

# Cortical Specialization for Processing First- and Second-order Motion

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**Distinct mechanisms underlying the visual perception of luminance- (first-order) and contrast-defined (second-order) motion have been proposed from electrophysiological, human psychophysical and neurological studies; however a cortical specialization for these mechanisms has proven elusive. Here human brain imaging combined with psychophysical methods was used to assess cortical specializations for processing these two kinds of motion. A common stimulus construction was employed, controlling for differences in spatial and temporal properties, psychophysical performance and attention. Distinct cortical regions have been found preferentially processing either first- or second-order motion, both in occipital and parietal lobes, producing the first physiological evidence in humans to support evidence from psychophysical studies, brain lesion sites and computational models. These results provide evidence for the idea that first-order motion is computed in V1 and second-order motion in later occipital visual areas, and additionally suggest a functional dissociation between these two kinds of motion beyond the occipital lobe.**

**Keywords:** brain imaging, fMRI, motion perception, second-order, vision, visual cortex

## Introduction

Our visual world contains both luminance- (first-order) and contrast-defined (second-order) information (Schofield, 2000). Separate mechanisms for processing first- and second-order stimuli, both stationary and moving, have been demonstrated by electrophysiological and psychophysical studies (for reviews, see Smith, 1994; Baker, 1999; Clifford and Vaina, 1999; Baker and Mareschal, 2001; Chubb *et al.*, 2001; Lu and Sperling, 2001). The idea of separate neuronal substrates is also supported by reports describing a double dissociation of deficits for either first-order (Greenlee and Smith, 1997; Vaina *et al.*, 1998, 1999, 2000) or second-order motion (Plant *et al.*, 1993; Plant and Nakayama, 1993; Vaina and Cowey, 1996; Greenlee and Smith, 1997; Braun *et al.*, 1998; Vaina *et al.*, 1999) perception in brain-damaged subjects. Comparing the location of lesions affecting first- and second-order motion perception, Greenlee and Smith (1997) reported extensive overlap in a standard space (Seeger, 1978), whereas Vaina and co-workers (Vaina and Cowey, 1996; Vaina *et al.*, 1998, 1999, 2000) found separate sites in medial and lateral occipital lobe, respectively. Models of motion detection, derived from these psychophysical, electrophysiological and neurological studies, propose parallel mechanisms at separate cortical sites, i.e. extraction of first- and second-order information at early (V1) and later cortical stages, respectively (Chubb and Sperling, 1988; Wilson *et al.*, 1992; Clifford and Vaina, 1999). Thus separate mechanisms have been proposed for processing first-

and second-order motion but direct evidence for such cortical specializations has proven elusive.

Previous human brain imaging attempts have implicated a variety of areas in processing both first- and second-order stimuli (Smith *et al.*, 1998; Somers *et al.*, 1999; Wenderoth *et al.*, 1999; Sasaki *et al.*, 2002; Dupont *et al.*, 2003; Seiffert *et al.*, 2003), with some responding more to second-order motion (Smith *et al.*, 1998; Wenderoth *et al.*, 1999). These previous studies employed differently constructed first- and second-order stimuli, as is common in psychophysical experiments where only certain stimulus attributes can be used for a given task. However, in the brain imaging data, differential responses can be elicited by differences in processing at any level, e.g. stimulus, task or attentional. In particular, second-order stimuli necessarily contain first-order carriers, whereas the first-order stimuli did not contain any second-order structure, i.e. both kind of stimuli contain first- but not second-order structure. Thus, the previous experiments might have been biased towards detecting responses to second-order attributes, which could explain why no cortical regions were selectively activated by first-order motion. In addition, attentional modulation can substantially affect neuroimaging responses (Beauchamp *et al.*, 1997; O'Craven *et al.*, 1997; Somers *et al.*, 1999), and could potentially confound the interpretation of the results (Huk *et al.*, 2001). Therefore a careful control of attention is a prerequisite (i) to avoid activations elicited by differential attentional requirements of the experimental conditions, and (ii) to minimize attentional tracking proposed to occur in second-order motion (Seiffert and Cavanagh, 1998; Derrington and Ukkonen, 1999).

Here a single kind of stimulus is used (Fig. 1), constructed of Gabor micropatterns in limited-lifetime stochastic motion to avoid attentional tracking (Baker and Hess, 1998). This stimulus contains both first- and second-order structure within the same image, related to the luminance-carrier and contrast-envelope of the Gabor micropatterns, respectively. Stimulus parameters, as delineated in previous psychophysical experiments (Boulton and Baker, 1993a,b, 1994; Bex and Baker, 1997; Baker and Hess, 1998; Clifford *et al.*, 1998; Bex and Baker, 1999; Clifford and Vaina, 1999; Ledgeway and Hess, 2000; Dumoulin *et al.*, 2001), were manipulated (i) to force the subjects' direction-discrimination by either first- or second-order mechanism, and (ii) to equate the stimulus conditions for their psychophysical performance. The stimuli were presented in the magnetic resonance scanner as they would be in a psychophysical experiment, and the subjects were required to perform a psychophysical task. This task (i) verified similar psychophysical performances for the different conditions within the MR environment, (ii) focused and maintained the subjects' attention on the motion of the stimulus,

and (iii) allowed for a more direct comparison of the brain imaging and psychophysical data. Using this single stimulus paradigm with its inbuilt controls for differences in spatial and temporal stimulus properties, we show cortical specializations for processing either type of motion, in both the occipital and parietal lobe.

## Materials and Methods

### Subjects

Eight experienced psychophysical observers were used as subjects (all male, mean age 36 years, age range 25–51 years), four of whom were naïve to the purpose of the study. The subjects were instructed to fixate at a provided fixation-point and trained prior to the scanning session to familiarize them with the task and to equate the stimulus conditions. All observers had normal or corrected to normal visual acuity.

### Gabor Micropattern Stimulus

The visual stimuli (Fig. 1) were generated using the VideoToobox (Pelli, 1997) on a Macintosh G4 Powerbook, and displayed on a LCD projector (NEC Multisync MT820). The stimuli were presented on a rear-projection screen placed in the bore, which was viewed by means of a mirror mounted above the eyes of the subject. The total visual display subtended 15° (horizontal and vertical) at the viewing distance of 1 m. The projector intensity non-linearity was measured using a photometer (United Detector Technology S370), and corrected using internal look-up tables. The monitor was operated using its green video input only.

The stimuli contained non-overlapping Gabor micropatterns each consisting of a one-dimensional sinuswave carrier enclosed by a two-dimensional Gaussian envelope:

$$L(x, y) = L_0 \left[ 1 + C \frac{\exp\left(-\frac{x^2}{2\sigma_x^2} - \frac{y^2}{2\sigma_y^2}\right)}{\sin\left(\frac{2\pi x}{\lambda} + \phi\right)} \right] \quad (1)$$

where  $L_0$  is the mean luminance,  $C$  is the contrast,  $\sigma$  is the sigma of the Gaussian envelope,  $\lambda$  and  $\phi$  the wavelength and phase of the carrier luminance sinuswave. The orientation of the Gabors was perpendicular to their direction of motion, i.e. vertical. Each stimulus presentation lasted 1600 ms. Two kinds of Gabor micropatterns were used, which only differed in their motion trajectories. One set of micropatterns moved coherently in fixed displacements, the others were randomly replotted. The average probability of a micropattern moving coherently was determined by the coherence level. The Gabors had a limited-lifetime, after which they were replotted in a random position, and it was freshly determined whether each would move coherently or not for the next set of displacements. Micropatterns falling in a central circular zone of radius  $4^\circ$  were not plotted to avoid attentional tracking. The net direction of motion of the Gabor patterns was either to the left or to the right. For a more detailed description of the limited-lifetime Gabor stimuli, see Baker and Hess (1998) and Ledgeway and Hess (2000). The subjects performed a two-alternative forced-choice (2AFC) direction-discrimination task and their responses were recorded.

