

## Static images of novel, moveable objects learned through touch activate visual area hMT+

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### ARTICLE INFO

#### Article history:

Received 12 August 2009

Revised 28 September 2009

Accepted 29 September 2009

Available online 6 October 2009

#### Keywords:

Dynamic object recognition

Haptics

hMT+

Multisensory perception

Object recognition

### ABSTRACT

Although many studies have found similar cortical areas activated during the recognition of objects encoded through vision or touch, little is known about cortical areas involved in the crossmodal recognition of dynamic objects. Here, we investigated which cortical areas are involved in the recognition of moving objects and were specifically interested in whether motion areas are involved in the recognition of dynamic objects within and across sensory modalities. Prior to scanning, participants first learned to recognise a set of 12 novel objects, each presented either visually or haptically, and either moving or stationary. We then conducted fMRI whilst participants performed an old-new task with static images of learned or not-learned objects. We found the fusiform and right inferior frontal gyri more activated to within-modal visual than crossmodal object recognition. Our results also revealed increased activation in area hMT+, LOC and the middle occipital gyrus, in the right hemisphere only, for the objects learned as moving compared to the learned static objects, regardless of modality. We propose that the network of cortical areas involved in the recognition of dynamic objects is largely independent of modality and have important implications for understanding the neural substrates of multisensory dynamic object recognition.

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### Introduction

Although there is extensive research on visual, haptic, and visuo-haptic object recognition, most of these studies have focused on the recognition of static objects (e.g., Amedi et al., 2002, 2005; Ernst et al., 2007; Grill-Spector et al., 1998, 1999; Newell et al., 2001). However, real world object recognition not only involves static objects but many objects can either move independently or have moveable parts for particular functions (e.g., door handles and hand whisks). Despite this fact, our knowledge of how information about moving objects is processed for the purpose of recognition is mainly limited to visual object recognition and relatively little is known about haptic or cross-modal recognition of moving objects.

Many behavioural studies have suggested efficient sharing of information across vision and touch for the purpose of the recognition of static objects (e.g., Easton et al., 1997; Reales and Ballesteros, 1999). Later neuroimaging investigations revealed an overlap between the cortical areas involved in visual object recognition and those involved in the recognition of objects encoded through touch (Amedi et al., 2001, 2005; Lacey et al., 2009; Malach et al., 1995; Sathian and Zangaladze, 2002). In particular, haptic object recogni-

tion activates the lateral occipital complex (LOC; Amedi et al., 2001), an area which is consistently activated during the visual recognition of objects. Together, these studies demonstrate that efficient behavioural performance in crossmodal object recognition is underpinned by shared neural systems often identified as being within so-called visual areas.

Recent research into the visual recognition of moving objects has suggested that objects are stored in memory as spatio-temporal representations such that both the characteristic motion and shape of an object are relevant cues for recognition (e.g., Newell et al., 2004; Setti and Newell, 2009; Stone, 1998). Other evidence, particularly from studies on the perception of faces, has supported the findings that motion information can affect recognition in that changes in the characteristic dynamic patterns of faces can disrupt the recognition of familiar faces (Hill and Johnston, 2001). Thus, evidence from behavioural studies suggests that motion and shape information are integrated in the representation of objects and faces.

Other evidence from neuroimaging studies has suggested that the processing of shape and motion information in object perception is underpinned by the same neural systems. For example, although it has been established that real visual-motion information activates area hMT+ (i.e., V5; Tootell et al., 1995b; Zeki, 1991, 1993), it has also been shown that area hMT+ is activated to apparent motion, that is, visual-motion aftereffects caused by outwardly moving concentric circles (Tootell et al., 1995a). In other words, activity in hMT+ can be elicited by the perception of motion and not just by motion information directly available in the visual stimulus itself. This

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suggests that neural activation (as measured by blood oxygen-level dependent or BOLD responses) in area hMT+ may be both top-down dependent and stimulus dependent (see also Alford et al., 2007; Beauchamp and DeYoe, 1996). Adding to the evidence that activity in hMT+ can be modulated by top-down processes, further brain imaging studies have also shown that the mental imagery of motion (Cohen et al., 1996; Goebel et al., 1998; O'Craven and Kanwisher, 2000) and illusory motion (Tootell et al., 1995a) activate the same brain regions as the direct perception of motion. Moreover, Kourtzi and Kanwisher (2000) compared BOLD activation to participants viewing still images in which motion was implied (e.g., an athlete performing an action) or no motion was implied (e.g., an athlete at rest). They found greater activation in area hMT+ in the right hemisphere when presented with images containing implied motion compared to the no-motion images. Interestingly, this effect was not restricted to images of humans and animals, but to motion implied in scenes as well (e.g., a waterfall) suggesting that activation to either direct or implied motion is not category specific.

Area hMT+ is not just related to the processing of motion in the visual modality, but has also been shown to be related to motion stimuli presented via the auditory (Poirer et al., 2005; Smith et al., 2007) and tactile modalities (Hagen et al., 2002; Ricciardi et al., 2007). For example, Hagen and colleagues examined the effect of tactile stimulation on a participant's passive hand using paint brushes which were moved across the hand. They found increased activation in area MT/V5 compared to static stimulation (i.e., brushes held in place; see also Blake et al., 2004). Specifically, activation in area MT was lower in the tactile motion condition than in the visual-motion condition (outwardly moving concentric circles). These results are contrary to other studies that found no activation in this area to vibration or light touch stimulation on the skin (Coghill et al., 1994; Fox et al., 1986, 1987; Pardo et al., 1991; Seitz and Roland, 1992). However, Hagen et al. suggest that this is because these previous studies used stimuli that did not provide a true perception of tactile motion. In other words, they did not use a stimulus that was perceived as a single entity moving in space.

