front of the subject. The fixation point was a small green circle with a diameter of 0.1° shown in the middle of the screen (0° eccentricity). The time delay of the projected stimuli was carefully checked and confirmed to be less than 1 ms.

The visual stimuli were bright photopic white bars on a dark background, presented with bar widths set to 0.05° and bar heights to 5° for optimal response (Felleman and Kaas, 1984). Control experiments testing a number of similar bar sizes and luminances indicated that there was no significant difference in the evoked response when these parameters were moderately varied. Motion displacement was horizontal and stimuli were centered vertically. The direction of motion was alternating – centripetal (IN) and centrifugal (OUT), towards and away from the point of fixation. One of the bars was presented at 1° (MacKay and Rietveld, 1968), while its more temporal counterpart was displaced further on the left correspondingly by 0.05°, 0.1°, 0.2°, 1°, 3° and 5°, away from the center of the screen. SOA onset-to-onset intervals were set to random durations ranging from 2000 to 3000 ms to avoid the 1400 ms trace lifetime of motion (Uusitalo et al., 1997), which indicates how long the preceding stimuli might affect the following one. The inter-stimulus intervals (ISI) without visual stimuli on screen were minimized to the screen's refresh interval of 16.7 ms for maximal evoked response magnitude (Kawakami et al., 2000), so that the calculated apparent speeds of the motion stimuli were 3°/s, 6°/s, 12°/s, 60°/s, 180°/s and 300°/s. The mean foreground luminance L_F of the stimuli was ~ 204 cd/m^2 and the background luminance L_B was ~ 4 cd/m^2, so that the stimulus contrast was $(L_F - L_B)/(L_F + L_B) = 0.98$. Brightness was measured from the subject's position by a luminance meter MINOLTA LS-110.

A total of 6×2 experimental conditions were presented in the left visual field, including apparent motion stimuli at 6 displacements and two directions of motion for each of them. Each of the 12 experimental conditions was repeated at least 220 times within 6 sessions on 3 separate days for

