

Functional MRI studies of human visual motion perception: Texture, luminance, attention and after-effects

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Motion of an object is thought to be perceived independently of the object's surface properties. However, theoretical, neuropsychological and psychophysical observations have suggested that motion of textures, called "second-order motion", may be processed by a separate system from luminance-based, or "first-order", motion. Functional magnetic resonance imaging (fMRI) responses during passive viewing, attentional modulation and post-adaptation motion after-effects (MAE) of these stimuli were measured in seven retinotopic visual areas (labeled V1, V2, V3, VP, V4v, V3A and LO) and the motion-sensitive area MT/MST (V5). In all visual areas, responses were strikingly similar to motion of first-order and second-order stimuli. These results differ from a prior investigation (Smith et al., 1998), because here the *motion-specific* responses were isolated. Directing attention to and away from the motion elicited equivalent response modulation for the two types. Dramatic post-adaptation (MAE) differences in perception of the two stimuli were observed, and fMRI activation mimicked perceptual changes, but did not reveal the processing differences. In fact, no visual area was found to selectively respond to the motion of second-order stimuli, suggesting that motion perception arises from a unified motion detection system.

Introduction

The visual percept of motion can be induced by diverse physical characteristics, even while the experience of motion is remarkably similar. This raises a paradoxical question. Are different neural circuits activated by different stimuli— or — is the same neural circuitry activated because we have the same phenomenological percept? Here we have employed human functional MRI studies to investigate this question in the context of a prominent dichotomy in the motion perception literature.

Strong theoretical and perceptual distinctions are made between two categories of moving stimuli, called first-order and second-order (Cavanagh & Mather, 1989). Perception of moving luminance edges (first-order motion; Figure 1B) is well-described by a set of luminance-driven, low-level detectors that are filters oriented in space and time (Adelson & Bergen, 1985; vanSanten & Sperling, 1985; Watson & Ahumada, 1985). However, motion can also be perceived in stimuli lacking moving luminance cues, where motion is given by second-order properties, such as texture contrast (Figure 1, C and D; Chubb & Sperling, 1988; Cavanagh & Mather, 1989). Important perceptual differences exist between the two stimulus types. Prolonged viewing of unidirectional, luminance-based motion gives rise to a subsequent motion after-effect (MAE) in which physically stationary patterns will appear

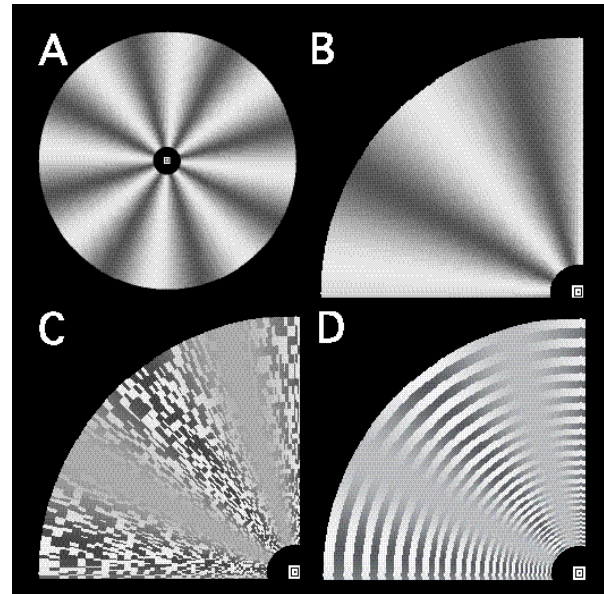


Figure 1: A) Visual display: Motion appeared in the annulus (inner radius $\sim 1.5^\circ$; outer radius $\sim 12^\circ$ visual angle) centered about a fixation marker. Subjects were required to maintain fixation on the central point throughout each scan, while the gratings rotated clockwise or counter-clockwise at 2 cyc/sec. B-D) Partial displays of stimuli used: B) Luminance condition: A luminance-based sine-wave radial grating. C) Contrast-Modulated Noise stimulus: A sinusoidal contrast modulation of a pattern of random checks, flickering at 37.5 Hz. D) Contrast-Modulated Rings stimulus: A sinusoidal contrast-modulation of a set of concentric rings.

to move (Wohlgemuth, 1911; Mather, Verstraten & Anstis, 1998). Curiously, this does not always occur with second-order motion (Derrington & Badcock, 1985; Cropper & Hammett, 1997; though see Ledgeway, 1994). Numerous other perceptual differences have been discovered, such as in opto-kinetic nystagmus (Harris & Smith, 1992) and spatial facilitation (Ashida, Seiffert & Osaka, 2001). Thus, theoretical and perceptual characteristics have indicated that there are fundamental processing differences between first-order and second-order motion perception.

Three leading hypotheses describe the possible neural basis of first- and second-order motion perception. First, the two types of motion may be processed by separate neural substrates located in distinct cortical areas. The amount of neural separation between these two processes has varied from model to model, from pre-processing stage

differences (Chubb & Sperling, 1988; Wilson, Ferrera & Yo, 1992; Zhou & Baker, 1993; 1994; 1996; Solomon & Sperling, 1994; Demb, et al., 2001), to separate cortical representations (Lu & Sperling, 1995; Vaina & Cowey, 1996; Clifford & Vaina, 1999). Second, the two types of motion may be processed in the same (or similar) channels located within the same cortical areas (Cavanagh & Mather, 1989; Johnston, McOwen & Buxton, 1992; Johnston & Clifford, 1995; Greenlee & Smith, 1997). Third, form-driven or attentional tracking of moving features may support second-order motion more than luminance-based motion (Seiffert & Cavanagh, 1998; Derrington & Ukkonen, 1999). Focused attention following moving features may be required to process second-order, but not first-order, motion (Lu, Liu & Dosher, 2000; Ashida, Seiffert & Osaka, 2001).

We tested these hypotheses using fMRI during motion perception. Previous neuroimaging experiments have suggested that an area of visual cortex (i.e. V3) may explicitly represent second-order motion (Smith et al., 1998; Wenderoth et al., 1999). However, the specific contribution of a specialized motion system is hard to assess with these results because experiments compared results from second-order to first-order stimuli directly, without comparing the isolated, motion-specific response to each stimulus type. The current study improves on this previous work by implementing multiple comparisons to isolate motion specific responses, as well as testing responses to higher-level, attentional and lower-level, adaptation effects. To anticipate, we found many areas of cortex were activated in similar ways by both types of motion.

