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Longer VEP latencies and slower reaction times to the onset of second-order motion than to the onset of first-order motion

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Abstract

We compared visual evoked potentials and psychophysical reaction times to the onset of first- and second-order motion. The stimuli consisted of luminance-modulated (first-order) and contrast-modulated (second-order) 1 cpd vertical sine-wave gratings drifting rightward for 140 ms at a velocity of 6 °/s. For each condition, we analysed the latencies and peak-to-baseline amplitudes of the P1 and N2 peaks recorded at Oz. For first-order motion, both P1 and N2 peaks were present at low (3%) contrast (i.e., depth modulations) whereas for second-order motion they appeared only at higher (25%) contrasts. When the two types of motion were equated for visibility, responses were slower for second-order motion than for first-order motion: about 44 ms slower for P1 latencies, 53 ms slower for N2 latencies, and 76 ms slower for reaction times. The longer VEP latencies for second-order motion support models that postulate additional processing steps for the extraction of second-order motion. The slower reaction time to the onset of second-order motion suggests that the longer neurophysiological analysis translates into slower detection.

Keywords: First-order motion; Second-order motion; Visual evoked potentials; Reaction times; Latencies

Our visual system is engineered to permit the efficient extraction of motion information that arises either from spatiotemporal changes in luminance (first-order cues) or from spatiotemporal changes in other physical characteristics of an image, such as its texture, that are visible even when there is no change in mean luminance (second-order cues). Our ability to detect objects defined by image attributes other than luminance is well documented both for the perception of motion (Badcock & Derrington, 1985; Cavanagh & Mather, 1989; Chubb & Sperling, 1988) and for spatial vision (McGraw, Levi, & Whitaker, 1999; Hess, Ledgeway, & Dakin, 2000).

Several lines of evidence suggest that first- and second-order motion are analysed by different signal processing mechanisms. Neurons in the cat's striate cortex have different spatial and temporal frequency tuning for first-order stimuli than they do for second-order stimuli (Zhu & Baker, 1993; Mareschal & Baker, 1998, 1999). Humans do not integrate alternating frames containing first- and second-order local motion into an unambiguous percept of motion (Legdeway & Smith, 1994), and their sensitivity to first- or second-order local motion is not affected by adaptation to motion of the other type (Nishida, Ledgeway, & Edwards, 1997). We recently found that sensitivity to second-order motion develops more slowly than sensitivity to first-order motion (Ellemberg et al., in press), and is more profoundly degraded by early visual deprivation caused by dense central congenital cataract (Ellemberg et al., submitted), at least under some conditions. Further, neuropsychological studies report a 'double dissociation' where lesions in some areas cause deficits in the perception of second-order motion while relatively sparing first-order motion (Plant & Nakayama, 1993; Vaina & Cowey, 1996), and lesions in other areas cause deficits in the perception of first-order motion with little if any effect on second-order motion (Greenlee & Smith, 1997; Vaina, Makris, Kennedy, & Cowey, 1998; Vaina, Soloviev, Bienfang, & Cowey, 2000). Finally, functional magnetic resonance imaging studies indicate that, although some visual areas (including V1, V2, and V5) respond equally to both types of motion, areas V3 and

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VP respond more strongly to second-order motion than to first-order motion (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998).

The detection of motion has been modeled using the principles of motion energy, supported both by psychophysical and neurophysiological data (Adelson & Bergen, 1985; Emerson, Bergen, & Adelson, 1992). The extraction of simple motion energy begins with orientation-selective filtering from neurons that signal the difference in average luminance within their receptive fields, and thus behave like linear filters. A phase-independent measure of motion energy arises when the squared responses of such bandpass linear spatio-temporal filters, akin to simple cells, are summed by direction-selective linear filters, akin to complex cells in V1. However, this mechanism is blind to second-order stimuli because it relies on the presence of spatial Fourier components in the luminance domain that move consistently in one direction. Computational modeling suggests that the detection of second-order motion requires not only a first stage linear filter but also additional processing steps (Wilson, Ferrara, & Yo, 1992; Chubb & Sperling, 1988, 1989).

