NeuroImage 84 (2014) 420–427

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Tactile and visual motion direction processing in hMT+/V5

Bianca M. van Kemenade [a,b,*], Kiley Seymour [b,c], Evelin Wacker [d], Bernhard Spitzer [e], Felix Blankenburg [a,e,f], Philipp Sterzer [a,b,f]

[a] Berlin School of Mind and Brain, Humboldt Universität zu Berlin, Berlin, Germany
[b] Department of Psychiatry and Psychotherapy, Campus Charite Mitte, Charité-Universitätsmedizin Berlin, Berlin, Germany
[c] Department of Cognitive Science, Macquarie University, Sydney, Australia
[d] Institute for Clinical Teratology and Drug Risk Assessment in Pregnancy, Charité University Medicine Berlin, Germany
[e] Dahlem Institute for Neuroimaging of Emotion, Freie Universität Berlin, Berlin, Germany
[f] Bernstein Center for Computational Neuroscience, Berlin, Germany

ARTICLE INFO

Article history:
Accepted 3 September 2013
Available online 12 September 2013

Keywords:
Tactile
Visual
Motion
Multisensory
fMRI

ABSTRACT

The human motion complex hMT+/V5 is activated not only by visual motion, but also by tactile and auditory motion. Whilst direction-selectivity has been found within this complex for visual and auditory stimuli, it is unknown whether hMT+/V5 also contains direction-specific information from the tactile modality. In the current study, we sought to investigate whether hMT+/V5 contains direction-specific information about visual/tactile moving stimuli. Leftward and rightward moving stimuli were presented in the visual and tactile modalities in an event-related fMRI design. Using region-of-interest-based multivariate pattern analysis we could decode the two motion directions for both tactile and visual stimuli in hMT+/V5. The activity patterns of the two modalities differed significantly, indicating that motion direction information from different modalities may be carried by distinct sets of neuronal populations. Our findings show that hMT+/V5 contains specific information about the direction of a moving stimulus in both the tactile and visual modalities, supporting the theory of hMT+/V5 being a multimodal motion area.

Introduction

The human motion complex, area hMT+/V5, is a cortical brain region located on the lateral surface of the occipital lobe, typically within the posterior limb of the inferior temporal sulcus (Zeki et al., 1991). Traditionally, hMT+/V5 has been regarded as a purely visual area, involved in visual motion processing. In monkey MT, cells respond to moving visual stimuli in a direction-selective fashion (Albright, 1984; Malonek et al., 1994; Van Essen et al., 1981; Zeki, 1974). Similarly, fMRI studies have provided evidence for direction-selective motion processing also in the human motion complex hMT+/V5 (Kamitani and Tong, 2006; Seymour et al., 2009). Furthermore, hMT+/V5 has been implicated in biological motion processing (Peelen et al., 2006; Thompson and Baccus, 2012). Area MST, a subregion with hMT+/V5, has additionally been associated with self motion detection and perception (Britten, 2008; DeAngelis and Angelaki, 2012) and optic flow processing (Smith et al., 2006). Recent work suggests that hMT+/V5 may be a multimodal or supramodal area that also has a role in tactile (Beauchamp et al., 2007; Blake et al., 2004; Hagen et al., 2002; Ricciardi et al., 2007; Sani et al., 2010; Wacker et al., 2011) and auditory (Poirier et al., 2005, 2006; Wolbers et al., 2011) motion processing. These studies have found activity in hMT+/V5 in response to tactile or auditory moving stimuli. Furthermore, area MST has been found to process vestibular cues (DeAngelis and Angelaki, 2012; Fetsch et al., 2007; Gu et al., 2007). Direction-specific information within hMT+/V5 has been found for auditory stimuli in blind individuals (Wolbers et al., 2011); yet it is unknown whether hMT+/V5 also represents direction-specific information from non-visual modalities in sighted individuals.

Here, using functional magnetic resonance imaging (fMRI), we investigated whether hMT+/V5 contains direction-specific information relating to both visual and tactile motion stimuli. In order to identify direction-specific signals, we used multi-voxel pattern analysis (MVPA). This is a method that tests multiple voxels at a time to detect information contained within the patterns of activity, and is therefore more sensitive to subtle differences in activity patterns compared to univariate analyses that test only one voxel at a time (e.g. Haynes and Rees, 2006; Norman et al., 2006). We hypothesized that both visual and tactile motion directions would be represented in area hMT+/V5.

Materials and methods

Participants

28 participants with normal or corrected-to-normal vision took part in a behavioural training session prior to the fMRI experiment. Three

* Corresponding author at. Klinik für Psychiatrie und Psychotherapie—CCM, Charité Universitätsmedizin Berlin, Charitеplatz 1, 10117 Berlin, Germany.
E-mail address: biancavankemenade@gmail.com (B.M. van Kemenade).

1053-8119/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2013.09.004

participants were excluded because of poor performance during this task (for details, see Design & procedure section). Thus, the remaining fMRI sample consisted of 25 subjects. Data from three additional subjects were excluded after the fMRI experiment because of excessive head motion during scanning; therefore, the data of 22 subjects were included in the analysis (11 females, 11 males, 21 right-handed, 1 left-handed, age 19–33; mean age 25). All participants gave written informed consent to participate in the experiment, which was approved by the local ethics committee.

Stimuli

Tactile stimulation was applied to the finger tips of both index fingers simultaneously. We applied our stimuli bilaterally in order to maximize the signal in the brain, since tactile stimuli seem to activate hMT+/V5 less strongly than visual stimuli (Blake et al., 2004). The stimuli were delivered by two piezoelectric Braille displays (4 × 4 quadratic matrix, 2.5 mm spacing), each consisting of 16 pins that moved up and down (Fig. 1). The pins were driven by a programmable controller (Piezostimulator, QuaeroSys, St. Johann, Germany). During each tactile trial, the pins were driven for 4000 ms by a 1 Hz sinusoidal signal. All pins forming a diagonal moved together; the next diagonal moved π/4 phase after the previous diagonal. In this way, the diagonals were propelled across the display, creating the sensation of a wave travelling continuously across the fingertip. The displays were rotated 45°, so that the wave was moving horizontally over the finger tip rather than in a diagonal direction. The movement was either propelled to the left or to the right to create leftward and rightward motion trials. The tactile displays were attached to a small wooden table placed on the subjects' lap. Subjects were instructed to lightly place their index fingers on the displays.

Visual stimuli were closely matched to the tactile stimuli. Two 4 × 4 dot displays (width 2.5°) were presented against a black background, rotated 45°, analogous to the tactile displays. They were presented on either side of the screen simultaneously, the edge of each display being 4.9° from the central fixation cross, viewed from a distance of approximately 70 cm. The brightness of the dots was controlled by a 1 Hz sine function and the phase of the sine wave was shifted across the diagonals of the display, as in the tactile stimuli. This created the percept of a continuous wave-like motion translating from left to right and vice versa. All stimuli were presented using Cogent (http://www.vislab.ucl.ac.uk/), on a Dell Latitude d531 laptop running Matlab (Mathworks).