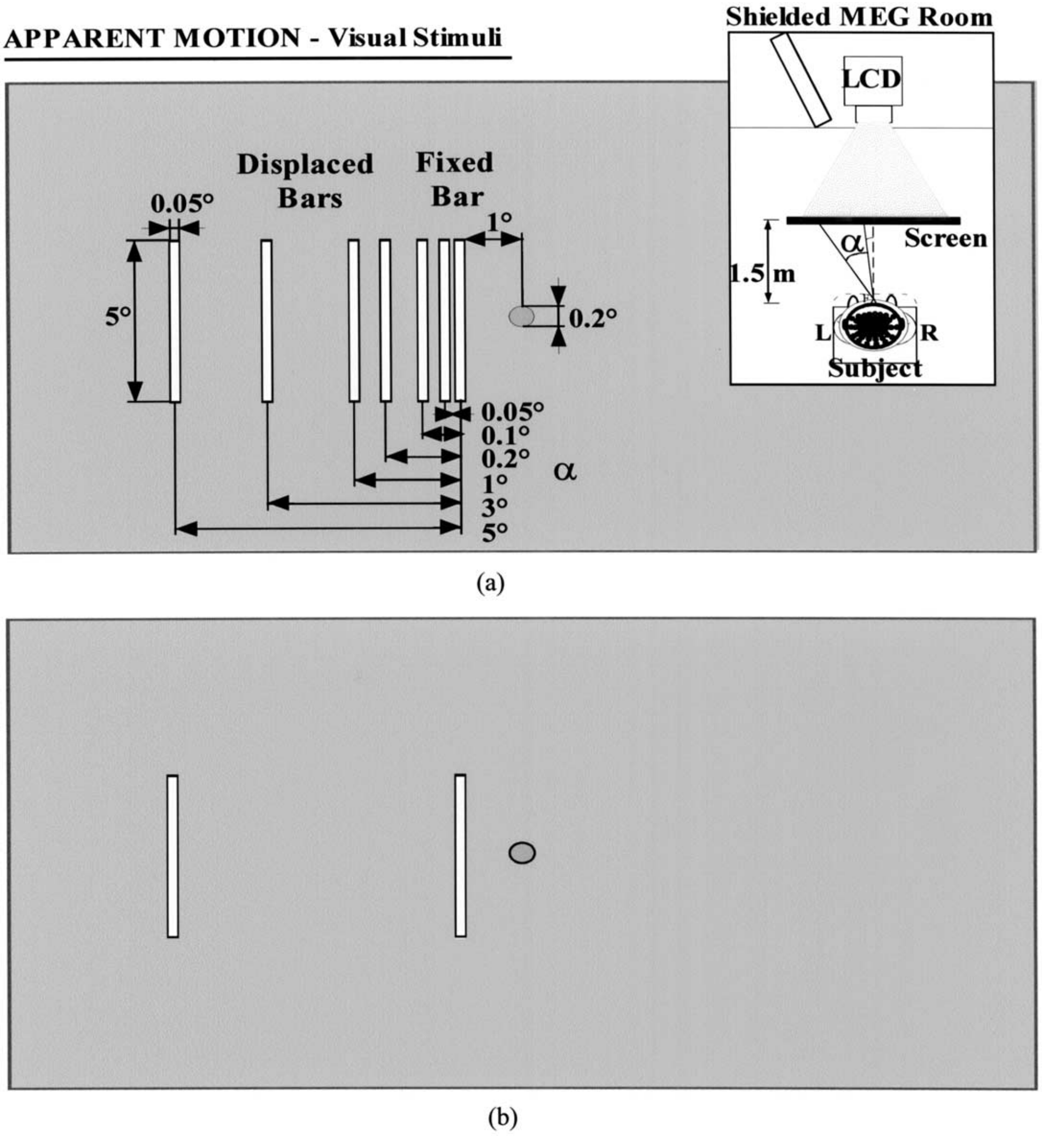

Fig. 1. Experimental setup for apparent motion MEG experiments with bar displacement stimuli (0.05° × 5°) in healthy human subjects. A static bar was fixed at an eccentricity of 1° left of gaze center and a moving bar was displaced by 0.05°, 0.1°, 0.2°, 1°, 3°, or 5° arcs. The applied experimental paradigm for visual stimulation is shown on the upper side (a), while an example for two-frame apparent motion with 5° displacement is demonstrated on the lower side (b).

every subject. In addition, short presentation breaks with a 20 s duration between every 50 stimuli were introduced in order to neutralize the effects of prolonged attention and fatigue towards the end of each session. One important point in our presentation paradigm was to present all 6 types of stimuli (displacements) in random order within a session. This was done to facilitate direct comparisons even after transient shifts in attention (Baylor et al., 1979), alertness and other commonly observed non-visual exogenous factors, as well as to reduce the systematic bias due to previous stimuli exposure (Baylor et al., 1979; Sekuler, 1996). In that way, non-visual variability between displacements was kept to a minimum. Inter-session variability of individual subjects was evaluated by 5° displacement test runs before each session.

2.4. Data processing

More than 15,000 single trials recorded in this study were individually examined. Trials were carefully tested, classified and rejected off-line on the basis of each subject's blinking artifacts and each individual's intrinsic cerebral noise levels. All decisions to reject a trial as containing artifacts were based on magnetic flux density levels during the 200 ms pre-stimulus period. A trial was rejected if for any parieto-occipital channel the median pre-stimulus noise exceeded the corresponding median levels of the previous trial by more than 200%, or if noise outliers within the trial exceeded the median pre-stimulus levels by 200%. The percentage of rejected trials ranged from 2% to 15% depending on the subject. The single trials, which were not rejected, were then baseline-corrected and averaged for each experimental condition. The averaged MEG data were bandpass-filtered between 0 and 40 Hz using a 10th order Butterworth filter.

Since all individual MEG sensor recordings in an average trial usually have slightly varying waveforms in time (Skrandies, 1995), a common measure of deviation from the baseline was necessary to find the peak latency and magnitude of the evoked response. An appropriate single measure was the root-mean-square (RMS), a statistic, quantifying the deviation from the baseline over time that takes account of the signal offset. In our study, the RMS was calculated from the magnetic flux densities for a 20 channel parieto-occipital subset of sensors over the visual cortex. The area covered by these sensors was approximately the same as in the experiments of Kaneoke et al. (1997, 1998). As shown in Fig. 2b, the M1 peak was estimated as the point of maximal RMS deflection (Ritter et al., 1988) between 0 and 200 ms after motion onset. In order to be considered valid for further analysis, a RMS peak had to exceed the baseline pre-stimulus median RMS by at least a factor of two (Raiguel et al., 1999). The RMS peak magnitude and the latency were calculated for the evoked responses of each subject, for each stimulus speed and direction, and then used in the subsequent apical (peak) analysis.

In accord with other studies (Lesevre and Joseph, 1979; Uusitalo et al., 1997), the consistent reproducibility of the evoked magnetic field responses for each subject was accompanied by a considerable inter-subject variability in waveforms, probably reflecting differences in cortical anatomy. To enable pooling of all data, the subject-parameter space was calibrated by normalizing the peak latency and magnitude for each subject individually by her/his mean values over all tested displacements. This procedure was similar to the peak amplitude normalization by maximum levels, proposed by Ritter et al. (1988). In that way, the results in our study were based on relative changes with increasing speed (normalized mean peak latency, normalized mean peak RMS magnitude) rather than on original values.

