Motion Standstill Leads to Activation of Inferior Parietal Lobe

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Abstract: Previous studies on motion perception revealed motion-processing brain areas sensitive to changes in luminance and texture (low-level) and changes in salience (high-level). The present functional magnetic resonance imaging (fMRI) study focused on motion standstill. This phenomenon, occurring at fast presentation frequencies of visual moving objects that are perceived as static, has not been previously explored by neuroimaging techniques. Thirteen subjects were investigated while perceiving apparent motion at 4 Hz, at 30 Hz (motion standstill), isoluminant static and flickering stimuli, fixation cross, and blank screen, presented randomly and balanced for rapid event-related fMRI design. Blood oxygenation level-dependent (BOLD) signal in the occipito-temporal brain region MT/V5 increased during apparent motion perception. Here we could demonstrate that brain areas like the posterior part of the right inferior parietal lobule (IPL) demonstrated higher BOLD-signal during motion standstill. These findings suggest that the activation of higher-order motion areas is elicited by apparent motion at high presentation rates (motion standstill). We interpret this observation as a manifestation of an orienting reaction in IPL towards stimulus motion that might be detected but not resolved by other motion-processing areas (i.e., MT/V5). *Hum Brain Mapp* 27:340–349, 2006.

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INTRODUCTION

The ability to perceive objects in motion, regardless of whether the motion is real or illusory, is one of the major properties shown by the human brain in daily life. “Motion standstill” is a phenomenon, first described by Julesz and Payne [1968], which occurs when motion is so fast that the moving visual stimuli are perceived as static. Previous studies have attempted to explore the mechanism of the perception of this motion illusion. Results from psychophysical visual investigations with isoluminant chromatic motion stimuli and rotating luminance gratings suggest a distinction between three different-motion processing mechanisms [Cavanagh 1992; Lu et al., 1999a; Lu and Sperling 2001]: (1)

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luminance-based process (motion process responsive to moving luminance patterns); (2) a feature-based process (motion process responsive to moving modulations of feature type); and (3) a salience-based mechanism. The low-level visual processing includes luminance- and feature-based motion. A higher-level, salience-based mechanism allows the processing of visual stimuli by computing a neural representation of visual space even when no substantial difference in luminance exists.

Brain imaging studies revealed several motion-sensitive areas: recent functional magnetic resonance imaging (fMRI) studies identified as motion-sensitive areas the so-called "human motion complex" (or middle temporal complex, MT/V5) [Zeki et al., 1991], the extrastriate visual area V3A [Tootell et al., 1995; Tootell and Taylor 1995], the superior temporal sulcus (STS) [Noguchi et al., 2005; Sunaert et al., 1999], and the intraparietal sulci (IPS) [Bremmer et al., 2001; Corbetta and Shulman 2002]. In particular, activation in MT/V5 has been reported to be induced even by a simple movement of a dot pattern when the load on attention for performing a relevant linguistic task was low [Rees et al., 1997]. This finding suggests that all these areas might be responsible for a low-level motion perception.

Other fMRI studies, dealing with illusory movement, revealed that the MT/V5 constituted an optimal candidate region for conscious perception of both real and illusory motion [Seghier et al., 2000; Tootell et al., 1995; Zeki et al., 1991, 1993]. However, recent brain imaging studies cast some doubt on a possible specific role of MT/V5 areas in motion detection. For example, Orban et al. [1998] proposed that lingual and cuneal regions are sensitive to real motion, whereas MT/V5, as reported also in other studies [Chawla et al., 1998; Sunaert et al., 2000], could be merely involved in motion speed discrimination. In conclusion, a definitive model about the role of MT/V5 as a motion- and/or speed-sensitive brain region has not been achieved yet and its supposed specificity for human motion perception is still controversial.

Furthermore, several studies have indicated that MT/V5 cannot be regarded as a "stand-alone" motion perceptive area, since the perception of moving objects seems to involve both low-level and high-level brain areas sensitive to motion. Recently, it was shown that activation in the temporoparietal junction (TPJ), including the inferior parietal lobe (IPL), is evoked by salient stimuli and during the detection of low-frequency stimuli at an attended location [Kirino et al., 2000]. The issue of the representation of motion perception has been more specifically addressed in a recent fMRI study [Claeys et al., 2003] in which the authors proposed that high-level motion processing engages the IPL. The authors reported activation of IPL for isoluminant color grating motion and for apparent motion with a temporal frequency of 7 Hz. However, IPL did not respond to 2-Hz apparent motion. Motion processing in IPL might therefore be driven by both salience-based and luminance-based apparent motion. Furthermore, the authors reported an activation due to lower-level, luminance-based features in the

traditional motion-sensitive regions (i.e., MT/V5, V3a, STS). This suggests that salience, as well as presentation rate, exert some influence on the activation of higher-order motion brain areas.