Apart from these four main stimulus types (tactile/visual, moving leftward/rightward), random-motion trials were additionally included to keep participants attentive; participants were instructed to press a button when they detected such a trial. These random-motion trials were generated using the same driving signals as for left- and rightward motion, but assigning these signals randomly to the individual pins of the display. Each individual pin thus still moved up and down in the exact same way as in the other stimuli, but the percept would be of pins moving randomly rather than together in a coherent wave-like manner. The same procedure was applied for the visual random-motion stimuli, in which the change in brightness was randomly assigned to the individual dots, thereby creating a percept of random visual motion. Furthermore, 18% null events were included, during which only the fixation cross was presented.

Fig. 1. Piezoelectric display used for tactile stimuli. The display consists of 16 pins that moved up and down. All pins forming a diagonal were moving together; each diagonal followed the next so that the diagonals were propelled across the display, inducing the percept of a wave travelling across the finger tip.

To localise hMT+/V5 a standard functional localiser was used (Huk et al., 2002; Tootell et al., 1995). Radially moving dots (speed: 8°/s) were contrasted with static dots, both presented centrally within a circular aperture with a diameter of 14.6° (200 dots per display, dot width 0.164°). Based on previous reports that tactile motion solely activated subregion MST within the hMT+/V5 complex (Beauchamp et al., 2007), we modified our localiser to allow for the separation of MST from MT within this complex. Therefore, the dots were also presented to either side of the screen (4.9° between the edge of the stimulus and the fixation cross; Huk et al., 2002). Each cycle of moving or static dots lasted 14 s and was repeated four times per run. Two runs were conducted. This localizer was presented using Psychtoolbox (Brainard, 1997).

Design & procedure

Subjects first performed a two-stage behavioural training to become familiar with the experimental stimuli and task. Only subjects achieving above-chance performance in both experiments were included in the fMRI experiment. The first behavioural training stage tested subjects' ability to discriminate between leftward and rightward moving stimuli. Tactile and visual stimuli moving leftward or rightward were presented bilaterally in random serial order for 4 s, followed by a 2 s response interval. By pressing the right or left button on a foot-switch, participants had to indicate whether the stimulus had moved towards the right or left. No random-motion trials were included in this experiment. Participants could train as long as they wished, up to a maximum of 6 runs of 28 trials (7 trials per condition) during which feedback was provided. Afterwards, two runs without feedback, each comprising 60 trials (15 trials per condition), were performed. The second stage of behavioural training simulated the main experiment that would be conducted in the fMRI scanner. In addition to leftward and rightward motion trials, this experiment also contained random-motion trials (3 tactile, 3 visual per run). Participants were instructed to attend closely to the stimuli, and to press a button with the right foot only when they detected a random-motion trial. Again, they could train for as long as they wished, with feedback, up to a maximum of 6 runs of 30 stimuli each. After that, two runs of 66 trials (15 trials per condition plus 6 random-motion trials) without feedback were presented. White noise was presented throughout both experiments to mask the noise generated by the tactile stimulator.

During the fMRI experiment, participants performed the same task as in the second behavioural training stage — i.e. they were instructed to pay close attention to the stimuli and to press a button with the right foot when they had detected a random-motion trial. Participants were asked to respond only after the stimulus had disappeared. During each run, the four main stimulus types (tactile/visual, moving leftward/rightward), random-motion trials, and null events were presented in random serial order. Each run comprised 44 trials: 8 trials for each main stimulus type, 8 null events, 2 tactile random-motion trials and 2 visual random-motion trials. Stimuli were presented for 4 s, followed by an inter-trial interval of varying duration (3.2, 5.6, or 8 s). Each participant in the fMRI experiment performed a single scanning session consisting of eight experimental runs, two runs of hMT+/V5 localiser, and a structural scan (see below).

Data acquisition

Functional MRI data were acquired using a 3 T TIM Trio scanner (Siemens, Erlangen, Germany), using a 12-channel head-coil. A gradient

echo EPI sequence was used (TR: 2.4 s, TE: 30 ms, flip angle: 78°, slice thickness: 2.5 mm, gap: 20%, voxel size: 3 × 3 × 3 mm). Per run, 196 volumes for the main experiment and 145 volumes for the hMT+/V5 localiser were obtained, each containing 39 slices covering the whole brain, acquired in descending order. Initial volumes were not removed, as the scanner sent the first trigger pulse (that started the experiment) only after T1 equilibration had occurred. Anatomical images were obtained using a T1-weighted MPRAGE sequence (TR: 1.9 s, TE: 2.52 ms, flip angle: 9°).

Data preprocessing

Data were analysed using Statistical Parametric Mapping (SPM8, Wellcome Department of Imaging Neuroscience, University College London, UK). Preprocessing of the experimental runs for the multivariate analyses was confined to slice time correction and realignment. For the additional univariate analysis that was carried out on this data, additional coregistration, normalisation, and smoothing were performed, whereby each participant's anatomical scan was coregistered to their functional images and normalised to the standard Montreal Neurological Institute (MNI) template. The resulting parameters were then used to normalise the functional images to the MNI template, after which the data were smoothed ($8 \times 8 \times 8$ mm^3 full-width at half-maximum). The hMT+/V5 localiser data were slice time corrected and realigned. No normalization was performed, but the data were spatially smoothed with a smoothing kernel of $5 \times 5 \times 5$ mm^3 full-width at half-maximum to maximise signal from noise in single subject data. Individual hMT+/V5 ROIs were defined using the activity from contrasting moving with static dots based on uncorrected p-values, whilst taking anatomical landmarks into account (Dumoulin et al., 2000). MST was defined as the area that showed ipsilateral activation. MST was then subtracted from hMT+/V5, and MT was defined by using anatomical criteria (Dumoulin et al., 2000) on the voxels that remained after subtraction. However, our attempt to identify MT and MST resulted in relatively small ROIs (average size: 176 and 116 voxels, respectively, compared to 277 voxels in hMT+/V5). Furthermore, MST could not be identified and separated from MT in 5 subjects. Altogether, our MT and MST ROIs did not permit reliable decoding. We therefore primarily focus on hMT+/V5 as a whole in this study, but include the separation of MT and MST as an additional univariate analysis.