Others have suggested that area hMT+ may not be a multisensory motion processing area but that the neural activation to motion encoded from other modalities may be mediated by visual imagery. In an attempt to dissociate tactile motion from visual imagery in sighted participants, Blake et al. (2004) used fMRI to measure activation when participants determined the direction of a rotating globe by either touching, viewing, or imagining the globe. They found increased activation in area hMT+ when touching a rotating globe relative to visual imagery of the rotating globe or even imagining their finger tapping. Similar to the Hagen et al. study, activation to the tactile stimulus was lower than when viewing rotating dots but was nevertheless significantly greater than baseline. Moreover, studies on participants who are visually impaired have also found that tactile motion was sufficient to activate area hMT+ in the absence of visual stimulation or even visual familiarity with the stimuli (Goyal et al., 2006; Ricciardi et al., 2007). Taken together, these studies suggest that visual imagery does not fully account for activations in area hMT+ induced by stimulation from modalities other than vision. Instead, these findings suggest that area hMT+ may be a general motion processing area.

There is evidence that changes in activation in brain areas associated with both the appearance and function of objects occurs as a consequence of learning. For example, Weisberg et al. (2007) explicitly investigated the role of learning in visual object recognition using novel objects which were attributed with a particular shape and function. They scanned participants in two fMRI sessions, before and after learning the novel objects. Before the training session, activation in areas in the fusiform gyrus commonly associated with object shape properties was found to the static visual presentation of the objects. During training, participants manipu-

lated each object and learned its particular shape and function. Following training, Weisberg et al. reported activation to the static images of the objects which was more focused in fusiform areas but also activation was found in other areas of the brain normally associated with object motion (the left middle temporal gyrus) and object manipulation (left intraparietal sulcus and premotor cortex). They attribute this activation to learned tool use and object functionality. Interestingly, in their study, still images of the objects were sufficient to activate motion areas in the cortex. As such, the activation was due to motion information implied in the image of the object and not related to motion available in the stimulus or to direct tool-use itself. However, as the function of each object was learned through both viewing and haptic manipulation it is unclear if this change in BOLD activation in area hMT+ is due to recalled visual object motion acquired during the training session or imagined action motion of the hands manipulating the object. Valyear et al. (2007) found that action-related activation for tools and other objects is localized in the posterior intraparietal sulcus (IPS) and not hMT+, suggesting that the motion of body parts during tool use is unlikely to activate area hMT+. On the other hand, others have argued that knowledge of tool-use and tool-motion is sufficient to activate ventral areas in the cortex, particularly those in lateral temporal areas which are activated by either static images or moving images of familiar tools (Beauchamp et al., 2002).

In the current fMRI study, we examined the neural substrates underlying the recognition of dynamic objects learned through either vision or touch. In particular, we investigated whether the cortical areas underpinning visual object recognition and visual object motion are also active to images of objects previously learned through touch alone. To that end, we trained participants outside the scanner to recognise a series of novel object shapes which were moving or stationary using either vision or haptics. In the scanner, we presented static, greyscale images of the learned objects to the participants who performed an old/new recognition task. We hypothesised that there would be significantly greater BOLD activation in areas hMT+ to static images of objects visually learned as moving compared to those learned as stationary objects. However, we were unclear as to whether moving objects learned through haptics would also selectively activate this motion area. These results could have important implications in understanding the role of area hMT+ in crossmodal processing. While previous studies have shown that area hMT+ is involved in processing motion information within vision and touch, it is unknown if area hMT+ processes implied motion in other modalities. Also, these results will further determine whether this information is shared across modalities. We were also interested in whether the lateral occipital complex (LOC) was activated by images of the learned objects irrespective of learning modality and learned motion. We propose that if motion is integrated into a single representation of the object then we would expect to find increased activation in LOC as well as hMT+ to images of objects learned as moving. If motion is processed as a separate feature from shape information then we would not expect to see any change in activation in area LOC across the image types.

## Methods

### Participants

Seventeen participants (10 female and 7 male) between the ages of 20 and 48 years (mean age 30.38 years) took part in this experiment. All participants were right hand dominant, reported to have normal or corrected to normal vision and were native English speakers. All procedures were approved by the School of Psychology, Trinity College Dublin and, accordingly, informed consent was obtained prior to the experiment.