Materials and Methods

MR Imaging and Analysis

Nine subjects (1 male), ages 18-40, with normal or corrected-to-normal vision participated with informed consent (Massachusetts General Hospital Human Studies Protocol #96-7464). Volunteers were scanned on a 3 Tesla General Electric Signa MR imager. A custom-built, bilateral quadrature transmit-receive surface coil (Nova Medical), placed at the back of the skull. Imaging details are similar to those described elsewhere (Tootell, et al., 1997; Somers et al., 1999). High resolution (1.0 X 1.0 X 1.3 mm) structural images were obtained for the purpose of 3-D brain reconstruction (Dale, Fischl & Sereno, 1999) using either a 2 T Siemens MR scanner using MP-RAGE or on a 1.5 T GE MR scanner using SPGR (TE = 3.3 milliseconds; TR = 30 msec). Computer representations of each cortical hemispheric surface were unfolded and flattened (please refer to Sereno et al., 1995; Figure 3 inset).

Retinotopic mapping of visual field representations was used to define regions of interest (ROIs). Cortical representations of retinal eccentricity and polar angle were mapped in separate runs, using previously described methods (see Sereno et al., 1995). T2*-weighted gradient-echo, echo-planar images were collected from 16 slices (4 mm thick) oriented approximately perpendicular to the calcarine sulcus (TE = 50 msec; TR = 4 sec; in-plane resolution 3.1 X 3.1 mm). These data were used to functionally identify six retinotopic visual cortical regions: V1, V2, V3, VP, V3A, and V4v (see Figure 3;

Tootell et al., 1995a) and the coarsely retinotopic lateral occipital cortex (LO) (Tootell and Hadjikhani, 2001; Levy et al., 2001). LO was defined as the retinotopically-specific region situated between V3A, V4v and MT (see Tootell & Hadjikhani, 2001). The human homologue of the MT/MST complex (MT+), also known as areas V5, was functionally identified using very low contrast moving and static luminance-defined stimuli, as previously described (Tootell et al., 1995a).

Imaging parameters for the motion perception studies were similar to the retinotopic studies (except the TR = 2 sec). After averaging across time within conditions, t-tests were performed voxel-by-voxel and significance (p) values were projected onto flattened cortical maps. Within each ROI, MR signal from all voxels was selectively averaged (with 4 sec delay for hemodynamics). Time course data were normalized as percent signal change from the mean activation of the initial fixation-only period within each scan and averaged across subjects

Visual Stimulation & Eye Movement Measurements.

Visual stimuli were projected (NEC MT-800 LCD, 800X600@75Hz) into the patient chamber onto a rear projection screen and viewed via an adjustable mirror. Motion stimuli were presented peripherally in an annulus centered about a fixation point. Specific description of the stimulus for each experiment is given below. Subjects were required to maintain fixation on the central point throughout each scan. Eye position was monitored (250 Hz sample rate) in the scanner for three subjects in the attention experiment, using MR-compatible eye-tracking goggles (OBER2 system by Permobil MeditechAB).

Passive Viewing Experiments

Scans consisted of 9 blocks or epochs, each 28 seconds long. The first epoch consisted of a fixation target only. Each of the four passive viewing test conditions – static and moving forms of both first- and second-order stimuli – was presented twice in the last eight epochs. The stimuli were sinusoidal gratings configured radially in an annulus about a central fixation point (Figure 1A) as in previous work (Seiffert & Cavanagh, 1998). In moving epochs, the gratings rotated at 2 cycles/second. The first-order stimulus was always a luminance grating (Figure 1B). Two forms of second-order stimuli were employed. Each used contrast modulations (CM) of a carrier texture. For the "CM Noise" stimulus, the carrier was a random binary noise pattern (Figure 1C) flickering at 37.5 Hz. For the "CM Rings" stimulus, the carrier was a set of thin, concentric rings (about 0.2° wide) in which the rings were drawn perpendicular to the orientation of contrast envelope (Figure 1D).

Motion sensitive areas were isolated by the standard method of comparing activation to moving and static forms for both types of stimuli to control for response to the visual pattern (see Culham et al., 2001 for review). This comparison can reveal responses to transients in addition to that to motion per se. As a control for transient-driven responses, the "static" control display for the CM Noise stimuli was a field of random noise flickering at 37.5 Hz. In some conditions, this control was shown without contrast modulation across space or time to ensure that flicker was controlled across the full extent of the visual space tested. Great care was taken to

minimize first-order (luminance) artifacts in the second-order stimuli (see Smith & Ledgeway, 1997). The projector and associated scanner optics were linearized, and stimuli were also checked perceptually; second-order modulations disappeared when vision was sufficiently blurred, and failed to produce motion after-effects.

Low and moderate contrast stimuli were tested in separate sessions. Low contrast stimuli were set so that individual subjects could faintly, but consistently see both static and moving patterns: 3% contrast for Luminance, 10-12% maximum contrast for CM Rings, and 8-10% maximum contrast for CM Noise. Moderate contrasts were ten times the static pattern detection thresholds, about 10% contrast for Luminance and 25% contrast for the rings stimulus, and . Total number of subjects per condition was as follows: Low-contrast CM Rings = 7, Moderate-contrast CM Rings = 6, Low-contrast CM Noise = 7, Moderate-contrast CM Noise = 4. Not all subjects participated in all stimulus conditions, so the more conservative, between-subjects statistical analysis was used on this data. One subject was omitted because of reported sleepiness during the study. For analyses, then, the total number of subjects was 23 (46 hemispheres).

Attentional Modulation Experiment

In our second experiment, we explored the effects of directing attention toward, and distracting attention away from, first- and second-order motion. Stimuli were composed of a central target (~1 σ radius) and a surrounding annulus (from ~3 σ to ~12 σ) with a gap between them (Figure 1A). Subjects were required to maintain central fixation, but attend to one of the two different display components. For one task, subjects identified letters presented at the fovea, and for the other subjects discriminated motion direction extrafoveally. Both tasks were a one-back comparison of the current trial to the previous trial. Importantly, the stimuli for both tasks remained on the screen throughout each task, and a cue shown before each epoch of trials directed attention to the task to be performed. After an initial fixation-only period, subjects alternated between letters and motion tasks between blocks. Task order was counterbalanced across subjects.