Two different versions of this stimulus were used with different spatial ( $\lambda = 1.4^\circ$  and  $1.9^\circ$ ) and temporal properties (16 exposures of 100 ms and 20 exposures of 80 ms). In both conditions the envelope size ( $\sigma$ ) was  $3/4\lambda$  and the contrast ( $C$ ) was 30%. To force the detection of the direction of motion by the first-order mechanism a displacement of  $1/4\lambda$ , a lifetime of 1 with a fixed carrier-phase ( $\phi = 0$ ) and a lower coherence level were used. To ensure that a second-order mechanism is mediating the subject's directional judgments, the carrier-phase was randomized on each exposure ( $-\pi < \phi < \pi$ ) at a displacement of  $1/2\lambda$ . These conditions are known to force the detection of the direction of motion by either mechanism (Baker and Hess, 1998; Ledgeway and Hess, 2000; Dumoulin *et al.*, 2001), which was verified during initial psychophysics. Both coherence and lifetime were adjusted for each subject in order to equate the psychophysical direction-discrimination

of the first- and second-order conditions, but were kept constant during the experiment. Both lifetime and coherence parameters vary the stimulus signal-to-noise ratios (SNR) to equate the psychophysical performance (and thus perceptual SNR), with the aim of achieving similar neuronal load. Thus, at least perceptually, the stimuli did not contain different SNR levels. Typically, a coherence level of 50% and 90% and a lifetime of 1 and 5 was used for the first- and second-order conditions, respectively. Thus stimulus parameters were varied to force the detection of the direction of motion by either mechanism (displacement, lifetime and carrier-phase) and to equate the subjects' psychophysical performances (lifetime and coherence). A subset of the four conditions provide a control to assess the effect of displacement (velocity) manipulation (see Fig. 1), and a separate coherence control experiment investigated the effect of the coherence manipulation.

Presentations of a mean-luminance block (21 s) and two blocks containing the limited-lifetime Gabor stimuli (each 30 s) were repeated four times. Thus each block of the four Gabor stimulus conditions was shown twice in random order, giving a total of four first- and four second-order blocks. Stimulus presentations lasted 1.6 s and were time-locked to the acquisition of fMRI time-frames, i.e. every 3 s. In the remaining 1.4 s the subjects' responses were recorded. The subjects continually performed a 2AFC psychophysical task, i.e. a left-right direction-discrimination task when the motion stimuli were presented and a black-white fixation-dot polarity task during blank periods. All subjects reported the tasks to be challenging, including the fixation-dot polarity task. Difficulties with the latter can be attributed to (i) time constraints, (ii) the stimulus design, i.e. in the blank periods both stimulus and response period contained a fixation-dot of random polarity, and (iii) the response requirements, i.e. the left and right response buttons did not map on to the black-white judgment as intuitively as in the left-right motion judgment.

### Mapping Stimuli

The visual stimuli used for identification of visual cortical areas were generated on a Silicon Graphics O<sub>2</sub> computer with OpenGL-based software and displayed with an LCD projector (NEC Multisync MT820). The total visual display subtended 34°. Standard stimuli were used to create polar-angle and eccentricity maps of the visual cortex (Engel *et al.*, 1994, 1997; Sereno *et al.*, 1995; DeYoe *et al.*, 1996; Dumoulin *et al.*, 2003). Rotating wedge and expanding annulus sections of a radial checkerboard were used for the phase-encoded retinotopic mapping. Both stimuli completed a full cycle in 12 time frames (0.03 Hz), giving a total of 10 cycles per scanning run. The contrast of the checkerboard was 100%, which was contrast reversing at 4 Hz. The wedge subtended 90°. Low contrast flickering stimuli (8 Hz, 6%) contrasted with stationary patterns were used to localize hMT+ or V5-complex (Tootell *et al.*, 1995; Dumoulin *et al.*, 2000).

### Magnetic Resonance Imaging

The magnetic resonance images were acquired with a Siemens Magnetom Vision 1.5 T MRI. The experiments were conducted with the subjects lying on their back with a surface-coil (circularly polarized, receive only) centered over their occipital poles. Head position was fixed by means of a foam head-rest and a bite-bar.

Multislice  $T_2^*$ -weighted gradient echo (GE) echo-planar imaging (EPI) functional MR images [ $T_R/T_E = 3000/51$  ms, flip angle = 90°, no. of slices = 25 (contiguous), slice thickness = 4 mm] were acquired using a surface-coil (receive only) with a  $64 \times 64$  acquisition matrix and a  $256 \times 256$  mm rectangular field of view. The slices were taken parallel to the calcarine sulcus and covered the entire occipital and parietal lobes and large dorsal-posterior parts of the temporal and frontal lobes. One hundred and ten measurements (time frames) were acquired. Ten fMRI scans were performed in each session.  $T_1$ -weighted anatomical MR images (aMRI) were acquired prior to the commencement of the functional scans. This aMRI utilized a three-dimensional GE sequence ( $T_R = 22$  ms,  $T_E = 10$  ms, flip angle = 30°,  $256 \times 256$  mm rFOV) and yielded 80 sagittal images with a thickness of 2 mm. The coherence control experiments were performed using identical MR parameters and setup using a Siemens Sonata 1.5 T MRI.

In separate sessions,  $T_1$ -weighted aMRI images were acquired with a head-coil, and also with a three-dimensional GE sequence, yielding 170 sagittal images comprising  $1 \text{ mm}^3$  voxels. Identification of the visual

areas was also performed in another separate session with identical parameters except for the number of time frames acquired and total runs which were 128 and 6–10, respectively. All studies were performed with the informed consent of the subjects and were approved by the Montréal Neurological Institute Research Ethics Committee.

### **Processing of Anatomical Images**

The anatomical MRI scans were corrected for intensity non-uniformity (Sled *et al.*, 1998; Arnold *et al.*, 2001) and automatically registered (Collins *et al.*, 1994) in a stereotaxic space (Talairach and Tournoux, 1988). The surface-coil aMRI, taken with the functional images, was aligned with the head-coil aMRI, thereby allowing an alignment of the functional data with a head-coil MRI and subsequently stereotaxic space. This alignment was performed with an automated script combining correction for the intensity gradient in the surface-coil aMRI (Sled *et al.*, 1998) and intra-subject registration (Collins *et al.*, 1994). A validation of this method was described in a previous study (Dumoulin *et al.*, 2000). The aMRIs were classified into gray matter, white matter and cerebrospinal fluid (Kollokian, 1996; Zijdenbos *et al.*, 1998), after which two cortical surfaces were automatically reconstructed at the inner and outer edge of the cortex (MacDonald *et al.*, 2000). The surface-normals of the cortical models were smoothed to produce an 'unfolded' model of the cortical sheet (MacDonald *et al.*, 2000). All processing steps were completely automatic and all the data are presented in a stereotaxic space (Talairach and Tournoux, 1988; Collins *et al.*, 1994).