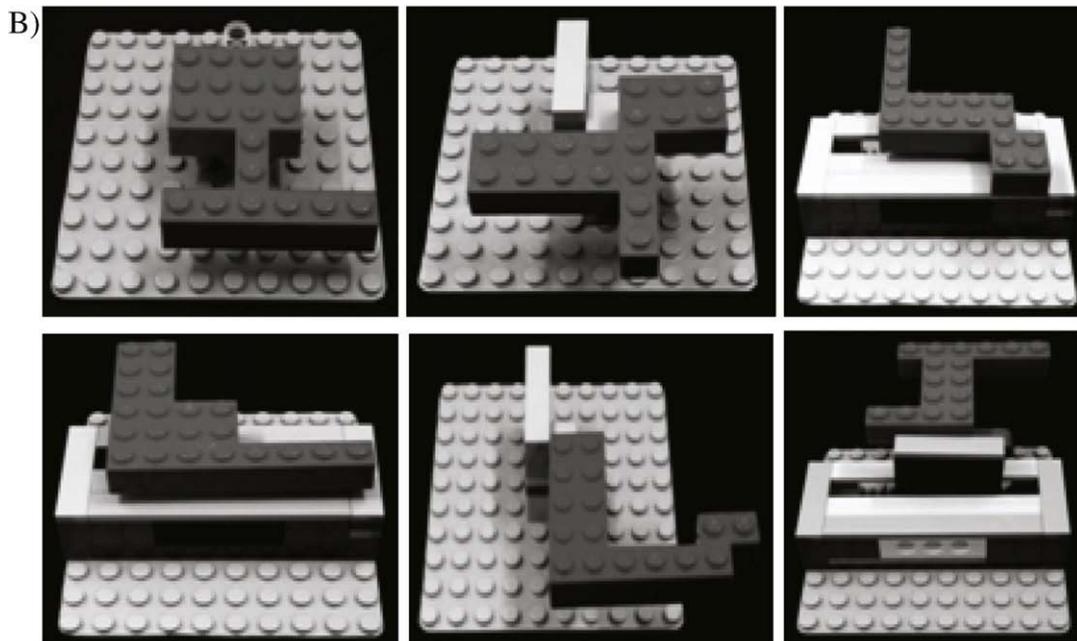
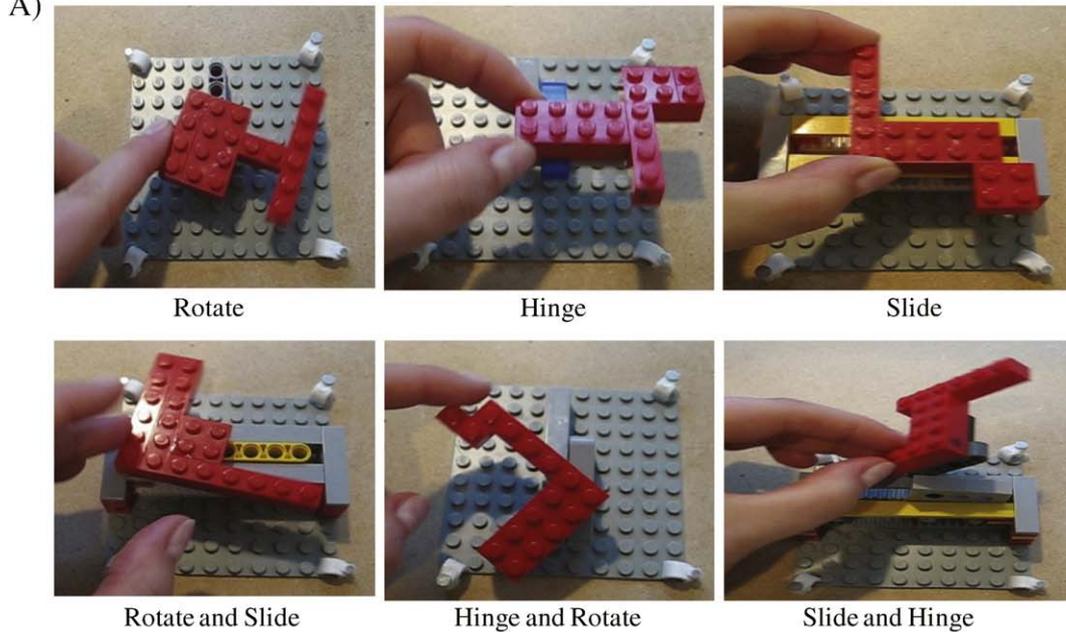
### Apparatus and stimuli

A set of 12 novel objects was created using Lego™ blocks and each was attached to a platform which prevented the participant from picking up the object. All objects were small enough to be easily palpated by the hands (8 cm × 8 cm). Each object shape was composed of between three and five blocks. For half of these objects, shape parts were built on a movable base structure which allowed the objects to be moved in one of six different ways, i.e., rotate, slide, pivot, slide and pivot, rotate and slide, and rotate and rotate (see Fig. 1 for an illustration of the shapes and motions). The remaining objects were similarly constructed but none of the parts were moveable.

In the learning phase, participants were presented with the 12 three-dimensional objects. High resolution photographs of these target objects were then taken from the viewpoint of the participant and converted to greyscale images using standard photo editing software. These images were used as stimuli during the testing session which took place in the fMRI scanner. We also constructed an extra set of eight objects, and images of these objects which were not presented to subjects prior to imaging were used as non-target stimuli in the fMRI task.

The test session of the experiment was programmed using “Presentation” software (Neurobehavioral Systems, California). Responses were recorded via an MR-compatible two-button response pad (Cambridge Research Systems).

#### A) Object motions:



**Fig. 1.** A subset of six objects and motions used in the learning session. Each object has a unique shape and motion pairing. (A) Still images of a participant's haptic exploration in the learning session. In the haptic-motion condition, participants moved the objects themselves. In the visual-motion condition, participants viewed the objects while the experimenter manipulated the object's motion. (B) Images used in the fMRI (test session).

A motion localizer stimulus was used to identify functional area hMT+ in each participant. The stimuli consisted of moving concentric circles (frequency 50 Hz) alternating with a static image (Hampson et al., 2004; Kourtzi and Kanwisher, 2000; Tootell et al., 1995b). The static image appeared as a single frame of the moving counterpart. These stimuli were created using the Visgen toolkit associated with Presentation.

#### *Design and procedure*

There were two sessions to the experiment: a learning session immediately followed by a test session. The learning session was conducted prior to neuroimaging and the test session occurred while the participant was in the MRI scanner. During the learning session, participants learned to associate a nonsense name to each target object. The task inside the scanner was based on an old-new recognition paradigm, where participants determined whether each visually presented object was previously learned (i.e., 'old') or not (i.e., 'new') regardless of the modality through which they were learned or whether they were moving or not during learning.