For the letters task, a series of five letters displayed at the point of fixation in rapid serial visual presentation (RSVP; Forster, 1970), followed by a fixation spot. On consecutive trials, subjects reported whether the same five letters appeared in the same order or one letter changed. RSVP timing parameters were adjusted to create high attentional demand while permitting subjects to perform well (5-20% error rates). The surround annulus contained either the luminance or the CM Rings grating that rotated in one direction and then stopped, synchronously with the end of the letter stream. In the motion task, subjects reported whether the direction of rotation was the same as, or different than, that of the preceding trial. Stimulus contrast (~3% Luminance, 8-12% CM Rings) was adjusted for each subject to create high attentional demand while permitting subjects to perform well (7% average error rate). This is the first presentation of the first- and second-order aspects of these data which were previously combined in a report of attentional modulations in primary visual cortex (Somers et al., 1999).

Motion After-effect Experiment

We tested the motion after-effect (MAE) for first-order and second-order motion in interleaved scans. Scans consisted of an initial fixation condition (16 sec), an MAE condition (120 secs) and a control condition (120 secs). Both MAE and control conditions consisted of a motion adaptation period (60 secs), and a static test period (60 secs). The direction of motion was constant in the MAE adaptation, but reversed every 2 seconds in the control condition. Rapid direction reversals do not allow for directional adaptation necessary for MAE (Wohlgemuth, 1911). Individual scans used only one type of motion stimulus: CM Rings (moderate contrast of 25%) or luminance gratings (moderate contrast of 10%) in both periods and conditions. Three to six scans of each condition were averaged together. Perceptual MAE duration was measured by button press and the MAE percept was confirmed by verbal report after each scan.

Results

Passive Viewing

We compared the activation produced by passive viewing of moving and static forms of first- and second-order stimuli. The goal was to isolate activation likely involved in the processing specific to second-order motion, so multiple comparisons between conditions were performed. To further increase the likelihood of detecting the specific brain areas that were sensitive to second-order motion, we tested two different forms of second-order stimuli (CM Rings and CM Noise, see Figure 1, C and D), at two different pattern contrasts (low or moderate). A system selective for second-order motion should respond independently of these factors. Results from the two contrast levels were qualitatively similar, so only the results from the low contrast condition are shown.

Our first comparison was between activation to moving second-order and moving first-order stimuli. Responses were taken relative to the baseline activity in which subjects maintained fixation on a central point and no peripheral stimulus was presented. Results showed in all areas responses to first-order motion were very similar to the responses to second-order motion ($r = 0.729$). Percent signal change relative to fixation baseline for the low contrast condition only is plotted in the top two graphs of Figure 2. Overall, this comparison revealed a higher response to second-order moving stimuli than first-order moving stimuli ($F(1,42)=34.03$, $p<10^{-6}$), which was significant for each visual area with a peripheral representation (all $F(1,42) > 15.0$, $p<10^{-3}$; area LOC, $F(1,42) < 1$). Similar effects were also reported previously (Smith et al., 1998).

A closer look showed that the CM Noise second-order motion consistently produced stronger activation than Luminance motion across all visual areas, but the CM Rings pattern did not ($F(8,336) = 12.72$, $p<10^{-6}$). This is likely due to the fact that the CM Noise carrier pattern was dynamic, whereas the CM Rings and Luminance carrier patterns were not, and therefore the CM Rings was a better comparison stimulus. Interestingly, one area that did respond significantly higher to CM Rings than Luminance motion was peripheral representation of area LO (LOP, $t =$

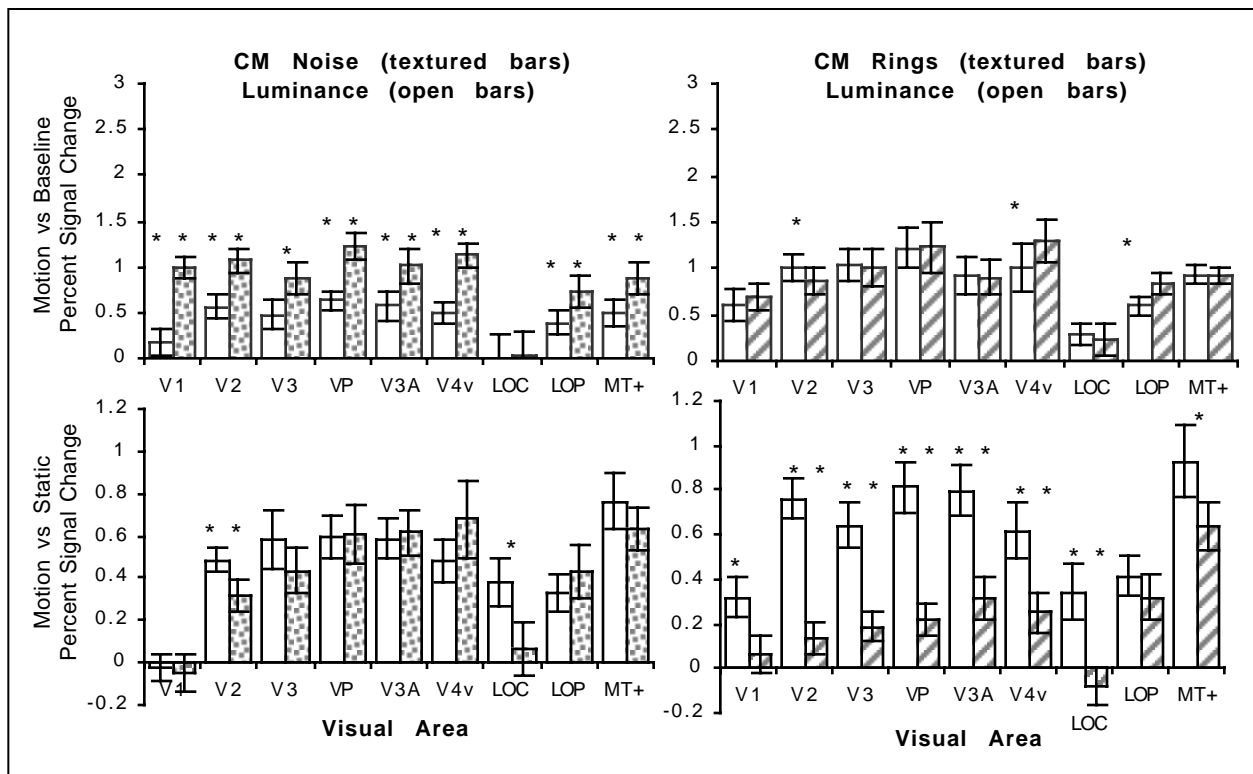


Figure 2: TOP: Percent signal change from moving stimulus minus fixation baseline plotted for each visual area for the low contrast conditions only, separately for each stimulus type. Contrast-modulated Noise stimuli plotted on the left, and contrast-modulated Rings on the right, for the low contrast stimuli. For each, luminance-based motion response from the same session is plotted with open bars and the second-order stimulus is plotted with textured bars. BOTTOM: Percent signal change from moving stimulus minus static stimulus plotted for each visual area. Unlike the top graphs, this is the motion-specific response. Error bars are standard error of the mean, and stars indicate a significant differences between first-order and second-order responses (* = $t > 2.0$, $p < .05$; ** = $t > 4.0$, $p < .005$).