In a series of experiments, Baker and colleagues found neurophysiological evidence for this additional processing (Zhu & Baker, 1993; Mareschal & Baker, 1998, 1999; for a review see Baker, 1999). They recorded responses from neurons in areas 17 and 18 of the cat's brain to luminance gratings (first-order) and to contrast envelope gratings (second-order) which had been created by multiplying a static high spatial frequency sinusoidal grating (carrier) with a drifting low spatial frequency sinusoidal grating (envelope). Neurons were tuned to a narrow range of spatial frequency that was much higher for the second-order carrier than for the first-order luminance grating. Further, in these same neurons, the preferred range of spatial frequency was lower for the second-order contrast envelope than for the first-order luminance grating. These data support a 'filter-rectify-filter' model, in which an early linear filtering occurs when neurons in areas 17 and 18, that are sensitive to high spatial frequencies, respond to the carrier grating. This is followed by a non-linear processing stage (e.g., full-wave rectification) that introduces first-order characteristics into the neural representation of the second-order image, and a second stage filtering by neurons that are sensitive to lower spatial frequencies and respond to the spatial and temporal properties of the stimulus. This processing scheme by itself cannot account for responses to luminance gratings because the spatial frequency tuning of the early and late filters do not overlap.

Wilson et al. (1992) proposed a similar model for the detection of contrast modulations contained in the motion of plaid patterns. Their quantitative model predicts that the additional steps necessary to extract second-order motion, whereby the image is filtered at one scale, undergoes a nonlinearity, and is then filtered at a different scale, require additional processing time. The purpose of the present study was to test this hypothesis by comparing the time required for the human visual system to process first-order versus second-order motion. We compared visual evoked potential (VEP) latencies and psychophysical reaction times to the onset of first-order versus second-order motion.

VEPs provide a useful means to investigate the neurophysiological processes underlying different aspects of visual function. Motion-onset elicits a strong VEP, which is dominated by a positive peak (P1), which appears between 100 and 130 ms, and a negative peak (N2), which appears between 150 and 200 ms (Clarke, 1973; Göpfert, Müller, & Hartwig, 1984; Bach & Ullrich, 1994, 1997; Kubova, Kuba, Spekreijse, & Blakemore, 1995). Several pieces of evidence indicate that the N2 peak is associated mainly with motion processing, whilst the P1 peak is mainly associated with pattern processing. First, the amplitude of the N2 but not of P1 is reduced by adaptation to motion (Bach & Ullrich, 1994; Hoffmann, Dorn, & Bach, 1999). Second, consistent with evidence that motion processing mechanisms have a low contrast threshold and a rapid contrast gain, the N2 but not the P1 is relatively independent of contrast (Kubova et al., 1995; Bach & Ullrich, 1997). Third, consistent with evidence that motion processing mechanisms are more sensitive in the periphery, the N2 can be elicited farther off in the periphery than the P1 (Kuba & Kubova, 1992).

Only one study compared VEPs to the onset of first- versus second-order motion in humans (Victor & Conte, 1992). Victor and Conte report no difference between VEPs elicited by first- versus second-order motion. Their stimuli consisted of a vertical bar made of randomly positioned light and dark noise dots that moved against a static background of randomly positioned light and dark noise dots. During movement of the first-order stimulus, luminance was kept constant. During movement of the second-order stimulus, the squares in the moving bar flickered randomly. However, the noise dots were large (>4 arc min) and, according to Smith and Ledgeway (1996), second-order stimuli made from a carrier of noise dots exceeding 2 arc min contain significant first-order artifacts. Thus, Victor and Conte's second-order stimuli likely contained first-order cues, an artifact that could explain the similarity of their VEP responses under the two conditions.

In the present study, we used stimuli that were constructed to ensure that they did not contain any luminance artifacts (noise dots subtending 1.4 arc min). We also used first-order stimuli with spatial and temporal characteristics that carefully matched those of the second-order stimuli. The stimuli consisted of two-dimensional noise patterns added to (first-order) or multiplied with (second-order) sinusoidal gratings. With visibility equated for first- and second-order stimuli, both VEP latencies and psychophysical reaction times were slower for second-order motion than for first-order motion.