Univariate analysis

We first performed univariate analyses to make sure that our stimuli activated our region of interest, and to ensure that decoding performance was not based on coarse univariate differences. The preprocessed data were analysed using the general linear model (GLM). Regressors modelling each stimulus type were convolved with the canonical hemodynamic response function implemented in SPM8 and included in the GLM. Furthermore, motion parameters were included as regressors of no interest. Null events were included in a separate regressor to obtain a baseline estimate. Random-motion trials, which contained no direction-specific motion signals, were modelled as a covariate of no interest and excluded from further analysis. T-contrasts of tactile and visual stimuli (excluding random-motion trials) were compared against null events (baseline) and passed on to the group-level analysis. Unless stated otherwise, all reported areas of activation are based on a threshold of $p < 0.05$, family-wise-error (FWE) corrected across the whole brain. The SPM anatomy toolbox (Eickhoff et al., 2005) was used to identify activated regions. A separate ROI analysis was included to investigate a potential difference between leftward and rightward motion within our hMT+/V5, MT, and MST ROIs. Thus, mean beta values for left- and rightward moving stimuli against baseline were extracted from each individual hMT+/V5, MT, and MST ROI and scaled with reference to the local mean within the ROI. These beta values are parameter estimates resulting from the GLM and reflect the extent to which a particular regressor (i.e. left- and rightward motion for each modality) explains the observed BOLD signal. Subsequent paired-sample t-tests to compare leftward and rightward beta values were performed for each modality.

Multivariate pattern analysis

For MVPA, the raw data were only slice time corrected and realigned. No other preprocessing was performed, such that data were not transformed to any standard anatomical template. We then used a general linear model to estimate the responses. Regressors for each stimulus type were defined separately for each experimental run in order to allow for estimation of one single beta-estimate for each stimulus type per run. Furthermore, head movement parameters were included as regressors of no interest. MVPA was performed using the Decoding toolbox (Görgen et al., 2012) which implements LibSVM software (http://www.csie.ntu.edu.tw/~cjlin/libsvm). A linear support vector machine (SVM) with a fixed regularization parameter $C = 1$ was used as a classifier. Leave-one-run-out cross-validation was performed using the run-wise beta-estimates from the GLM analysis. That is, beta-estimates from all but one run were used in the training set, and the beta-estimates from the remaining run functioned as a test set to probe the accuracy of the trained SVM classifier. In each cross-validation, a different run was used as a test set, resulting in 8 cross-validations in total. Decoding accuracy was calculated by averaging the decoding accuracies for each cross-validation. This procedure was used in ROI-based decoding, using only voxels from the predefined ROIs, and in searchlight decoding, in which a sphere with a radius of 4 voxels searched through the whole brain to identify brain areas with significant decoding accuracies (Kriegeskorte et al., 2006). For ROI-based decoding one-sample t-tests against 50% were used to determine the significance of the decoding accuracy on the group level. In view of the recent debate concerning the use of t-tests in MVPA (Schreiber and Krekelberg, 2013; Stelzer et al., 2013), we performed permutation testing on our ROI-based decoding. Following the method described by Stelzer et al. (2013), we decoded with all possible combinations of label assignments for each subject. We then randomly selected one of these decoding accuracies from each subject and calculated the average decoding accuracy. This procedure of random selection and calculation of average decoding accuracy was repeated 10,000 times. Based on the resulting distribution of average decoding accuracies, a cut-off of 95% was used to determine the significance of our results. For the searchlight decoding, the resulting whole-brain maps were normalised and smoothed with a 6-mm full-width at half-maximum Gaussian kernel, after which they were passed on to the group-level analysis. An additional searchlight analysis with a radius of 6 voxels was performed to investigate whether the size of the radius played a role. Since we obtained the same results with both radii, we do not further report the searchlight with a 6 voxel radius in the Results section.

Pattern similarity

Following our decoding analysis, voxel pattern similarity across modalities was examined using a cross-classification strategy, in which a classifier was trained on one modality and was tested on the other modality, and vice versa, using the voxels from our predefined hMT+/V5 ROIs. This procedure helped to determine whether motion decoding across modalities relied on independent or overlapping voxels. Additionally, we tested how (dis)similar the activity patterns of the two modalities within hMT+/V5 were using an analysis as described by Seymour et al. (2009). Linear support vector machines assign a weight to each voxel that indicates its importance in the classification. A given weight map of n voxels can be considered a vector in n-dimensional space. The angle between two such weight vectors indicates their similarity. We calculated the angle between voxel weight maps that were generated by the classifier in the learning phase for

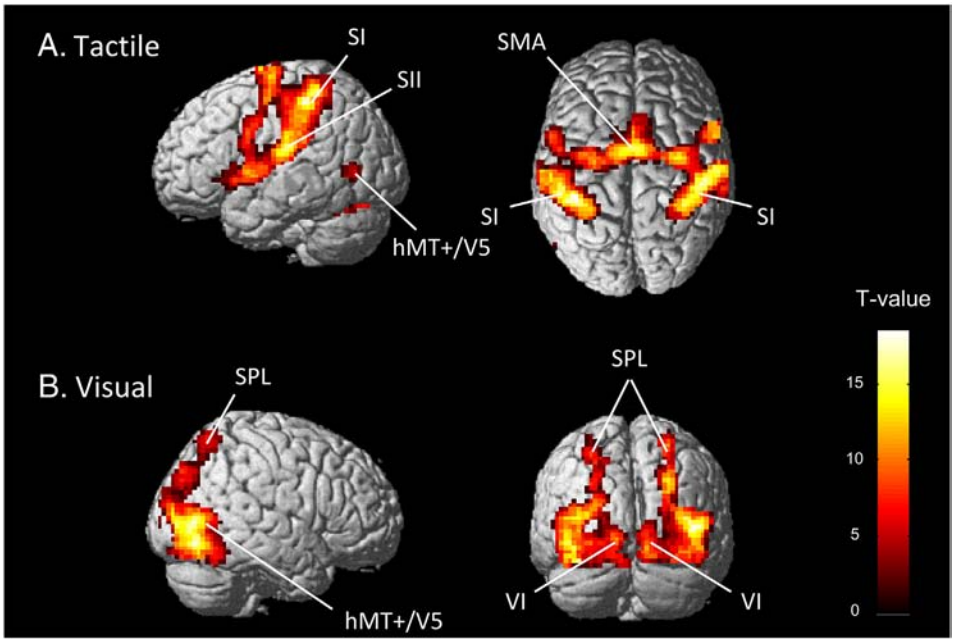

Fig. 2. Neural network associated with tactile motion processing. Tactile stimuli were contrasted with fixation, revealing a distributed network including SI and SII, supplementary motor area (SMA), and hMT+/V5 (A). Contrasting visual stimuli with fixation revealed various clusters including V1, hMT+/V5 and superior parietal lobule (SPL) (B). For a full list of activations, see Table 1. Activation maps are shown at a threshold of $p < 0.05$ (whole-brain FWE corr.).

motion direction in the tactile and visual stimulus conditions, respectively, for each individual participant. We also calculated the mean angle resulting from 1000 random permutations of the weight values, which yields the expected angle given the assumption of no relation between the two weight vectors (Seymour et al., 2009). Next, we tested across subjects whether the angle between the weight maps differed significantly from the expected angles. We carried out the analysis by using only voxels whose weights exceeded ±2 standard deviation for either modality. If the angular differences are significantly smaller than expected by chance, this would indicate a positive relation, meaning that voxels informative for tactile motion direction are also informative for visual motion direction, and vice versa. If the angular differences are significantly larger than expected by chance, a negative relation is indicated, meaning that the better a given voxel coded for tactile motion direction, the worse it coded for visual motion direction, and vice versa. No significant angular differences would indicate no relation between voxels coding for tactile vs. visual motion direction (Seymour et al., 2009).