#### *Learning session (behavioural)*

The learning phase consisted of four separate learning blocks: two haptic-only blocks and two vision-only blocks. Each block consisted of three objects. Within each sensory block all objects were presented as either fixed in position (i.e., static) or were movable. The presentation order of these four blocks was counterbalanced across participants. During this session all target objects were placed behind a curtain which obscured the object from the participant's view. To ensure that participants adequately learned each target object and all of its properties, they were instructed to explore all aspects of each target object. To aid explanation, participants were provided with examples of manipulable objects in the real world which comprise several features and functions such as a door handle, a stapler or a hand whisk. These example objects have a characteristic shape and motion and were provided as an indication of the range of object types that could be tested but there was no emphasis given to a particular feature (i.e., neither motion nor shape was singled out for attention).

During haptic learning, participants reached underneath the curtain with both hands to feel the object for 30 s. All object parts of each target could be freely explored during haptic learning. For the moving target objects, the objects did not move independently but could be moved by the participant during active exploration. During visual learning, participants lifted the curtain for 10 s to see the object and lowered it when instructed by the experimenter. For the moving visual target objects, participants viewed the target object while the experimenter moved the object. In the visual-static block, participants viewed the stationary object for 10 s and participants were encouraged to remain still. However, their heads were not fixed in place.

To ensure that participants were exploring all aspects of the objects for recognition, participants were required to associate each object with a given nonsense name (e.g., "nof," "zam," "kuk"). Within each block of trials, an object was presented four times in succession and the experimenter provided the name of each object to the participant. At the end of each block, the target objects were randomly presented to the participant one at a time, and he or she was required to recall the correct name of the object.

After conducting all four blocks of learning, participants were then tested on their object-name recall. Participants were randomly presented with objects across all conditions. They were informed beforehand in which modality the object would be presented but not whether the object would be moving or static. This was an unspeeded task, thus participants could take as long as they needed to answer correctly. All responses were recorded by the experi-

menter. The learning session was repeated until participants were able to recall the names of the objects with an accuracy of over 90% correct (i.e., 11 out of 12 correct responses). On average, training lasted approximately 60 min. Participants were brought to the fMRI scanner immediately after training to take part in the test session.

#### *Test session (neuroimaging)*

Prior to functional acquisition during the test session, we acquired structural scans, which lasted approximately 12 min. During the test session, participants were presented with static visual images only of the target objects which they learned during the learning session. The main test session was based on a 2 × 2 repeated measures design with learning modality (haptic or visual) and learned motion (static or motion) as factors. For the purposes of this test, participants were told to ignore the names of each object but instead indicate whether the object was previously learned or not.

The test session was separated into six runs, with each run lasting approximately 6 min. The protocol was based on an event-related design which was implemented with a jittered inter-trial interval (ITI) of 6, 8, 10 or 12 s. A trial began with a red fixation cross which was presented for the duration of the ITI. This was immediately replaced by a blue fixation cross which was presented for 2 s. Participants were instructed that the blue fixation cross signalled the imminent appearance of a stimulus object. A static image of an object was then presented for 4 s. Following the trial, participants were given 2 s to indicate whether the object image they saw was one they had learned before or not. Images of objects were presented in a random order across all runs. In 60% of trials the old object was presented with a new object presented in the remaining trials. There were 120 trials in total with 8 repetitions of each old object and 3 repetitions of each new object. This was done to ensure that participants did not become familiar with the new stimuli.

Following the test session, participants were presented with visual images designed to localise functional area hMT+. There were 12 interleaved blocks of 6 moving and 6 static visual images in total, with each block lasting 16 s. The participants were required to look at the fixation point at the centre of each visual image but they were not required to perform a task. The entire scanning session lasted approximately 50 min.

#### *fMRI data acquisition and data analysis*

Scanning was performed with a Philips Intera Achieva 3.0 Tesla whole-body MR system (Philips Healthcare, The Netherlands) equipped with a mirror that reflected a 1024 × 768 display, projected on a panel placed behind the participant's head outside the magnet. The mirror was mounted on the head coil in the participant's line of vision.

Imaging started with 31.5 s of standard scout images to adjust for head positioning, followed by a reference scan to resolve sensitivity variations. Imaging used a parallel SENSitivity Encoding (SENSE) approach (Pruessmann et al., 1999) with reduction factor 2. One hundred and eighty high-resolution T1-weighted anatomic MPRAGE axial images (FOV 230 mm, thickness 0.9 mm, voxel size 0.9 × 0.9 × 0.9) were then acquired (for a total duration of 5.43 min), to allow subsequent activation localization and spatial normalization.

The functional scans consisted of 32 non-contiguous (10% gap) 3.5 mm axial slices covering the entire brain were collected using a T2\* weighted echo-planar imaging sequence (TE = 35 ms, TR = 2000 ms, FOV 224 mm, 64 × 64 mm matrix size in Fourier space). The spontaneous changes in frequency were automatically corrected by the Intera Achieva by means of dynamic stabilization (real-time frequency adjustment) after each TR.

The analyses of the functional activations were restricted to trials to which the participant responded correctly. This was done to ensure that we were analyzing brain activation related to an accurate

perception of the learned object. The six functional task runs were concatenated (yielding 771 volumes) and motion corrected. Four separate time-series regressors were created by convolving the timing of each object stimulus (i.e., haptic motion, haptic static, visual motion and visual static) with a gamma-variate function to account for the BOLD hemodynamic response function and the regression analysis was conducted using the '3dDeconvolve' program in AFNI (Cox, 1996). The magnitude of the signal change from baseline associated with each regressor was carried forward to group analyses. Spatial smoothing was then applied for all time points of activation using a 3-mm full width half-maximum Gaussian kernel. For group analysis, individual brains were converted into standard anatomical space (Talairach and Tournoux, 1988).

