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Research Report

Motor experience with graspable objects reduces their implicit analysis in visual- and motor-related cortex

Todd C. Handy[a,*], Christine M. Tipper[a], Jana Schaich Borg[b], Scott T. Grafton[b], Michael S. Gazzaniga[b]

[a]Department of Psychology, University of British Columbia, 2136 West Mall, Vancouver, BC, Canada V6T 1Z4
[b]Center for Cognitive Neuroscience, Dartmouth College, Hanover, NH 03755, USA

ARTICLE INFO

Article history:
Accepted 8 April 2006
Available online 9 June 2006

Keywords:
Motor cortex
Visual expertise
Object perception
Action
fMRI

ABSTRACT

Motor-related regions of parietal and prefrontal cortices have been shown to selectively activate when observers passively view objects that afford manual grasping. Yet, it remains unknown whether these cortical responses depend on prior motor-related experience with the object being observed. To address this question, we asked participants to undergo fMRI scanning while viewing exemplars of two different categories of graspable objects: one associated with extensive motor experience (door knobs) and one associated with no self-reported motor experience (artificial rock climbing holds). Despite participants' lack of experience grasping climbing holds, these objects were found to generate a systematic response in several visuomotor-related regions of cortex—including left PMv and left AIP. Interestingly, however, the response to door knobs did not include activity in any motor-related regions, being limited instead to a comparatively small bilateral area of lateral occipital cortex, relative to the more spatially extensive response in occipital and temporal cortex that was observed for climbing holds. This result suggested that object-specific responses in both visual- and motor-related cortex may in fact negatively correlate with object-specific motor experience. To test this possibility, we repeated the experiment using participants having extensive self-reported experience grasping climbing holds (i.e., veteran indoor rock climbers). Consistent with our hypothesis, both climbing holds and door knobs generated activity limited to lateral occipital cortex. Taken together, these data support the proposal that repeated real-world motor experience with an object category may lead to reduced implicit analysis in both motor- and visual-related regions of cortex.

Visually guided hand actions are a cornerstone of human behavior. Although these actions may seem effortless to most, they involve a complex interplay between visual and motor functions in the brain (e.g., Milner and Goodale, 1995). Indeed, significant portions of parietal and prefrontal cortices are dedicated to the transformation of visual object representations into object-specific motor programs (e.g., Jeannerod, 1997, 2001; Jeannerod et al., 1995). As a consequence, when a graspable object such as a coffee cup comes into view, a variety of parietal and prefrontal regions have been shown to respond to that object independent of the observers intention to act—a phenomenon we will refer to here as an implicit visuomotor response, or iVMR (e.g., Chao and Martin, 2000; Grafton et al., 1997; Faillenot et al., 1997;

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* *Corresponding author.*
E-mail address: tchandy@psych.ubc.ca (T.C. Handy).

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doi:10.1016/j.brainres.2006.04.059

Grèzes and Decety, 2002; Handy et al., 2003, 2005; Martin et al., 1995, 1996). While the existence of iVMRs has been well-documented in both human and non-human primates, a critical question remains: what is the role of motor experience in the generation of iVMRs?

One hypothesis is that the generation of an iVMR depends on actual experience grasping the specific type of object being viewed. From this perspective, an iVMR would reflect a learned, object-specific motor association acquired through repeated real-world interactions. The greater one's experience–or expertise–manually interacting with an object, the more likely that object would generate an iVMR when viewed. However, an alternative hypothesis posits that iVMRs may be generated by any object that conforms to a grasp—appropriate shape, even in the absence of any prior motor-related experience with that object. According to this account, object-specific motor experience would not be a necessary antecedent for an iVMR. Rather, the presence or absence of an iVMR would depend on the physical parameters of the object itself, and in particular, whether the object surface appears to afford manual grasping.