An increase of the presentation rate, far above the frequency used in the study by Claeys et al. [2003], leads to the above-described phenomenon called motion standstill. So far, motion standstill has been investigated using chromatic display [Lu et al., 1999a,b]. The authors suggested that the isoluminant color motion was only perceived by a salience-based motion system. In the present study we used only black and white stimuli to produce the effect of motion standstill. To our knowledge, it is the first investigation of the phenomenon of motion standstill with fMRI. The goal was twofold: clarifying whether motion standstill is processed in traditional motion-processing areas only (i.e., MT/V5, V3A, STS, IPS) or if additional brain areas are also involved in this process. Furthermore, we addressed the question of whether motion standstill differs from simple perception of flicker. These issues were investigated with the fMRI method, which offers good spatial resolution.

SUBJECTS AND METHODS

Subjects

Thirteen volunteers (8 women, 5 men) participated in the first experiment. Age (mean $\pm$ SD) was 29.7 ± 4.6 years. All were staff members or students at the Karolinska Institutet of Stockholm (Sweden). All subjects were right-handed, as assessed by the Edinburgh Inventory [Oldfield, 1971]. Vision was normal or corrected-to-normal in all subjects, and none had a history of major medical, neurological, or psychiatric diseases, nor did they receive psychotropic medication, as ascertained by a 1-hour nonstructured clinical interview. All participants had normal structural MRI, as confirmed by the evaluation of an expert radiologist (M.K.W.). The study was approved by the local ethical committee and written informed consent was obtained from all subjects.

An additional four subjects (3 females, ages 27.4, 27.11, and 23.8 years, and 1 male, age 33.1 years) were investigated in a second fMRI experiment.

Experimental Paradigm

A schematic view of the stimulation paradigm is shown in Figure 1. The first experiment consisted of the visual presentation against a black background of nine white dots ($\varnothing$ 0.9°) arranged in a circle with a radius of 10°. The dots were alternating in position by a 20° shift. The alternation rate of these 9 dots was set either to 4 Hz (resulting in the perception of nine apparently moving dots: "slow motion"), or to 30 Hz (resulting in the perception of eighteen static dots: "motion standstill"). Additionally, four types of control stimuli were presented: static 9 dots (corresponding, in terms of luminance and visual information delivered to the subject, to the "slow motion") and static 18 dots (corresponding to the "motion standstill"), blank screen, and fix-

ation cross. Stimuli were presented to the subjects by a goggle system (VisuaStim XGA; Resonance Technology, Northridge, CA). The parameters of this system were: field of view = 30°, refresh rate = 60 Hz, resolution = 1024 × 768. The alternation rate of 30 Hz was measured with photodiodes directly placed in front of the goggle system and linked to a digital storage oscilloscope. Stimuli were presented for 3,000 ms, followed by a blank screen (interstimulus interval: 3,000 ms). Each stimulus category was presented 40 times: the resulting 240 stimuli were randomized and the stimulus categories were balanced. Subjects were asked to give a motor response by pressing a button with the right index finger whenever they perceived either the impression of a “motion standstill” or a “slow motion” pattern. Response times and omission rate to each stimulus was recorded by an MRI-compatible optical keypress device which was interfaced to an external personal computer running the experimental paradigm outside the scanner room.

A second experiment was conducted with the same stimulation paradigm as described above but with different control stimuli. Here the 4 Hz “slow motion” category was contrasted with 9 dots presented at a flicker frequency of 4 Hz. The 30 Hz “motion standstill” category was contrasted with 9 dots flickering at 30 Hz (the isoluminant control category) and by 18 dots flickering at 30 Hz (a control category with two times higher luminance). Stimulus display time, interstimulus interval, total number of stimuli, and number of stimuli for each category were unchanged.

fMRI Acquisition

All images were acquired using a 1.5 T whole-body MRI system (Siemens Vision, Erlangen, Germany) equipped with a standard RF head coil. Head motion was minimized within the coil using a vacuum deflatable pillow and an open-cell polyurethane foam. The fMRI session included the acquisition of a set of 3-D T_1 -weighted (magnetization prepared rapid acquisition gradient echo, MP-RAGE) images, providing 170 sagittal slices with 1.0 mm thickness, 256 × 256 mm field of view (FOV), and a matrix size of 256 × 256. Further scan parameters were: 11.4 ms repetition time

Figure 1.