1. Methods

1.1. Observers

The subjects were 8 adults (mean age = 24.6 years, range 19–34 years). All had normal or corrected-to-normal acuity with no history of visual disorders. The procedures were explained and informed consent was obtained.

1.2. Apparatus

The stimuli were generated by a Power Macintosh computer with Pixx 1.55 software, and were displayed on a 53 cm View Sonic monitor. The monitor had a frame rate of 75 Hz and a pixel resolution of 1600×1200. VEPs were recorded by a Grass system model 79D.

1.3. Stimuli

The stimuli consisted of 1 cpd vertical sinusoidal gratings that were 15° wide and 15° high when viewed from a distance of 114 cm. The stimuli were made of two-dimensional random noise (the carrier), the luminance of which was binary. Each noise element subtended 1.4×1.4 arc min. The first-order stimuli were created by adding the noise carrier to a luminance-modulated sinusoidal grating. This produced a sinusoidal modulation of luminance across the carrier, which appeared like a conventional luminance-modulated sinusoidal grating. The depth modulation (Michelson contrast of the grating's luminance) was defined as:

$$\text{depth modulation} = (L_{\max} - L_{\min})/(L_{\max} + \mathrm{L}_{\min})$$

where $L_{\max}$ and $L_{\min}$ are the maximum and minimum mean local luminance averaged over adjacent pairs of noise dots.

The second-order stimuli were created by multiplying the carrier with a luminance-modulated sinusoidal grating. This produced a sinusoidal modulation of the contrast of the carrier. The stimulus consisted of a series of alternating regions of higher and lower contrast between noise dots, with every region having the same mean luminance. The depth modulation of the grating's contrast envelope was defined as:

$$\text{depth modulation} = (C_{\max} - C_{\min})/(C_{\max} + C_{\min})$$

where $C_{\max}$ and $C_{\min}$ are the maximum and minimum mean local contrasts (Michelson) in the stimulus.

The space- and time-average luminance of the stimuli and background were maintained at 35 $\mathrm{cd\,m^{-2}}$. Gamma-correction was verified by means of a Minolta chroma-meter CS 100. The depth modulation of the first-order images was linearly related to the voltage of the *Z*-axis. Using the same procedure as Smith and Ledgeway (1996), we calibrated the second-order images to ensure that gamma-correction was accurate with respect to the characteristics of these stimuli. Specifically, we measured the local luminance values of a stationary and of a drifting second-order stimulus, and adjusted the gamma correction factor to eliminate any differences in luminance between the high and low contrast regions of the envelope. The correction factor was verified regularly throughout the course of the study. Further, small noise dots (1.4×1.4 arc min) were used to ensure that the second-order stimuli did not contain detectable local luminance cues (Smith & Ledgeway, 1996).

Each type of motion (first- and second-order) was presented at five depth modulations: 3.25, 12.5, 25, 50, and 100%. The gratings moved rightwards at a velocity of 6 °/s. During each recording session the sequence consisted of an abrupt onset of continuous motion for 140 ms, followed by a long stationary phase that was again immediately followed by an abrupt onset of motion, so forth and so on. Therefore, the grating was always present on the screen. The stationary phase varied randomly from 3.5 to 5.5 s to minimize the effects of adaptation. The duty cycle of the motion to stationary phase averaged 3.3%.

1.4. Procedure

In a Faraday chamber, participants viewed the screen binocularly from a distance of 114 cm. The participants were instructed to fixate a small transparent cross (0.25°) positioned at the centre of the display. Each subject completed 10 conditions (two types of motion × 5 levels of depth modulation). The order of presentation was randomized across the 10 conditions to control for any effects of habituation and/or fatigue. An experimental session, including electrode placement, lasted about two hours.