2.5, $p < .05$), which is similar in location to areas previously reported as second-order motion selective (area V3B in Smith et al., 1998), and selective to motion-defined boundaries (area KO in Orban et al., 1995; Van Oostende et al., 1997; Dupont et al., 1997; see also Tootell & Hadjikhani, 2001). In the current study, area V4v also showed consistently higher activation to the second-order CM-Rings motion ($t = 2.5$, $p < .05$). Interestingly, these areas have been implicated in the perception of object form and texture contours (Amedi et al., 2001; Kastner, De Weerd & Ungerleider, 2000; Mendola et al., 1999; Grill-Spector et al., 1998, 2000; De Weerd, Desimone & Ungerleider, 1996; Malach et al., 1995). Note that the feature tracking account predicts that areas involved in processing form or contour are a necessary part of motion detection, as the relevant contours must be localized before they can be tracked (Seiffert & Cavanagh, 1998; 1999; Derrington & Ukkonen, 1999). In addition, evidence from neuropsychology shows that brain area LO may be necessary for the normal perception of second-order motion (Plant & Nakayama, 1993; Vaina & Cowey, 1996).

However, these responses cannot be directly attributed to motion processing of second-order stimuli, because the fixation baseline was used as the comparison. The resultant activity, therefore, represented all differences between the first and second-order stimuli, including the presence of texture patterns. The second-order static patterns contained more high-spatial frequency

information (and high-temporal frequency for the CM-Noise) and would thus be expected to produce greater activation responses than static first-order stimuli. It is important to factor out this difference by comparing the difference in activity evoked from moving and static second-order stimuli. This comparison, however, does not determine whether or not there are processing differences between perception of first-order and second-order motion. The proper comparison for this issue is a double subtraction. Response to motion minus response to static for each stimulus type (first-order and second-order) must be subtracted between stimulus types to determine if the motion-specific response was different for first- and second-order stimuli. This comparison correctly isolates the second-order motion process, by removing the differences between responses to first- and second-order patterns, and the response to static stimuli of the same type. Previous neuroimaging experiments of second-order motion did not include this analysis in the experimental design (Smith et al., 1998).

We compared activation to moving compared to not moving stimuli to measure the response specific to motion processing. The bottom graphs in Figure 2 plot this motion-specific response in average percent MR signal difference across visual areas for the different stimulus types. Reliable responses to second-order motion were found across all labeled visual areas, indicating that, despite the constant mean luminance in the second-order stimuli, the moving contrast modulation was differentially

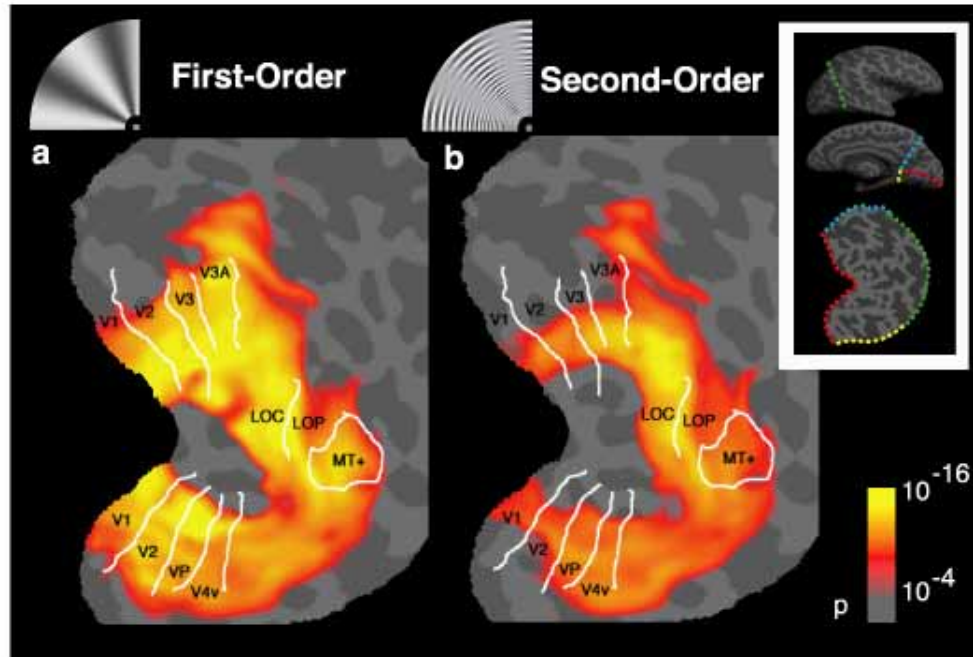


Figure 3: First- and second-order motion-specific activation patterns. (a) Luminance modulated (first-order) and (b) CM Rings (second-order) stimuli were presented in moving and static forms. Pseudocolor codes statistical significance (p-values) of responses to motion greater than static (red-yellow) in one subject's hemisphere for the two stimulus types. INSET: Lateral (top) and medial (middle) views of an inflated representation of a subject's right hemisphere show cuts used to make the flattened visual cortical patch (bottom).

activating cortex ($F(1,42)=81.88$, $p<10^{-6}$). We observed significant motion-specific responses to second-order stimuli in areas V1 and V2. Average percent MR signal change was 0.16% for V1 ($t(45)=2.8$, $p<.01$), and 0.33% for V2 ($t(45)=7.2$, $p<10^{-6}$), averaged across second-order type (CM Rings and CM Noise) and contrast (not shown in Figure 2). This finding suggests that the earliest cortical representations may be sensitive to the motion of second-order stimuli, consistent with neurophysiological observation (Zhou & Baker, 1993; 1994; Chaudhuri & Albright, 1997). However, this result is also in contrast to a conclusion of Smith et al. (1998) that second-order motion is first represented explicitly in VP and V3. Note that motion-specific responses to CM Noise stimuli were overall stronger than to the CM Rings stimuli, which may originate from local luminance imbalances which can occur in contrast-modulated white noise texture such as this (Cropper & Johnston, 2001). Also, consistent with prior reports (O'Keefe & Movshon, 1998; Smith et al., 1998), the strongest motion-specific responses for second-order stimuli were found in the classical, motion-sensitive area, the MT Complex (0.62% signal change, $t=10.46$, $p<10^{-6}$) and V3A (0.53% signal change, $t=9.64$, $p<10^{-6}$), averaged across second-order type and contrast. Comparing responses between stimulus types allows us to determine whether the motion-specific response was different for first- and second-order stimuli (difference between bars in Figure 2 bottom). Once again, it was clear that responses were very similar across the two stimulus types. Interestingly, the motion response to luminance stimuli was higher than that for contrast-modulated stimuli for almost all of the visual areas, for all second-order types (first-order = 0.56% signal change, and second-order =

0.38% signal change, $F(1,42)=18.84$, $p<10^{-4}$). The result comes about from the fact that the response to the static second-order stimulus was much higher than that to the static first-order stimulus, as one would predict from the complexity of the texture. Thus, taking the static component out of the motion response reduced the second-order much more than the first-order response.

