The constructive nature of vision: direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery

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Abstract
Echoplanar functional magnetic resonance imaging was used to monitor activation changes of brain areas while subjects viewed apparent motion stimuli and while they were engaged in motion imagery. Human cortical areas MT (V5) and MST were the first areas of the ‘dorsal’ processing stream which responded with a clear increase in signal intensity to apparent motion stimuli as compared with flickering control conditions. Apparent motion of figures defined by illusory contours evoked greater activation in V2 and MT/MST than appropriate control conditions. Several areas of the dorsal pathway (V3A, MT/MST, areas in the inferior and superior parietal lobule) as well as prefrontal areas including FEF and BA 9/46 responded strongly when subjects merely imagined moving stimuli which they had seen several seconds before. The activation during motion imagery increased with the synaptic distance of an area from V1 along the dorsal processing stream. Area MT/MST was selectively activated during motion imagery but not during a static imagery control condition. The comparison between the results obtained with objective motion, apparent motion and imagined motion provides further insights into a complex cortical network of motion-sensitive areas driven by bottom-up and top-down neural processes.

Introduction
Perceptual illusions and visual imagery are important paradigms for the experimental study of constructive aspects of vision and the generation of visual percepts that goes beyond the information contained in the mere physical composition of the stimuli (Zeki et al., 1993). Certain types of illusions arise when the physical properties of a stimulus are supplemented by perceptual features that rely on the assumptions of the brain about what it expects in the outside world. For example, when stimuli separated in space are turned on and off in alternation at appropriate temporal intervals (Kolers, 1972), subjects perceive one stimulus moving between the two stimulus positions (apparent motion) rather than two stationary flickering stimuli. Visual imagery, on the other hand, may be performed in the complete absence of visual stimuli. Thus, when a subject is requested to imagine a previously seen visual scene, the task usually consists in the construction of a visual image purely from stored information. In order to study constructive aspects of motion perception we reduced gradually the amount of objective motion perception and increased the amount of internally generated motion representations in a series of experiments using objectively moving stimuli, apparent motion stimuli, stimuli inducing apparent motion of figures defined by illusory contours and motion imagery conditions. Part of this work has previously appeared in abstract form (Goebel et al., 1996, 1997).

Previous brain imaging studies using either positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) have shown that human cortical areas MT (V5) and MST respond with increased activity to moving stimuli (Watson et al., 1993; Tootell et al., 1995b; McCarthy et al., 1995) and stationary stimuli inducing illusory motion (Zeki et al., 1993; Tootell et al., 1995a). We investigated to what extent apparent motion stimuli also activate the motion-selective areas MT and MST. As it is known that these areas respond to some degree to flickering stimuli (Tootell et al., 1995b), appropriate control conditions had to be specified which differ from the apparent motion stimuli only in the relative timing of appearing objects. Additionally, form–motion interactions were investigated by inducing apparent motion of squares whose outlines were defined by illusory contours. This paradigm integrates two perceptual illusions and should provide additional insight into the interaction of brain regions responsible for extracting different stimulus properties.

We further investigated whether the areas activated by apparent motion stimuli are also activated when moving stimuli are solely imagined. Previous brain imaging studies have shown that mental imagery activates some of the same brain regions as in visual perception (e.g. Kosslyn et al., 1995). It is, however, unclear whether small circumscribed extrastriate visual areas responsible for the analysis of specific stimulus properties can be selectively activated by imagery. We examined this issue for the motion-selective areas MT and MST by comparing their response patterns during imagery of moving stimuli with imagery of static stimuli.

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Materials and methods

Subjects

Ten subjects without a neurological or psychiatric history participated in this study. Their ages ranged from 25 to 32 years, and there were six males. Informed consent was obtained from each subject.

Experimental protocol

Visual stimuli were delivered under computer control (Digital DECpc Celebris XL, 590, Digital Equipment, Munich, Germany) to an LCD display panel (Sharp QA-1000, Sharp Corporation, Osaka, Japan) and a high-luminance overhead projector (Elmo HP-285P, ELMO Co., Ltd, Nagoya, Japan) in experiments 1–3 and to a high-luminance LCD projector (EIKI LC-6000, Eiki GmbH, Idstein, Germany) in experiment 4. Subjects were in a supine position and viewed the screen through an adjustable mirror fixed to the head coil. The image was back-projected on to a frosted screen positioned at the foot end of the scanner. Visual stimuli were generated in real time using the ELSA Winner 2000 ProX graphics adapter and the ELSA Powerlib C library.

