Apparent Motion: Event-Related Functional Magnetic Resonance Imaging of Perceptual Switches and States

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When spatially segregated visual stimuli are presented in alternation, subjects may perceive a single stimulus moving between the two positions (apparent motion). By adjusting spatial and temporal parameters, an ambiguous condition can be created in which perception of back-and-forth motion alternates with the perception of two stationary blinking stimuli. We presented subjects with such ambiguous stimuli, asked them to signal periods of perceived motion and blinking, and measured brain activity with functional magnetic resonance imaging. Multiple regression analysis revealed that early visual areas responded with equal strength during both perceptual conditions, whereas hMT+(V5) (the human motion complex that includes the human homolog of MT and its satellites) was more active during the perception of apparent motion. These results indicate that neurons in hMT+ participate in the constructive process that creates a continuous motion percept from a discontinuous visual input.

Key words: multistable vision; motion perception; apparent motion; apparent motion breakdown; human motion complex; MT; V5; perceptual switches; functional magnetic resonance imaging; BOLD; event-related

Moving visual stimuli are known to enhance activity in various regions of the primate brain, particularly in monkey temporal areas MT and MST (Zeki, 1974; Van Essen et al., 1981; Mikami et al., 1986; Tanaka et al., 1986; Dodd et al., 2001) and in hMT+, the human motion complex that includes the human homolog of MT and its satellites (Zeki et al., 1991; Tootell et al., 1995; Sunaert et al., 1999). Such activation has also been demonstrated for stationary flashed stimuli if their timing and spatial arrangement are adjusted to give rise to apparent motion perception (Korte, 1915; Kolers, 1972; Newsome et al., 1986; Mikami, 1991; Goebel et al., 1998). Additional evidence for a close relationship between perception of visual motion and these areas comes from the demonstration that direct electrical stimulation (Salzman et al., 1992; Salzman and Newsome, 1994) or indirect transcranial magnetic stimulation (Pascual-Leone and Walsh, 2001) of neurons in MT/MST influences motion perception. A common feature of all of these stimulation experiments is that changes in perception are studied as the dependent variable following manipulations that alter neuronal responses. Here we treat neuronal activity in the hMT+ as the dependent variable and examine whether it changes as a function of perception, even if there is no change of stimulation conditions.

To induce a bistable percept, we used two squares presented alternately on either side of the fixation point (see Fig. 1). Depending on stimulation parameters, subjects perceived either two independently blinking squares or a single square moving back and forth between the two locations. For a particular parameter setting specific for each subject, this stimulus becomes ambiguous: subjects perceive it as moving and blinking in alternation. This phenomenon is also known as apparent motion breakdown effect (De Silva, 1928; Kolers, 1964; Tyler, 1973; Selmes et al., 1997) and has been attributed to neuronal adaptation (Clatworthy and Frisby, 1973, Anstis et al., 1985). In the present functional magnetic resonance imaging (fMRI) study, stimulus parameters were adjusted for each subject until switches between apparent motion and blinking squares (breakdown and recovery of apparent motion) were reported. Stimulus parameters were then fixed for the recording sessions during which subjects reported perceptual switches by pressing one of two response buttons.

MATERIALS AND METHODS

Stimulus. The stimulus consisted of two white blinking squares (size, 1.3° visual angle; contrast, 94%; luminance, 6 cd/m^2) presented on a dark screen to either side of the fixation point (see Fig. 1*A*). The stimulus parameters varied across subjects as follows: distance between the centers of the squares between 11.7 and 13.5° (average, 13°), stimulus duration between 116 and 166 msec (average, 146 msec), and interstimulus interval between 50 and 67 msec (average, 52 msec).

The human motion complex was mapped in separate experiments for four subjects comparing responses to 400 stationary white dots with responses to a motion stimulus that consisted of 400 white dots moving radially outward on a dark screen (visual field, 30 × 23°; dot size, 0.06 ×

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0.06°; dot velocity, 3.6–14.4°/sec). This stimulus is known to produce a clear hMT response (Tootell et al., 1995; Goebel et al., 1998). Stimuli were generated by computer and back-projected onto a frosted screen with a liquid crystal display projector. Subjects viewed the screen through a mirror fixed to the head coil.