2.5. Statistical analysis

Statistical evaluation of peak latency or magnetic flux density (magnitude) was performed under various experimental conditions using mean values and standard deviations (x ± SD). Two-factor repeated-measures analyses of variance (ANOVA) as well as *t* tests were applied in order to verify whether data series were drawn from populations with the same mean value.

3. Results

For each of the 6 subjects, the M1 peak magnitude in these average trials increased monotonically with greater spatial separation between the moving stimuli (higher speed) (Fig. 2a). The relatively weak magnitude response to 0.05° displacement (Fig. 2a, upper left) was in agreement with subject-reported difficulties in detecting such a minimal motion separation. Apparent motion perception problems were

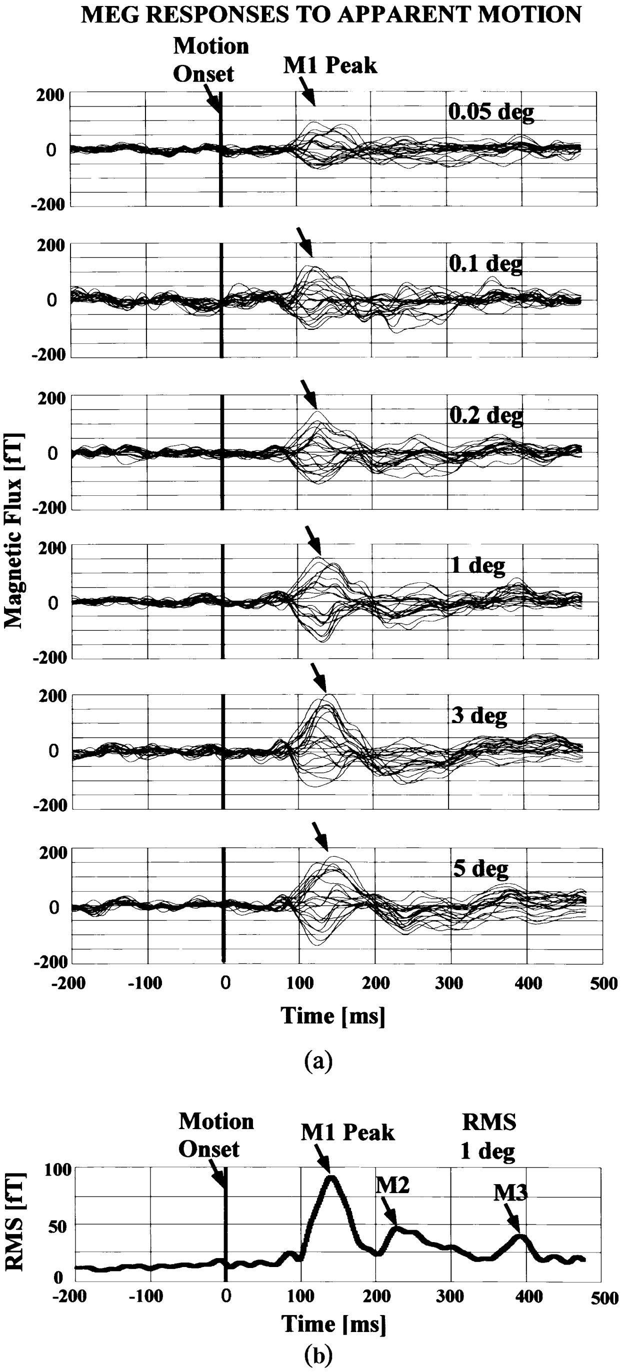

Fig. 2. (a) Mean evoked field responses to apparent motion stimuli as a function of horizontal displacement in the left visual hemifield using only right parieto-occipital sensors from whole-head MEG recordings. Data are shown for one subject; the responses from other subjects were similar. Displacement of stimuli (apparent speed) increases downwards from top to bottom. (b) Root-mean-square (RMS) curve for 1° spatial separation. The M1 locator algorithm performed a global iterative top-to-bottom search within the 0…200 ms time range, looking for the first RMS maximum that exceeded twice the pre-stimulus median level. Located peak magnitude and latency values were used in the subsequent apical analysis.

reported only when the smallest 0.05° displacements were randomly mixed with larger displacements, and could be compensated by an increased level of attention.