Visual stimuli presented. **A:** Nine white dots ($\varnothing$ 0.9°) arranged in a circle with radius of 10° on black background. Dots were alternating in position by a 20° shift. Illusionary stimuli used in the first and second experiments originated by an alternation rate of the 9 dots corresponding to 4 Hz (the illusionary perception is “slow motion”), or to 30 Hz (the illusionary perception is that of 18 dots “motion standstill”). **B:** Control categories in the first experiment were 9 static dots and 18 static dots. **C:** Control categories in the second experiment were 9 dots presented at flicker frequency of 4 Hz and 18 dots flickering at 30 Hz. Not shown in this schematic view are two categories that are displayed in each experiment: blank screen and fixation cross. Each stimulus category was presented 40 times: the resulting 240 stimuli were randomized and the stimulus categories were balanced.

(TR), 4.4 ms echo time (TE), and a flip angle of 15° (FA). Functional images were acquired using a multislice single-shot T_2^* -weighted echo planar imaging sequence, with 16 interleaved axial oblique slices, positioned in-line with the bicommissural axis; 720 dynamic scans were collected in each subject (TR = 2,000 ms, TE = 40 ms, FA = 90°, slice thickness = 4 mm, gap thickness = 1 mm, matrix size = 64 × 64, FOV = 240 × 240 mm).

fMRI Analysis

Analysis of the fMRI data was performed using BrainVoyager 4.9 (Brain Innovation, Maastricht, The Netherlands). Preprocessing of the images included the removal of low-frequency drifts, 3-D motion detection and correction, and spatial smoothing with 4 mm FWHM. Coregistration of the 2-D functional to the 3-D structural images was performed using the scanner's slice position parameters of the T_2^* -weighted measurements and the T_1 -weighted anatomical measurements. Spatial resolution of the functional dataset was interpolated to isovoxel 1 mm³. Finally, the anatomical and functional datasets were transformed into the normalized Talairach space [Talairach and Tournoux, 1988].

All voxels with t -test value > 7.6 were defined as regions of interest (ROIs). The reconstruction of the hemodynamic response function within these ROIs was performed using a general linear model (GLM) to estimate the finite impulse response (FIR) associated with each stimulus category. For each stimulus type the convolution of the discrete time points with the event sequence was built (i.e., a "1" was placed in the row corresponding to the time at which each image was acquired and in the column corresponding to the appropriate point of the hemodynamic response). For the extraction of the event-related responses we used 10 FIR time bins (with TR = 2 s; this corresponds to the time interval 0–20 s after stimulus onset). The hemodynamic response function can substantially vary between subjects [Aguirre et al., 1998], and therefore we decided to define the peak values of the event-related response in each individual and for each stimulus, a method repeatedly used in previous fMRI studies [Huk et al., 2001; Noguchi et al., 2005]. Peak values of the event-related data were chosen as the average of the three highest consecutive values in the BOLD event-related data for each subject and for each category in the statistical analysis [Lehmann et al., 2004].

In addition to the conventional normalization of individual functional time series in the standard Talairach space, an improved correspondence of cortical regions across subjects was obtained by using a cortex-based intersubject alignment [Fischl et al., 1999].

Statistical Analysis

An analysis of variance (ANOVA) with subjects as the random factor and category as fixed factor was calculated. Furthermore, an ANOVA for repeated measures was performed with the average of three highest BOLD peak values of the corresponding hemodynamic response function in order to test the effect of stimulus for each resulting brain

area (factor category). Post-hoc pairwise comparison was performed using Scheffe's tests. The software system Statistica v. 6 (StatSoft, Tulsa, OK, 2001) was used.