For the single localiser run, a separate square-wave regressor was convolved with a gamma-variate function, contrasting the moving and static concentric circles and then motion corrected.

We conducted a repeated measures, voxel-wise,  $2 \times 2$  random effects ANOVA on the activation, with learning modality (vision or touch) and learned motion (motion or static) of the target object as factors. The results of this group analysis were *F*-maps indicating the extent to which each factor or the interaction between factors modulated brain activity for each voxel. Voxels were then thresholded at  $p \leq 0.005$  which, when combined with a cluster size criterion of  $285 \text{ mm}^3$ , resulted in a false positive level of  $p \leq 0.05$  (corrected) as calculated by Monte Carlo simulation.

We were also specifically interested in determining if object area LOC and motion area hMT+ were activated by images of objects previously learned either visually or haptically or as static or movable objects. To that end, we created 5 mm radius ROI spheres based on the coordinates of hMT+ as revealed by the localiser (Talairach coordinates: 40, -71, 4) and on the coordinates for LOC (Talairach coordinates: 43, -73, -18) provided by Malach et al. (1995). For both ROIs,  $2 \times 2$  repeated measures ANOVAs were conducted with learning modality and learned motion as factors.

## Results

### Behavioural results

Accuracy averaged across participants and conditions during the test session was 65%. A one-way ANOVA found no significant difference in accuracy across conditions [ $F(4,65) < 1$ , n.s.]. Performance in each target condition was greater than chance level (15%) with significant differences between chance performance and the haptic-motion condition (mean = 64.58% [ $\chi^2 = 206.30$ ,  $p < 0.0001$ ]), haptic-static condition (mean = 68.15%) [ $\chi^2 = 247.22$ ,  $p < 0.0001$ ], visual-motion condition (mean = 58.93%) [ $\chi^2 = 142.04$ ,  $p < 0.0001$ ], visual-static condition (mean = 72.62%) [ $\chi^2 = 292.96$ ,  $p < 0.0001$ ], and the correct recognition of new objects (chance = 40%; mean = 66.37%) [ $\chi^2 = 46.25$ ,  $p < 0.0005$ ].

### fMRI results

As previously stated, fMRI analyses were restricted to the correct responses alone to ensure that activations were related to the veridical percept of the object. Furthermore, we excluded activations to the presentation of the new objects from any further analyses as these responses were not of relevance to the investigation (but were nevertheless important for the task).

### Whole-brain analysis

Fig. 2 illustrates the cortical areas which were selectively activated by either learning modality (vision or haptics) or object motion (moving or stationary). The voxel-wise analysis revealed two areas where activation was modulated by the modality through which the objects were learned. There was a significant difference in

BOLD activation in the right fusiform gyrus (Talairach coordinates: 47, -61 -18) [ $F(1,14) = 29.21$ ,  $p < 0.001$ ] for learning modality, with greater activation for the objects previously learned through the visual modality than those learned through touch (regardless of motion). Interestingly, an effect of learned motion approached significance in the right fusiform gyrus [ $F(1,14) = 4.04$ ,  $p = .064$ ] with greater activation to objects learned as moving than those learned as static. There was no interaction between the two main factors here. We found greater activation in the right inferior frontal gyrus (Talairach coordinates: 50, 16, 20) for objects learned through vision compared to those learned through touch [ $F(1,14) = 36.19$ ,  $p < 0.001$ ]. There was no main effect of motion [ $F(1,14) > 1$ , n.s.] nor was there an interaction between these two factors [ $F(1,14) > 1$ , n.s.] on activations in the right inferior frontal gyrus.

The only cortical area within which there was greater activation to objects previously learned as moving than those learned as static was in the right middle occipital gyrus (Talairach coordinates: 15, -91, 14) [ $F(1,14) = 33.30$ ,  $p < 0.001$ ]. There was no main effect of learning modality [ $F(1,14) < 1$ , n.s.] nor was there an interaction between these two factors [ $F(1,14) < 1$ , n.s.].

Finally, we found a significant interaction between the factors learning modality and object motion at learning, in activations in two cortical areas, namely, the left precuneus (Talairach coordinates: -10, -39, 44) [ $F(1,14) = 25.62$ ,  $p < 0.001$ ] and the right postcentral gyrus (Talairach coordinates: 17, -46, 66) [ $F(1,14) = 22.54$ ,  $p < 0.001$ ]. These interactions are depicted in Fig. 2. Both areas were deactivated when presented with images of the haptic-motion and visual-static learned objects. In contrast, these areas were more activated when participants were presented with images of either the haptic-static or visual-motion learned objects.