### **Preprocessing of Functional Images**

The first eight scans of each functional run were discarded due to start-up magnetization transients in the data. All remaining scans in each functional run were normalized for variations in mean spatial slice intensity across the different slices and blurred with an isotropic three-dimensional Gaussian kernel [full-width half-maximum (FWHM) = 6 mm] to attenuate high-frequency noise. The functional scans were corrected for subject motion within each fMRI scan and between scans with the AIR package (Woods *et al.*, 1992; Jiang *et al.*, 1995; Woods *et al.*, 1998). Functional scans were excluded from further analysis if artifacts were found (e.g. large subject motion or spurious spikes) or if the subjects' psychophysical responses for any given condition contained more than 40% errors. In total, 13 out of 108 fMRI scans were excluded from further analysis, primarily due to imaging artifacts.

### **Identification of Visual Areas**

Early visual cortical areas were identified using volumetric phase-encoded retinotopic mapping (COBRA package; Dumoulin *et al.*, 2003). By combining eccentricity and polar-angle phase-maps with the anatomical MRI, the visual field signs of different visual areas could be segmented. Neighboring visual areas could be identified due to opposite field signs, i.e. V1, V2, V3/VP, V3a, V3b, V4v and V7 (Sereni *et al.*, 1994, 1995; Dumoulin *et al.*, 2003). Areas V3b and V7 could be identified lateral and anterior to area V3A, due to their change in field sign relative to this area. Therefore, only one border could be identified with certainty, i.e. the V3A border. Thus, only parts of these two areas are identified in all subjects, containing quadri-field and hemi-field representations, respectively (Dumoulin *et al.*, 2003). Area MT (or V5) was identified using a low-contrast flickering stimulus (Tootell *et al.*, 1995; Dumoulin *et al.*, 2000). This activation region is usually termed hMT+ (or V5-complex) to indicate that parts of adjacent cortical areas might be included.

### **Statistical Analysis**

The fMRI data were analyzed using software developed by Worsley *et al.* (2002). This statistical analysis is based on a linear model with correlated errors. Runs, sessions and subjects were combined using a linear model with fixed effects and standard deviations taken from the previous analysis on individual runs. A random effects analysis was performed by first estimating the ratio of the random effects variance to the fixed effects variance, then regularizing this ratio by spatial smoothing with a 15 mm FWHM Gaussian filter. The variance of the effect was then estimated by the smoothed ratio multiplied by the fixed effects variance to achieve higher degrees of freedom. The resulting *t*-statistical images were thresholded for peaks and cluster

sizes using random field theory (Worsley *et al.*, 1996). In determining significant clusters and peaks in the first- versus second-order comparison, the search region was restricted to voxels within the brain which responded to the 'stimulus' versus 'blank' comparison ( $t = 1.96$  corresponding to an uncorrected  $P = 0.05$ ; however, the results were robust over a range of thresholds  $1 < t < 4$ ).

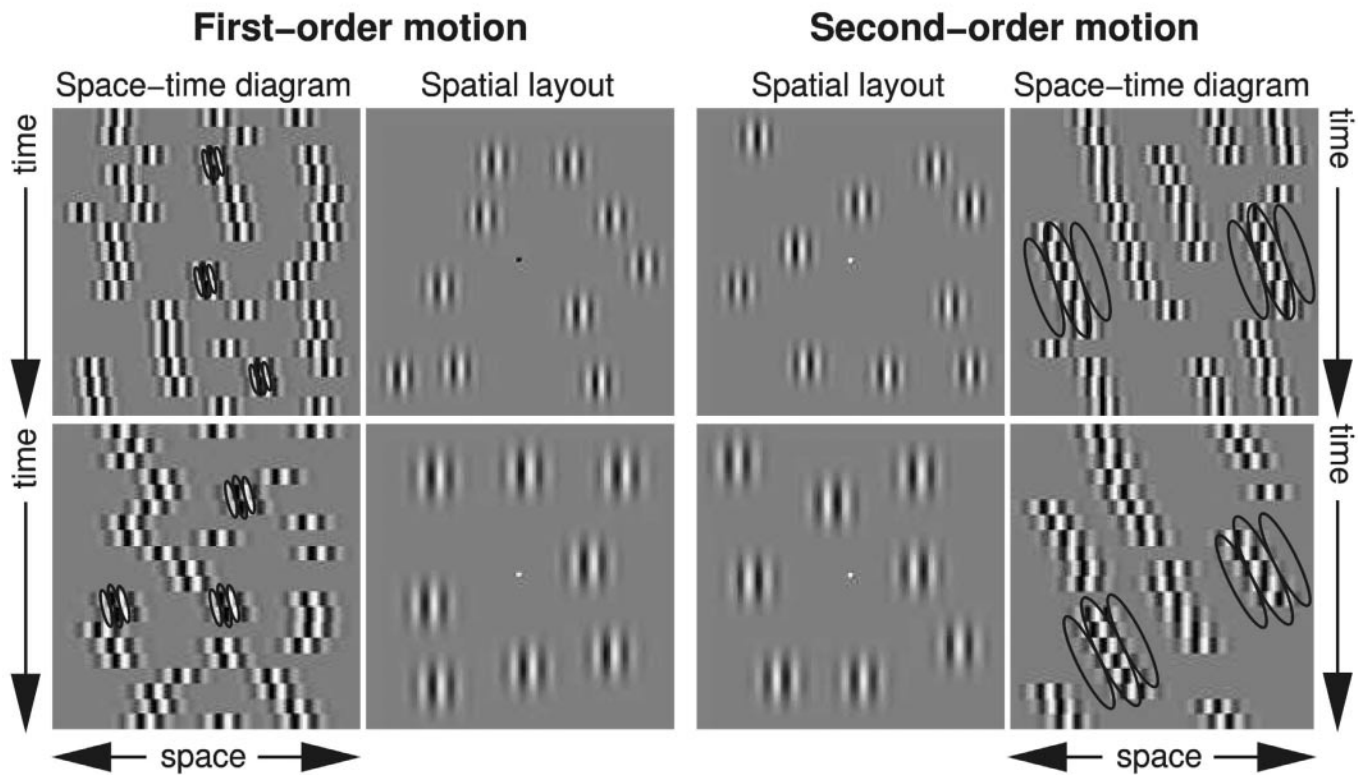
The volume-of-interest analysis of the identified visual areas (V1–V7) was done in an identical fashion. Prior to the statistical analysis, time-series of voxels responding to motion stimuli within a volume-of-interest (VOI) (left and right hemispheres) were averaged together, and voxels displaying artifacts were excluded.

## **Results**

The motion stimuli had virtually identical spatial and temporal properties (see Fig. 1), and even though all conditions contain stochastic first- and second-order information, the correct net direction of motion can only be determined by one mechanism. Drawn on the space-time diagrams are hypothetical filters signaling the motion-direction of certain Gabor micropatterns. In the first-order configurations (Fig. 1, left panels) the net direction of motion can correctly be determined by a standard (first-order) quasi-linear filter (Adelson and Bergen, 1985; Van Santen and Sperling, 1985) responding to the luminance-carrier; previous psychophysical studies (Baker and Hess, 1998; Ledgeway and Hess, 2000; Dumoulin *et al.*, 2001) indicate that in those conditions a second-order mechanism does not contribute to judgments of the net direction of motion. In the second-order conditions (Fig. 1, right panels) the carrier-phase is randomized on different exposures, eliminating direction-discrimination based on first-order mechanisms. Here the mechanism signaling the correct direction of motion has been shown to be based on the contrast-envelope of the micropatterns, i.e. second-order information, because the average luminance in the different subfields of the filter are identical (Baker and Hess, 1998; Bex and Baker, 1999; Ledgeway and Hess, 2000; Dumoulin *et al.*, 2001).