In fact, no visual area produced reliably greater motion-specific response to second-order motion than first-order motion, across both second-order patterns and contrast levels. Stronger first-order than second-order response is opposite to the results relative to fixation baseline, here (Figure 2 top), and in a previous report (Smith et al., 1998). Interestingly, neurophysiological studies have also found stronger motion-sensitive responses to luminance-based stimuli as compared to second-order stimuli (O'Keefe & Movshon, 1998; Zhou & Baker, 1993; 1994; Chaudhuri & Albright, 1997). Our results stand in direct contrast to a principal conclusion of the Smith et al. (1998) study, that VP and V3 gave greater responses to second-order motion than to first-order motion. The discrepancy of results is likely due to the fact that the present work takes into account the responses to the static patterns. Taken together the results indicate that the higher responses to second-order stimuli (in V4v and LO in Figure 2 top, and in VP and V3 in Smith et al., 1998) can be attributed to response to the static patterns, rather than reflecting motion processing, per se.

The similarity between first-order and second-order motion processing is further supported by data from individual subjects. In Figure 3, activation maps of a representative subject show the motion-specific response for the luminance stimulus compared to the CM Rings

stimulus at low contrasts. Clearly the motion response for the first-order stimuli was very similar to (and somewhat stronger than) that for the second-order stimuli. These results concur with reports that consistency in neural response was the most striking effect observed between first- and second-order motion, both in neurophysiology (O'Keefe & Movshon, 1998) and neuropsychology (Greenlee & Smith, 1997). Weaker motion-specific MRI response is also consistent with psychophysical observations that second-order motion perception is often weaker and less consistent, especially with peripheral presentation as used here (Pantle, 1992; Smith, Hess, & Baker, 1994; Zanker, 1997)

Attentional Modulation

Behavioral Data

Subjects' direction of attention was manipulated through the use of two different tasks. In the letters comparison task, a stream of letters (presented foveally) were compared to the previous stream. Timing parameters for the letter task were manipulated on a subject by subject basis to create high attentional demand while maintaining high performance yielding 90.4% correct on average (standard error = $\pm 6.7\%$). In the motion task, the direction of motion of the extrafoveal grating was compared to the direction on the previous trial. Subjects also performed well on this task, yielding an average correct performance of 95.1% (± 8.5). Performance on this task did not differ statistically with the type of motion stimulus presented ($F(1,5)=2.8$, $p>.15$).

MRI Data

Attentional modulation was measured as the difference in activation found when attention was directed to the motion task compared to the letters task (Figure 4). Overall average attentional modulation was 0.76% signal change, which was significant ($F(1,11) = 157.45$, $p<10^{-7}$) and was about 81% of the stimulation modulation found in the Passive viewing experiment. Attentional modulation interacted with visual area ($F(8,88) = 28.22$, $p<10^{-7}$) in that attentional modulation was retinotopically specific, with more response in peripheral areas when attention was directed towards the periphery and away from the fovea, and vice versa. This result was dealt with in detail in our previous report of these averaged data (Somers et al., 1999, see also Gandhi, Heeger & Boynton, 1999; Martinez et al., 1999).

For the present study, we were interested in the effects of stimulus type. Previous work showed that motion perception of second-order stimuli seems to rely on focused attentional resources to a greater extent than first-order motion (Lu et al., 2000; Ashida et al., 2001). The purpose of directing subjects attention toward and away from the motion stimulus was to assess the role of attentional focus in motion processing. If second-order motion processing requires more attentional focus than first-order motion processing, then one might expect that removing attentional focus from second-order motion would modulate activity to a greater extent. Because fMRI responses reflect perceived contrast differences (Boynton et al., 1998; Engel & Furmanski, 2001), one might expect greater attentional modulation with second-order than with

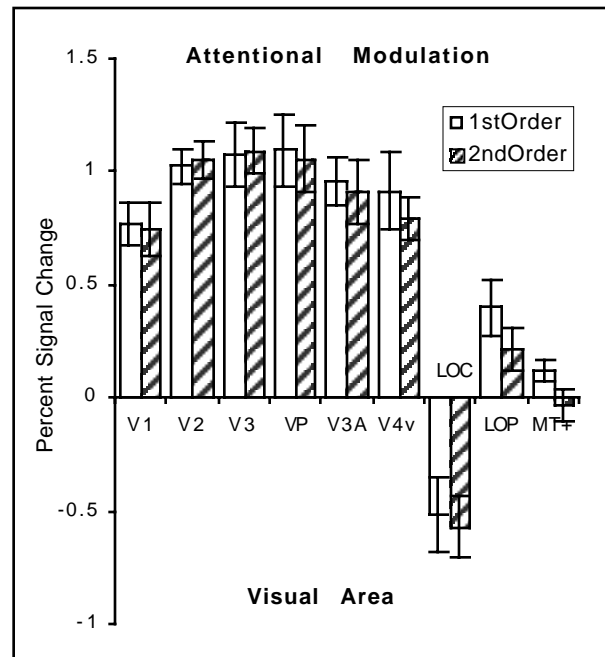


Figure 4: Percent signal change from Motion Task minus Letters Task plotted for each visual area, separately for the two stimulus types. Luminance-based (first order) motion is plotted with open bars and the CM Rings (second order) stimulus plotted in textured bars. Error bars are standard error of the mean. There are no significant differences between first-order and second-order results (all $t < 1.8$, ns). Note: Area LOC shows the reverse attentional modulation because of its retinotopic representation (see text).

first-order stimuli, as has been shown for perceived contrast with psychophysics (Lu et al., 2000). However, second-order and first-order stimuli yielded equal levels of attentional modulation (interaction $F(1,11)=1.1$, ns). As shown in Figure 4, each visual area showed strikingly similar attentional modulation for first-order and second-order stimuli (t -test for all visual areas, $t < 1.75$, $p>.10$). Furthermore, activation during attention to motion, compared to the fixation baseline condition, was also very similar for first-order and second-order stimuli (not shown, $F(1,11)<1$). These results suggest that neural response to the different stimulus types was not differentially affected by the direction of attention. Consonant with our overall conclusion, we consider the similarity of response to the two stimulus types is the most compelling aspect of the data. However, future experiments pitting attention to motion versus attention to some other component of the same stimulus, will properly determine the motion-specific attentional modulation and may show more stimulus-specific trends.