Procedure. Subjects ($n = 8$) reported their current perceptual state by pressing one of two optic fiber response buttons with their right hand (see Fig. 1*B*). Stimulus presentation lasted 46 sec and was preceded and followed by a 17 sec fixation period, during which only the fixation cross was present. Each subject was exposed to 12 stimulation blocks presented in three successive runs of scanning. Subjects were instructed to fixate throughout the experiment. Eye position was controlled in three subjects by an infrared eye-tracking system (Ober2; Permobil Meditech, Timra, Sweden). Four subjects participated in a separate experiment designed to map hMT+, in which objective motion and static control stimuli were each presented in six blocks of 16 sec and alternated with fixation periods of equal duration.

Functional image acquisition and analysis. Blood oxygenation level-dependent fMRI (BOLD) (Ogawa et al., 1990) was acquired with a 1.5 tesla Magnetom Vision Scanner (Siemens, Erlangen, Germany) using a gradient echo planar imaging (EPI) sequence (one volume is equivalent to 16 axial slices; repetition time, 2081 msec; echo time, 69 msec; flip angle, 90°; field of view, 210×210 mm^2; voxel size, $3 \times 3 \times 5$ mm^3). A high-resolution T1-weighted anatomical scan was acquired for each subject for reference in single-subject analysis. The first slice scan time within a volume was used as a reference for alignment by linear interpolation of the following slices of that volume to correct for the temporal slice scan time shifts. Data analysis and visualization were performed with the fMRI software package BrainVoyager 4 (BrainInnovation, Maastricht, The Netherlands) (Goebel et al., 1998). Before analysis, the data were preprocessed as follows: (1) three-dimensional motion correction; (2) spatial smoothing of EPI images with full width at half maximum of 8 mm for the group analysis and 4 mm for the single-subject analysis; (3) trend removal by temporal fast Fourier transform-based high-pass filtering, removing components with a period longer than 84 sec; and (4) transformation into Talairach (Talairach and Tournaux, 1988) coordinate space. The cortical sheets of the individual subjects and a template brain were reconstructed as polygon meshes based on the high-resolution T1-weighted structural three-dimensional recordings. The white–gray matter boundary was segmented, reconstructed, smoothed, morphed, and flattened as described in detail previously (Linden et al., 1999; Kriegeskorte and Goebel, 2001). A morphed surface always possesses a link to the folded reference mesh so that functional data can be correctly projected onto partially inflated, as well as flattened, representations.

The subjectively defined perceptual phases between two successive switches were used for multiple linear regression analysis of the BOLD signal time course. Using an empirically founded model (Boynton et al., 1996) of the temporal dynamics of the fMRI signal, hemodynamic predictors were computed from the subjects' indications of perceptual phases, and a general linear model (GLM) was computed for every voxel (see Fig. 1*C*). To exclude unspecific stimulus onset effects, the first perceptual phase of each stimulation block was excluded. A contrast analysis of the predictors comprising the remaining perceptual phases was used to find regions in which average activity was higher during phases of apparent motion perception than during phases of blinking perception in group analysis and single-subject analysis of eight subjects (see Fig. 2). Event-related average time courses were computed for each subject. Segments representing the same perceptual conditions were averaged over successive runs (see Fig. 3).

In a second GLM analysis, the predictors were modeled to comprise only transient switch-related activity. The predictor model was built as described for the phase-related GLM, except that the switch-related predictors had a duration of one volume (2 sec).

The hMT+ was located with a two-predictor GLM analysis of the objective motion experiment, using one predictor for the radial motion condition and one for the static condition. Contrast analysis between these predictors permitted identification of regions with the highest activity difference between motion and static conditions.