The average psychophysical data for all subjects are shown in Figure 3 for the different conditions. The percent error and standard deviations for first- and second-order motion conditions were  $7.3 \pm 10.5$  and  $8.9 \pm 9.7$ , respectively. The results show that (i) the subjects were able to do the tasks, (ii) the tasks were challenging enough to engage their full attention (rarely 0% errors performance occurred), and (iii) the psychophysical performances for the conditions were not significantly different ( $P > 0.2$ ).

The first fMRI statistical analysis aimed at identifying cortical regions involved in processing *all* stimulus aspects. Since any first- and second-order differences would be expected to occur in these cortical regions, any further statistical comparisons will be restricted to this region. This statistical comparison, i.e. motion versus blank conditions, indicates a widespread activation (Fig. 4, thin black lines). In early visual areas, this activation region corresponds to the cortical representation of the eccentric locations where the Gabor stimulus was presented, as it should. This statistical map is very similar to *t*-statistical maps comparing each individual stimulus configuration to the blank-periods (correlation:  $r_{xy} = 0.85$ ), which therefore allows the further statistical analysis to be restricted by the combined statistical map. Furthermore, this result indicates that similar areas are involved in processing any version of the stimulus, which is in agreement with previous studies investigating first- and second-order motion (Smith *et al.*, 1998; Somers *et al.*, 1999; Wenderoth *et al.*, 1999; Dupont *et*



**Figure 1.** Spatial layout and space–time diagrams of the four conditions of the visual stimulus. The top and bottom rows differ only in stimulus parameters controlling velocity. The central four panels show four representative spatial layouts, flanked by corresponding examples of space–time diagrams having an overall direction of motion (displacement direction) to the right. The left four panels are examples of the first-order stimulus conditions whereas the right four panels illustrate second-order stimulus configurations. The spatial and temporal properties of both first- and second-order stimulus conditions are virtually identical. A few hypothetical filters are drawn on top of the space-time diagrams illustrating that on the left panels first-order mechanisms underlie the perceptual judgments, whereas in the right panels the overall direction of motion can only be determined by second-order mechanisms. In the first-order configurations (left side) a displacement of quadrature phase, a lifetime of 1 and a lower coherence (50%) was used, parameters known to favor processing by first-order mechanisms. In the second-order conditions (right side) the carrier-phase was randomized on each exposure, forcing the perceptual judgments by a second-order mechanism. The first- and second-order conditions have slightly different velocities (different displacements with identical temporal properties). As a control condition, the spatial and temporal properties of the top and bottom stimulus versions were chosen in such a way that the second-order (top-right) condition has the same velocity as the first-order (bottom-left) condition, allowing for a velocity-matched control. The contrast of the Gabor micropatterns is higher than in the actual stimulus (30%) for illustration purposes.

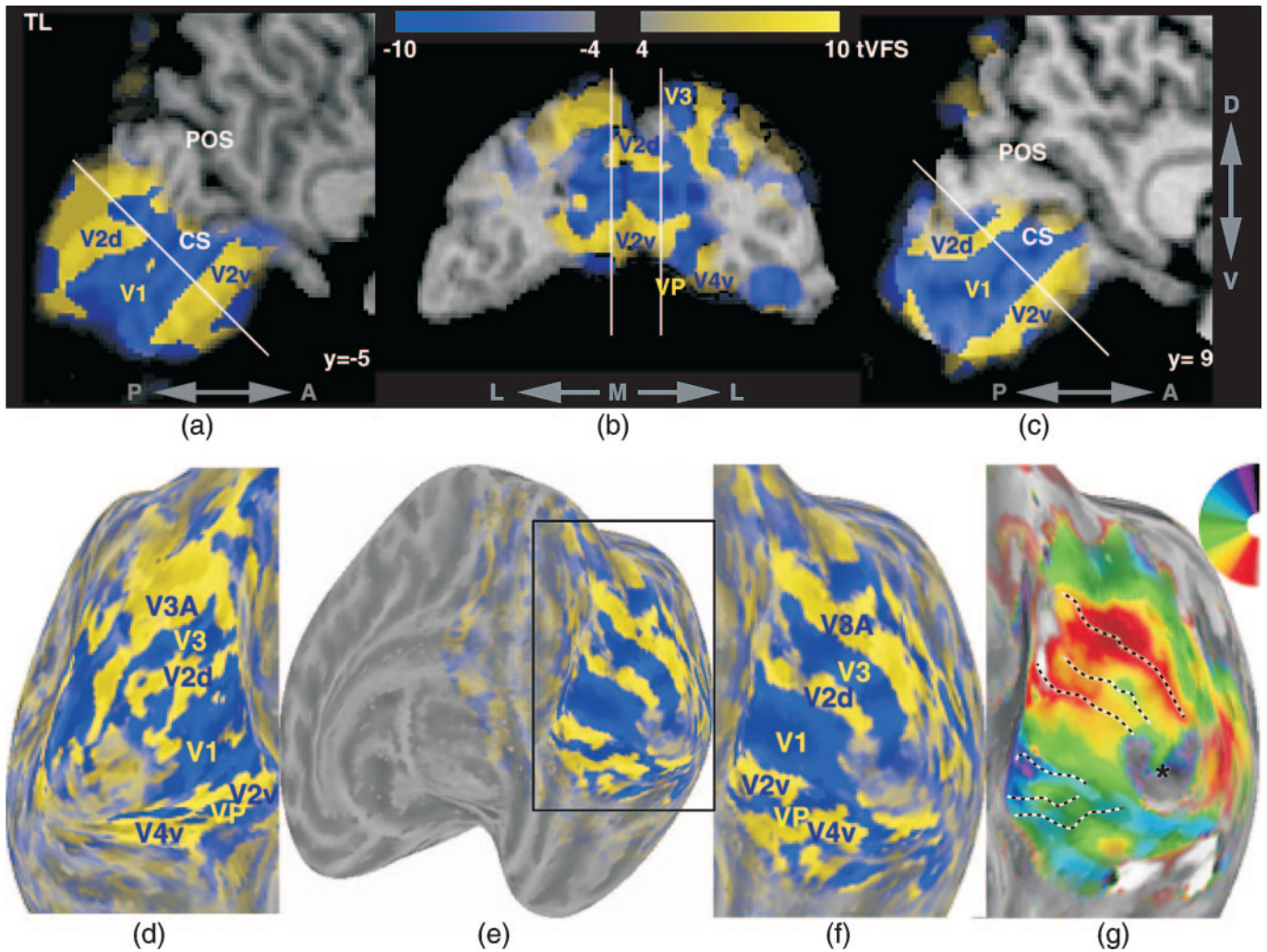
*al.*, 2003; Seiffert *et al.*, 2003;). This is not surprising since this is a highly unspecific comparison and the blank periods do not provide a resting baseline. That is, it is an unspecific comparison because we are comparing stimulus ‘present’ versus ‘absent’. Therefore, this activation distribution is not motion specific. And furthermore, any stimulus version always contained both first- and second-order noise. Lastly, it does not represent a resting baseline because these activation patterns are also produced by changes in ‘more eccentric’ versus ‘foveal’ spatial-attention (Tootell *et al.*, 1998; Watanabe *et al.*, 1998; Gandhi *et al.*, 1999; Smith *et al.*, 2000; Sasaki *et al.*, 2001). In summary, comparing ‘stimuli’ versus ‘blank’ is a highly unspecific comparison where all aspects contribute to, and thus can only be used for, the identification of cortical areas processing *any* stimulus aspects.