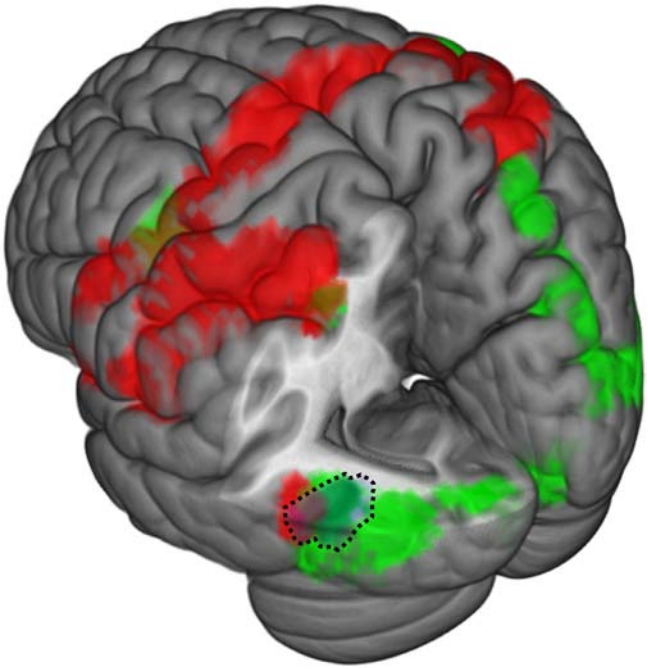

Fig. 3. Overlap between visual and tactile activation. Tactile activity is shown in red, visual activity in green, both at a threshold of $p < 0.05$ (FWE corr.). A normalised hMT+/V5 ROI based on the second-level MT localiser data ($p < 0.05$, FWE corr.) is depicted by the dotted line, and shows an overlap in activity between the two modalities.

Results

Behavioural performance

The average accuracy on the motion direction discrimination task outside the scanner was 86.4% (SEM = 2.51) for tactile trials and 99.5% (SEM = 0.16) for visual trials. On the detection task, participants detected on average 86% (SEM = 3.69) of all random-motion trials. Visual random-motion trials were detected more often than the tactile random-motion trials (95.4% (SEM = 2.56) vs. 76.5% (SEM = 6.06), respectively). During the fMRI experiment, participants detected on average 87.7% (SEM = 2.5) of all random-motion trials, 99.1% (SEM = 0.46) of visual and 76.3% (SEM = 5.1) of tactile random-motion trials.

Univariate analysis

Contrasting tactile motion trials with baseline revealed activated clusters in the bilateral primary somatosensory cortex in the postcentral gyrus (SI; areas 1, 2, 3), secondary somatosensory cortex/parietal operculum (SII; OP1, OP4), cerebellum, in the right insula, supplementary motor area (SMA), inferior parietal cortex (IPC), and in the left hMT+/V5 and thalamus ($p < 0.05$, FWE corr.; Fig. 2 & Table 1). The contrast between visual motion trials and fixation yielded activation in the bilateral striate and extrastriate cortex, middle occipital gyrus, in right hMT+/V5, superior occipital gyrus, fusiform gyrus, superior parietal lobule (SPL), and left thalamus ($p < 0.05$, FWE corr.; Fig. 2 & Table 1). The overlap between tactile and visual activation is shown in Fig. 3,

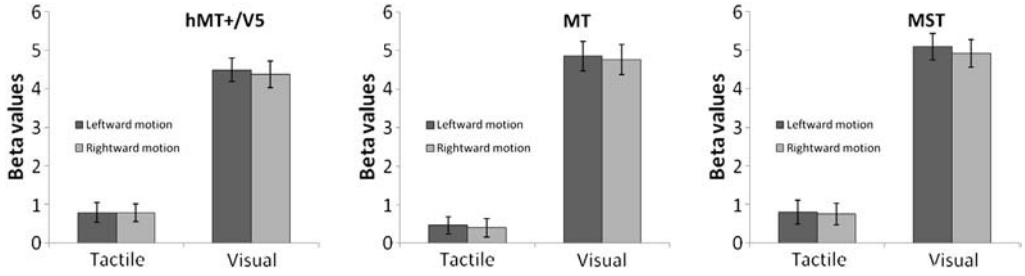

Fig. 4. Univariate region-of-interest (ROI) analysis. Weighted mean beta estimates for leftward and rightward moving stimuli, contrasted against baseline, were extracted from the individual hMT+/V5, MT, and MST ROIs and scaled using the within-ROI mean. Betas for leftward and rightward moving stimuli were then compared within modality using paired sample t-tests. No significant differences between leftward and rightward moving stimuli were found for either ROI (hMT+/V5: $p = 0.96$ (tactile) and $p = 0.24$ (visual), MT: $p = 0.66$ (tactile) and $p = 0.53$ (visual), MST: $p = 0.71$ (tactile) and $p = 0.18$ (visual)). Error bars denote standard errors of the mean (SEM).

showing that our stimuli activated our region of interest. No differences between leftward and rightward motion were found in either modality when contrasting leftward with rightward stimuli. To increase sensitivity, we performed a separate analysis on our hMT+/V5, MT, and MST ROIs. Mean beta values were extracted from each individual ROI and scaled with reference to the local mean within that ROI. Leftward and rightward beta values were tested per modality with paired-sample t-tests. Again, no significant differences between leftward and rightward motion were found in either modality, in either hMT+/V5, MT or MST (Fig. 4). The decoding performance of our subsequent MVPA analysis could thus not be based on univariate differences.

Multivariate pattern analysis

ROI-decoding revealed significant above-chance decoding of leftward and rightward moving stimuli within hMT+/V5 for both tactile and visual stimuli (55.9%, $p = 0.04$; 58.1%, $p = 0.005$, respectively; Fig. 5). Permutation testing confirmed that our results were significantly different than can be expected by chance (tactile: $p = 0.01$; visual: $p = 0.002$). Additional explorative searchlight decoding across the whole brain yielded clusters containing direction-specific information in the bilateral primary somatosensory cortex (bilateral area 3b, left area 1, right area 2 and 3a) for tactile stimuli ($p < 0.001$, uncorr., extent thresh. = 10), but not in hMT+/V5. For visual stimuli, the searchlight analysis ($p < 0.001$, uncorr., extent thresh. = 10) across the whole brain showed no significant effects, also not in hMT+/V5. Potential clusters with direction information in this area may not have been detected in normalized searchlight maps due to the large variability in size and location of hMT+/V5 in individuals (Dumoulin et al., 2000; Huk et al., 2002).