The cortical activation strength over the relevant parieto-occipital visual areas was quantitatively measured by RMS curves, as shown in Fig. 2b in the case of 1° displacement. In most cases, M1 (100…200 ms), M2 (200…300 ms) and M3 (~400 ms) peak cortical activities could be observed (Bakardjian et al., 1998). The mean M1 peak latency of the visual evoked responses in two-bar apparent motion was 140 ± 10.6 ms when averaged over all subjects, displacements and directions. The individual mean M1 latencies were 126.4 ± 6.2, 129.6 ± 6.2, 140.8 ± 3.6, 142.4 ± 6.6, 145.6 ± 6.0, and 155.2 ± 3.9 ms.

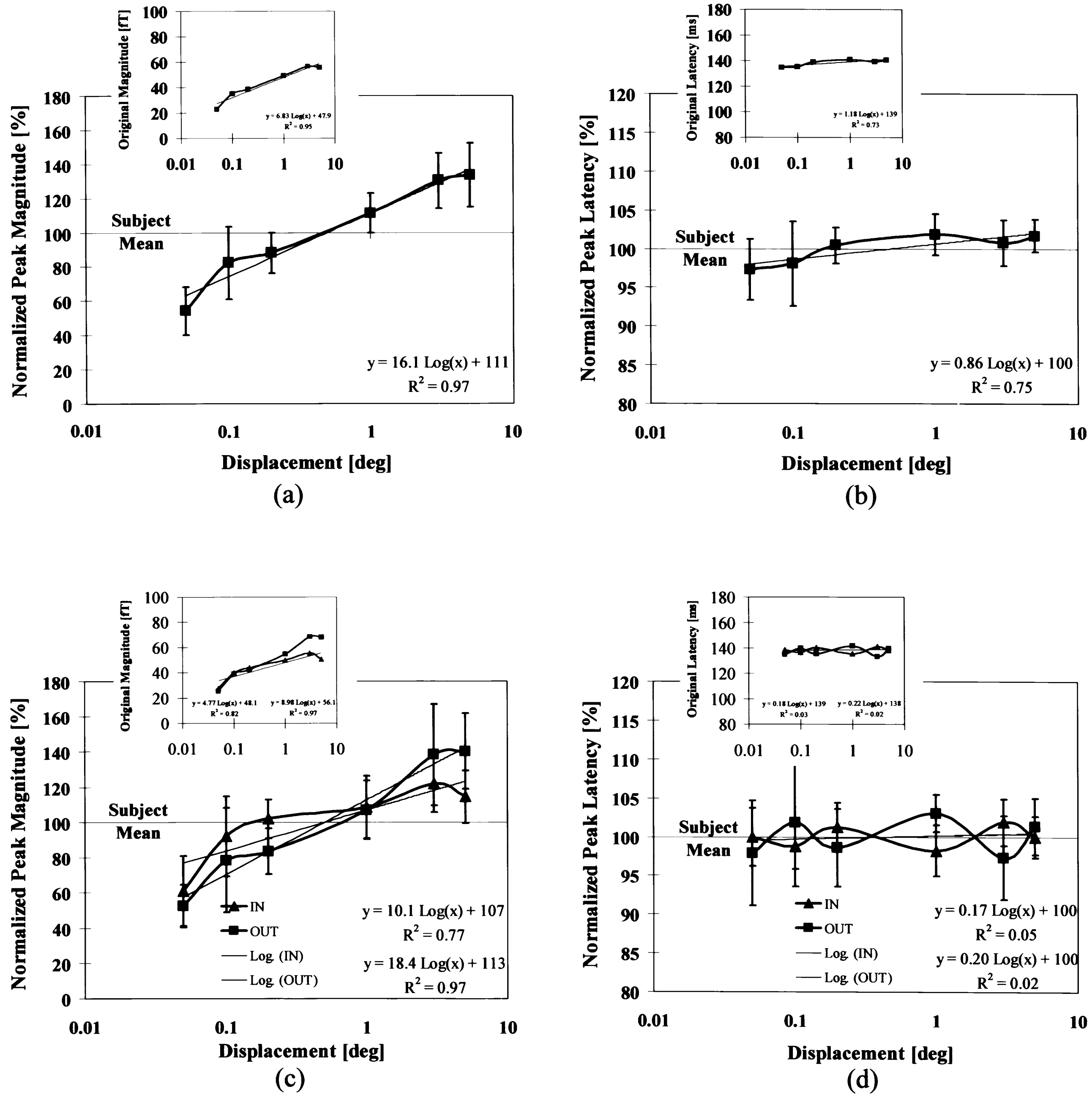

Fig. 3. Apical (peak) analysis of apparent motion peak visual evoked field (VEF) latency and magnitude for two-bar stimulus displacements (angular velocities) using large stimulus onset intervals and minimal blank inter-stimulus intervals. The strongest effects were observed for high-velocity stimuli (speed anisotropy of the VEF magnitude), while there was no significant change in peak latency with velocity. Individual averages for each subject were removed by normalization in order to facilitate an inter-subject comparison. Curves show mean values, lines display the best logarithmic fit and vertical bars represent standard deviation. (a,b) The peak latency and magnitude values when the direction of motion was also averaged. (c,d) The influence of motion direction (IN/OUT) on VEF changes due to bar displacement. Note weak magnitude preference for OUT-going stimuli at faster speeds and for IN-going direction in slower motion. Small boxes show original values before normalization.