Motion After-effect

Behavioral Data

As is typically observed, subjects reported that adaptation to unilateral motion of first-order stimuli produced strong subsequent motion after-effects (MAE) during the static test, while adaptation to second-order stimuli did not. MAE duration to first-order stimuli was,

on average, 14.0 seconds long (± 5.6 sec), which was comparable to previous measurements for the conditions used (Hershenson, 1993). In contrast, four of seven subjects never reported a MAE with the second-order stimulus, and the additional three subjects reported them only occasionally, with very short duration (1.30 ± 0.7 seconds). MAE was never reported during the control test after adaptation to reversing motion when subjects were directly asked, though subjects occasionally made anticipatory button press responses of approximately 1 second.

MRI Data

Previous work has found significant differential responses during the experience of the motion after-effect primarily in motion-sensitive area MT (Tootell et al., 1995b; Culham, et al., 1999). The top graph in Figure 5, corresponding to the first-order stimulus, replicates previous work, in that the MT Complex activation during the static test period was significantly higher after unidirectional motion adaptation, and during experience of the motion after-effect (MAE), compared to control. Recall that the static stimuli presented in these conditions were identical, yet greater activation was observed when the after-effect was seen. The middle graph in Figure 5 shows the same time-course for tests with the second-order stimulus (CM Rings). The difference between MAE and control activation levels was considerably reduced, and the curves fell within each other's standard error (vertical lines in Figure 5), corresponding to the absent or weak second-order MAE experienced by our subjects. Removing those subjects who briefly experienced the MAE did not reduce the size of this difference.

It is perhaps not surprising that the activity in MT was not dramatically different for second-order stimuli between tests after unidirectional motion adaptation and control. First, recent evidence suggests that the stronger fMRI response in area MT during the MAE reflects greater attention allocated to the compelling perceptual illusion than the control condition (Huk et al., 2001), so the lack of a perceptual effect would predict no fMRI effect. Second, only early visual areas, such as V1 and not MT, may show adaptation effects to second-order stimuli, because global luminance motion signals are balanced in these stimuli, but local differences may still produce local motion adaptation effects. Some models of second-order motion emphasize early stage non-linearities as the source for the motion signal (Wilson, Ferrera & Yo, 1992; Zhou & Baker, 1993; 1996). Analysis in early retinotopic visual areas, rather than MT, may be more appropriate to reveal adaptation differences.

Similar results were also found across all visual cortical areas. Comparing activation during the adaptation periods (compared to baseline) revealed robust activation over a broad range of cortical areas for both stimulus types (similar to Figure 3). However, the patterns were dramatically different for the motion after-effect comparison (Figure 6). For first-order stimuli, the MAE produced a pattern of activation very similar to, though lower amplitude than, that obtained for viewing real motion stimuli. For second order stimuli, no MAE activation was observed in this subject, consistent with the absence of a MAE experience. Analysis across visual

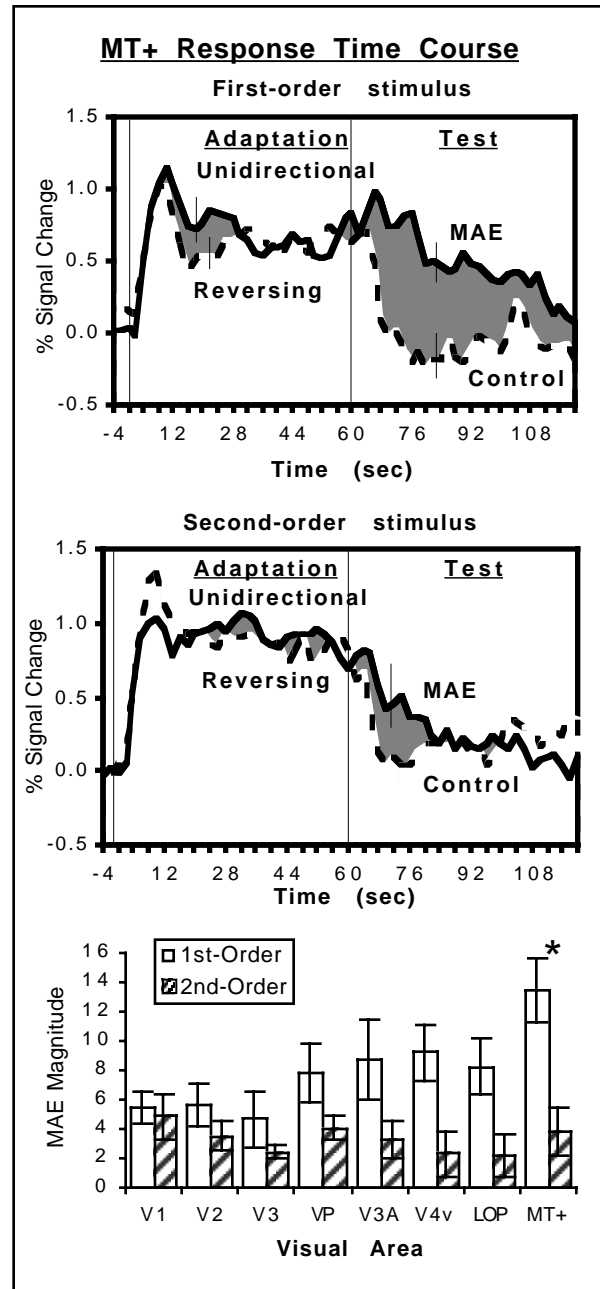


Figure 5: TOP: Percent signal change from Area MT+ in the two adaptation and test conditions, shown separately for the first-order stimulus (Luminance; upper) and second-order stimulus (CM Rings; middle). Solid line shows adaptation to unidirectional motion followed by its static test (MAE), and the dashed line shows adaptation to reversing motion (control) followed by its test. Time is measured relative to the onset of the adaptation stimulus. Thick vertical lines show the average standard error of the mean for each condition. BOTTOM: Averaged MAE Magnitude shown separately for each stimulus type and visual area. Error bars show the standard error of the mean. Star shows the significant difference between first-order and second-order stimuli (* = $t > 3.0$, $p < .05$)