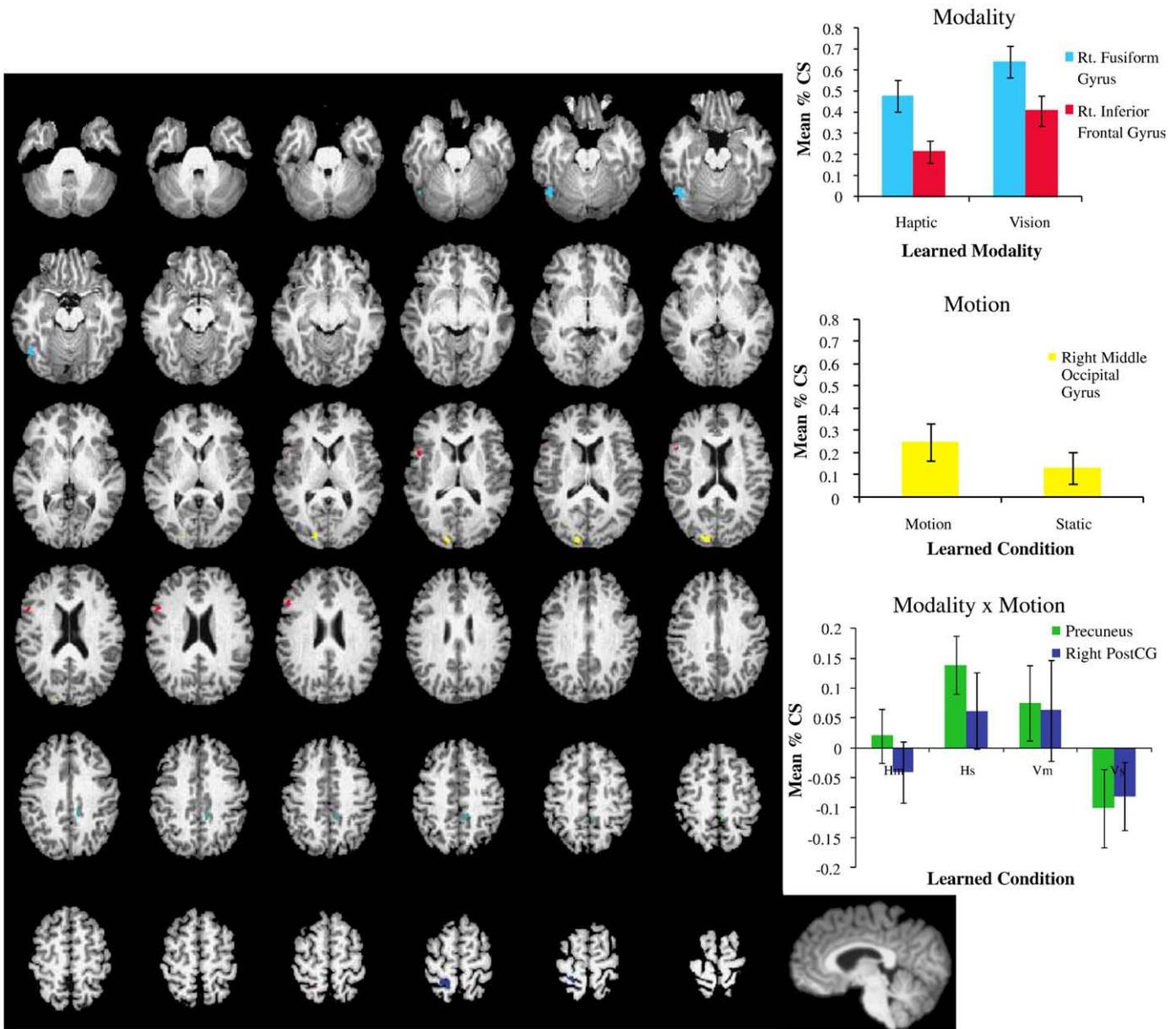
### Regions of interest

Further examination of the whole-brain analysis revealed areas hMT+ and LOC were activated in the object motion condition at the  $p = 0.01$  (uncorrected) level. This cluster did not survive correction for multiple comparisons. Therefore, we conducted a ROI analysis on each of these areas, based on the a priori hypothesis that BOLD activation in these areas would be modulated by implied motion.

Area hMT+ was localised by measuring the BOLD activation, contrasted between the moving and static stimulus blocks. The centre of mass for this cluster (Talairach coordinates: 40, -71, 4) was then used to create a region of interest sphere with a radius of 5 mm. These coordinates are in line with previous studies (Beauchamp et al., 1997, 2007; Kourtzi et al., 2002; Ricciardi et al., 2007; Tootell et al., 1995b).

A  $2 \times 2 \times 2$  repeated measures ANOVA was conducted on activations in hMT+, with hemisphere (right or left), learning modality (touch or vision), and object motion (moving or static) as factors. Fig. 3A depicts the effects of each factor on activations in this area. There was a main effect of hemisphere, with significantly greater activation in the right hemisphere compared to the left [ $F(1,14) = 9.16$ ,  $p < 0.01$ ]. There was no main effect of learning modality [ $F(1,14) < 1$ , n.s.]. However, there was a significant main effect of motion [ $F(1,14) = 9.65$ ,  $p < 0.01$ ] with greater BOLD activations to static images of objects previously learned as moving than images of objects learned as stationary. There was a significant interaction between hemisphere and object motion [ $F(1,14) = 10.45$ ,  $p < 0.01$ ]. Only activation in the right hemisphere was modulated by object motion.

A similar  $2 \times 2 \times 2$  repeated measures ANOVA was performed on activations within the right LOC with hemisphere (right or left), learning modality (touch vs. vision) and object motion (moving vs. static), and as factors. There was a main effect of hemisphere with greater activation in the left hemisphere compared to the right [ $F(1,14) = 6.05$ ,  $p = 0.03$ ]. There was no difference in activations to object images across the different learning modalities [ $F(1,14) < 1$ , n.s.].



**Fig. 2.** Activations represent the results from the voxel-wise whole-brain,  $2 \times 2$  random effects ANOVA, with modality (vision vs. touch) and motion (motion vs. static) as factors. Graphs represent the clusters of significant activation for each main effect and interaction between the factors. Error bars represent the SEM. Images are using the neurological convention.