Cortical responses were recorded from Oz (as defined by the international 10–20 system) with reference to linked earlobes. The ground electrode was placed at Fpz (centre of the forehead). We used Ag/AgCl electrodes that were fixed on the scalp with Ten 20_{TM} and $\mathrm{EC}_{2\mathrm{TM}}$ conducting cream. Electrode impedance was kept below 5 K ohms. Prior to each recording session, a 5 μV, 20 ms pulse was recorded to calibrate the acquisition system. The recording epoch was 500 ms, and started 55 ms prior to the onset of motion. Each VEP was the average of 100 trials. This produced 10 averaged responses (or VEPs) per subject.

Reaction time. Reaction time was recorded simultaneously by asking subjects to press a computer-monitored push-button as soon as they detected the onset of the motion. Any response produced prior to, or over 1 s after, the motion-onset was rejected. As a result, 4.9% and 4.5% of the responses to the onset of first- and second-order motion, respectively, were not included in the analyses of the reaction times.

1.5. Data analysis

The biopotentials were acquired with an analog band-pass ranging from 0.1–100 Hz and were stored for subsequent off-line averaging and analysis. Biopotentials for each response in the same condition (motion type and contrast) were averaged for each subject. EEG recordings contaminated with eye movement artifacts, detected with a threshold criterion of 100 μV, were eliminated before the averaging. Fewer than 6% of the trials were rejected for any given condition.

P1 and N2 peak amplitudes were measured relative to the baseline, which was calculated from the average amplitude of the first 30 ms after the onset of averaging (see Ellemberg, Hammarrenger, Lepore, Roy, & Guillemot, 2001; Bach & Ullrich, 1997; Kubova et al., 1995).

1.6. Control experiment to measure the direction discrimination thresholds of the first- and second-order stimuli

For the same numerical value of depth modulation (i.e., amplitude modulation of the sine function or Michelson contrast), second-order stimuli are much less visible than are first-order stimuli. This could be a potential confound as it is well documented that VEP latency and reaction time increase and VEP amplitude decreases as the visibility or contrast of a grating decreases (Breitmeyer, 1975; Parker & Salzen, 1977; Vassilev & Strashimirov, 1979; Jakobsson & Johansson, 1992; Bonnet, Thomas, & Fagerholm, 1996). Therefore, in a control experiment we measured thresholds for detecting the direction of motion of the first- and second-order images and then compared the latencies and reaction-times for the first- and second-order conditions whose depth modulation was at a constant multiple of those thresholds. This procedure ensures that the first- and second-order stimuli's depth modulations are comparably above the subjects' threshold.

The observers were 6 of the 8 subjects who participated in the VEP study. The apparatus and stimuli were the same as those described above.

1.7. Procedures

Subjects viewed the stimuli binocularly, from 114 cm. To determine thresholds for direction of motion, subjects were instructed to fixate the centre of the screen and were asked to judge whether the stripes were moving leftward or rightward. The subjects entered their responses by pressing one of two keys on the keyboard.

All subjects were tested in each of two conditions: first- and second-order motion at 6 °/s. Half of the participants first completed trials with first-order motion; the other half first completed trials with second-order motion. Thresholds for the discrimination of the direction of motion (left versus right) were calculated with a Maximum Likelihood-TEST staircase procedure (Harvey, 1986), and were defined as the minimum contrast (i.e., depth modulation) necessary to detect the direction of motion. For the staircase procedure, the maximum values for the first- and second-order stimuli were 50% and 100% contrast, respectively. The minimum values for first- and second-order motion were 0.1% and 1.0% for first- and second-order respectively. In the two conditions, the number of steps between the maximum and minimum was set at 20. Before beginning the test with each type of motion (first- or second-order), each subject was given a practice staircase with feedback after each trial. At the end of each practice run, subjects were asked if they understood the task and if so, testing began. For each subject, each threshold was calculated from the mean of two complete staircases.