Binocular eye positions were sampled with 100 Hz. Radio frequency (rf)-induced artifacts were removed by a sequence-triggered threshold algorithm. The traces were analyzed by a threshold-based algorithm and calibrated with 5° reference saccades. This procedure allowed detection of saccades >1° and eye blinks.
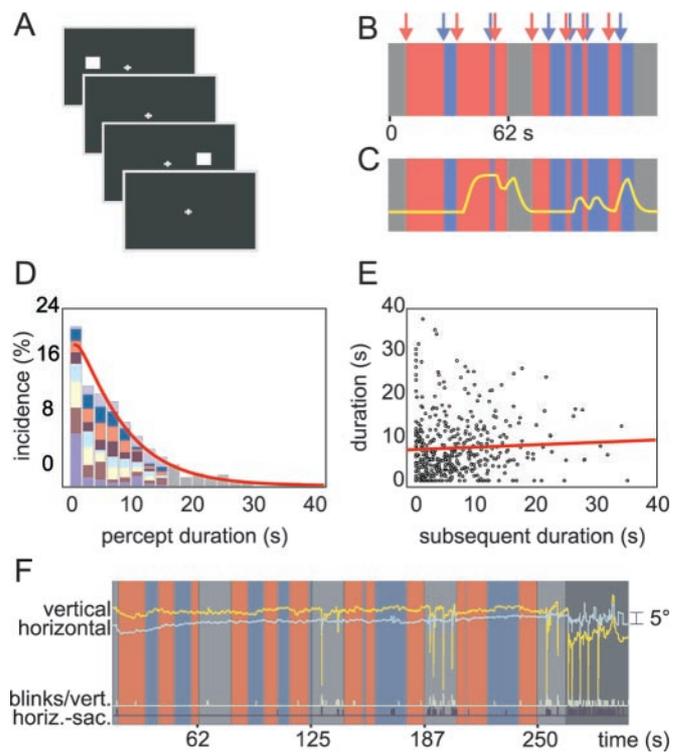

Figure 1. *A*, The apparent motion stimulus: a white square presented alternately at two positions. Stimulus parameters were adjusted for each subject in the scanner until perceptual switches between apparent motion and blinking squares were reported. *B*, This bistable stimulus was continuously presented in blocks of 46 sec preceded and followed by 17 sec of fixation (*gray blocks*). Subjects indicated whether they perceived motion (*red periods*) or blinking (*blue periods*) by pressing one of two response buttons (*red* and *blue arrows*). *C*, The expected hemodynamic response time course for the separate perceptual conditions (*yellow* for apparent motion). The first perceptual phase of each stimulation block was represented as a separate predictor in multiple regression analysis and was omitted from additional analysis. *D*, *E*, Temporal dynamics of perceptual switches. *D*, Histogram of percept durations during fMRI experiments accumulated over all subjects. Each *column* refers to the acquisition time of one brain volume (2 sec). Individual (*colored bars*) and cumulative distribution of percept duration follows approximately a gamma distribution (*red line* for cumulative distribution), which is a typical feature of a broad range of multistable phenomena (for review, see Leopold and Logothetis, 1999). *E*, Consecutive percept durations are uncorrelated. *F*, Eye position trace averaged over both eyes after rf artifact rejection during an experimental run and a successive calibration period (*dark gray*). Occurrence of eye movements as detected by thresholding algorithm (>1°) is indicated in the *bottom row*. *blinks/vert*, Vertical eye movements including eyeblinks; *horiz.-sac.*, horizontal saccades.