RESULTS

Test Performance

The mean ($\pm$ SD) motor reaction time for the perception of slow motion was 512.1 ($\pm$ 281.5) ms and for the perception of motion standstill was 528.1 ($\pm$ 254.6) ms (this difference in reaction time was not statistically significant). Subjects responded to 4 Hz and 30 Hz but not to the flicker control conditions. Due to the simple nature of the task the subjects responded to all presented stimuli and there were no significant differences between omission rates for the two stimulus categories in which a button press was required.

fMRI Results

The ANOVA with subjects as the random factor showed significant category effect ($F_{(4,48)} = 38.44$; $P < 0.0001$). The GLM analysis showed that the contrast between apparent motion stimuli and static stimuli categories vs. the fixation category yielded a significant activation in the early visual areas (calcarine cortex), as illustrated in Figure 2A. The Talairach coordinates corresponding to the center of gravity for each identified ROI and the results of the repeated measure ANOVA for within-subject effects, as well as the average and SDs of the three highest peak values, time parameters, and maximum peak values for each category are summarized in Table I. The comparison between apparent motion and static stimuli revealed activation of the right and left MT/V5, as depicted in Figure 2B. The contrast between slow motion and static 9 dots stimulus categories, as illustrated in Figure 2C, yielded significant activation of the right MT/V5. Finally, a comparison between motion standstill with static 18 dots stimulus categories yielded significant activation of the left MT/V5, left inferior frontal gyrus (IFG) corresponding to BA 45, right IFG corresponding to BA 44, and bilateral IPL corresponding to BA 40, as illustrated in Figure 2D.

The averaged event-related responses for early visual area are shown in Figure 3 and were obtained from the region displayed in Figure 2A. The averaged event-related responses for all other identified regions are shown in Figure 4a–f.

The results of the post-hoc pairwise comparison are summarized in Table II. The post-hoc comparison between motion standstill and slow motion revealed a statistical tendency to significance ($t_{(1,12)} = 3.3$; $P < 0.06$) only for the right IPL (r-IPL posterior).

BOLD responses, as depicted in Figure 4, are higher for the apparent motion stimulus category rather than for static stimuli. Generally, the right and left MT/V5 regions appeared to be more involved in the processing of slow motion than for motion standstill stimuli. In contrast, the right IPL region (r-IPL posterior) appeared more active for motion

Figure 2.

Group GLM contrast analysis detects regions in which: **(A)** activity is higher during perception of visual stimuli than during fixation cross. Activation in the human early visual areas (Talairach coordinates: 7-85 0); **(B)** activity is higher during perception of illusionary stimuli (both motion standstill and slow motion) than during “static” stimulation. Activation is observed bilaterally in human motion complex MT/V5; **(C)** activity is higher during the perception of slow motion stimulus (4 Hz) as compared to static 9 dots stimulus in right human motion complex MT/V5; **(D)** activity is higher during the perception of motion standstill stimulus (30 Hz) as compared to static 18 dots stimulus. These regions corresponds to left MT/V5, left BA45 (gyrus frontalis inferior), right BA 44 (gyrus frontalis inferior), and bilaterally in the posterior part of BA 40 (inferior parietal lobe; gyrus supramarginal). Right top corner: color scale represents values of *t*-test; significance level indicated ($P(\text{corrected}) < 0.00001$).

standstill than for slow motion stimuli. In all identified regions but early visual areas the activation for “static 9 dots” was higher than for “static 18 dots” stimuli but the difference was not statistically significant.

Figure 3.

BOLD signal time course in cortical early visual areas averaged over 13 subjects. The region is shown in Figure 2A.

The cortex-based intersubject alignment revealed a second region in right IPL (Talairach coordinates: $x = 60$, $y = -31$, $z = 32$; *t*-value: 5.5; $P < 0.0001$) for the contrast between motion standstill and slow motion (r-IPL anterior). However, no significant differences were obtained for the contrast between motion standstill and static 18 dots. Instead, using the contrast between motion standstill stimulus as compared to all other categories, there was also significant activation in the anterior cingulum cortex (ACC) (Talairach coordinates: $x = 1$, $y = 23$, $z = 29$; *t*-value: 4.0; $P < 0.0001$).

The results of the second experiment are shown in Figure 5. In right IPL (r-IPL posterior) the highest activation was observed by motion standstill. Activation due to slow motion and due to the flickering control categories was lower. Activation of early visual areas, bilateral MT/V5, and r-IPL posterior due to motion standstill and slow motion are comparable to the results of the first experiment. No statistical differences were observed in the ACC (*t*-value: 0.96; $P = \text{n.s.}$) for the comparison between motion standstill and flickering control categories.