Activation tasks

Each experiment consisted of 104–128 measurements, each sampling 10–15 oblique transversal slices running either approximately in parallel to the calcarine fissure (experiments 1–3) or approximately in parallel to the AC-PC line (experiments 3 and 4). Each experimental condition lasted 24 s. This allowed the acquisition of eight measurements per condition. In experiment 4, the initial and final fixation condition consisted of only four measurements. In all conditions a small fixation cross appeared in the centre of the screen. The fixation cross was the only stimulus present during fixation conditions and imagery conditions. Each experiment included an objective motion stimulus consisting of 400 white dots moving radially outward on a black background (visual field: 30° wide by 23° high, dot size: 0.06° × 0.06° dot velocity: 3.6–14.4°/s). This stimulus is known to produce a clear MT/MST response without provoking eye movements (Tootell et al., 1995b). Additionally, a static stimulus which consisted of 400 stationary dots was used in each experiment.

Apparent motion I

In the first experiment, perception of apparent motion was induced with two concentric rings (diameters: 3° and 10°) that appeared in parallel to the calcarine fissure (experiments 1–3) or approximately in parallel to the AC-PC line (experiments 3 and 4). Each experimental condition lasted 24 s. This allowed the acquisition of eight measurements per condition. In experiment 4, the initial and final fixation condition consisted of only four measurements. In all conditions a small fixation cross appeared in the centre of the screen. The fixation cross was the only stimulus present during fixation conditions and imagery conditions. Each experiment included an objective motion stimulus consisting of 400 white dots moving radially outward on a black background (visual field: 30° wide by 23° high, dot size: 0.06° × 0.06° dot velocity: 3.6–14.4°/s). This stimulus is known to produce a clear MT/MST response without provoking eye movements (Tootell et al., 1995b). Additionally, a static stimulus which consisted of 400 stationary dots was used in each experiment.

Apparent motion II

In the second experiment the stimuli used to generate the perception of apparent motion were squares whose outlines consisted of subjective contours (Kanizsa, 1979). These illusory squares were presented in alternation on the left and right side of the fixation spot (Fig. 3A). In order to generate the percept of an appearing and disappearing square the four ‘pacmen’ defining a square were opened and closed simultaneously so that observers (n = 7) saw either a Kanizsa square or four filled circles (diameter: 0.9°) at the respective location. Kanizsa squares were centred at an eccentricity of 4.5° and were 2.2° in length. In the control condition without motion cues the illusory Kanizsa squares appeared and disappeared simultaneously on both sides of the fixation cross whereas in the apparent motion condition they appeared and disappeared in alternation (Fig. 3A). Despite this change in relative timing across hemifields, stimulation conditions within each hemifield remained the same in both conditions. In the control condition subjects reported that they were seeing two squares appearing and disappearing in alternation while in the apparent motion condition they reported that they were seeing a single square moving between the two stimulus locations. In two additional no-contour control conditions the pacmen were opened outward and thus did not produce illusory squares (Fig. 3A). A sequence of 13 stimulation conditions was used consisting of fixation, objective motion, fixation, static, fixation, subjective-contour apparent motion, fixation, subjective-contour flickering control, fixation, no-contour apparent motion, fixation, no-contour flickering control, fixation.

Motion imagery I

In the third experiment we examined whether motion-sensitive areas are activated when subjects solely imagine moving stimuli. After subjects (n = 5) had seen one of three motion stimuli for 24 s (radially moving dots, apparent motion of subjective contours or rotating grating), they were required to fixate a cross for 24 s. This long interval was introduced in order for the haemodynamic response to return to baseline level before the start of the following imagery condition. After this fixation period, the fixation cross was turned off for 200 ms, which signalled to the subject that they should now try to imagine the previous motion stimulus as intensely as possible while fixating the cross. After 24 s, the cross was turned off again for 200 ms. This signalled to the subject the end of the imagery condition. Motion stimuli were the same as described above except the rotating grating (diameter: 16.7°, frequency: 15) which rotated with 170°/s. The experiment was repeated twice. Activity was measured in 12 slices approximately parallel to the calcarine fissure and in 15 axial slices with a transversal-to-coronal angle of 5–10° with respect to the AC-PC line. The sequence of 15 stimulation conditions consisted of fixation, static, fixation, motion I (radially moving dots), fixation, motion imagery I, fixation, motion II (subjective-contour apparent motion stimulus of experiment II), fixation, motion imagery II, fixation, motion III (rotating grating), fixation, motion imagery III, fixation. The sequence of stimulation conditions (triplets of motion–fixation–imagery) was randomized across subjects.