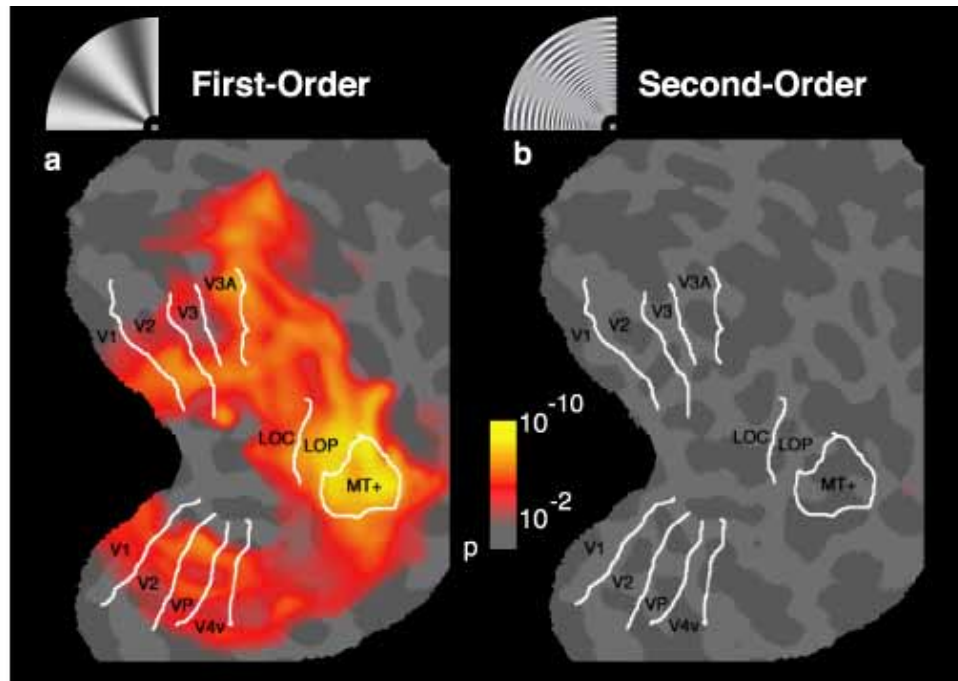


Figure 6: Post-adaptation activation in MAE paradigm for (a) first-order and (b) second-order stimuli. Motion after-effect activation is quantified by comparing responses during the two static epochs: after single-direction motion adaptation and after direction-reversing motion adaptation. Activation found during perception of the Motion After-Effect illusion (first-order motion) is very similar to that found during presentation of real motion (Figure 3). No differences were found for the second-order stimuli, consistent with reports of no MAE percept.

areas, therefore, did not reveal any early stage adaptation to second-order stimuli.

To quantify the MAE activation, we calculated a summary statistic, MAE Magnitude, which was a measure of the area between the two response curves in Figure 5 (top graphs). MAE Magnitude was calculated by, first, adjusting the values in the control condition to match the MAE condition at the beginning of the test period, then taking the percent signal change difference between the MAE and control conditions, summed across all time points prior to convergence (Figure 5 bottom graph). The MT Complex produced the largest MAE Magnitude, in the first-order condition (Mag = 13.5, $t=6.17$, $p<.001$), and a non-significant MAE Magnitude in the second-order condition (Mag = 3.8, $t=2.26$, $p>.06$). Across all subjects, the difference between first and second-order was statistically significant for the MT Complex ($t=3.15$, $p<.05$), but not for any other visual area (all $t<2.2$, $p>.07$) yielding an interaction between visual area and stimulus type ($F(7, 42)=3.60$, $p<.005$). The difference between areas was best characterized by a linear increase in first-order MAE Magnitude from early visual areas to later visual areas (from 4.6 to 13.5, linear contrast $F=13.2$, $p<.05$), similar to previous reports (Tootell et al., 1995b, their Table 1). Contrastingly, for the second-order stimulus, average MAE Magnitude was approximately the same for each visual area (mean = 3.3 ± 0.3 , linear contrast $F<1$). Thus, although the MRI response to first- and second-order motion is very similar, motion processing of the two stimulus types is fundamentally different, as one leads to an after-effect while the other does not.

The small MAE effect that was observed for the second-order stimulus deserves further explanation. This

effect was not carried by those subjects who reported short MAE experiences, as the MAE Magnitudes were not reduced when these subjects were omitted. A possible explanation is that visual areas were indeed coding a directional adaptation effect for the second-order stimulus, which was not experienced by the subjects. However, given that the size of the MAE Magnitude was consistent across areas, it is more conservative to assume that these significant differences were not indicative of any special process. Another possibility is that these trends may have arisen because subjects were attending more to the display during the anticipation of a second-order MAE. Recent results show that the larger fMRI response during the MAE may be entirely accounted for by subject attention (Huk et al., 2001). In support of this idea, subjects took longer to respond to the second-order static test when responding after unidirectional motion than the reversing control ($t=3.29$, $p<.05$), even for those subjects who reported no MAE percept (difference = $1.75 \text{ secs} \pm 0.84$). Regardless of the cause of the small MAE effect, it is clear that no single visual area preferentially responded after adaptation, bolstering the conclusion that second-order motion is processed with the same visual areas as first-order motion.

Discussion

Equivalent visual motion perception can be induced by stimuli with different characteristics. Here we have tested the following question: Are different neural representations used for different stimuli, or is the same neural circuitry used to produce the same percept? The

striking similarity of the neuroimaging activation collected while subjects view, attend to or experience motion of the two stimulus types supports the latter option. Passively viewing the two types of motion elicited very similar responses across visual areas and stimulus types (Figure 3). No single visual area was found to be specifically tuned to the motion of one stimulus type over another, though often areas responded more strongly to first- over second-order motion (Figure 2 bottom). Indeed, activation differences between types were found to be similar across visual areas, as if the bank of responsive areas worked in concert. Notably, motion-specific responses were observed in all 8 visual cortical areas studied, which appears at odds with the view (Zeki, 1978; Zeki et al., 1991) that motion processing is localized to a specialized region (i.e., MT). In addition, there were no differences in the attentional modulation for the different motion-defined stimuli, although allocating attention selectively to or away from motion produced strong modulation of response overall (Figure 4). Finally, though post-adaptation observations (the Motion After-Effect) demonstrated dramatic perceptual and neuroimaging differences between stimuli (Figure 5), activation echoed the perceptual experience of motion and not the stimulus properties (Figure 6). Consistently across different tasks, stimulus types and visual areas, we have found support for the notion that the brain has an extensive, yet unified, visual motion processing system whose response closely relates to motion perception.