The second statistical analysis compared first- versus second-order motion responses. This statistical comparison was constrained to the cortical regions found to process any of the stimulus attributes, thereby increasing statistical sensitivity. To identify the cortical regions involved in any processing steps related to motion stimuli, the *t*-statistical map was thresholded (Fig. 4, thin lines, correspond to  $t = 1.96$ ). To not exclude, *a priori*, certain regions due to an overly restricted search

region, this threshold was generously chosen ( $t = 1.96$  corresponding to an uncorrected *P*-value of 0.05). However, the final results did not critically depend upon, and were robust over, a wide range of thresholds ( $1 < t\text{-threshold} < 4$ ). The results of this statistical analysis are shown in Figure 4. Significant *t*-statistical clusters and peaks ( $P < 0.05$ ) in the resulting *t*-map were determined (Worsley *et al.*, 1996) and are identified in Figure 4 and Table 1. Cortical specializations for processing first- and second-order motion were found both in occipital and parietal lobes.

In the parietal lobe, cortical specializations for processing first- and second-order motion were found in the left precuneus (PC) and bilateral anterior superior parietal lobule (ASPL) within the dorsal part of the intraparietal sulcus (IPS). These ASPL regions are known to respond to motion stimuli (Sunaert *et al.*, 1999) and also to attentional tasks such as motion tracking (Culham *et al.*, 1998, 2001; Jovicich *et al.*, 2001). In the same contiguous ASPL cluster in the right hemisphere, a visually distinct peak ( $t = 5.14$ ,  $P < 0.001$ , *xyz*-coordinates = 18, -66, 54) was found more posterior within the middle superior parietal lobule (MSPL).

In the occipital lobe, a clear segregation of regions preferentially responding to each of the two types of motion was



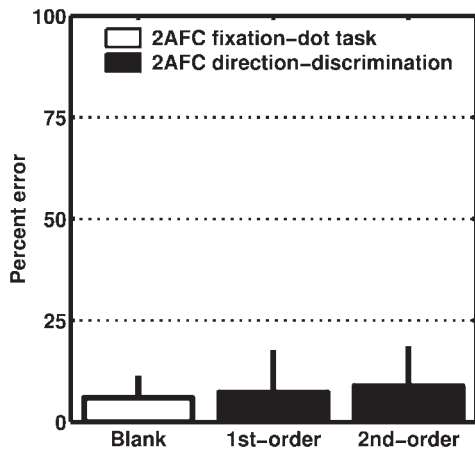
**Figure 2.** Example of volumetric visual area identification (Dumoulin *et al.*, 2003) for one subject (TL). The top row (a–c) shows the volumetric visual field sign maps (VFS) weighted by t-statistical maps (tVFS). On the sagittal slices (a,c) the parietal-occipital sulcus (POS) and calcarine sulcus (CS) have been identified. The bottom row shows the same data (same colormap range) on unfolded cortical surfaces of the left (d) and right (e,f) hemisphere. The bottom row also shows an example of the polar-angle phase map (g), where the borders of the areas are drawn based on the tVFS-changes. The polar-angle map is used in combination with the eccentricity map and the surface-normals to compute the VFS.

found. Responses driven more by second-order motion are apparent in higher visual areas at the edge and beyond the early retinotopically mapped visual cortex. Several peaks reach significance, all in the lateral occipital cortex (LO), in the vicinity of area hMT+. Drawn on top of the activation maps are the statistical probability anatomical map (SPAM) of area hMT+ taken from the five subjects in whom it was identified. The hMT+ SPAM suggests that the largest peak found to preferentially process second-order motion stimuli is slightly posterior to hMT+, and not hMT itself (indicated in Fig. 4). Stronger fMRI (but not significant) responses elicited by first-order motion stimuli are located in the early visual areas (medial occipital cortex, MO). They are mentioned, however, because they are of interest, since activations would be predicted in V1 and V2 based on current models (Wilson *et al.*, 1992) and lesion studies (Vaina *et al.*, 1998). When this V1/V2 prediction is taken into account, this MO-cluster does reach significance ( $P = 0.01$  uncorrected). These occipital specializations (MO and LO) are in agreement with the lesion sites described by Vaina and co-workers (Vaina and Cowey, 1996; Vaina *et al.*,

1998, 1999, 2000), as illustrated in Fig. 4, which were associated with selective deficits of first- and second-order motion perception.

To further identify the origin of the fMRI peaks in the occipital lobe (Fig. 4), a VOI analysis was performed in five subjects on the first seven visual areas: V1–V7 including hMT+ (Fig. 5). Areas V3b and V7 are included in this analysis because they may partially overlap with the LO-cluster, even though they are incompletely localized. However, including or excluding areas V3b and V7 in the VOI analysis does not alter our results or conclusions in any way. The complete MO-cluster was covered by these visual areas, which was not the case for the LO-cluster. The unidentified parts of the LO-cluster were processed as a separate VOI, and most likely consist of several visual areas. This VOI is termed as LO- to indicate that identified visual areas have been removed from this VOI. Thus all occipital activations found in the stereotaxicanalysis were processed in the VOI analysis.

The VOI results (Fig. 5, top panel) provide evidence for a stronger involvement of early visual areas (V1 and V2) in



**Figure 3.** Subjects' psychophysical performance during the MR scans. Percent error and standard deviations of the subjects' performance during the fMRI scans are plotted for three conditions. All tasks comprised psychophysical two-alternative forced choice (2AFC) judgments. During the blank periods, the subjects judged the fixation-dot polarity (black-white). When the Gabor-stimuli, either first- or second-order version, were presented the subjects performed a direction-discrimination (left-right) task. The results show that the subjects were able to do either task and that the responses to first- and second-order stimulus conditions were statistically indistinguishable ( $P > 0.2$ ), indicating that the conditions were equated for their psychophysical performance.

processing first-order motion, a trend that decreases and eventually reverses in higher visual areas. Significant differential activations are found in VOIs V1 and LO-. These results suggest that V1 (and V2:  $P = 0.09$ ) are responsible for the MO activation, and because no significant activation was determined for hMT+ ( $P = 0.17$ ), also confirm the previous suggestion that the main LO-activation peak is not hMT+.