Motion imagery II

In the fourth experiment, imagery of moving stimuli was compared with the imagery of static stimuli. The experimental procedure was the same as in the previous experiment, except that either a static or a moving stimulus was shown prior to the respective imagery period. One static stimulus consisted of the standard static control condition (400 randomly positioned dots). A stationary frame of the subjective-contour apparent motion stimulus of experiment 2 was used as the second static stimulus. The dynamic versions of these stimuli (radially outward moving dots, subjective-contour apparent motion stimulus) were used in the two motion conditions. Activity was measured in

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15 slices approximately parallel to the calcarine fissure and in 15 axial slices with a transversal-to-coronal angle of 1–5° with respect to the AC-PC line. The sequence of 17 stimulation conditions consisted of fixation, static I (stationary dots), fixation, static imagery (SI) I, fixation, motion I (radially moving dots), fixation, motion imagery (MI) I, fixation, static II (stationary frame of subjective-contour apparent motion stimulus of experiment 2), fixation, static imagery II, fixation, motion II (subjective-contour apparent motion of experiment 2), fixation, motion imagery III, fixation. In the first and last fixation condition only four measurements were acquired resulting in 128 (15×8 + 2×4) measurements.

Eye movements
In order to verify whether subjects were able to fixate the cross during apparent motion and motion imagery conditions, the third experiment was performed outside the scanner monitoring eye movements with horizontal and vertical electro-oculograms.

Magnetic resonance imaging acquisition
Echoplanar images were collected on a 1.5-T scanner (Siemens Magnetom Vision, Siemens, Erlangen, Germany) using the standard head coil and a gradient echo echoplanar sequence (TR = 3000 ms, TE = 66 ms, flip angle = 90°, FOV = 210 mm × 210 mm, slice thickness = 3 mm, imaging matrix = 64 × 64, voxel size = 3.2 × 3.2 × 3 mm). In experiments 2–4 the Siemens Magnetom gradient overdrive was used allowing functional scans with high spatial resolution (TR = 3000 ms, TE = 69 ms, flip angle = 90°, FOV = 210 × 210 mm, slice thickness = 3 mm, imaging matrix = 128 × 128, voxel size = 1.6 × 1.6 × 3 mm). Before each set of functional scans in experiments 1 and 2, we recorded a T1-weighted series of images with the same orientation, slice thickness, and field of view as the functional scans. In experiments 3 and 4, a T1-weighted 3D MP RAGE scan lasting 8 min was recorded in the same session as the functional measurements. Additional T1-weighted 3D data sets tuned to optimize the contrast between grey vs. white matter were recorded for each subject in separate recording sessions lasting 24 min.

Data analysis
Data analysis, including preprocessing (motion correction, Gaussian spatial (FWHM = 3 pixel) and temporal (FWHM = 2 measurements) smoothing, linear trend removal), correlation analysis, determination of Talairach coordinates, volume rendering, surface rendering and cortex flattening was performed using custom software (BrainVoyager, Goebel, 1996, 1997) on a DEC Alpha 500 MHz Personal Workstation with the Windows NT 4.0 operating system. Statistical mapping, motion correction and Talairach transformation was cross-validated for three subjects using AFNI 96 (Cox, 1996) on a Pentium 166 MHz Gateway 2000 PC running the Linux 2.0 operating system. Prior to statistical analysis the time series of functional images was aligned for each slice in order to minimize the effects of head movement. For each slice the third recorded functional image was used as a reference image to which all other images of the slice time series were registered. In order to evaluate statistically the differences between experimental conditions cross-correlation analysis was applied. For the computation of correlation maps, the stimulation protocol served as the basis of appropriate reference functions reflecting experimental and control conditions (experimental condition = 1, control condition = 0). On a pixel-by-pixel basis the signal time course was cross-correlated with a reference function (Bandettini et al., 1993). Pixels were included into the statistical map if the obtained correlation value was greater than 0.4, given lag values of 1 and 2 (corresponding to a 3–9 s delay after the beginning of a stimulation condition in order to adapt to the haemodynamic response). Cross-correlation maps were superimposed both on the original functional scans as well as on to T1-weighted 2D or 3D anatomical reference scans.