Finally, we pooled the fMRI data and compared the BOLD signals that contained the motion response with the BOLD signals without motor response. For the comparison be-

TABLE I. Summary of identified brain regions with Talairach coordinates, repeated-measures ANOVA for categories, mean of the three highest peak values of BOLD response, time parameters, and maximum peak values

Brain area	Talairach coordinate for center of gravity (x, y, z)	Repeated measures ANOVA		Stimulus categories	Three highest peak values (mean $\pm$ SD)	Average peak value at lag (s)	Maximum peak value
		F(3,48)	P				
Early visual areas	7, -85, 0	0.36	n.s.	Motion standstill	0.677 $\pm$ 0.221	5.5	0.855
				Slow motion	0.732 $\pm$ 0.193	5.8	0.899
				Static 18 dots	0.795 $\pm$ 0.192	5.5	0.97
				Static 9 dots	0.672 $\pm$ 0.164	5.4	0.814
MT/V5 right	45, -69, 0	6.74	<0.001	fixation cross	0.063 $\pm$ 0.118	6.5	0.168
				Motion standstill	0.457 $\pm$ 0.146	5.2	0.592
				Slow motion	0.586 $\pm$ 0.175	5.5	0.732
				Static 18 dots	0.094 $\pm$ 0.149	6	0.237
MT/V5 left	-47, -69, 0	7.82	<0.0001	Static 9 dots	0.256 $\pm$ 0.155	6	0.393
				Motion standstill	0.526 $\pm$ 0.187	5.5	0.693
				Slow motion	0.612 $\pm$ 0.205	5.1	0.806
				Static 18 dots	0.152 $\pm$ 0.127	5.5	0.273
IPL right posterior	39, -55, 33	3.31	<0.028	Static 9 dots	0.379 $\pm$ 0.144	5.2	0.506
				Motion standstill	0.391 $\pm$ 0.149	5.8	0.518
				Slow motion	0.277 $\pm$ 0.152	5.8	0.413
				Static 18 dots	0.164 $\pm$ 0.165	6.2	0.32
IPL left posterior	-35, -56, 33	2.30	n.s.	Static 9 dots	0.319 $\pm$ 0.125	6.3	0.433
				Motion standstill	0.163 $\pm$ 0.133	5.8	0.288
				Slow motion	0.096 $\pm$ 0.144	5.5	0.225
				Static 18 dots	-0.01 $\pm$ 0.114	6.5	0.075
IFG right	43, 3, 29	1.83	n.s.	Static 9 dots	0.172 $\pm$ 0.125	5.5	0.267
				Motion standstill	0.342 $\pm$ 0.181	5.5	0.51
				Slow motion	0.237 $\pm$ 0.167	5.5	0.402
				Static 18 dots	0.114 $\pm$ 0.169	5.2	0.264
IFG left	-48, 32, 8	5.64	<0.002	Static 9 dots	0.288 $\pm$ 0.167	4.9	0.443
				Motion standstill	0.142 $\pm$ 0.118	6.2	0.236
				Slow motion	0.032 $\pm$ 0.15	5.2	0.158
				Static 18 dots	-0.076 $\pm$ 0.153	5.7	0.022
				Static 9 dots	0.074 $\pm$ 0.124	6.2	0.178

All values are listed for illusory stimulus categories and for their corresponding control stimuli.

tween response vs. nonresponse we found no significant differences within r-IPL anterior (t -test value = -1.3726; P = 0.3331) and within r-IPL posterior (t -test value = -0.0245; P = 0.5981).

DISCUSSION

Here we demonstrate that the perception of motion involves several distinct brain areas, as depicted in our BOLD responses. We found activation of the right IPL (r-IPL posterior) specific for motion standstill. Additionally, unilateral activation of the right IFG (BA 44), left IFG (BA 45), and ACC was observed for the contrast between motion standstill and static 18 dots stimuli. As expected according to previous studies, we found a bilateral MT/V5 activation. Furthermore, a higher-order motion area located in the right IPL (r-IPL anterior) was activated by motion [Claeys et al., 2003]. In the second experiment with flickering control stimuli the findings for the regions right IPL (r-IPL posterior) and bilateral MT/V5 and specific for motion standstill were reproduced.