The inter-subject variability was significant both for the original peak magnitudes ($P = 8 \times 10^{-6}$) and for the original peak latency ($P = 9 \times 10^{-7}$), when tested by single-factor ANOVA. That variability, however, was speed-dependent, so that for lower stimulus speeds (smallest displacements 0.05° and 0.1°) the coefficient of variation between subjects for all normalized magnitude and latency values was twice as great than the one for faster motion.

Fig. 3 illustrates the main dependencies between the motion-related spatial displacement/speed and the normalized evoked M1 response parameters. In this figure, the peak magnitude and latency values were normalized for each subject individually before averaging the peak data from all subjects. During the normalization procedure, each subject's peak magnitude or latency average value across all tested speeds was taken as her/his 100% reference in order to remove offset differences in the individual responses. The peak magnitude (Fig. 3a) increased substantially, while the peak latency (Fig. 3b) was not influenced by the degree of stimulus separation.

A two-factor repeated-measures ANOVA confirmed that spatial separation significantly influenced the M1 peak magnitude ($P = 1.5 \times 10^{-7}$), while it did not have a significant effect on peak latency ($P = 0.22$). Furthermore, Student's t test was performed on the 3 smallest and the 3 largest displacements for all subjects in order to investigate the effect of the stimulus speed more precisely. Results showed that the original peak magnitudes were significantly different ($P = 0.01$), while shifts in the peak latency were not ($P = 0.36$). In addition, heteroscedastic t tests of peak values between individual displacements for all subjects were performed to uncover a potential change in the visual processing mechanism as the stimulus speed increased. Results from these tests demonstrated that interactions between magnitude and displacement were independent ($P < 0.05$) with the exception of 0.1° versus 0.2° ($P = 0.4$) and 3° versus 5° ($P = 0.8$), as can also be seen in Fig. 3a. There were no independent interactions between the peak latency and displacement. In light of reports in the literature that higher response rates in individual neurons were related to shorter onset latencies (Raiguel et al., 1999), a Spearman rank order correlation test was performed. It showed that for all subjects and displacements there was no direct association ($r = -0.15$, $P = 1.0$) between the original mean peak magnitude and latency values in the evoked MEG responses. A weak association ($r = 0.83$, $P = 0.1$) was indicated only for the normalized inter-subject averages (Fig. 3a,b).

All observed evoked magnitude changes could be described analytically in 2D space by a logarithmic fit (Fig. 3). The data generally conformed to Fechner's law (Fechner, 1860/1966; Palmer, 1999), which outlines the logarithmic relationship between the intensity of a perception response I and the stimulus strength S,

$$I = k^{*}\log(S) + n \qquad (1)$$

According to that principle, the mean normalized peak magnitude $M_{\mathrm{N}}^{\mathrm{INOUT}}$ (Fig. 3a) and latency $L_{\mathrm{N}}^{\mathrm{INOUT}}$ (Fig. 3b) were described as a function of the spatial separation between moving stimuli D by the following equations

$$M_{\mathrm{N}}^{\mathrm{INOUT}}\,[\%] = 16.1^{*}\log(D) + 111 \qquad (r = 0.98,\ P < 0.02) \qquad (2)$$

$$L_{\mathrm{N}}^{\mathrm{INOUT}}\,[\%] = 0.86^{*}\log(D) + 101 \qquad (r = 0.87,\ P < 0.1) \qquad (3)$$

The role that the horizontal motion direction played in the evoked responses is shown in Fig. 3c for the peak magnitude and in Fig. 3d for the latency.

An ANOVA test indicated that direction itself did not exert a significant influence upon the mean M1 magnitude ($P = 0.40$) or upon the latency ($P = 0.79$). This fact allowed us to increase the signal-to-noise ratio by averaging the IN–OUT trial data for subsequent processing (Fig. 3c,d). Nevertheless we should note that the peak magnitude differences between the IN and OUT directions for increasing stimulus velocities were marginally significant ($P = 0.09$), where the normalized mean IN magnitudes were relatively stronger for small displacements (low speeds), while the OUT magnitudes may have increased more rapidly at higher speeds.