The data for statistical comparisons consisted of the mean time course of all voxels of an analysed area. Based on this data the mean of the raw fMRI signal for each subject and condition in a given experiment was computed. These mean values were analysed using ANOVA and post hoc pairwise comparisons using stimulus condition as a within-group factor. The obtained P-values were corrected for multiple comparisons. Values of percentage signal change averaged across subjects were computed on the basis of the difference between the mean values of the fMRI signal in each experimental condition and the mean fMRI signal in the fixation periods for each individual subject.

Statistical maps were transformed into the high-resolution 3D data sets and interpolated to the same resolution (voxel size: 1.0 × 1.0 × 1.0 mm). For each subject the structural and functional 3D data sets were transformed into Talairach space (Talairach & Tournoux, 1988) which allowed us to compare activated brain regions across different experiments and across different subjects and to determine Talairach coordinates of these regions. Talairach transformation was performed in two steps. The first step consisted in rotating the 3D data set of each subject to be aligned with the stereotactic axes. For this step the location of the anterior commissure (AC) and the posterior commissure (PC) as well as two rotation parameters for mid-sagittal alignment had to be specified manually. In the second step the extreme points of the cerebrum were specified. These points together with the AC and PC coordinates were then used to scale the 3D data sets into the dimensions of the standard brain of the Talairach and Tournoux atlas using a piecewise affine and continuous transformation for each of the 12 defined subvolumes.

Striate and extrastriate cortical areas V1, V2, V3, VP, V3A and V4v were discriminated based on anatomical location and functional properties (Seren et al., 1995; Tootell et al., 1996; Van Essen & Drury, 1997). The delineation of these areas was validated for each subject using results from separate recordings for generating retinotopic maps (compare Engel et al., 1994; Sereno et al., 1995, DeYoe et al., 1996), sampling 12 contiguous slices approximately in parallel to the calcarine fissure (TR = 3000 ms, TE = 69 ms, flip angle = 90°, FOV = 200 mm × 200 mm, slice thickness = 3 mm, gap thickness = 0 mm, imaging matrix = 128 × 128, voxel size = 1.6 × 1.6 × 3 mm). Within the same recording session, an eccentricity mapping and a polar angle mapping experiment were performed. In the eccentricity mapping experiment, white and black checks flickering at 4 Hz formed into a ring-shaped configuration. The ring started with a radius of 1° and slowly expanded to a radius of 12° within 96 s. In the polar angle mapping experiment, flickering white and black checks formed into a ray-shaped configuration subtending 22.5° in polar angle. The ray started at the left horizontal meridian and slowly rotated clockwise for a full cycle of 360° within 96 s. Each mapping experiment consisted of four repetitions of a full expansion or rotation, respectively. Retinotopy of eccentricity and polar angle was revealed with cross-correlation analysis selecting the lag value resulting the highest correlation value for a particular voxel. The obtained lag value finally determined the pseudocolour for that voxel as well as for corresponding polygons on reconstructed surfaces (Fig. 1B,C). The recorded high resolution T1-weighted 3D recordings were used for surface reconstruction (Fig. 1A) of the posterior part of subjects’ brains including mainly the occipital lobe. The white
Fig. 1. Results of boundary determination of retinotopic cortical areas V1, V2, V3, VP, V3A and V4v of one subject. (A) Lateral view of the reconstructed surface of the posterior portion of the left hemisphere of the subject’s brain. The statistical map comparing the objective motion condition with the static condition is projected to the reconstructed surface revealing motion-selective areas including V3A, MT/MST as well as a region in the inferior parietal lobule (IPL). (B) Ventromedial view of the same surface after cortex ‘inflation’. The retinotopic eccentricity map is projected on to the reconstructed surface. Retinotopic responses are represented by using a pseudocolour scale. Responses ranging from central to peripheral stimulation are coded red through yellow through green through blue. Black lines show cuts 2.5 cm anterior to the occipital pole and roughly along the fundus of the calcarine sulcus. (C) Flattened visual cortex of the posterior part of the hemisphere. The polar angle map is projected on to the flattened surface representation. Responses to right upper visual field are coloured yellow (horizontal meridian) to red (vertical meridian), responses to right lower visual field are coloured blue (horizontal meridian) to green (vertical meridian). Area boundaries (white lines) are drawn at vertical and horizontal meridian representations. (D) The same statistical map as in (A) comparing objective motion condition and static condition projected to the cut and flattened cortex showing activity in areas V1, V2d and V3A.
matter within this region was segmented with a region-growing method. The surface reconstruction procedure started with a sphere (recursively tessellated icosahedron) which slowly wrapped around the segmented white matter. In order to avoid topological defects and to let the surface smoothly grow into deep sulci, we defined a dynamic mesh algorithm which automatically invents new polygons at places where the length of triangle edges is more than 1.2 times the average edge length. Within a typical surface reconstruction run, the mesh grows from initially 20 480 triangles to 60 000–80 000 triangles. The reconstructed white matter surface is finally expanded into the grey matter. In order to avoid cross-talk during sampling of functional data between both banks of a sulcus, the final surface (Fig. 1A) is, however, kept closer to the white matter border (below the estimated position of layer 4). Prior to surface flattening, the cortical surface was inflated and cut along the calcaine fissure and along a coronal slice = 3 cm anterior to the occipital pole (Fig. 1B). The surface was then slowly unfolded against a coronal plane at the occipital pole minimizing areal distortions. Based on the polar angle mapping experiment which includes stimulation of the horizontal and vertical meridian, the boundaries of retinotopic cortical areas V1, V2, V3, VP, V3A and V4v were defined on the cortical surface for each subject (Fig. 1C,D).