2. Results

Fig. 1 shows the averaged potentials evoked by the onset of first- and second-order motion for one representative subject. The solid lines represent the waveforms elicited by the onset of first-order motion and the dashed lines represent the waveforms elicited by the onset of second-order motion. First-order motion elicited VEPs at the lowest depth modulation tested (3.25%). Second-order motion-onset produced a flat line for depth modulations of 12.5% and less, both for the P1 and N2 peaks. This was true in every subject tested. Fig. 1 indicates that the P1 and N2 peaks had longer latencies for second-order motion than for first-order motion.

Fig. 2 represents the mean amplitudes of the P1 (top graph) and N2 (bottom graph) for the eight subjects as a function of depth modulation for first- (solid circles) and second-order (open circles) motion-onset. Interestingly, the slopes of the amplitude response functions were similar for the two types of motion: the P1 peak had a slow gain, it increased in amplitude with increasing depth modulation and did not appear to saturate, whilst the N2 peak attained its maximum response at the lowest depth modulation to which there was any response. The amplitude of P1 was lower for second-order motion, whereas the amplitude of N2 was higher for second-order motion.

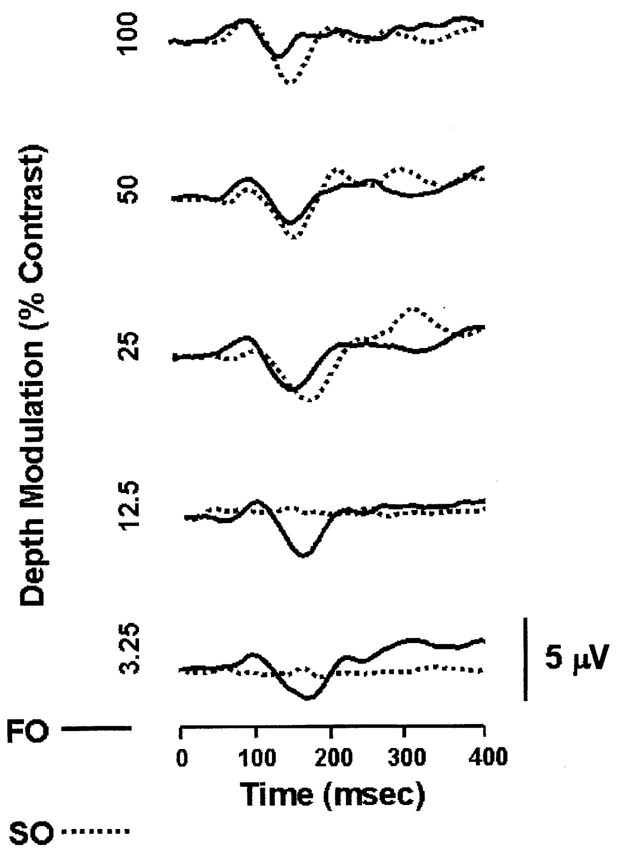

Fig. 1. First- (solid line) and second-order (dashed line) motion-onset VEPs for one subject, as a function of depth modulation. Depth modulation represents modulation of the luminance of first-order gratings and modulation of the contrast of second-order gratings.

Fig. 3 shows the mean latencies of the P1 (top graph) and N2 peaks (bottom graph) for the eight subjects as a function of depth modulation for first- (solid circles) and second-order (open circles) motion-onset. For each condition where both first- and second-order motion-onset elicited evoked potentials (i.e., $\geqslant 25\%$ depth modulation), peak latencies were longer for second-order motion than for first-order motion, and this is true for both the P1 and the N2 peaks. Latencies elicited by second-order motion-onset were on average 69 ms and 73 ms longer for the P1 and N2 peaks, respectively. For both types of motion, the latencies of P1 and N2 became slightly shorter as depth modulation augmented.

Fig. 4 presents reaction times for the detection of first- (solid circles) and second-order (open circles) motion-onset. Visual detection was on average 104 ms slower for second-order motion than for first-order motion. For both types of motion the detection data are comparable to the VEP data: subjects detected the onset of first-order motion at depth modulations as low as 3.25%, but did not detect second-order motion when depth modulation was 12.5% or less.