The following linear regression equations described the normalized directional peak magnitudes and latencies of the log-linear plots in Fig. 3:

$$M_{\mathrm{N}}^{\mathrm{IN}}\,[\%] = 10.1^{*}\log(D) + 107 \qquad (r = 0.88,\ P = 0.05) \qquad (4)$$

$$M_{\mathrm{N}}^{\mathrm{OUT}}\,[\%] = 18.4^{*}\log(D) + 113 \qquad (r = 0.98,\ P < 0.02) \qquad (5)$$

$$L_{\mathrm{N}}^{\mathrm{IN}}\,[\%] = 0.17^{*}\log(D) + 100 \qquad (r = 0.22,\ P > 0.5) \qquad (6)$$

$$L_{\mathrm{N}}^{\mathrm{OUT}}\,[\%] = 0.20^{*}\log(D) + 100 \qquad (r = 0.14,\ P > 0.5) \qquad (7)$$

where D is the visual stimulus displacement in degrees.

4. Discussion

Our MEG experiments demonstrated an apparent speed anisotropy (alterations in peak strength and latency of the evoked responses due to motion stimulus velocity change) in which visually-evoked responses, as exemplified by the M1 peak, increased in magnitude with larger stimulus displacement and hence with increasing speed, although latencies remained relatively unchanged.

The results in our study are consistent with several previous EEG reports on evoked responses after displacements of random dots (Nakamura and Ohtsuka, 1999) and checkerboard patterns (Wu et al., 1992; Parry-Jones and Fenwick, 1979). However, unlike our own stimuli, those used in these previous studies may have been poorly unsuitable for studying speed anisotropy. The primary goals of experiments with checkerboard stimuli have generally been to establish clinical methodology for assessing the optical pathways (Parry-Jones and Fenwick, 1979) or to investigate the relationship between visually-evoked potentials and the number of stimulated retinal receptors (Wu et al., 1992). Since the bright checks in the pattern were regularly interspersed with darker inter-check areas of the same size, the shifting of the checkerboard pattern structures in these studies was restricted from a zero movement to a full displacement of a single check size. Another drawback of these stimuli may have been the enhanced contribution to the evoked response by cortical areas (Lesevre and Joseph, 1979) associated with the processing of visual form. That is why motion stimuli with increased spatial localization might also have advantages when investigating the influence of speed on cortical responses. Manning et al. (1988) argued that apparent motion elicited by 0.5° × 3° bar stimuli is initially processed in the occipital cortex with further processing taking place in the temporal and parietal cortices. Their EEG study employed continuously cycling red LED stimuli flashed for 80 ms at apparent speeds of 2°/s, 4°/s, 6°/s and 8°/s and indicated that the latency of the evoked peak negativity around 150–175 ms did not change with higher speed, while the amplitude decreased for electrode O2.

However, in their 37 channel MEG studies using apparent motion 0.1° × 2° bar stimuli, Kaneoke et al. (1997, 1998) argued that increasing stimulus displacement/speed from 3.3°/s to 333°/s produced a significant decline in the M1 peak latency, from 182 to 74 ms. Response magnitudes were not discussed in their reports. Our attempt to verify these experiments was unable to reproduce them satisfactorily. We performed more than 200 MEG experiments on 11 subjects in which the timing of all components in our stimulus generation procedures was carefully tested in relation to the MEG recording onset in order to avoid image exposure aliasing. The influence of the stimulus size, form and brightness was studied on 3 of the subjects and we found that these factors were not significant in relation to the peak latency. Consequently, we concluded that the differences lie in the technical details of the two experimental setups and we could find no flaws whatsoever, neither in our setup, nor in our analytical methods.

Our results presented in this report demonstrated clearly a lack of a significant M1 peak latency change, while there was a strong trend for the M1 response magnitude to increase logarithmically with apparent motion speed. Interestingly, a recent short report by the research group including Kaneoke et al. (Kawakami et al., 2000) described using a laser beam to simulate apparent motion and compared it to real motion. Their results showed a much more complex dependency of response latency to stimulus speed in contradiction to their previous reports (Kaneoke et al., 1997, 1998). In a paper (Kawakami et al., 2002) published during the review process of the current report, the same group diverged from their initial findings and argued that the peak latency changed at increasing apparent speeds according to a U-shaped curve with the minimum value at 100°/s. They also showed increasing peak amplitudes, similar to the results in the current study. These results strongly conflicted their previous findings. Although we are unable to offer an explanation for this discrepancy, it at least confirmed once again how crucial all stimulus delivery details are for studying evoked peak latencies in response to apparent motion stimuli.