In order to delineate MT/MST as well as other motion-selective areas we defined regions that were significantly more strongly activated during the objective motion condition than during the static condition as regions of interest (Tootell et al., 1995b). In experiments 3 and 4, additional regions of interest (ROIs) were defined a posteriori by comparing all imagery conditions with the fixation conditions.

Results

Apparent motion I

Area V1 responded with largely similar activation levels to all stimulation conditions, the lowest activation being in both two ring conditions. In area V3A, the objective motion condition, the apparent motion condition and the flickering control evoked similarly large responses, but in contrast to V1 the stationary stimulus was significantly less effective ($P < 0.01$, Fig. 2B). Area MT/MST responded strongly to both the apparent and the objective motion stimulus but much less to both flickering control conditions ($P < 0.01$, Fig. 2B). The flickering control I condition produced a stronger MT/MST response than the flickering control II condition and was used for statistical comparisons. The results indicate that the MT/MST complex is the first area in the dorsal pathway that responds selectively to apparent motion. A response pattern very similar to that of MT/MST was found in the intraparietal sulcus.

Apparent motion II

Figure 3B shows that area V1 responded with similar activation levels to all subjective-contour and no-contour conditions. Area V2 but not
Fig. 3. Main experimental conditions and results of experiment 2. The sequence of stimulation conditions consisted of: fixation, objective motion, fixation, static, fixation, subjective-contour apparent motion (SCAM), fixation, subjective-contour flickering control (SCFC), fixation, no-contour apparent motion (NCAM), fixation, no-contour flickering control (NCFC). (A) In the subjective-contour conditions four circles or four ‘pacmen’ figures appeared on the left and the right side of the fixation cross. By showing the four ‘pacmen’ figures or the four filled circles observers saw either a Kanizsa square or four disks at the respective location. In the subjective-contour apparent motion condition the Kanizsa squares appeared in alternation on each side. In the subjective-contour flickering control the Kanizsa squares appeared and disappeared simultaneously. (B) Signal time course in cortical area MT/MST (top) and statistical comparison of activation levels in V1, V2, V3A and MT/MST (bottom) averaged over seven subjects. Mean per cent signal change ± SEM is displayed for each condition. (C) Location of area MT/MST of one subject. A correlation map (r = 0.3) was superimposed on a respective functional scan which was obtained with an EPI sequence with high spatial resolution (voxel size: 1.6 × 1.6 × 3 mm).

V1 and V3A responded significantly more strongly to the two conditions with illusory contours than to the respective control conditions with the outward turned pacmen (P < 0.01). The stimulus generating apparent motion of figures defined by subjective contours activated MT/MST more than the flickering squares (P < 0.01) and these in turn were more effective than the outward turned pacmen that did not define Kanizsa squares (P < 0.01). Unexpectedly, the difference between the apparent motion and the flickering control condition was smaller than in the first experiment, although the amount of stationary flicker was reduced in the second experiment.