Fig. 5 shows the mean discrimination thresholds (%) of the 6 subjects for the direction of first- and second-order motion. Thresholds for the discrimination of the direction of first- and second-order motion were 0.4% and 12% depth modulation, respectively. These values are consistent with the results from a previous study in which we used the same stimuli and procedure (Ellemberg et al., in press).

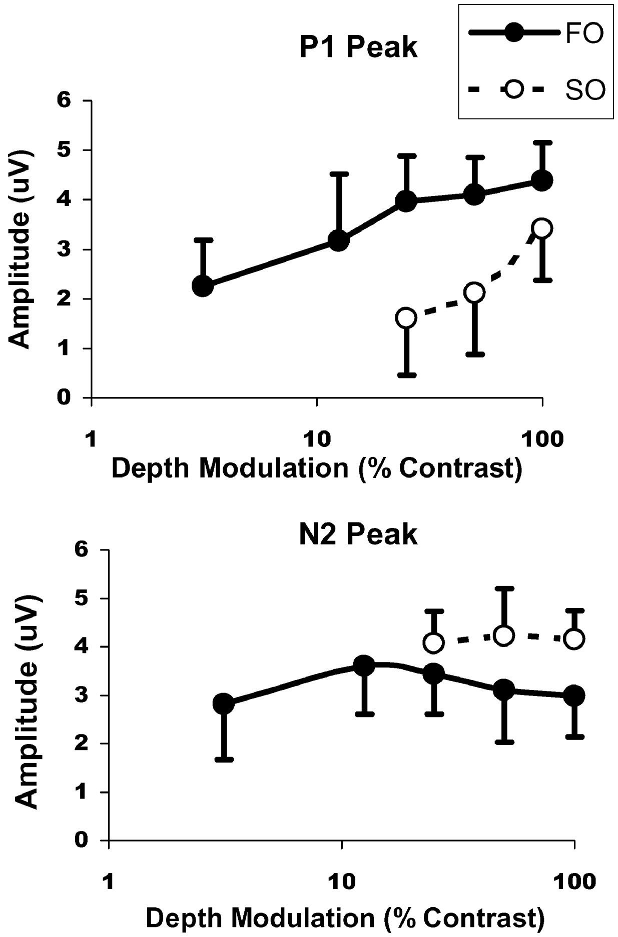

Fig. 2. Mean amplitudes (±1 S.E.) of P1 (top panel) and N2 peaks (bottom panel), for the eight subjects as a function of depth modulation. Solid circles and open circles present the data for first- and second-order motion-onset, respectively. See Fig. 1 for other details.

To control for the differences in visibility between the two types of motion, we compared the conditions with the minimum depth modulation for first-order motion (3.2%) and the maximum depth modulation for second-order motion (100%). At these values, depth modulation was a factor of 8.2 (first-order) to 8.3 (second-order) above the threshold. This permitted us to compare the results for the first- and second-order conditions that were comparably above threshold. Two separate one-tailed t-tests indicate that the P1 ($t = 5.980$, $p < 0.01$) and N2 ($t = 6.220$, $p < 0.01$) latencies were significantly longer for second-order than for first-order motion-onset, by 44 and 53 ms, respectively. Reaction times were also 76 ms slower for the detection of second-order than for the detection of first-order motion-onset