The bottom panel shows the same VOI results with two control conditions, illustrating that the results cannot be accounted for in terms of the different stimulus parameters (displacement and coherence) used. Firstly, the results might be explained by the velocity differences between first- and second-order conditions (due to different displacements, see Fig. 1). Although a net velocity difference existed among our four stimulus configurations, one particular pair of first- and second-order conditions were velocity matched. A comparison of these two conditions alone revealed a similar activation pattern (data shown for VOI analysis, Fig. 5, bottom panel, gray bars), indicating that velocity differences cannot account for the observed activation pattern, and furthermore may even have decreased activations in the early visual areas. A second possibility is that first- and second-order stimuli may have different stimulus SNR levels due to the different coherences and lifetimes used. The different stimulus SNR levels were used to equate the conditions for their psychophysical performance (and thus perceptual SNR), with the aim to achieve similar neuronal load. Thus perceptually the stimuli did not contain different SNR levels, which is more important than stimulus SNR levels, since neuronal activity has been shown to correlate with perception (Newsome *et al.*, 1989; Britten *et al.*, 1992; Parker and Newsome, 1998; Grill-Spector *et al.*, 2000), rather than physical stimulus properties even in early visual cortex (Ress and Heeger, 2003). Nevertheless, control experiments were performed, using first-order motion, comparing the same coherence levels (50% and 90%) as used in the first- and second-order conditions. This data revealed a different and non-significant activation pattern (data

**Table 1**

Brain regions where a significant difference ( $P < 0.05$ , except MO) in processing either stimulus condition was found,  $P$ -values are indicated for the clusters and the peak  $t$ -statistical value (corrected for multiple comparisons: Worsley *et al.*, 1996, 2002) with corresponding  $x, y, z$  stereotaxic coordinates (Talairach and Tournoux, 1988; Collins *et al.*, 1994). MO is shown in the table as well, because it does reach significance ( $P = 0.01$ ) when taking predictions into account from current models (Wilson *et al.*, 1992) and lesion data (Vaina *et al.*, 1998, 2000); furthermore the MO activations reveal a trend that is significant in the VOI analysis (Fig. 5)

	Brain region	$P$ -value	$t$ -peak ( $P$ -value)	Coordinates		
				$x$	$y$	$z$
First-order	Left precuneus (PC)	0.01	4.03 (0.21)	-8	-52	30
	Right medial occipital lobe (MO)	0.14	3.26 (>0.7)	14	-94	14
Second-order	Right lateral occipital lobe (LO)	0.00	5.23 (0.00)	44	-78	8
	Left lateral occipital lobe (LO)	0.00	4.80 (0.01)	-32	-74	20
	Right anterior superior parietal lobule (ASPL)	0.00	6.08 (0.00)	36	-44	54
	Left anterior superior parietal lobule (ASPL)	0.01	6.18 (0.00)	-32	-46	50

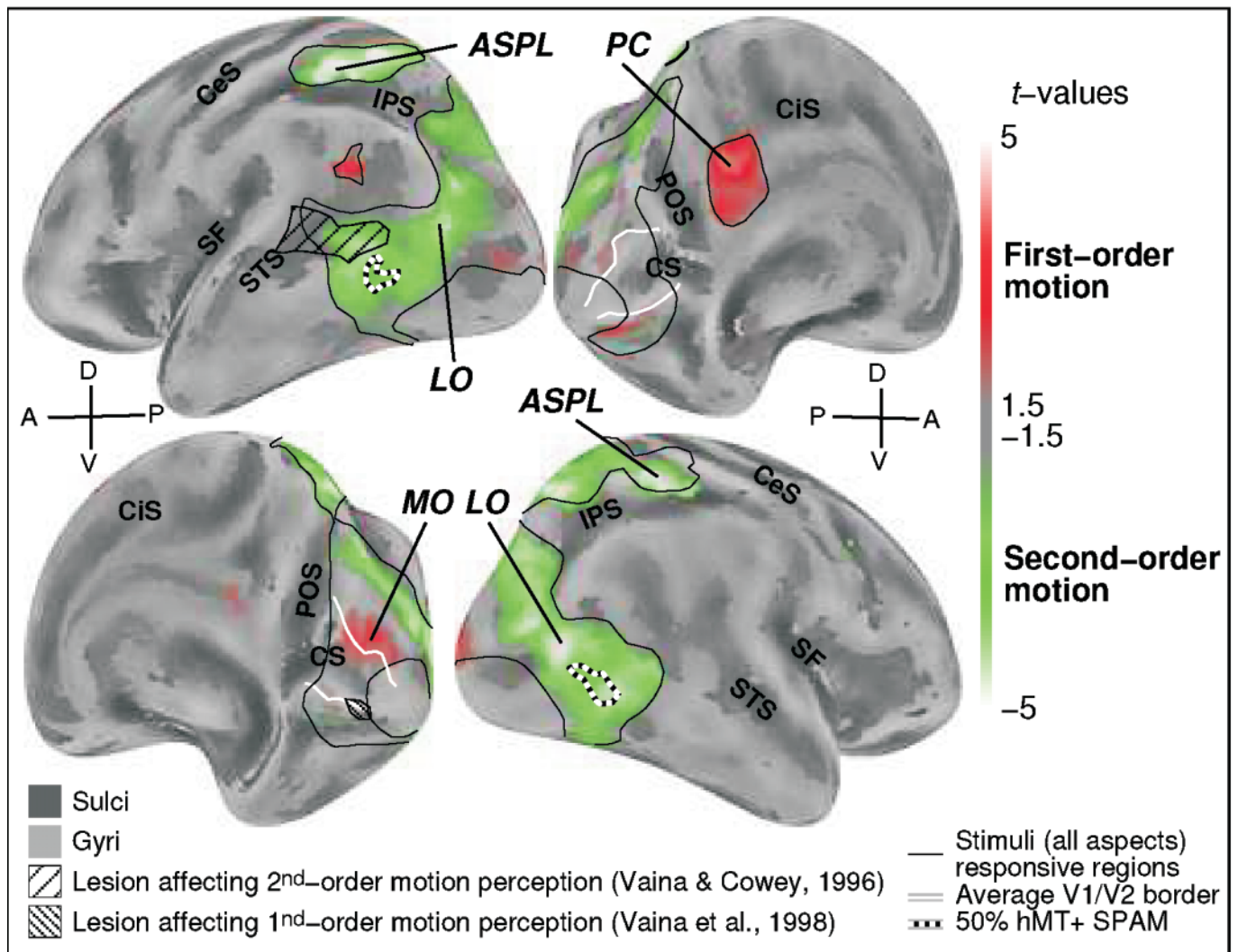
shown for VOI analysis, Fig. 5, bottom panel, white bars). Based on this result the possibility of a coherence confound seems very unlikely. We conclude that the different pattern of cortical activation produced by first- and second-order motion suggests a relative cortical specialization for the processing of these two different types of visual motion.

The coherence control indicates no significant differences of 50% versus 90% coherent motion, including area hMT+ (slightly stronger response to 50% coherent motion, if anything). This differs from that expected from previous fMRI and multi-unit electrophysiology studies (Heeger *et al.*, 1999; Rees *et al.*, 2000; Braddick *et al.*, 2000; Singh *et al.*, 2000; Braddick *et al.*, 2001) that find a stronger response to coherent motion in hMT+ (but for an opposite result see McKeefry *et al.*, 1997). This can be attributed to, firstly, stimulus construction, i.e. the stimulus is constructed differently than in the previous studies, being narrow-band in both orientation and spatial frequency. Secondly, subjects were able to correctly detect the direction of motion in both conditions, indicating that perhaps the coherence differences, both suprathreshold, were not large enough to replicate the previous studies (using 0–100%). Thirdly, direction-discrimination for the 50% coherence condition is slightly harder, thereby requiring more attention which will increase hMT+ activation (O'Craven *et al.*, 1997).

A methodological implication of these results is that a VOI analysis alone may lead to misinterpretations when neighboring areas are not processed. More specifically, taken with the  $t$ -statistical maps in Fig. 4, the bias of hMT+ to second-order motion (significant when uncorrected  $P$ -values are used) could be explained by a smearing of the activity of the adjacent area (LO-peak) due to blurring, resampling and partial volume effects, an interpretation which might be missed if the neighboring cortex was not also analyzed.