Activation of MT/V5

Although no standard mapping procedure to identify MT/V5 was used in the present study, the Talairach coordinates of MT/V5 match those reported in the literature [Goebel et al., 1998]. An involvement of MT/V5 regions has been reported for the detection of real motion [Dukelow et al., 2001], illusory motion [Tootell et al., 1995; Zeki et al., 1993], apparent motion [Goebel et al., 1998; Kaneoke et al., 1997; Muckli et al., 2002], imagined motion [Goebel et al., 1998], as well as “implied” motion (i.e., a still image of a moving object, conveying dynamic information about the object’s position) [Kourtzi and Kanwisher, 2000], clearly indicating an important role of this brain area in illusory motion perception.

We observed that human MT/V5 was involved in the processing of apparent motion, showing different responses depending on the frequency of the presented stimuli. In fact, we observed higher activation in MT/V5 for slow apparent motion as compared to motion standstill. This finding is in line with previous studies [Huk et al., 2001; Sunaert et al.,

Figure 4.

BOLD signal time course in cortical areas obtained as contrast between illusory stimuli and “static” stimulation (a,b), and as contrast between motion standstill stimulus (30 Hz) and static 18 dots stimulus (c–f). Vertical scale: averaged percentage signal change; horizontal scale: stimulus onset time in seconds. Legends as well as scales are equal in all plots and only shown in a.

2000] and especially with the inverted “U” dependency of MT/V5 on speed reported by Chawla et al. [1998]. They used dots moving at constant speed (the velocities used are

well below the velocities used in our study for motion standstill), radially from the center of the screen, as stimulus material to demonstrate the dependency on speed of MT/V5

TABLE II. Summary of post-hoc pairwise comparison between categories performed using Scheffe’s tests within the identified brain regions with Talairach coordinates for center of gravity

Brain area	Talairach coordinate for center of gravity (x, y, z)	Motion standstill vs. static 18-dot stimuli		Slow motion vs. static 9-dot stimuli	
		t(1,12)	P	t(1,12)	P
MT/V5 right	45, -69, 0	8.9	<0.0001	3.9; p	<0.0001
MT/V5 left	-47, -69, 0	4.7	<0.0001	4.3	<0.0001
IPL right posterior	39, -55, 33	3.3	<0.006	0.4;	n.s.
IPL left posterior	-35, -56, 33	5.3	<0.0001	0.7;	n.s.
IFG right	43, 3, 29	5.2; p	<0.0002	0.9;	n.s.
IFG left	-48, 32, 8	1.5;	n.s.	3.5	<0.004

Figure 5.

Second experiment: BOLD peak values (with standard deviation) for illusionary motion stimuli (motion standstill (black bars) and slow motion (dark gray bars) and for control stimuli (18 dots presented at flicker frequency of 30 Hz (white bars) and 9 dots presented at flicker frequency of 4 Hz (light gray bars)). Vertical scale: averaged percentage signal change; horizontal scale: brain regions right IPL posterior, MT/V5 right and left and early visual areas.

and V3a activation. This result was obtained in a whole brain fMRI measurement and was subsequently replicated by the same group [Chawla et al., 1999].

It has been reported that motion standstill can occur when the spatiotemporal resolution of the shape and color systems exceeds that of the motion system: at higher presentation frequencies (>8 Hz) the motion system for this salience-based stimulus breaks down [Lu et al., 1999a]. In our study, the effect of motion standstill was produced with high alternation frequency of nine white dots displaced by 20° (velocity above 100° visual angle/s). Is it possible that motion standstill can also occur with luminance-based objects when the temporal resolution of the physical stimulus exceeds the resolution of the motion systems in MT/V5? In this case, motion standstill would be the result of a speed effect of the first-order luminance-based apparent motion.

The response in MT/V5 for real and apparent motion is similar as long as the speed of the apparent motion does not exceed the temporal resolution of the human visual system. The upper limit for temporal resolution has been reported to be in the 4–8 Hz range [Verstraten et al., 2000]. Above this rate, perception of the sequence of changes in the positions of dots is no longer possible. In the present experiment the motion standstill stimulus clearly differs from the static 18 dots stimulus in terms of physical properties. However, both stimuli are perceived as 18 dots. In fact, all the subjects could distinguish between both types of stimuli. This is also reflected by the observed BOLD response in MT/V5, which was found to be more pronounced for the motion standstill stimulus, indicating that the process of motion analysis had already started.