Comparison with previous studies

Previous studies have examined whether there are independent, specialized cell classes for processing second-order motion. Single-unit recordings in the monkey motion-sensitive area, MT, have found that, though some of these neurons were responsive to non-luminance motion (Albright, 1992), cells were always more responsive to luminance-based motion (Olavarria et al., 1992; O'Keefe & Movshon, 1998). Responses of neurons earlier in the visual stream show similar results, responding to both luminance and non-luminance stimuli (cat Area 18: Zhou & Baker, 1993, 1994, 1996; Mareschal & Baker, 1999; monkey V1: Chaudhuri & Albright, 1997). However, studies also observed that stimuli elicited similar response profiles across other attributes, such as direction selectivity, supporting the notion that neurons are not subdivided into two separate groups of detector types (Olavarria et al., 1992; O'Keefe & Movshon, 1998). Taken together, these studies fail to support the hypothesis that specialized second-order motion detectors exist within either MT or V1. However, these studies could not address the possible existence of separate brain regions specialized for second-order motion.

Neuropsychological studies of second-order motion deficits have yielded interesting, yet inconclusive results. Double dissociation between first- and second-order motion perception in two patients with different brain damage strongly suggested that separate processing must occur (Plant & Nakayama, 1993; Vaina & Cowey, 1996; Vaina, et al., 1999). However, localization of the system based on lesion location has remained elusive. Patient lesions do not include standard motion-sensitive areas, such as MT, but other areas nearby, such as the lateral occipital gyrus (Plant & Nakayama, 1993; Vaina &

Cowey, 1996), suggesting that the important analysis may occur in areas processing object form (Amedi et al., 2001; Grill-Spector et al., 1998, 2000; Malach et al., 1995). However, some researchers have observed that there is high overlap of lesion location between patients with first-order and second-order motion deficits, with only slight differences to support a partial dissociation (Greenlee & Smith, 1997).

Previous neuroimaging studies have also supported the separate brain region hypothesis. Smith and colleagues (1998) provided the first MRI analysis of first- and second-order motion processing. They concluded that second-order motion may be detected in V3/VP and then passed on for further processing to V3A, V3B (similar in location to LO; see Methods), and MT/V5. Similar observations attributed to V3 were made in an independent PET study with second-order plaid stimuli (Wenderoth et al., 1999). These previous studies compared second-order motion responses directly to first-order motion responses without taking out the response to the static stimulus of each type, so these studies could not verify that the differences shown were due to a separate motion system. Though the motion-specific responses to second-order stimuli were measured in one study (Smith et al., 1998), they were not compared to corresponding motion-specific responses to first-order stimuli. In order to determine the motion-specific response differences, the current study factored out the activation to the static pattern for both first-order and second-order stimuli to determine if the brain activation related to different motion perception systems.

Though there are differences, there are many similarities between our results and previous work. Our initial analysis, of activation to moving stimuli with respect to a fixation baseline, produced results consistent with Smith et al. (1998). Two areas responded reliably more to second-order motion: area LOP (similar in location to V3B; Smith et al., 1998), and area V4v (see Figure 2, top graphs). In addition, our results confirm the finding of Smith and colleagues that the MT complex and V3A show the largest motion-specific responses, for both first- and second-order stimuli (Figure 2, bottom graphs). Also consistent is the finding that intermediate visual areas (such as V3/VP and LO/V3B) show an intermediate magnitude, and early areas (V1 and V2) show the lowest magnitude.

Our results differ from prior imaging studies in two primary ways. First, sensitivity to second-order stimuli was observed in V1 and V2, suggesting that these, and not V3/VP (Smith et al., 1998), are the first areas in the cortical hierarchy to respond to these stimuli. In fact, we observed that the retinotopically-consistent parts of all visual areas responded well to second-order motion (Figure 2 top). Second, we directly compared the motion-specific responses to first- and second-order stimuli by subtracting out the activity related to static presentation of each stimulus type to isolate the responses to motion (Figure 2 bottom). None of the visual areas were found to respond more to the motion of second- than to first-order stimuli, and responses overall visual areas were remarkably similar (Figure 3). These results suggest that the V4v and LOP responses in our first analysis, and the V3/V3B responses reported in previous work (Smith et al., 1998; Wenderoth et al., 1999) are likely driven by the static textures or

complex structure of the second-order stimuli, and do not represent responses from a specialized motion detection system. In addition, our experiments with the attentional modulation of motion perception found remarkably similar modulation in the response of all areas to first- and second-order motion (Figure 4). Finally, though large differences in responses to first- and second-order stimuli were found after adaptation to unidirectional motion (MAE), results did not isolate any visual area that might be specialized for analysis of second-order motion (Figure 6). These results are most consistent with the conclusion that the motion-sensitive areas respond similarly to the motion of first- and second-order patterns, without separating into different detector types.

Implications for models of motion processing

The introduction of the stimulus class known as "second-order motion" arose because well-supported neural models of motion detection (Adelson & Bergen, 1985; vanSanten & Sperling, 1985) could not account for psychophysical observation that second-order stimuli produced reliable motion perception (Chubb & Sperling, 1988; Cavanagh & Mather, 1989). Three types of new models were proposed: 1) Independent, specialized detectors for the analysis of second-order motion (Chubb & Sperling, 1988; Lu & Sperling, 1995). 2) Unified motion analysis by the same, multi-dimensional, set of units (Johnston et al., 1992; Johnston & Clifford, 1995). 3) Feature tracking of defined contours that mediated second-order motion more than first-order (Seiffert & Cavanagh, 1998, 1999; Derrington & Ukkonen, 1999; Ukkonen & Derrington, 2000). Clearly, the present results provide no support for the first model type, as no specialized motion areas have been found. It's possible that specialized detectors exist on a smaller cortical scale than we could record with fMRI, although evidence from single-unit studies also doesn't support this notion (O'Keefe & Movshon, 1998). These data are most consistent with the unified motion processing account, because the observed motion-responsive brain areas seemed to work as a unit. Motion detectors of such a system must have nonlinear stages to detect second-order stimuli such as these (Johnston et al., 1992; Johnston & Clifford, 1995). However, our finding that brain areas that do respond more to second-order stimuli more likely reflect processing of form, also may support the feature tracking account. Overall, these data suggest that models of motion perception need to provide a unified approach to motion analysis, even for stimuli of different types.

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