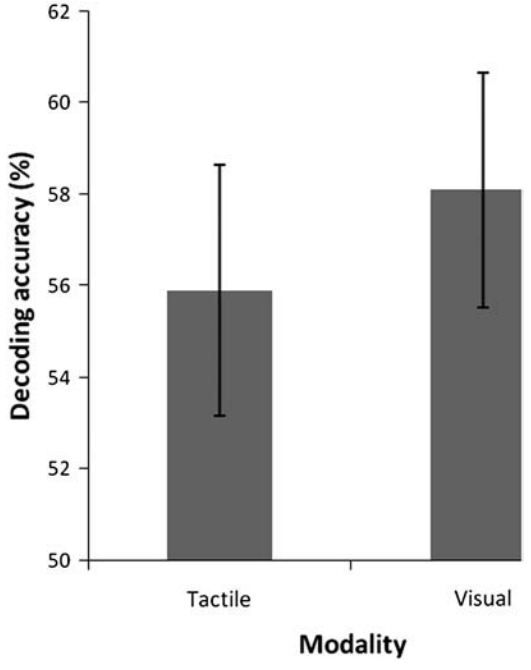

Fig. 5. Decoding performance. Using multi-voxel pattern analysis (MVPA), leftward and rightward moving stimuli could be decoded with above-chance accuracy within hMT+/V5 for both modalities (tactile: 55.9%, $p = 0.04$; visual: 58.1%, $p = 0.005$). Chance level is 50%. Error bars denote standard errors of the mean (SEM).

Cross-classification and pattern similarity

Training on tactile stimuli and testing on visual stimuli using voxels from our hMT+/V5 ROIs yielded no significant results. Similarly, training on visual stimuli and testing on tactile stimuli resulted in chance decoding performance (accuracy 50.5%, $p = 0.69$; 51.9%, $p = 0.08$, respectively). This was also the case when the analysis was performed

Table 1
Regions active during tactile and visual motion trials. Areas were identified using the SPM anatomy toolbox (Eickhoff et al., 2005). Coordinates are in MNI space. T-values are based on $p < 0.05$ (whole brain FWE corr.). R = right hemisphere, L = left hemisphere.

Region	Hemisphere	X	Y	Z	T-value
Visual stimuli					
Middle temporal gyrus (hMT+/V5)	R	51	−73	4	12.91
Inferior temporal gyrus	R	42	−64	−8	12.93
Inferior occipital gyrus (V4)	R	45	−82	−2	11.95
	L	−27	−82	−8	12.10
Superior occipital gyrus	R	27	−76	34	10.59
Fusiform gyrus	R	39	−49	−17	10.59
	L	−42	−61	−20	12.31
Calcarine gyrus (V1)	L	−9	−97	−5	10.52
Middle occipital gyrus	R	36	−88	10	10.20
	L	−36	−91	10	10.08
Lingual gyrus (V2)	R	12	−85	−14	9.75
	L	−12	−91	−11	8.77
Lingual gyrus (V1)	R	12	−91	−5	9.72
V3v	R	30	−79	−11	9.75
Superior parietal lobule	R	24	−64	64	8.94
Thalamus	L	−18	−31	1	9.79
Tactile stimuli					
Insula	R	39	−1	0	18.52
Postcentral gyrus (SI)	R	45	−31	52	16.57
	L	−39	−37	52	15.26
OP1 (SII)	R	54	−22	19	15.64
	L	−54	−22	19	16.30
OP4 (SII)	L	−45	−7	10	15.60
Supplementary motor area	R	3	−4	73	13.50
Intraparietal cortex	R	57	−19	31	13.35
Cerebellum	R	21	−67	−20	9.54
	L	−24	−61	−26	12.20
Middle temporal gyrus (hMT+/V5)	L	−51	−67	4	8.99
Thalamus	L	−15	−22	10	7.87

on only the 7 participants who had above chance decoding performance for both modalities (49.1%, $p = 0.36$; 49%, $p = 0.36$).

The pattern similarity was investigated using an analysis of the classifier weights. The angles between the weight maps of the two modalities differed from the angles produced by a permutation test procedure performed on the same weight maps more than expected by chance (difference between weight map angles and permutation angles in radians: mean = 0.1967, SEM = 0.0217, $p < 0.001$). This indicates that the weight maps for tactile and visual motions within hMT+/V5 were negatively correlated, meaning that the more a voxel contributed to decoding of tactile motion direction, the less it contributed to decoding of visual motion direction, and vice versa.

Discussion

In the current study we investigated tactile and visual motion direction processing in area hMT+/V5. We first performed univariate analyses to make sure that our stimuli activated our region of interest, and to ensure that decoding of motion direction could not be based on univariate differences. The univariate analyses did not reveal any fMRI signal differences between leftward and rightward motion, neither for tactile nor for visual stimuli. Our visual stimuli may not have been optimal for driving hMT+/V5, as they were designed to match the spatio-temporal properties of the optimized tactile stimuli. Furthermore, since subjects did not perform a motion discrimination task, we could not take out potential unrecognized trials, which may have influenced the neural signals. We cannot completely rule out that the lack of directionality differences in the univariate analyses is due to the properties of our stimuli or potential unrecognized trials. However, univariate differences would suggest a large scale representation of direction selectivity. This is inconsistent with the physiology of MT, since MT is known to encode direction information in a columnar fashion (Albright et al., 1984), best assessed with MVPA. It is therefore more plausible that MVPA would be better to assess direction selectivity in this area than univariate methods. Indeed, the MVPA approach showed that both tactile and visual motion directions could be decoded above chance from fMRI signal patterns within hMT+/V5. Univariate analysis tests only one voxel at a time to reveal areas involved in the task, whereas multivariate pattern analysis tests multiple voxels at a time to detect specific information contained within the pattern of activity (Haynes and Rees, 2006; Norman et al., 2006). The information that univariate analysis and MVPA can detect is therefore different. As we might have expected, our results indicate that the MVPA approach, which takes activity patterns into account rather than averages across voxels, is more sensitive than standard univariate analysis to reveal a discrimination of both visual and tactile motion directions within hMT+/V5 activity patterns. Cross-classification between the two modalities did not yield significant results and analysis of the voxel weight maps showed that the activity patterns in the two modalities differed significantly, suggesting that separate neuronal populations code for motion direction across modalities.