## Discussion

Here we have shown relative cortical specializations using fMRI for first- and second-order mechanisms in both occipital

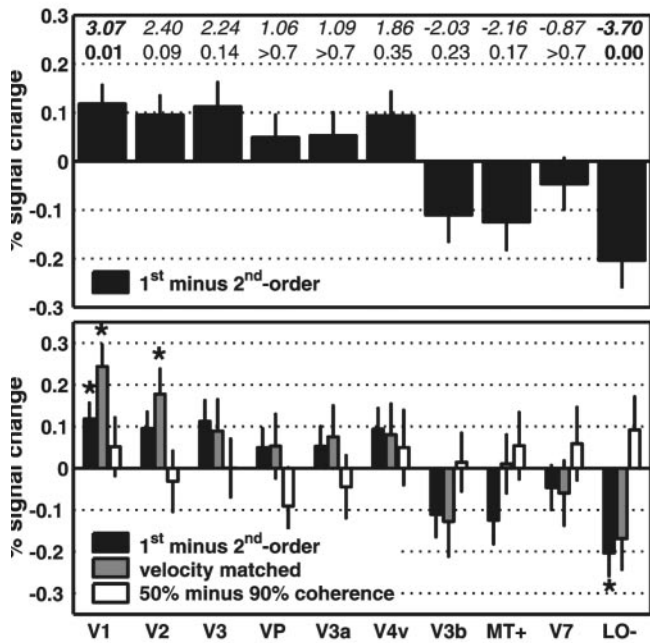


**Figure 4.** Average  $t$ -statistical map ( $n = 8$ ) comparing first- and second-order motion conditions displayed on their average unfolded cortical surfaces. The oblique lateral and medial views (left and right) of the left hemisphere are shown in the top row whereas the oblique medial and lateral views (left and right) of the right hemisphere are shown in the bottom row. On their averaged surfaces major anatomical structures can be identified (MacDonald et al., 2000) and some are labeled to facilitate orientation on the surfaces. On the lateral views the central sulcus (CeS), Sylvian fissure (SF), superior temporal sulcus (STS) and intraparietal sulcus (IPS) are labeled. On the medial side the locations of the cingulate sulcus (CiS), parietal-occipital sulcus (POS) and calcarine sulcus (CS) are indicated. Relevant regions are indicated (for  $t$  and  $P$ -values see Table 1). Significant stronger responses to second-order motion is found both in the anterior superior parietal lobule (ASPL) and in lateral occipital regions (LO). Areas responding more to first-order motion are found in the precuneus (PC) and medial occipital cortex (MO). The MO-activation show a trend that is disclosed significantly in the VOI-analysis (Fig. 5). Regions responding to all stimulus and task aspects are delineated with black lines (corresponding to  $t = 1.96$ , uncorrected  $P = 0.05$ ); in early visual areas this indicates the eccentricity range where the stimuli were presented. On the medial views the average V1/V2 border is indicated with white lines. The average location of hMT+ is indicated by black-white iso-probability lines (50%) of the hMT+ statistical probabilistic anatomical map (SPAM) on the lateral views. The hMT+ iso-probability lines suggest that the main second-order LO-activation peak is most likely not MT. Also, the lesion locations of subjects RA (bottom left) and FD (top left) are indicated, who were selectively impaired in first- and second-order motion perception, respectively (Vaina and Cowey, 1996; Vaina et al., 1998). The lesion data was provided by Dr Vaina.

and parietal cortex. We also have shown that these differences cannot be accounted for in terms of the parameters chosen to equate psychophysical performance and to force the observers' perceptual judgments by either mechanism (Fig. 5). Due to the nature of the stimulus construction, all stimulus conditions contained both first- and second-order structure; consequently only a *relative* cortical specialization could be determined, i.e. all areas responded to all stimulus conditions but to a different degree.

Our results agree with previous studies on that we find similar areas responding to either type of stimulus (Smith et al., 1998; Somers et al., 1999; Wenderoth et al., 1999; Sasaki et

al., 2002; Seiffert et al., 2003; Dupont et al., 2003); however, the relative cortical specialization reported here is in conflict with previous imaging studies, where no cortical specialization (Somers et al., 1999; Dupont et al., 2003; Seiffert et al., 2003) or some areas responding more to second-order motion were found (V3/VP: Smith et al., 1998; Wenderoth et al., 1999). All the previous studies used different stimuli for the first- and second-order conditions, where both first- and second-order conditions contained first-order structure. This may explain why no areas have been found that respond more strongly to first-order motion. Furthermore, any differential fMRI activity may be elicited by any of the spatial and/or temporal stimulus



**Figure 5.** Comparison of activation to first- and second-order motion in occipital visual areas. The LO-activation that was not covered by the identified visual areas is plotted as area LO-. Average fMRI percent signal changes and standard deviations for comparing first- and second-order stimulus conditions are plotted for the identified visual areas. The top part shows the results for each visual area comparing first- versus second-order motion (see Fig. 4). The results reveal the general trend that first-order motion is processed relatively more in early visual areas, a trend that disappears and then reverses in higher visual areas. The t-statistical (top) and corresponding Bonferroni-corrected *P*-values (bottom) comparing first- and second-order stimulus conditions for each area are shown as well. These *t*- and *P*-values indicate a significantly ( $P < 0.05$ ) stronger response to first-order motion in V1 and significantly stronger response to second-order in the undefined LO regions (LO-). These MR signal changes are relatively small, which can be attributed to the following facts. Firstly, all stimulus conditions contain first- and second-order noise, only the net-direction of motion can be determined by one mechanism. Secondly, this is a relative difference since all areas respond to all stimuli (but to a different degree). The bottom part shows the same results (black) with the results for two control conditions (gray and white). Significant values ( $P < 0.05$ , corrected) are indicated with stars. The first control (gray bars) addressed whether the activation pattern can be explained by velocity differences present between the first- and second-order conditions. To this aim, first- and second-order conditions were compared where the velocities were equal (see Fig. 1). The pattern is similar to the original results indicating that velocity differences cannot explain the first- and second-order activation pattern. The second comparison, white bars, shows a control for coherence, which was used to equate the psychophysical performances for the first- and second-order conditions. In this control condition coherence was varied for a first-order stimulus version, taking coherence levels used in the first- and second-order comparison. A different pattern is found than for the first- and second-order activations illustrating that different coherence levels cannot explain the patterns found.

differences, rather than the different kinds of motion. More recent studies have tried to address this issue by comparing stationary versus moving stimulus conditions in a full factorial design (Dupont *et al.*, 2003; Seiffert *et al.*, 2003), perceptually equating the different motion types by either stimulus contrast (Seiffert *et al.*, 2003), or by adding first-order noise (Dupont *et al.*, 2003). However, the neuronal activity associated with these different motion stimuli may not have been equated since these kinds of *local* second-order stimuli require longer durations (about a factor of 10) to detect the direction of motion (Derrington *et al.*, 1993; Ledgeway and Hess, 2002), which is reflected in longer reaction times and longer VEP

latencies to the onset of second-order motion independent of stimulus contrast (Elleberg *et al.*, 2003). All these potential problems are resolved in our paradigm because, firstly, the stimulus conditions have virtually identical spatial and temporal properties, making our design unbiased for activation by either type of motion, and bypassing the problem of differential spatial/temporal versus motion activation. Secondly, our *global* stimulus conditions were equated for perceptual coherence, where the need to integrate different local motion vectors resolves the problem of a different neuronal processing of local stimulus elements. Thus our results that differ from previous studies can be explained by our different approach, where subjects were performing a psychophysical task in the scanner while controlling for differences in spatial and temporal properties, psychophysical performance and attention.