RESULTS

Psychophysics

All subjects experienced frequent perceptual transitions during the experiment. Perceptual phases lasted between 2.3 and 10.6 sec (lower to upper percentile), with an average of 7.7 sec (median, 5.6 sec). The distributions of phase durations are strongly shifted toward the left and can be approximated in each individual by a gamma distribution. Six of eight individual fits showed no significant deviation ($p > 0.2$; Kolmogorov–Smirnov test), but two fits deviated significantly ($p < 0.05$) (Fig. 1*D*). These distributions of phase durations agree with the temporal dynamics of perceptual switches, such as occur with binocular rivalry (Levelt, 1965; Walker, 1975; Lehky, 1988; Leopold and Logothetis, 1999) or with ambiguous figures like the Necker cube, or shape from
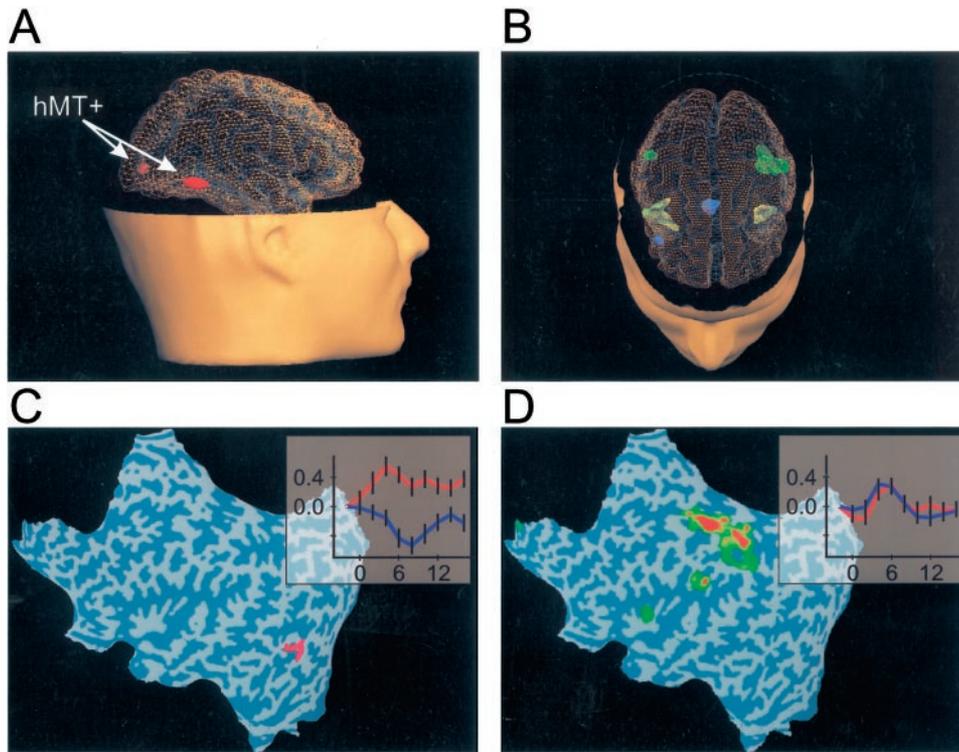
Figure 2. *A*, *B*, Group analysis shown on transparent template brains. *C*, *D*, The corresponding analyses performed for a single subject and presented on flat maps for the left hemisphere. *A*, *C*, GLM contrast analysis detects regions in which activity is higher during the perception of motion than during blink perception. The clusters correspond to the human motion complex of the left and right hemispheres. *C*, Single subject's flattened hemisphere with the corresponding event-related time course of hMT+. Signal time courses after perceptual switches from blinking to motion are shown in *red* and after switches from motion to blinking in *blue*. *Dark* and *light shading* indicates gyral structure (*dark*, concavity; *light*, convexity). *B*, *D*, Results from the switch-related GLM analysis of group data (*B*) and single-subject data (*D*). GLM detects regions with transient switch-related activity in motorsensory and somatosensory cortex, insular cortex, right middle frontal cortex, SMA, and middle frontal cortex. Event-related time course from left motorsensory and somatosensory cortex is shown for the selected subject. Template brain in *A* and *B* is courtesy of the Montreal Neurological Institute.

shading (Taylor and Aldridge, 1974). The temporal dynamics of multistable perception are usually characterized by stochastic independence of consecutive phases (Walker, 1975). We confirmed such independence in six of eight subjects ($r = -0.02$, -0.03, -0.04, 0.12, -0.17, and -0.18) (Fig. 1*E*). However, two subjects exhibited significant dependencies ($r = -0.31$, $p < 0.01$; $r = 0.37$, $p < 0.01$).

Eye movements
Horizontal saccades above 1° were rare and occurred with a frequency of 0.3–0.8/min during fixation, 0.3–1.9/min during perceived motion, and 0–1.2/min during perception of blinking (differences between perceptual conditions were not significant; $t < 1.5$; $p > 0.1$). No saccades above 5° were detected during the fMRI experiments. Vertical saccades and eye blinks occurred more often during the fixation period (7–19/min; significance in all subjects, $t > 2.8$; $p < 0.01$) than during the visual stimulation (motion, 1.7–4.3/min; blinking, 0.6–1.1/min). The probability of eye movements was not increased around perceptual switches. On average, the positions of the eyes were similar for both perceptual conditions ($t < 0.7$; $p > 0.5$).