Above-chance decoding of leftward and rightward tactile motion direction in hMT+/V5 shows that this area is not just active when tactile motion is present, but also contains information about its direction. This finding extends existing knowledge on the involvement of visual area hMT+/V5 in tactile motion processing. Since hMT+/V5 can be activated by visual imagery (Goebel et al., 1998), it has been suggested that the activation of hMT+/V5 in tactile motion trials might be merely due to visual imagery, and not essentially involved in tactile motion perception (Hagen et al., 2002). Whilst our finding cannot completely rule this out, previous reports that congenitally blind individuals exhibit hMT+/V5 activation in response to tactile motion strongly speak against the possibility that the responses of hMT+/V5 to tactile motion stimuli might reflect visual imagery only (Matteau et al., 2010; Ricciardi et al., 2007; Sani et al., 2010). Furthermore, earlier work also showed that a condition in which participants had to imagine touching a rotating tactile globe did not yield hMT+/V5 activation (Blake et al., 2004). Moreover, recent studies using TMS applied over hMT+/V5 during tactile motion trials significantly impaired accuracy, reaction times, (Ricciardi et al., 2011), and speed perception (Basso et al., 2012), providing evidence that hMT+/V5 is in fact necessary for tactile motion perception. Lastly, our similarity analysis of voxel weight angles assigned by the classifier in the learning phase indicated that the activity patterns of tactile and visual motion trials differed significantly from each other. Together, these findings suggest that visual imagery does not play a crucial role in the recruitment of hMT+/V5 for tactile motion processing. Our finding that motion direction information is represented in hMT+/V5 supports the idea that the activation of this area is not just an epiphenomenon, but plays a supportive role in tactile motion perception.

It is not uncommon to find activity in areas traditionally considered as 'unisensory' in response to stimuli from a different modality. In fact, more and more studies report activity from various modalities in 'unisensory' areas (for reviews see Ghazanfar and Schroeder, 2006; Kayser, 2010). For example, auditory cortex can be activated by visual presentation of silent lipreading (Calvert et al., 1997; Pekkola et al., 2005) or by somatosensory stimuli (Fu et al., 2003; Schurmann et al., 2006) in sighted individuals. Although multisensory integration was previously thought to occur first in higher level areas, such studies point towards the possibility that multisensory integration already takes place earlier in lower areas. Indeed, early multisensory integration has been reported repeatedly (for review, see Kayser and Logothetis, 2007). For example, early audio–tactile interactions have been found in the somatosensory cortex (Foxe et al., 2000), or audio–visual interactions in the visual cortex (Molholm et al., 2002). Specifically, several studies have found evidence for multisensory motion processing within hMT+/V5, specifically audiovisual interactions (Alink et al., 2008; Lewis and Noppeney, 2010; Sadaghiani et al., 2009; Scheef et al., 2009), but also visuo-tactile interactions (Chan et al., 2010). The present finding of motion direction-selective information in hMT+/V5 for both tactile and visual motions supports the view of hMT+/V5 as a multimodal area and goes beyond previous work in showing that hMT+/V5 processes motion signals from different modalities in a direction-selective fashion.

We found no evidence for overlapping neuronal representations of motion direction across modalities, as indicated by the lack of significant decoding performance in our cross-validation analysis. Though the difficulty of the tactile and visual tasks differed as indicated by the behavioural performance in the training phase, this is an unlikely cause for a complete lack of cross-classification decoding. Importantly, an analysis of voxel weight angles assigned by the classifier in the learning phase indicated that the patterns of the two modalities differed significantly from each other. This finding suggests that motion direction information from different modalities may be carried by distinct sets of neuronal populations within hMT+/V5. This may seem surprising in light of several studies reporting multisensory interactions in visual and tactile motion processing (Bensmaia et al., 2006; Conrad et al., 2012; Konkle et al., 2009; Lunghi and Alais, 2013; Lunghi et al., 2010). However, our findings do suggest that at the coarse level, as investigated with univariate analyses, coding of visual and tactile motions cannot be distinguished. Moving to the more fine grained level, which is assessed with MVPA, we see distinct coding of the two modalities. This mapping arrangement may indicate that visual and tactile motions are coded by different neuronal populations that interact tightly to enable multisensory integration. Alternatively, our experimental set-up may not have been suitable for cross-classification specifically. It has been proposed that tactile representations are remapped to external locations with reference to egocentric space (Azanón and Soto-Faraco, 2008), which is suggested to occur in a head-centred framework (Butz et al., 2010). Visual motion might also be processed within hMT+/V5 in an external, not retinal, framework (d'Avossa et al., 2007). It is therefore possible that, when lying in a supine position within the scanner with the arms downwards from a head centred view, the tactile stimuli presented to the fingertips may have been remapped to the space behind the

participant, whereas the visual stimuli would be perceived to be in front of the participant. Although the perceived direction was the same, the spatiotopic representation of 'in front' versus 'behind' could potentially have led to different activity patterns, which would not be cross-classifiable. Since our main aim was to classify tactile motion direction, this set-up was well-suited for the current study, as it elicited strong tactile motion perception. However, we speculate that a setup in which visual and tactile stimuli were spatially colocalised could potentially have led to the activation of overlapping neuronal populations within hMT+/V5. Therefore, future studies addressing differences in spatial positioning of our stimuli will determine more confidently whether overlapping neuronal populations underlie motion direction encoding within hMT+/V5.

One could also argue that the tactile and visual modalities are too different to elicit similar neural responses. There are indeed psychophysical differences between these modalities (Marks, 1983). For example, tactile distance perception does not match visual distance perception. Also, temporal acuity is much poorer in the tactile domain compared to the visual domain (Marks, 1983). However, several studies show that tactile and visual stimuli are processed in a similar way (Gori et al., 2011). For example, like in visual motion perception, the perceived direction of tactile motion is first mediated by local motion detectors, subject to the aperture problem. Cues from local motion detectors and terminators are then gradually integrated to yield the veridical motion direction, analogous to the visual processes (Pei et al., 2008). Furthermore, tactile motion is subject to similar illusions observed with visual motion, such as the motion after-effect (Watanabe et al., 2007). Moreover, a number of studies show cross-modal effects between vision and touch. For example, visual motion influences the perceived speed of tactile motion (Bensmaia et al., 2006), tactile and visual apparent motion quartets interact with each other (Conrad et al., 2012), tactile stimuli interact with vision during binocular rivalry with sensitivity to matching spatial frequency (Lunghi et al., 2010) and orientation (Lunghi and Alais, 2013), and motion after-effects can transfer between vision and touch (Konkle et al., 2009). Such specific interactions suggest a common mechanism. Nevertheless, because differences still exist between the modalities, it is unclear whether the neural mechanisms would be comparable.

In summary, we have shown that hMT+/V5 contains information about the direction of a moving stimulus, both in the tactile and in the visual modality. To our knowledge, this study is the first to report evidence for direction selectivity in tactile motion processing in area hMT+/V5. Though our findings are preliminary and need to be confirmed by future studies, they provide an initial insight into the nature of tactile motion processing within hMT+/V5, supporting the notion of hMT+/V5 as a multimodal motion processing area.

Acknowledgments

This work was supported by the German Research Foundation (Emmy Noether Programme, STE-1430/2-1). BVK was funded by the Berlin School of Mind and Brain, and by the Stichting dr. Hendrik Muller's Vaderlandsch Fonds. KS was funded by the Alexander von Humboldt Foundation. We would like to thank Thomas B. Christophel, Martin N. Hebart, and Kai Görgen for helpful discussions on multivariate pattern analysis.