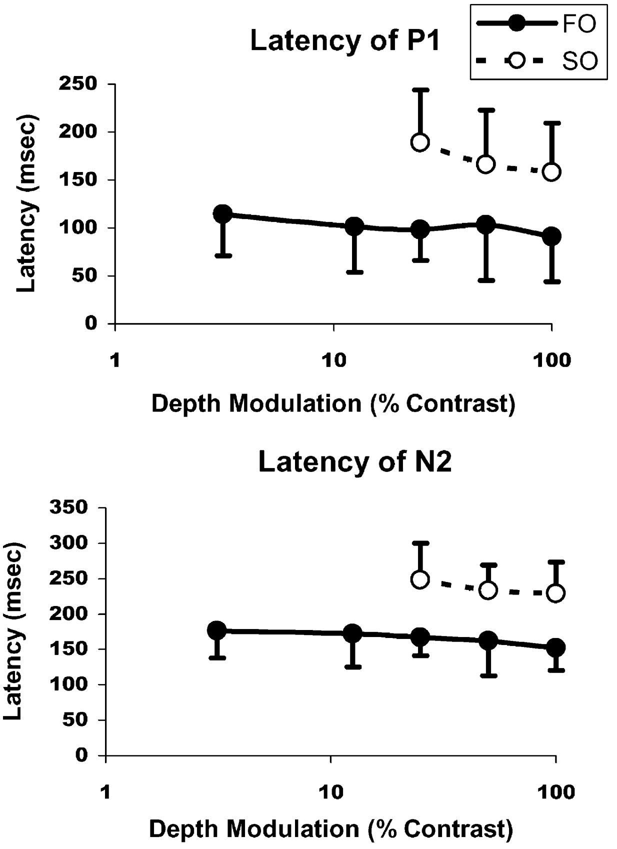

Fig. 3. Mean latencies (±1 S.E.) of P1 (top panel) and N2 peaks (bottom panel), for the eight subjects as a function of depth modulation. Solid circles and open circles present the data for first- and second-order motion-onset, respectively. See Fig. 1 for other details.

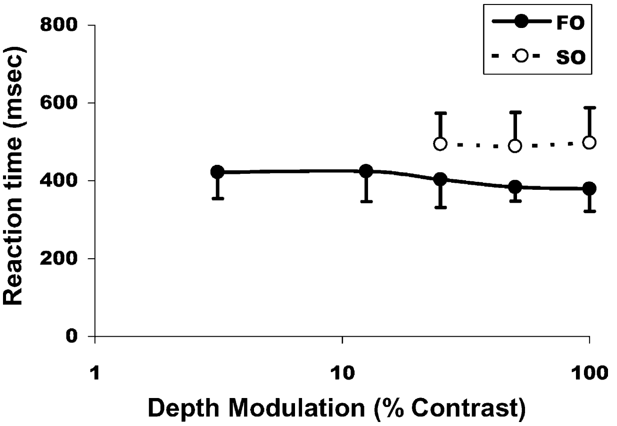

Fig. 4. Mean reaction times (±1 S.E.) for the eight subjects as a function of depth modulation. Solid circles and open circles present the data for first- and second-order motion-onset, respectively. See Fig. 1 for other details.

($t = 2.558$, $p < 0.02$). Further, for these depth modulations, the amplitudes of the P1 ($t = 3.078$, $p < 0.02$) and N2 peaks ($t = 3.531$, $p < 0.01$) were about 1.5 times greater for second-order motion than for first-order motion.

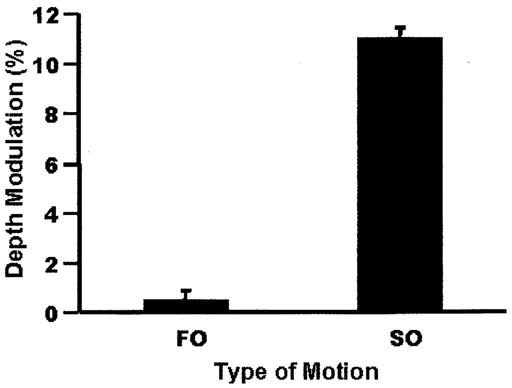

Fig. 5. Mean thresholds of the depth modulation (% contrast) (±1 S.E.) for six subjects, for the accurate discrimination of the direction of first- and second-order motion. See Fig. 1 for other details.

3. Discussion

When the suprathreshold visibility of the two types of motion where equated,VEP latencies for both the P1 and the N2 peaks were longer for the onset of second-order motion than for the onset of first-order motion. Further, subjects took longer to report the onset of second-order motion than the onset of first-order motion. The longer VEP latencies indicate that the neurophysiological analysis of second-order motion necessitates more time, and the slower reaction times suggest that the longer neurphysiological response translates into a slower detection. Taken together these findings are consistent with the hypothesis that first- and second-order motion are analysed by different signal processing mechanisms, and support models that suggest additional processing steps for the extraction of second-order motion.