Group analysis
The GLM group analysis of contrast differences between episodes with differing percepts revealed regions with higher activity during perception of motion than during perception of blinking. Figure 2, *A* and *B*, shows the clusters with the highest contrast. At this threshold, each voxel in the map is significant at $p < 0.0001$ (Bonferroni corrected for 49,125 comparisons in voxel space). The reverse contrast does not label a single voxel at this threshold (data not shown). By their coordinates in Talairach space [centers of gravity of the clusters, right hemisphere (RH), $x = 48$, $y = -72$, $z = -1$; left hemisphere (LH), $x = -47$, $y = -70$, $z = 2$], clusters were identified as corresponding to the hMT+ of both hemispheres.

The GLM group analysis of transient signal changes revealed

an increase in activity for both perceptual switches in the primary motor and somatosensory cortex (RH, $x = 51$, $y = -37$, $z = 34$; LH, $x = -46$, $y = -29$, $z = 37$), in the insular cortex (RH, $x = 45$, $y = 6$, $z = 19$; LH, $x = -39$, $y = 4$, $z = 11$), in the right middle frontal cortex ($x = 43$, $y = 31$, $z = 22$), in the supplementary motor area (SMA), and in the medial anterior cingulate ($x = 3$, $y = 9$, $z = 45$). Most of this activity can be attributed to the preparation and execution of the right-hand motor responses.

Single-subject analysis
Single subjects were analyzed in the same way for areas activated more strongly during the percept of motion than during that of blinking. In agreement with the group analysis, hMT+ was the region that showed the strongest and most consistent difference in activation when the percept switched from blinking to motion. In all eight subjects, the contrast analysis revealed activation of hMT+. In five subjects, hMT+ was activated only in the left and in three in both hemispheres (Fig. 3). The identified hMT+ clusters were subjected to an event-related time course analysis. BOLD signal was averaged using the subjects' button presses as trigger. This resulted in average signals comprising the volume during which the perceptual transition occurred plus the eight volumes after the transition (corresponding to an interval of -2 to $+16$ sec). Because the next transitions are likely to occur within this time interval and because these switches sometimes occur quite soon, subsequent switches tend to blur the time course of individual responses. Figure 3 shows these time courses for hMT+ of the left and right hemisphere of each subject. The *colored bars* below the time courses indicate the persistence of the percepts signaled by the subjects. Signal intensity rises after perceptual transitions from blinking to motion (*red*) ($t = 3.7$; $p < 0.01$) and falls after transitions from motion to blinking (*blue*) ($t = 0.9$; NS). The *white panels* in Figure 3 correspond to hemispheres whose hMT+ exhibited no differential activation during the mo-
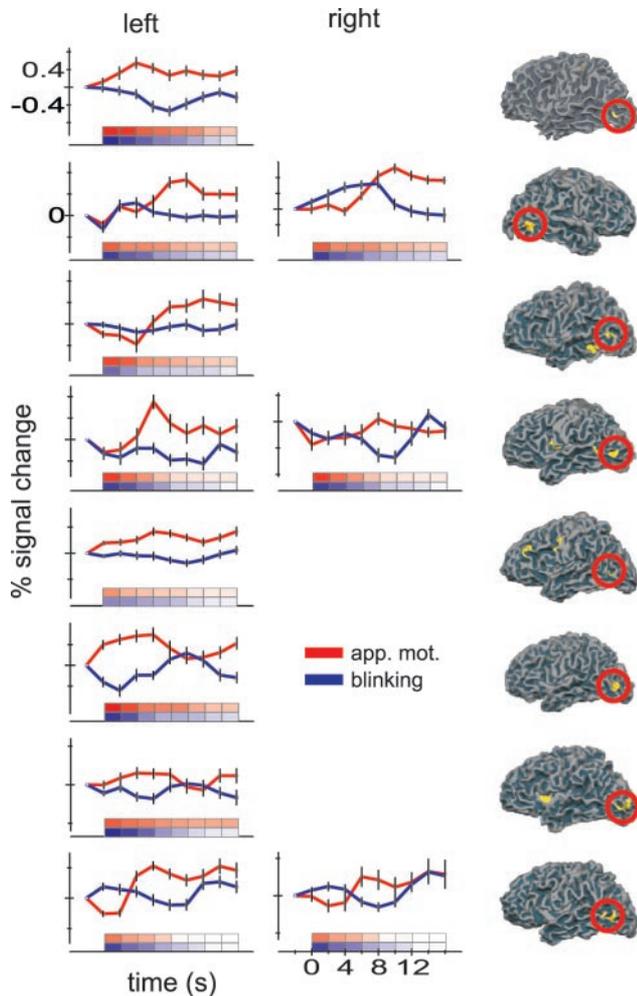
Figure 3. Individual analysis of eight subjects. In the *right column*, activated clusters are superimposed onto individual reconstructions of the cortical sheet of the left or right hemisphere. Regions in which activity is stronger during motion than during blinking are marked in *yellow*. Regions with the same activity during both conditions are not marked. Event-related average time courses of human motion complex clusters are shown in the *left* and *middle column* for left and right hMT+. (Locations are indicated by *red circles*.) Signal time courses after perceptual switches from blinking to motion are shown in *red* and after switches from motion to blinking in *blue*. Whiskers correspond to ±1 SEM. Each of the *colored rectangles* below the time courses represents a functional volume (2 sec). The *color* indicates the proportion of averaged time courses on which the percept endured. *Dark color* (intensity, 100%) indicates that the respective percept (motion, *red*; blinking, *blue*) was present at that functional volume on every one of the averaged time courses. *White color* (intensity, 0%) indicates that the percept had switched again on all averaged time courses. *app. mot.*, Apparent motion.