However, in MT/V5 we also observed significant differences in the control categories between 9 dots and 18 dots (both experiments, static and flicker). Surprisingly, the magnitude of BOLD signal for the 9 dot control stimuli in MT/V5 exceeded the magnitude of the 18 dots control stimuli. This phenomenon is contrary to the activation in early

visual areas, which shows stronger activation in the 18 dots control category. The results in early visual areas can be attributed to luminance effects. Baseline problems could explain this discrepancy, although the averaged time course in the early visual region shows a clear distinction between fixation cross and all other stimulus categories. An alternative explanation could be an “expectancy of movement” for the 9 dot control stimuli. In fact, for the first 250 ms the two categories (slow motion and 9 dot control stimuli) are identical. Since the first 9 dot stimuli presented to the subjects are moving, an anticipation of motion may be evoked during the 9 dot control stimuli. On the contrary, based on the presented stimuli, the 18 dot control stimuli are not expected to move.

If this explanation for the control stimuli holds, then the differences between motion standstill and slow motion in MT/V5 might originate from a presentation frequency which exceeds the temporal resolution of MT/V5. In this case, the motion stimuli that cannot be allocated to a clear direction in space may provoke a pronounced shift of attention in order to achieve a consistent explanation. At the time we are not aware of other explanations for the surprising effect of the control stimuli in MT/V5. Future investigations with an appropriate design will have to provide further insights.

Activation of the Anterior Part of the Right IPL (r-IPL Anterior)

In addition to the activations in MT/V5, we observed activation in the right IPL region for the motion stimuli. Activation in this region due to slow motion and due to the control stimuli (both experiments, static and flicker) was lower. The involvement of this region in motion processing has been described once before by Claeys et al. [2003], who characterized IPL as a potential higher-order motion region.

In their study, right IPL responded to isoluminance color gratings stimuli when the saliency of one color was increased. IPL also responded to apparent motion stimulation at a 7 Hz rate, but not at a 2-Hz rate. This finding is in line with our observation that the 30-Hz stimulus (but not the 4-Hz stimulus) evokes a response in the IPL, although the frequencies used in both studies substantially differ. A direct comparison is hence difficult.

Activation of the Posterior Part of the Right IPL (r-IPL Posterior)

In the posterior part of the right IPL we observed activation by motion standstill only. Presently, we are not aware of other studies showing activation of the r-IPL posterior originated by motion. Generally, the IPL region is known to show activations in multiple paradigms in all sensory modalities. Downar et al. [2000] recently reported that temporoparietal junction (including IPL) was also activated when visual and other sensory stimuli were suddenly changed; this finding was interpreted as a consequence of a reorienting attention-demanding task. In our study the activation of the r-IPL posterior was only present for the motion standstill stimulus. Other contrasts, including the reorientation of attention (i.e., slow motion vs. fixation cross), did not evoke an activation in the r-IPL posterior. Therefore, reorientation of attention to a sudden change in stimulation alone cannot fully explain activation in the r-IPL posterior. Nonetheless, modulation of the r-IPL posterior by visual attention cannot be ruled out. It seems reasonable to hypothesize that the activation in this area could be due to a special kind of arousal. This view is supported by the observed activation in right IFG (BA 44), left IFG (BA 45), and ACC also only by motion standstill. Taken together, by motion standstill we observed activation of a typical attention network [see Corbetta and Shulman, 2002, for a detailed review] (r-IPL posterior [BA 40], ACC, right IFG [BA 44] and left IFG [BA 45]). Furthermore, this network is also activated by visual [Kirino et al., 2000; Linden et al., 1999] and acoustic [Horn et al., 2003] target detection paradigms. Therefore, the r-IPL posterior can be regarded as a multimodal area, an area activated together with the anterior attentional network by orienting reaction towards unresolved or target stimuli.

In conclusion, our study confirms the previously reported activation of lower-order motion region MT/V5 in an apparent motion paradigm [Goebel et al., 1998; Muckli et al., 2002; Tootell et al., 1995; Zeki et al., 1993]. In line with the reported speed-dependency of these regions [Chawla et al., 1998, 1999] (the velocities used in these studies are well below the velocities used in our study), our observed response to slow motion is higher, if compared to motion standstill. Additionally, in the present study the activation of higher-order motion regions in the right IPL (r-IPL anterior) was observed with all motion categories. This result is in line with the work of Claeys et al. [2003]. In addition to this known higher-order motion region, we observed a specific activation by motion standstill in the r-IPL posterior and in an anterior attention network.

These findings support the hypothesis that motion standstill exceeding the temporal resolution of MT/V5 evokes a response in an attention network. This response can be caused by an orienting reaction with a stimulus-related arousal.

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