References

Albright, T.D., 1984. Direction and orientation selectivity of neurons in visual area MT of the macaque. J. Neurophysiol. 52 (6), 1106–1130.
Albright, T.D., Desimone, R., Gross, C.G., 1984. Columnar organization of directionally selective cells in visual area MT of the macaque. J. Neurophysiol. 51, 16–31.
Alink, A., Singer, W., Muckli, L., 2008. Capture of auditory motion by vision is represented by an activation shift from auditory to visual motion cortex. J. Neurosci. 28 (11), 2690–2697.
Azanón, E., Soto-Faraco, S., 2008. Changing reference frames during the encoding of tactile events. Curr. Biol. 18 (14), 1044–1049.
Basso, D., Pavan, A., Ricciardi, E., Fagioli, S., Vecchi, T., Miniussi, C., et al., 2012. Touching motion: rTMS on the human middle temporal complex interferes with tactile speed perception. Brain Topogr. 25 (4), 389–398.
Beauchamp, M.S., Yasar, N.E., Kishan, N., Ro, T., 2007. Human MST but not MT responds to tactile stimulation. J. Neurosci. 27 (31), 8261–8267.
Bensmaia, S.J., Killebrew, J.H., Craig, J.C., 2006. Influence of visual motion on tactile motion perception. J. Neurophysiol. 96 (3), 1625–1637.
Blake, R., Sobel, K.V., James, T.W., 2004. Neural synergy between kinetic vision and touch. Psychol. Sci. 15 (6), 397–402.
Brainard, D.H., 1997. The Psychophysics toolbox. Spat. Vis. 10 (4), 433–436.
Britten, K.H., 2008. Mechanisms of self-motion perception. Annu. Rev. Neurosci. 31, 389–410.
Butz, M.V., Thomaschke, R., Linhardt, M.J., Herbort, O., 2010. Remapping motion across modalities: tactile rotations influence visual motion judgments. Exp. Brain Res. 207 (1–2), 1–11.
Calvert, G.A., Bullmore, E.T., Brammer, M.J., Campbell, R., Williams, S.C., McGuire, P.K., et al., 1997. Activation of auditory cortex during silent lipreading. Science 276 (5312), 593–596.
Chan, J.S., Simoes-Franklin, C., Garavan, H., Newell, F.N., 2010. Static images of novel, moveable objects learned through touch activate visual area hMT+. Neuroimage 49 (2), 1708–1716.
Conrad, V., Vitello, M.P., Noppeney, U., 2012. Interactions between apparent motion rivalry in vision and touch. Psychol. Sci. 23 (8), 940–948.
D'Avossa, G., Tosetti, M., Crespi, S., Biagi, L., Burr, D.C., Morrone, M.C., 2007. Spatiotopic selectivity of BOLD responses to visual motion in human area MT. Nat. Neurosci. 10 (2), 249–255.
DeAngelis, G.C., Angelaki, D.E., 2012. Visual–vestibular integration for self-motion perception. In: Murray, M.M., Wallace, M.T. (Eds.), The Neural Bases of Multisensory Processes. CRC Press, Boca Raton (FL).
Dumoulin, S.O., Bittar, R.G., Kabani, N.J., Baker Jr., C.L., Le Goualher, G., Bruce Pike, G., et al., 2000. A new anatomical landmark for reliable identification of human area V5/MT: a quantitative analysis of sulcal patterning. Cereb. Cortex 10 (5), 454–463.
Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., et al., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. Neuroimage 25 (4), 1325–1335.
Fetsch, C.R., Wang, S., Gu, Y., Deangelis, G.C., Angelaki, D.E., 2007. Spatial reference frames of visual, vestibular, and multimodal heading signals in the dorsal subdivision of the medial superior temporal area. J. Neurosci. 27 (3), 700–712.
Foxe, J.J., Morocz, I.A., Murray, M.M., Higgins, B.A., Javitt, D.C., Schroeder, C.E., 2000. Multisensory auditory–somatosensory interactions in early cortical processing revealed by high-density electrical mapping. Brain Res. Cogn. Brain Res. 10 (1–2), 77–83.
Fu, K.M., Johnston, T.A., Shah, A.S., Arnold, L., Smiley, J., Hackett, T.A., et al., 2003. Auditory cortical neurons respond to somatosensory stimulation. J. Neurosci. 23 (20), 7510–7515.
Ghazanfar, A.A., Schroeder, C.E., 2006. Is neocortex essentially multisensory? Trends Cogn. Sci. 10 (6), 278–285.
Goebel, R., Khorram-Sefat, D., Muckli, L., Hacker, H., Singer, W., 1998. The constructive nature of vision: direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery. Eur. J. Neurosci. 10, 1563–1573.
Gori, M., Mazzilli, G., Sandini, G., Burr, D., 2011. Cross-sensory facilitation reveals neural interactions between visual and tactile motion in humans. Front. Psychol. 2, 55.
Görgen, K., Hebart, M.N., Haynes, J.D., 2012. The Decoding Toolbox (TDT): a new fMRI analysis package for SPM and MATLAB. Poster Presented at the 18th Annual Meeting of the Organization for Human Brain Mapping (http://f1000.com/posters/browse/summary/1092032).
Gu, Y., DeAngelis, G.C., Angelaki, D.E., 2007. A functional link between area MSTd and heading perception based on vestibular signals. Nat. Neurosci. 10 (8), 1038–1047.
Hagen, M.C., Franzen, O., McGlone, F., Essick, G., Dancer, C., Pardo, J.V., 2002. Tactile motion activates the human middle temporal/V5 (MT/V5) complex. Eur. J. Neurosci. 16 (5), 957–964.
Haynes, J.D., Rees, G., 2006. Decoding mental states from brain activity in humans. Nat. Rev. Neurosci. 7 (7), 523–534.
Huk, A.C., Dougherty, R.F., Heeger, D.J., 2002. Retinotopy and functional subdivision of human areas MT and MST. J. Neurosci. 22 (16), 7195–7205.
Kamitani, Y., Tong, F., 2006. Decoding seen and attended motion directions from activity in the human visual cortex. Curr. Biol. 16 (11), 1096–1102.
Kayser, C., 2010. The multisensory nature of unisensory cortices: a puzzle continued. Neuron 67 (2), 178–180.
Kayser, C., Logothetis, N.K., 2007. Do early sensory cortices integrate cross-modal information? Brain Struct. Funct. 212 (2), 121–132.
Konkle, T., Wang, Q., Hayward, V., Moore, C.I., 2009. Motion after effects transfer between touch and vision. Curr. Biol. 19 (9), 745–750.
Kriegeskorte, N., Goebel, R., Bandettini, P., 2006. Information-based functional brain mapping. Proc. Natl. Acad. Sci. U. S. A. 103 (10), 3863–3868.
Lewis, R., Noppeney, U., 2010. Audiovisual synchrony improves motion discrimination via enhanced connectivity between early visual and auditory areas. J. Neurosci. 30 (37), 12329–12339.
Lunghi, C., Alais, D., 2013. Touch interacts with vision during binocular rivalry with a tight orientation tuning. PLoS One 8 (3), e58754.
Lunghi, C., Binda, P., Morrone, M.C., 2010. Touch disambiguates rivalrous perception at early stages of visual analysis. Curr. Biol. 20 (4), R143–R144.
Malonek, D., Tootell, R.B., Grinvald, A., 1994. Optical imaging reveals the functional architecture of neurons processing shape and motion in owl monkey area MT. Proc. Biol. Sci. 258 (1352), 109–119.