tion percept. The locations of the selected regions of interest match well with estimates on the location of hMT+ based on cortical morphology (temporo-occipital border of inferior temporal sulcus) (Fig. 3, *right column*), on Talairach coordinates, or on the results of functional mapping (Fig. 4.). Despite non-optimal overlap in two of four subjects (Fig. 4C,D), the time courses showed the same characteristics for functionally mapped hMT+ regions.

DISCUSSION

Combining a bistable visual stimulus, perceived as stationary blinking or moving, with an event-related fMRI design revealed neuronal correlates of changes in perception that were not stimulus
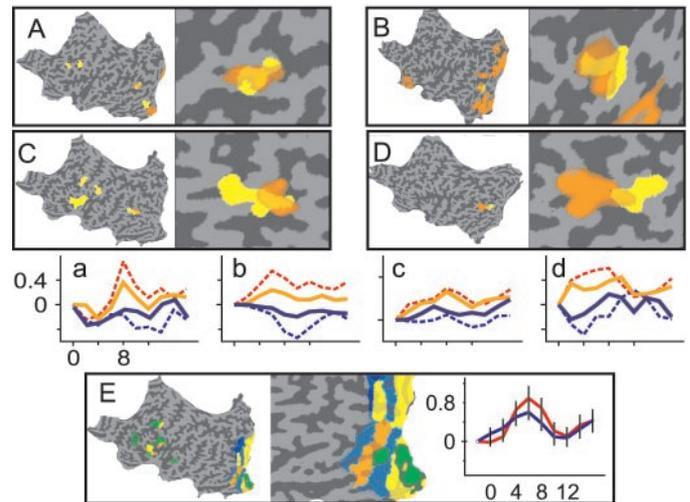

Figure 4. Functional mapping of hMT+ (*red*). *A–D*, Flattened hemispheres of four individual subjects with superimposed result of hMT+ mapping. Highest GLM contrast between objective motion and static dot pattern is shown in *orange*. Regions with higher activity to apparent motion (compare with Fig. 3) are superimposed in *yellow*. In each subject, a substantial proportion of the subjective contrast map overlaps hMT+ (as mapped by objective motion vs static dots), which is also shown at higher magnification. *a–d*, Corresponding event-related time courses are shown for both patches. *Solid lines* show time courses from the functionally mapped hMT+ region (*red* in *A–D*), and *dotted lines* are taken from Figure 3 (*yellow* in *A–D*). *E*, Early visual areas in some subjects (shown here for the subject from *C*) showed transient switch-related activity (*green*) in regions along the ventral horizontal meridian, which is consistent with upper visual field stimulation (Fig. 1*A*). This activity was not seen in the group analysis (Fig. 2). The event-related time course is from the ventral horizontal meridian within V1 (*right panel*). Retinotopic mapping of early visual areas was as reported by Goebel et al. (1998) (color codes: V1 and V3, *yellow*; V2 and V4, *blue*; VP, *orange*; V3a, *dark blue*).