However, we found a main effect of motion [ $F(1,14) = 7.87, p = 0.01$ ], with significantly greater BOLD response in right LOC when seeing a static object image that was previously learned as moving object compared to seeing an image of an object previously learned as stationary. There were no other significant interactions (Table 1).

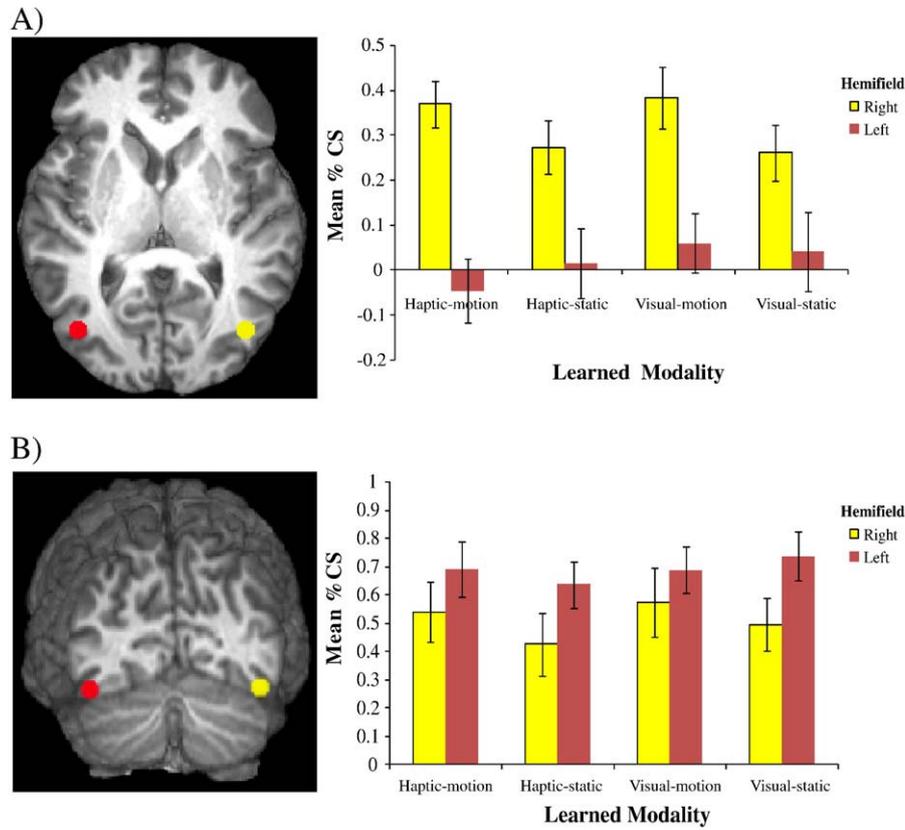
To assess the specificity of the ROI results, we conducted an additional 5 mm spherical ROI analysis on Brodmann area 17 (V1; Talairach coordinates: right: 10, -66, 17; left: -9, -67, 17) (Dougherty et al., 2003), a region in which we would not hypothesise activity to be influenced by learning modality or object motion. The same  $2 \times 2 \times 2$  repeated measures analysis performed for the previous ROI areas was also conducted here. There were no significant effects or interactions.

**Discussion**

In summary, prior to scanning, participants were trained to recognise a set of novel objects which either had moving or static

parts as experienced through either touch or vision. In the fMRI scanner, participants were presented with static images of these target objects and other non-target objects and were required to perform an old/new task. We found increased activation in several areas which was specifically related to the learning modality and whether the objects were learned as moving or not. In particular, activations in areas hMT+ and LOC within the right hemisphere differed for images of objects that implied motion and not images of objects that were stationary, regardless of modality.

This study investigated whether static images of moving objects previously learned through touch also activates hMT+, an area previously shown to be active for implied visual motion (Kourtzi and Kanwisher, 2000). By presenting static visual images, we were able to demonstrate that area hMT+ processes the implied motion from objects previously learned through touch as well as vision. Activation from the hMT+ localiser was found in only the right hemisphere which is similar to the results reported by Kourtzi and Kanwisher (2000). This lateralization of hMT+ activity could be due to a greater



**Fig. 3.** (A) Results from the hMT+ ROI analysis. The 5 mm sphere represents the Talairach coordinates from the hMT+ localizer task. (B) The results from the LOC ROI analysis. The 5 mm sphere represents the Talairach coordinates taken from Malach et al. (1995). For both analyses, results indicate the BOLD activation, thresholded to 0.005 and *p* correct to 0.05. Images are using the neurological convention.

involvement of the right hemisphere in spatial processing, whereas the left hemisphere is thought to be more involved in linguistic processing (Grèzes et al., 2001; Large et al., 2007; Van Boven et al., 2005; Vandenberg et al., 2006).

In a related study, James and Gauthier (2003) investigated cortical activations associated with learned associations between visually presented unfamiliar objects and either auditory, action or encyclopedic semantic labels presented verbally. They found that each concept activated sensory-specific networks. In particular, auditory concepts activated the superior temporal gyrus, whereas action concepts activated more posterior regions in the superior temporal sulcus. The authors conducted ROI analyses within these specific regions, however, and did not report activation specifically in area hMT+ for the presentation of novel visual objects associated with action concepts. It may be the case, therefore, that previous

direct sensory experience with moving objects may be necessary to activate this area (Beauchamp and Martin, 2007).