Motion imagery I

All subjects reported that they were able to evoke mentally a clear motion experience during the imagery periods. At the same time they judged their mental image to contain less detail than the percept which was generated when they were seeing moving contours. As
expected, the same areas as in the previous experiments responded to the initial presentation of the objectively and apparently moving stimuli (Fig. 4A,B). However, most of these areas also showed a surprisingly high activation during all three conditions of motion imagery. Interestingly, the imagery specific activation (ISA) defined as the ratio (motion imagery–fixation)/(objective motion–fixation) increased with the synaptic distance of an area from V1 along the dorsal processing stream (Fig. 4B, Fig. 5A). Area MT/MST was activated approximately half as much in the imagery conditions as in the motion conditions (ISA = 0.6). A close inspection of the time course of signal changes at individual voxels revealed that the ISA was different within subparts of the MT/MST complex. During motion imagery the upper anterior part of MT/MST (presumed MST) was activated almost as strongly as during presentation of objective motion stimuli (ISA = 0.8) while the lower posterior part (presumed MT) showed less activation (ISA = 0.4). A weak but significant activation with motion imagery was also found in areas V2 and V3A ($P < 0.01$), but no significant modulation was detectable in the primary visual cortex. In addition to MT/MST several cortical areas in the inferior and superior parietal cortex were strongly and bilaterally activated during motion imagery (Figs 4B and 5A). Comparing all imagery conditions with all fixation conditions revealed further regions including the dorsolateral prefrontal cortex, mainly the Brodmann area (BA) 9/46, a region close to the junction of the precentral sulcus and the superior frontal gyrus (BA 6) corresponding according to Paus (1996) to the human frontal eye field (FEF), the anterior cingulate gyrus and the insular gyrus (Fig. 5B). Activation of BA 9/46 was found bilaterally but was higher in the right hemisphere ($P < 0.01$). Most of these higher areas were more strongly activated during motion imagery than during the objective and apparent motion conditions. Mean Talairach coordinates of the areas that showed consistent activity in all subjects are presented in Table 1.

**Motion imagery II**  
The results obtained during motion imagery resemble those of the preceding experiment. A weak but non-significant activation with motion imagery was found in area V1 (Fig. 6B). All other analysed areas were significantly activated during motion imagery ($P < 0.01$). Although several areas of the dorsal pathway were also activated during static imagery, the activation was much weaker than during motion imagery in most areas. Area MT/MST (Fig. 6A,B) shows no significant enhancement during static and static imagery conditions but a strong enhancement ($P < 0.01$) during motion and motion imagery conditions (ISA = 0.6). Additional regions activated during both static and motion imagery (not shown in Fig. 6) included several small areas in the intermediate and inferior frontal gyri, regions in the insular gyrus as well as the anterior cingulate gyrus. The latter responded with roughly equal strength to both types of imagery but showed no response to other stimulus conditions.

**Eye movements**  
In analysing the EOG records of the first motion imagery experiment, less than five eye movements of 1° or more per subject during all experimental conditions were detected.

**Discussion**  
The comparison between the results obtained with objective motion, apparent motion and imagined motion provides new insights into a complex cortical network of motion-sensitive areas driven by bottom-up and top-down neural processes. It has to be conceded that
Fig. 5. Topological distribution of responses from experiment 3 of one subject. (A) Areas with significant responses during motion and/or motion imagery conditions in a volume rendered view of left (left side) and right (right side) hemisphere. Areas are coloured with respect to a continuum reaching from responses to motion but not to motion imagery (red) to responses to motion imagery but not to motion (green). Intermediate colours depict areas which respond to both conditions (e.g. yellow). White lines with tick marks indicate the coordinate space of the Talairach and Tournoux stereotactic brain atlas. Short yellow lines on left side indicate vertical position of axial slices shown in (B). IPL = area in the inferior parietal lobule, SPL = area in the superior parietal lobule. (B) Selected axial slices as marked in (A) showing several areas with significant responses during motion and motion imagery. Right hemisphere is shown on the left and the left hemisphere is on the right. White lines indicate the coordinate space of the Talairach and Tournaux stereotactic brain atlas. Colouring as in (A). Axial slice 1 shows bilateral activation of area MT/MST (yellow), V2 (red) and V3/V3A (red/orange). Axial slice 2 shows activation foci in the insular gyri (green) which cannot be seen on lateral view. Axial slice 3 shows BA 9/46 (green) and V3A (orange).