Our results are complementary to electrophysiological and psychophysical studies suggesting different mechanisms for processing first- and second-order motion (for reviews see Smith, 1994; Baker, 1999; Clifford and Vaina, 1999; Baker and Mareschal, 2001; Chubb *et al.*, 2001; Lu and Sperling, 2001). In particular, our results are largely in agreement with single-unit recordings, where neurons responding to first- and second-order motion have been reported in relatively early (V1 and V2, e.g. Zhou and Baker, 1993; Chaudhuri and Albright, 1997; Mareschal and Baker, 1998) and late (MT and neighbors, e.g. Albright, 1992; Geesaman and Andersen, 1996; O'Keefe and Movshon, 1998; Churan and Ilg, 2001) visual areas. This is in agreement with our finding that all areas responded to both first- and second-order stimuli. In agreement with our findings, electrophysiological studies describe a smaller proportion of neurons responding to second-order stimuli in early (area 17, 18) visual areas, where the response is weaker than to first-order stimulus versions (Zhou and Baker, 1993; Chaudhuri and Albright, 1997; Mareschal and Baker, 1998). Lastly, neurons in area MT and neighbors have been suggested to be 'form-cue-invariant' (Albright, 1992; Geesaman and Andersen, 1996) or at least to a larger degree than V1 (O'Keefe and Movshon, 1998), i.e. responses to both first and second-order motion. Consistent with this notion, hMT+ did respond to both stimuli, though differing from these single-unit recordings by a stronger, but not significantly ( $P = 0.17$ ), response to second-order motion.

Our results are in broad agreement with studies of brain-damaged subjects, where lesion sites in occipital and parietal lobes differentially affect first- or second-order motion perception (Plant *et al.*, 1993; Plant and Nakayama, 1993; Vaina and Cowey, 1996; Greenlee and Smith, 1997; Braun *et al.*, 1998; Vaina *et al.*, 1998, 1999, 2000). Lesions in the lateral parietal lobe have been reported to mainly affect second-order motion perception (Greenlee and Smith, 1997; Braun *et al.*, 1998); in agreement with these results we find stronger second-order activations in the lateral parietal lobe. Particularly in the occipital lobe, our locations of cortical specializations agree remarkably well with the lesion sites of Plant and Nakayama (1993), Greenlee and Smith (1997), and especially with the results of Vaina and co-workers (Vaina and Cowey, 1996; Vaina *et al.*, 1998, 1999, 2000) which provides a neurological 'double dissociation'. Plant and Nakayama (1993) and Vaina and co-workers (Vaina and Cowey, 1996; Vaina *et al.*, 1999) describe lesions in the lateral occipital lobe (roughly corresponding to the LO region found in this study, see Fig. 4), which selec-

tively affects second-order motion perception. With occipital-temporal lesions in roughly similar locations, second-order direction-discrimination was found to be more impaired by Greenlee and Smith (1997). Vaina *et al.* (1998, 1999, 2000) describes other subjects with lesions in the vicinity of V2, to be severely impaired in first-order but not second-order motion perception; this location corresponds closely to the stronger activation to first-order motion in our studies in the early visual areas V1 and V2 ( $P = 0.09$ , see Fig. 5).

Finally, relatively higher visual areas are involved in second-order motion perception, suggesting a more complex analysis, as predicted by current models, such as the filter-rectify-filter (FRF) model (Chubb and Sperling, 1988; Wilson *et al.*, 1992; Clifford and Vaina, 1999). Thus these results provide human imaging evidence for distinct first- and second-order motion mechanisms within and beyond the occipital lobe, which converges with psychophysical and electrophysiological studies, brain lesion sites and current models.

In addition to a VOI analysis on the early visual areas, a stereotaxic analysis was performed (Talairach and Tournoux, 1988; Collins *et al.*, 1994), revealing a cortical specialization in the parietal lobe. The ASPL region is known to be involved in motion processing (e.g. Sunaert *et al.*, 1999), but the PC cluster remains more surprising. Not much is known about cortical areas in the medial parietal lobe (in human or nonhuman primates: Culham and Kanwisher, 2001), but our results would implicate some areas of the medial parietal lobe in motion processing, especially first-order motion.

In view of the involvement of parietal areas, which have been implicated in motion tracking (Culham *et al.*, 1998, 2001; Jovicich *et al.*, 2001) and eye tracking (Petit *et al.*, 1997; Luna *et al.*, 1998, but see Verstraten *et al.*, 2001), it is worth asking whether the results imply a higher-level process (e.g. feature tracking) rather than a low-level mechanism (e.g. FRF model), as a substrate of second-order motion perception (Seiffert and Cavanagh, 1998; Derrington and Ukkonen, 1999). We would argue against a role of high-level feature tracking in our particular second-order motion task for the following reasons. Firstly, while psychophysical studies using similar Gabor stimuli have demonstrated both kinds of contribution, the stimulus parameters used here should strongly favor the low-level mechanism (Bex and Baker, 1999; Ledgeway and Hess, 2000). Secondly, in the motion tracking studies it is controversial whether those areas are driven by the attentional aspects of the task (Culham *et al.*, 2001; Jovicich *et al.*, 2001). Thirdly, the other areas of the cortical network previously implicated in the process of motion tracking (Culham *et al.*, 1998, 2001; Jovicich *et al.*, 2001) and/or eye tracking (Petit *et al.*, 1997; Luna *et al.*, 1998) were not activated or equally activated by both stimuli. Fourthly, early visual areas, such as V3 and V3A, involved in motion processing but not motion tracking, were equally activated by first- and second-order motion. And finally, similar parietal regions responding to attentional tracking also exhibit activation to general motion stimuli (Cornette *et al.*, 1998; Sunaert *et al.*, 1999). Taken together these statements argue against a role of attentional tracking in these second-order motion conditions.

If the occipital and not parietal activations are related to the extraction of first- and second-order motion, as predicted by the FRF model, how should the parietal activation be interpreted? Perhaps the first- and second-order pathways remain partly distinct, even after both kinds of motions have been

extracted, suggesting a differential contribution to higher visual functions. Thus the parietal activations could suggest a functional specialization of each mechanism. For example, the superior parietal lobule has been implicated in processing more complex motion stimuli such as biological motion (Grèzes *et al.*, 2001; Vaina *et al.*, 2001) and optic flow (De Jong *et al.*, 1994; Peuskens *et al.*, 2001; Prito *et al.*, 2001, but see Beer *et al.*, 2002). In the study of Peuskens *et al.* (2001) two visual motion sensitive areas were implicated in heading judgments: hMT+, including an adjacent area, and a dorsal intraparietal sulcus area, predominantly in the right hemisphere. This pattern is similar to that found for second-order motion activation in our study. Thus the parietal activations might indicate a functional specialization for second-order motion in optic flow analysis, a suggestion that has received recent psychophysical support (Gurnsey *et al.*, 1998; Dumoulin *et al.*, 2001).

## Notes

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