Marks, L.E., 1983. Similarities and differences among the senses. Int. J. Neurosci. 19 (1–4), 1–11.
Matteau, I., Kupers, R., Ricciardi, E., Pietrini, P., Ptito, M., 2010. Beyond visual, aural and haptic movement perception: hMT+ is activated by electrotactile motion stimulation of the tongue in sighted and in congenitally blind individuals. Brain Res. Bull. 82 (5–6), 264–270.
Molholm, S., Ritter, W., Murray, M.M., Javitt, D.C., Schroeder, C.E., Foxe, J.J., 2002. Multisensory auditory-visual interactions during early sensory processing in humans: a high-density electrical mapping study. Brain Res. Cogn. Brain Res. 14 (1), 115–128.
Norman, K.A., Polyn, S.M., Detre, G.J., Haxby, J.V., 2006. Beyond mind-reading: multi-voxel pattern analysis of fMRI data. Trends Cogn. Sci. 10 (9), 424–430.
Peelen, M.V., Wiggett, A.J., Downing, P.E., 2006. Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. Neuron 49 (6), 815–822.
Pei, Y.C., Hsiao, S.S., Bensmaia, S.J., 2008. The tactile integration of local motion cues is analogous to its visual counterpart. Proc. Natl. Acad. Sci. U. S. A. 105 (23), 8130–8135.
Pekkola, J., Ojanen, V., Autti, T., Jaaskelainen, I.P., Mottonen, R., Tarkiainen, A., et al., 2005. Primary auditory cortex activation by visual speech: an fMRI study at 3 T. Neuroreport 16 (2), 125–128.
Poirier, C., Collignon, O., Devolder, A.G., Renier, L., Vanlierde, A., Tranduy, D., et al., 2005. Specific activation of the V5 brain area by auditory motion processing: an fMRI study. Brain Res. Cogn. Brain Res. 25 (3), 650–658.
Poirier, C., Collignon, O., Scheiber, C., Renier, L., Vanlierde, A., Tranduy, D., et al., 2006. Auditory motion perception activates visual motion areas in early blind subjects. Neuroimage 31 (1), 279–285.
Ricciardi, E., Vanello, N., Sani, L., Gentili, C., Scilingo, E.P., Landini, L., et al., 2007. The effect of visual experience on the development of functional architecture in hMT+. Cereb. Cortex 17 (12), 2933–2939.
Ricciardi, E., Basso, D., Sani, L., Bonino, D., Vecchi, T., Pietrini, P., et al., 2011. Functional inhibition of the human middle temporal cortex affects non-visual motion perception: a repetitive transcranial magnetic stimulation study during tactile speed discrimination. Exp. Biol. Med. (Maywood) 236 (2), 138–144.
Sadaghiani, S., Maier, J.X., Noppeney, U., 2009. Natural, metaphoric, and linguistic auditory direction signals have distinct influences on visual motion processing. J. Neurosci. 29 (20), 6490–6499.
Sani, L., Ricciardi, E., Gentili, C., Vanello, N., Haxby, J.V., Pietrini, P., 2010. Effects of visual experience on the human MT+ functional connectivity networks: an fMRI study of motion perception in sighted and congenitally blind individuals. Front. Syst. Neurosci. 4 (159), 1–9.
Scheef, L., Boecker, H., Daamen, M., Fehse, U., Landsberg, M.W., Granath, D.O., et al., 2009. Multimodal motion processing in area V5/MT: evidence from an artificial class of audio–visual events. Brain Res. 1252, 94–104.
Schreiber, K., Krekelberg, B., 2013. The statistical analysis of multi-voxel patterns in functional imaging. PLoS One 8 (7), e69328.
Schurmann, M., Caetano, G., Hlushchuk, Y., Jousmaki, V., Hari, R., 2006. Touch activates human auditory cortex. Neuroimage 30 (4), 1325–1331.
Seymour, K., Clifford, C.W., Logothetis, N.K., Bartels, A., 2009. The coding of color, motion, and their conjunction in the human visual cortex. Curr. Biol. 19 (3), 177–183.
Smith, A.T., Wall, M.B., Williams, A.L., Singh, K.D., 2006. Sensitivity to optic flow in human cortical areas MT and MST. Eur. J. Neurosci. 23, 561–569.
Stelzer, J., Chen, Y., Turner, R., 2013. Statistical inference and multiple testing correction in classification-based multi-voxel pattern analysis (MVPA): random permutations and cluster size control. Neuroimage 65, 69–82.
Thompson, J.C., Baccus, W., 2012. Form and motion make independent contributions to the response to biological motion in occipitotemporal cortex. Neuroimage 59 (1), 625–634.
Tootell, R.B., Reppas, J.B., Dale, A.M., Look, R.B., Sereno, M.I., Malach, R., et al., 1995. Visual motion after effect in human cortical area MT revealed by functional magnetic resonance imaging. Nature 375 (6527), 139–141.
Van Essen, D.C., Maunsell, J.H., Bixby, J.L., 1981. The middle temporal visual area in the macaque: myeloarchitecture, connections, functional properties and topographic organization. J. Comp. Neurol. 199 (3), 293–326.
Wacker, E., Spitzer, B., Lutzkendorf, R., Bernarding, J., Blankenburg, F., 2011. Tactile motion and pattern processing assessed with high-field FMRI. PLoS One 6 (9), e24860.
Watanabe, J., Hayashi, S., Kajimoto, H., Tachi, S., Nishida, S., 2007. Tactile motion after effects produced by appropriate presentation for mechanoreceptors. Exp. Brain Res. 180 (3), 577–582.
Wolbers, T., Zahorik, P., Giudice, N.A., 2011. Decoding the direction of auditory motion in blind humans. Neuroimage 56 (2), 681–687.
Zeki, S.M., 1974. Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. J. Physiol. 236 (3), 549–573.
Zeki, S., Watson, J.D., Lueck, C.J., Friston, K.J., Kennard, C., Frackowiak, R.S., 1991. A direct demonstration of functional specialization in human visual cortex. J. Neurosci. 11 (3), 641–649.