Functional MRI provides an indirect measure of neuronal activity and that the interpretation of the metabolic signal with regard to cortical neuronal networks must be conducted in a very restrictive manner and concurrent evidence from other experimental approaches be sought. To this date, however, functional MRI is the method that allows the investigation of distributed areas in the human cerebral cortex that show task dependent coactivation at the highest spatial resolution.

**Activation by apparent motion stimuli**

Our results suggest that area MT/MST is the first cortical area along the dorsal stream that is capable of extracting apparent motion cues: In contrast to V1, V2 and V3A, its responses differed significantly between the apparent motion conditions and the respective flickering controls. Comparison of responses to illusory-contour and no-contour conditions suggests that area MT/MST is also capable of using illusory contour information for computing and representing apparent motion. Area V2 responded more strongly to the two illusory-contour conditions than to the two no-contour conditions suggesting that the illusory contour information is extracted at that level (von der Heydt et al., 1984; Hirsch et al., 1995; Ffytche & Zehi, 1996) and made available as input to area MT/MST.

In the second apparent motion experiment, the difference between the apparent motion and the flickering control condition was smaller.
TABLE 1. Talairach coordinates of areas V1, dorsal V2 (V2d) V3A, MT/MST, area in the inferior parietal lobule (IPL), area in the superior parietal lobule (SPL), frontal eye field (FEF) and area in Brodmann area 9/46 averaged over five subjects participating in all four experiments. SD = standard deviation [mm], L = left hemisphere, R = right hemisphere

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<th>Area</th>
<th>x (SD)</th>
<th>y (SD)</th>
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<td>–43.8 (7.9)</td>
<td>1.4 (4.7)</td>
<td>39.6 (4.7)</td>
<td>Superior part of precentral sulcus</td>
</tr>
<tr>
<td>R</td>
<td>43.6 (9.3)</td>
<td>2.6 (5.0)</td>
<td>40.8 (7.1)</td>
<td>Superior part of precentral sulcus</td>
</tr>
<tr>
<td>BA 9/46 L</td>
<td>–34.2 (5.2)</td>
<td>31.3 (11.4)</td>
<td>23.5 (7.9)</td>
<td>Intermediate frontal gyrus</td>
</tr>
<tr>
<td>R</td>
<td>38.0 (4.5)</td>
<td>26.8 (9.3)</td>
<td>29.8 (8.5)</td>
<td>Intermediate frontal gyrus</td>
</tr>
</tbody>
</table>

Our finding that V1 is not significantly active during imagery conditions is in agreement with several PET mental imagery studies (Roland & Gulyás, 1994; Mellet et al., 1996) but is in conflict with a recent PET study (Kosslyn et al., 1995) where significant activation of V1 was found when compared with a non-imagery listening control condition. In Kosslyn’s study, however, significant V1 activation was not detectable when compared with the resting baseline condition. Our results suggest that imagery related activation is much less pronounced in V1 than in the extrastriate areas V2 and V3A which were identified as significantly activated in our imagery experiments when matched against the visual fixation control condition.

The motion-sensitive MT/MST complex responded strongly when subjects merely imagined moving stimuli. As the MT/MST complex was selectively activated during motion imagery but not during static imagery, it is unlikely that the activated network of areas during imagery periods is merely the consequence of general activation related to vigilance.

Subjects reported that they were able to evoke mentally a clear motion experience during the imagery periods. At the same time they
judged their mental images to contain less detail when compared with seeing moving contours. One might speculate that these subjective reports reflect the lack of detectable V1 activity despite the strong activation of MT/MST during motion imagery and that the activation of area MT/MST during motion imagery mediates an experience of motion that is detached from figural details.

In addition to MT and MST, areas at higher levels of the dorsal pathway (Felleman & Van Essen, 1991) were strongly activated during motion imagery and during objective and apparent motion conditions. Although we have no information about the location of monkey areas VIP, LIP and 7a in humans, the activated regions in the inferior and superior parietal lobule could be the homologues of these areas. Like the activated region in the inferior parietal lobule (IPL, Fig. 4, Fig. 6), monkey area VIP responds to moving stimuli in a similar way as area MT (Colby et al., 1993). The activation of more dorsal parietal regions might be due to covert spatial attention shifts and spatial representations (see below), which would give them a similar function as monkey LIP (Goldberg et al., 1990) and 7a (Andersen et al., 1985). While dorsal pathway activity during motion imagery was most pronounced in the areas with the highest synaptic distance to V1, it showed the opposite behaviour during objective and apparent motion conditions. Furthermore, FEF and BA 9/46, regions which are known to be involved in spatial attention and visual short-term memory (Courtney et al., 1997) were almost exclusively activated during motion imagery. This pattern of activation suggests that attentional mechanisms involved in the generation and maintenance of the mental image generate a top-down information flow toward early visual areas (Sakai & Miyashita, 1994).