Interestingly, there was also a significant difference in BOLD activation in area LOC when participants were shown objects that were learned moving compared to objects which did not move during learning. However, the increased activation in LOC for the learned moving objects could be due to the additional information provided about the object while the object was moved (Gauthier et al., 2002; Grill-Spector et al., 1999) and not due to pure motion information. Gauthier et al. suggest that additional information enhances mental imagery in the superior and inferior parietal lobules, but they did not find that changes in viewpoint increased activation during an object recognition task in those areas of LOC. Thus, it is possible that the increase in BOLD response we see in LOC was not due to additional viewpoint information of the motion

**Table 1**  
A summary of BOLD activation when viewing static greyscale images of the target objects.

Brain area	Hemifield	Talairach coordinates			Learning conditions				Statistics	
		x	y	z	% Change score				F-stat	p-value
					Haptic motion	Haptic static	Visual motion	Visual static		
ROI										
MT+	Right/left	± 40	-71	4	0.411	0.302	0.395	0.294	9.65	<0.01
LOC	Right/left	± 43	-73	-18	0.541	0.425	0.572	0.495	7.87	0.01
Voxel-wise analysis										
Fusiform gyrus	Right	47	-61	-18	0.487	0.471	0.708	0.579	29.21	<0.0001
Inferior frontal gyrus	Right	50	16	20	0.241	0.19	0.406	0.41	36.188	<0.0001
Middle occipital gyrus	Right	15	-91	14	0.237	0.134	0.26	0.128	33.3	<0.0001
Precuneus	Left	-10	-39	44	0.02	0.139	0.075	-0.101	25.62	0.0001
Post-CG	Right	17	-46	66	-0.04	0.062	0.063	-0.081	22.54	0.0003

ROI statistics represent the main effects of object motion analyses. Voxel-wise statistics are the results of the 2 × 2 whole-brain analysis.

component but due to an integration of motion and shape information (see e.g., Kriegerkorte et al., 2003).

The whole-brain analysis revealed activation in the precuneus and right postcentral gyrus under certain conditions. The precuneus has been shown to be active during tasks involving visuo-spatial attention (see Cavanna and Trimble, 2006 for a review) as well as mental imagery of self-generated movement (Hanakawa et al., 2003). For example, Hanakawa et al. asked participants either to finger-tap in time to a visual cue or to imagine themselves finger tapping. They found greater activation in the precuneus for imagined finger tapping compared to real finger tapping. We found increased activation in this area for the haptic-static and visual-motion conditions compared to the haptic-motion and visual-static conditions. If the precuneus is involved in the mental imagery of self-generated motion we would have expected activation in the haptic-motion condition instead of the haptic-static condition. Increased BOLD activation in the right postcentral gyrus, the primary somatosensory processing area, was surprising given that participants did not feel the objects in the scanner. Activation in this brain region followed the same pattern as activation in the precuneus in that there was increased activation for the haptic-static and visual-motion conditions compared to the haptic-motion and visual-static conditions. This may suggest increased spatial attention or mental imagery (Corbetta, 1998; Hopfinger et al., 2000). Clearly further research is needed to interpret these interactions between learning modality and object position and the role of mental imagery.

The right fusiform gyrus was found to be more active when participants were presented with images of objects previously learned through vision than through touch. There was also a near significant difference of motion in this brain area with images of objects previously learned as moving producing greater activation than images of objects learned as stationary. This suggests that the motion of an object is a feature which is integrated into a representation of an object and is not processed independently of object shape (Wiggett et al., 2006).

Images of objects which were previously learned as moving also activated the right middle occipital gyrus. This area has been implicated in tasks in which object shape is derived from motion and not to coherent motion without shape (Braddick et al., 2000). Taken together, the results from these studies suggest that the middle occipital gyrus may be involved in the integration of shape and motion, and not just deriving shape from motion, and that activations in the rMOG are independent of the modality through which the moving object was initially learned.

In the learning phase, participants either manipulated the objects by touch or saw the objects being manipulated by the experimenter in the object motion conditions. Clearly, there was less interaction with the object features when the object was learned as stationary or when the object was learned through vision. Consequently, it may be argued that the activations in area hMT+ and the middle occipital gyrus are action related instead of object related. However, we do not believe this to be the case for several reasons. First, the difference in activations in area hMT+ to the images of objects learned as moving and those learned as stationary was modality independent. If activations were related to interaction with the objects then it might be expected that there would be greater activations to objects learned through the haptic modality than those learned visually. Second, it has been shown that object–hand interactions activate the precentral gyrus, pars triangularis and part opercularis in humans (BA44: Johnson-Frey et al., 2003). Johnson-Frey et al. presented still images of a hand grasping an object in a functional or non-functional way, or simply touching the object (the palm was facing away from the object) and found that prehensile action was sufficient to elicit activation in these areas. In other words, implied goal-directed action was enough to activate the inferior frontal gyrus. We did not find any significant changes in activation in these brain areas across the images

of objects learned through touch or vision. Instead, areas activated by images of objects learned as moving or not and learned through vision or touch tended to activate a network within ventral areas of the cortex commonly associated with object recognition.

In this study, we present new findings suggesting that the once so-called visual middle occipital gyrus, hMT+, and LOC are areas involved in the processing of implied motion of objects through vision and touch. More importantly, this processing of implied motion is shared across modalities. These results further elucidate the multisensory nature of information processing in the human brain for the purpose of object recognition and add to the growing evidence that object motion and shape is integrated for the purpose of recognition.

## Acknowledgments

This research was funded by the Irish Research Council for the Humanities and Social Sciences.

This work was supported by access to the IITAC advanced computing and visualisation facilities, funded by the HEA PRTL program and the NDP, provided by the Trinity Centre for High Performance Computing.

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