driven but must have resulted from changes of internal dispositions. The region exhibiting the strongest change of activity between different phases of perception was the human motion complex. Its activity increased for perceptual switches from stationary to moving patterns. This suggests an important role of hMT+ activity in the conscious perception of motion. In the monkey, close relationships between neuronal activity and perception have been established exploiting cortical microstimulation (Salzman et al., 1990; Celebrini and Newsome, 1995) or perceptual switches associated with ambiguous figures (Dodd et al., 2001) or binocular rivalry (Logothetis and Schall, 1989). The latter two studies, in particular, permit direct comparison with the present investigation because stimulation conditions were constant and neuronal activity changed in close relation with the objects the monkeys reported to perceive. The present results in human subjects agree well with previously obtained data from monkeys, because both indicate that perceptual switches are associated with strongest changes of neuronal activity in those cortical regions that are specialized for the analysis of the respective stimulus qualities: figural aspects in the inferotemporal cortex (Logothetis and Schall, 1989), motion attributes of three-dimensional figures in area MT (Dodd et al., 2001), and perceived motion in hMT+ (present study).

What then causes these switches in neuronal activity and perception? The BOLD signal reflects, rather indirectly, neuronal activity with poor spatial and temporal resolution, but it has the advantage that it can be measured in the whole brain within short time intervals. This allowed us to identify hMT+ as the area

whose activation reflected best the time course of perceptual states. Recent fMRI studies emphasized the importance of top-down modulation for the initiation of perceptual switches in binocular rivalry (Lumer et al., 1998; Tong et al., 1998; Leopold and Logothetis, 1999) and for distributing attention to specialized visual areas, including hMT+ (Beauchamp et al., 1997; Büchel and Friston, 1997; O'Craven et al., 1997; Kleinschmidt et al., 1998). Top-down effects have also been shown in mental imagery. Imagery of a moving pattern is associated with strong activation of both prefrontal cortex and hMT+ and less activation of lower visual areas, whereas perception of the real stimulus is associated with strong activation of both lower visual areas and hMT+ but less with prefrontal activity (Goebel et al., 1998). However, because there were no comparable correlations between perceptual switches and activation patterns in other areas, it is unlikely that the enhanced activity of hMT+ was secondary to enhanced activity in other cortical areas. Therefore, the possibility needs to be considered that the switch in perception from flicker to motion is actually a direct consequence of increased activity in hMT+. Thus, whereas imagery of motion seems to require top-down activation of hMT+, perception of both real and illusory motion might mainly require bottom-up activation of hMT+. A possible mechanism that could have caused the activity change in hMT+ and the concomitant perceptual switch is adaptation. Adaptation to real motion reduces the probability of perceiving both real and apparent motion (Anstis et al., 1985). Activity of hMT+ increased strongly after switches to perceived motion but decreased only little after switches to perceived blinking, indicating that activity of hMT+ adapts and returns to near baseline with the consequence that a switch to the blinking percept does not cause much additional decreases. If different networks represent flicker and motion and if these networks compete with one another (e.g., through reciprocal inhibition), adaptation weakening the network that is active and supporting perception, can lead to shifts of dominance between the networks and to concomitant switches between the respective percepts. Lehky (1988) has proposed such a reciprocal feedback inhibition model to explain multistable perception in binocular rivalry. A simulation based on this model reproduced the typical temporal dynamics of perceptual switches, which were also apparent in our behavioral data (Fig. 1D,E). This and the fact that hMT+ activity correlated best with the perceptual changes suggests that the perceptual switches were attributable to adaptation and competition within hMT+ and were not gated by top-down influences.

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