**Visuospatial mental operations and eye movements**

The strong activation of the higher areas of the dorsal pathway as well as the prefrontal areas FEF and BA 9/46 during imagined motion, might reflect processes of spatial attention and spatial working memory. In two recent PET studies of mental spatial exploration (Mellet et al., 1995) and spatial mental imagery generated from verbal instructions (Mellet et al., 1996), a similar bilateral occipitoparietal-frontal network was observed. It is unlikely that the strong activation of any of these areas is a direct consequence of eye movements. In PET studies of voluntary saccadic eye movements (Petit et al., 1993, 1996) activation at the cortical level was found in the precentral gyrus, the supplementary motor area, posterior parietal cortex, the right insula and left cingulate; a weak activation was also found in the right fusiform and lingual gyrus. As this activation pattern matches the results found during apparent motion and motion imagery only partially, we consider a strong contribution of eye movement related activity as unlikely.

In order to reduce the occurrence of eye movements, concentric rings were used as the apparent motion stimulus of the first experiment. In the motion imagery experiments the radially outward moving dot stimulus which probably did not provoke eye movements produced similar results as the apparent motion stimulus and the rotating grating. Experiment 3 was also replicated outside of the scanner in order to verify that subjects were able to fixate the cross during apparent motion and motion imagery.

From electrophysiological and brain imaging studies it is known that all of the activated higher areas of the dorsal pathway can become active in the absence of eye movements. Cells in the primate posterior parietal cortex are able to maintain activity about inferred moving stimuli in the absence of either sensory input or motor output (Assad & Maunsell, 1995). Areas in the superior parietal lobule (SPL) are activated in mental rotation tasks (Cohen et al., 1996) and in tasks which require imagined information about spatial relations in extrapersonal space (Decety et al., 1992) as well as covert spatial attention (Corbetta et al., 1995). Likewise, the FEF is activated when attention is directed towards remembered loci in extrapersonal space (Roland & Skinhøj, 1981) and it has been suggested that the FEF ‘keeps track of visuospatial information over time’ (Raichle, 1989). In the macaque monkey, the FEF is interconnected with the posterior part of the parietal lobe, especially the cortex in the intraparietal sulcus (IPS) which suggests functional coupling of these areas. This is supported by the presented results that the FEF and areas in the inferior and superior parietal lobe are coactivated during motion imagery. Small regions in the dorsolateral prefrontal cortex including BA 9/46 were strongly activated during motion imagery and to a lesser degree during objective motion, and this activation was consistently lateralized to the right hemisphere (Fig. 5). Such a lateralization of BA 9/46 activation to the right hemisphere was also found in association with a spatial working memory task (McCarthy et al., 1994). The activation of the anterior cingulate gyrus might be a correlate of a non-spatial, task-orientated attentional process (Posner & Petersen, 1990) as it was very marked during all mental imagery conditions but almost absent during all other stimulus conditions.

The described network of activated areas indicates that subjects engaged in processes of spatial attention and spatial working memory during motion imagery. The finding that areas of the dorsal processing stream as early as MT/MST are activated by the apparent motion of illusory contours and even by motion imagery nearly as strongly as by real, normally moving contours is an impressive demonstration of the constructive nature of visual processing. Moreover, it implies that these synthetic operations involve the same specialized areas that are held responsible for the analysis of real motion.

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**References**


Nature, 369, 525.
Cereb. Cortex, 1, 1–47.
NeuroImage, 3, 104–108.
NeuroImage, 3, S604.
NeuroImage, 5, S635.
NeuroImage, 3, S274.
NeuroImage, 5, S130.
Cold Spring Harbor Symposium on Quantitative Biology, LV, 729–739.
Science, 224, 1260–1262.
Neuropsychologia, 34, 475–483.
Trends Neurosci., 17, 281–287.
Brain Res., 222, 166–171.
Trends Neurosci., 17, 287–289.
Science, 268, 889–893.
Nature, 375, 139–141.
Trends Neurosci., 19, 481–489.
J. Neurosci., 17, 7079–7102.