In addition, there was also a certain controversy in the explanation of their initial peak latency results by these authors (Kaneoke et al., 1998) concerning the probable visual areas involved in generating the evoked apparent motion responses. They appropriately suggested that the marked differences in the evoked peak latencies caused by increasing stimulus speed might be explained by a decrease of synchronization delays in existing feedback loops between various visual areas. However, their own magnetic single-dipole estimations indicated that the M1 peak cortical activity itself arose locally only in the probable human homologue of the area MT/V5 for all tested stimulus velocities, so that the feedback desynchronization would have little effect on the visual circuitry as a whole. Somewhat surprisingly, a later study by Bundo et al. (2000), which used the same experimental setup as in the previous study of Kaneoke et al. (1997, 1998) and examined single mid-range 1° bar displacements, found that there were actually 3 possible cortical locations – temporo-occipital, occipital and parietal – of the apparent motion response depending on the subject's sulcal anatomy. As our experiments have also demonstrated, inter-subject variability (Patzwahl et al., 1996; Ahlfors et al., 1999) is a significant factor, which must be fully accounted for before summarizing results related to individual cortical anatomy.

In general, there may be at least 4 possible mechanisms producing the speed anisotropy observed in our results showing that a higher stimulus speed enhanced the evoked response and did not change significantly the peak latencies in apparent motion: extensive feedback/feedforward connections between visual areas, enhanced spatial integration at larger displacements, lateral inhibition at smaller displacements and low-level retinotopic effects. The first 3 of these mechanisms cannot be regarded as mutually exclusive.

The first, 'connectivity' hypothesis explains the observed speed anisotropy as the result of simultaneous motion processing within several reciprocally connected visual areas along the dorsal stream (Maunsell and van Essen, 1983; Jiang et al., 2002; Newsome et al., 1986). This theory is supported by the fact that the evoked M1 peak latencies around 140 ms that we measured were much too large to correspond to the activation of the neurons from any single extrastriate or striate visual area (Probst et al., 1993). Areas V1, V2 and MT/V5 are known to be concurrently active in visual motion (Zeki et al., 1991; Raiguel et al., 1989; Maunsell and van Essen, 1983). It is feasible to suggest that in our experiments the synchronized activity around peak M1 at the higher speed range probably reflected mostly visual processing outside the striate cortex because the striate cortex contributes mainly to the speed range below 20°/s

(Duysens et al., 1984; Orban et al., 1987; Pasternak et al., 1995). It is known that for motion stimuli MT/V5 neurons exhibit shorter latencies at higher speeds (Lisberger and Movshon, 1999; Raiguel et al., 1999). However, we demonstrated that peak latencies were independent of stimulus speed across a wide range of velocities. Our findings are supported by previous reports (Manning et al., 1988; Gallichio and Andreassi, 1982; Szirtes et al., 1988) showing that short neuronal onset latencies do not automatically imply earlier evoked latencies in stimulus-velocity-related MEG/EEG recordings. This may be due to the fact that the optimal motion preferences are different for various individual extrastriate neurons, so that even near-simultaneous activation in the neural population by a single visual stimulus would involve numerous non-optimal responses with lower firing rates and longer latencies. Furthermore, selective or distributed neuronal synchronization mechanisms (Kreiter and Singer, 1996) may also play an important role in the observed effect of evoked peak latency equalization, as well as cortical visual processing possibly being performed always at maximal speed.

The observed increase in the peak magnitude values for higher speeds in our data could also have been a manifestation of intensified feedback processing between the extrastriate and striate visual areas (Lamme and Roelfsema, 2000; Hupe et al., 2001; Bullier et al., 2001), as also indicated by the relatively large peak latency values. One such scenario has been suggested by Smith et al. (1998) who proposed that striate area V1 could be responsible for decoding the local spatial and temporal structure of the visual input, while the extrastriate area V5 (MT) is predominantly motion-specific. Since MT neurons alone may not be able to detect the particular speed at which the stimulus is moving, higher cortical areas could be also involved in motion speed estimation (Simoncelli and Heeger, 2001). Other possible explanations involving multi-area processing may include the activation of direct feedforward speed-sensitive pathways to the extrastriate cortex in addition to those through the primary visual cortex (Ffytche et al., 1995) or, alternatively, a ‘fast-lane’ mechanism, which switches from simple position tracking at low speeds in the striate cortex to motion-energy sensitivity at higher velocities (Seiffert and Cavanagh, 1999) in the extrastriate cortex.