Unlike the present study, Victor and Conte (1992) did not find any difference between VEPs elicited by first-order versus second-order motion. Their noise dots consisted of large squares (4.125 arc min) that likely contained luminance artifacts (see Smith & Ledgeway, 1996), essentially making the first- and second-order images equally visible to the first-order system. For this reason, we used noise dots subtending 1.4 arc min. and used the procedure described in Smith and Ledgeway (1996) to verify that there were no first-order artifacts in the second-order stimuli.

Some computational models suggest a common mechanism for the perception of first- and second-order motion (Victor & Conte, 1992; Baloch, Grossberg, Mingolla, & Nogueira, 1999; Benton, Johnston, & McOwan, 2000). Benton et al. (2000) proposed a single low-level luminance model that includes a nonlinear preprocessing stage which can detect second-order motion without additional processing. Baloch et al. (1999) formulated a single mechanism model that computes the interactions between ON and OFF cells within a single processing channel to account for some of the differences between the perception of first- and second-order motion that have been reported in the psychophysical literature. Single channel models cannot account for the findings from the present study. The longer latencies of VEPs and slower reaction times that we found for the onset of second-order motion imply that additional processing steps are involved in the extraction of second-order motion. The present findings are compatible with current models that suggest a 'filter-rectify-filter' sequence to extract the second-order content of images (Chubb & Sperling, 1988; Wilson et al., 1992; Nishida et al., 1997; Baker, 1999). These models postulate additional processing steps that include a non-linear operation that introduces first-order characteristics into the second-order image, and a second stage filtering.

The similar pattern of amplitude gain of the P1 and N2 peaks for first- versus second-order motion is consistent with evidence that the mechanisms underlying each of these two types of motion operate under similar principles. It is well documented that in humans, first-order motion is initially processed by a series of multiple scale bandpass and directionally selective mechanisms in area V1 (Anderson & Burr, 1987, 1998; Nishida et al., 1997). Nishida et al. (1997) provided evidence for a similar set of multiple bandpass mechanisms that are selective for the direction of second-order motion. They found that adaptation to second-order motion elevated thresholds for the detection of only this type of motion and that these aftereffects were both spatial frequency and direction selective. This is consistent with the findings of Zhu and Baker (1993, 1996), that neurons sensitive to second-order motion in cat areas 17 and 18 respond to limited ranges of envelope spatial frequency, as do neurons that are sensitive to first-order motion.

As noted in the Introduction, the N2 peak is generally accepted as the motion-onset response, whilst the P1 peak is accepted as the pattern processing response (Clarke, 1973; Bach & Ullrich, 1994, 1997; Kubova et al., 1995). Our data confirm this for both the first- and the second-order conditions. For both types of motion, the N2 peak attains its maximum response at the lowest depth modulation to which there is any response. This finding is consistent with evidence that motion processing mechanisms have a low contrast threshold and a rapid contrast gain. In contrast, the P1 had a slow gain, and its amplitude increased with increasing depth modulation. Our finding that both the P1 and N2 peak latencies were similarly reduced during the onset of second-order motion suggests that both the pattern and motion processing mechanisms underlying the analysis of second-order information involve additional processing steps.

In summary, our findings provide the first electrophysiological evidence in humans that is consistent with the hypothesis that the perception of first- and second-order motion is mediated by different neuronal mechanisms. Further, our findings suggest that, in humans, the perception of second-order motion requires more processing than does the perception of first-order motion. Our findings support the 'filer-rectify-filter' scheme proposed by most models of second-order processing (Chubb & Sperling, 1988; Wilson et al., 1992; Nishida et al., 1997; Baker, 1999). These models postulate additional processing steps for the extraction of second-order information that include a non-linear operation and a second stage filtering. In addition, we find that more time is required for the visual system as a whole to detect the onset of second-order motion. Therefore, we suggest that the longer neurophysiological processing of second-order motion results in the slower detection of its percept.

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