Another proposed hypothesis exploits the notion of enhanced spatial integration mainly in the extrastriate cortex due to increased neuronal receptive field (RF) sizes and to enhanced synchronization of activity in neurons where the RFs overlap to a greater extent with those of their neighbors. It is known that the RF sizes of extrastriate neurons are 60–100 times larger than the RFs of striate cells (Desimone and Ungerleider, 1986; Maunsell and van Essen, 1983). Also, RF sizes have been found to be larger away from the center of gaze (Tanaka et al., 1986; Felleman and Kaas, 1984). On the other hand, the percentage of cells with overlapping RFs is reportedly higher for velocity-high-pass (VHP) neurons (Duysens et al., 1984) at increasing eccentricities (Lagae et al., 1993; Curtis et al., 1985). Such neurons with overlapping RF and different preferred directions were reportedly shown to engage in much stronger synchronous activity by a single common moving bar stimulus, rather than by separate bar stimuli moving strictly in each individual neuron’s RF and preferred direction (Kreiter and Singer, 1996).

Lateral inhibition is a third possible mechanism which would be strictly apparent-motion-specific and would assume an increasingly weakening inhibition between interacting adjacent neural regions as the discrete stimulus displacements become larger (Castet, 1994). This is also a viable cortical mechanism in view of the saturating duration and contrast of our bar stimuli. This may also provide support for the idea that changes of evoked response strength in apparent motion were actually due to the relative displacement itself and not to the absolute eccentricity (Bakardjian et al., 1998; MacKay and Rietveld, 1968).

However, if our findings were merely due to the eccentricity bias (Rovamo and Raninen, 1984), according to the fourth hypothesis, a number of low-level retinotopic mechanisms could have contributed. Responsible local factors may have included retinotopic dependencies of the retinal photoreceptor diameters, the ganglion cell RF sizes (Ricco’s area), the relative density of lateral geniculate nucleus (LGN) fast-conducting Y-cells and the projection density from the retina to the striate cortex (cortical magnification). Nevertheless, the theoretical dependencies of all these local mechanisms on the retinal eccentricity, calculated from data in the literature, did not match the logarithmic increase in response magnitudes demonstrated in our experiments.

We cannot exclude the possibility that our peak latency magnitude results might be specific for the high-contrast, low-duty-cycle apparent-motion bar stimuli we have used in our experiments. Since by definition apparent motion is a sequence of spatially displaced flash onsets, it was necessary to verify if evoked responses to apparent motion were different from responses to simple bar appearance/disappearance. In a previous preliminary study (Bakardjian et al., 1998), we addressed this issue using the same experimental setup and performed a control experiment with randomly mixed apparent motion bar stimuli at the speed of 180°/s (spatial displacement of 3°) and the appearance/disappearance bar stimuli at the corresponding eccentricities. We demonstrated that while appearance response magnitudes declined at greater eccentricity, apparent motion responses were enhanced with increasing displacement. In addition, apparent motion responses were much stronger than their corresponding appearance-only counterparts. Peak evoked latencies did not change significantly under any of the experimental conditions and, again, they were much too large to correspond simply to the typical onset latencies of individual extrastriate neurons activated by flash stimuli (Schmolesky et al., 1998). Involvement of several visual areas and cortical feedback motion processing is a more feasible explanation for our findings than simple flash responses in the striate cortex, as shown by the peak magnitude differences. However, it is most likely that both appearance- and movement-related cortical neural generators are involved in apparent motion perception at the stage of stimulus classification (Ritter et al., 1982). Functional feedback connections between various visual areas are recruited very early in the evoked response, so that their presence may be difficult to detect using only time course measures such as peak latency and magnitude (Hupe et al., 2001).

Also, although a subject's motor reaction response latency to moving stimuli has been also shown to decrease across motion velocities (Hohnsbein and Mateeff, 1992; Burr et al., 1998; Novak et al., 1992), it probably cannot be linked directly to evoked peak latency measures due to the involvement of a number of supplementary high-level perceptional processes.

In summary, in our study we were particularly interested in ascertaining if measured visually-evoked M1 peak latency and strength would show dependency on horizontal apparent motion speed and direction as the range of the stimulus velocities expanded 100 fold. The magnitude of the peak cortical activation displayed a nonlinear increase without abrupt changes across stimulus speeds, which was well described by Fechner's logarithmic law. However, the mean peak latency did not vary substantially for higher stimulus velocities. In addition, the direction of motion had no significant effect on the peak magnitude and latency values. These findings may indicate that the speed-sensitive mechanisms in apparent motion are capable of global motion processing and require reciprocal feedback connectivity between the striate and extrastriate visual cortex.

Since there is a possibility that the results in our study may have been limited with respect to the particular type of stimuli applied, experiments with other apparent motion stimuli may be needed to further analyze the relationship between real and apparent motion perception. In view of practical applications for the demonstrated enhanced responses to fast apparent motion, specialized experimental designs may provide more insight into the exact origins of speed-dependent phenomena.

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