To distinguish between these competing possibilities, we asked participants to undergo fMRI scanning while they observed color digital photographs of three different types or categories of objects (Fig. 1). Two of the object categories were selected based on their common level of semantic familiarity to the participants through everyday experience, with one object category–door knobs–assumed to have well-learned unimanual motor associations, and one category–car tires–assumed to have a comparatively reduced level of acquired unimanual motor association, if any at all. The third object category was plastic indoor rock climbing holds, objects specifically designed for unimanual grasping. However, because we specifically selected for participants self-reporting no prior experience with rock climbing, these climbing holds were objects conforming to a grasp-appropriate shape, but that would have no learned motor association in the participant cohort.

Given this paradigm, we expected door knobs to generate an iVMR but not car tires. In turn, the key question was whether or not an iVMR would be observed for climbing holds. A positive result would support the hypothesis that iVMRs do not depend on object-specific motor experience, whereas a negative result would suggest that motor experience is in fact necessary for these cortical responses.

1. Experiment 1

1.1. Materials and methods

1.1.1. Participants

Sixteen right-handed volunteers were paid to participate in Experiment 1 (6 male, 10 female, age 18–32 years old, mean = 24.4 years). All had normal or corrected-to-normal vision, and all self-reported no experience with (or practical knowledge of) rock climbing, indoors or out. All procedures and protocols for participants were approved by the Dartmouth College Committee for the Protection of Human Subjects.

1.1.2. Stimuli and procedures

Participants performed a simple target detection task that required them to view color digital photographs of door knobs, car tires, and indoor rock climbing holds (Fig. 1) while waiting for an infrequent but suprathreshold square-wave target to be superimposed over the center of an object; the objects themselves were thus irrelevant to the task, in terms of the pictorial content displayed. On trials when a target was presented, participants made a manual response with the thumb, indicating that the target was detected; the responding thumb (left or right) was counterbalanced between participants. Each color photograph was approximately 5° wide by 4° tall, with the actual object approximately centered within the frame of the photo. The square-wave target was formed using black bars, was approximately 2° square, and was approximately 2 cycles/degree. Stimulus delivery was controlled using Presentation software (Neurobehavioral Systems, Inc., Albany, CA; http://nbs.neuro-bs.com/) and displayed via rear-projection on an LCD projector (Epson ELP-7000). Photographs were presented for 1750 ms, with a 750 ms ISI. Targets (when present) appeared for 200 ms and followed the photograph onset by 1000 ms.

Each block of trials contained a total of 24 presentations of each object type, with 21 of those presentations having no target and 3 presentations having a target. There were thus a total of 72 trials per block, with targets included on 12.5% of these trials. For each object category, there were 24 different exemplars of that object; on every trial, an object was selected from the appropriate category with replacement. The order of trial type (object category and target presence/absence) was randomized within and between trial blocks. Randomly interspersed with the 72 trials were 18 fixation-only intervals

Fig. 1 – Examples of the three object categories. The entire object set is available for web-based viewing and download (see Materials and methods).

lasting one, two, or three TRs in duration; these intervals were included in order to optimize deconvolution of the event-related hemodynamic response (e.g., Miezin et al., 2000). In addition, each block of trials began and ended with 25 s of fixation-only "rest". Each participant performed a total of 5 trial blocks, with each block corresponding to one "functional" scanning run, as described below. The actual 72 digital photographs used in the experiment are available for on-line viewing and downloading at (http://neuroimaging.psych.ubc.ca/climber.htm). Note that behavioral data for four subjects from Experiment 1 and two subjects from Experiment 2 are not included in the respective analyses due to failure of the data recording system at the time of scanning. However, on-line monitoring of performance suggested no abnormalities in their behavioral patterns.

1.1.3. *fMRI recording and analysis*

fMRI data were collected using a 1.5 T SIGNA scanner (GE Medical Systems, Milwaukee, WI) with a fast gradient system for echo-planar imaging (EPI). Dense foam padding was used for head stabilization. Scanning was performed in a dimly lit room, with the visual stimuli rear-projected to a screen behind the participant's head and viewed via a headcoil-mounted mirror. EPI images in-plane with the AC–PC line were acquired using a gradient-echo pulse sequence and sequential slice acquisition (TR = 2500 ms, TE = 35 ms, flip angle = 90°, 25 contiguous slices at 4.5 mm skip 1 mm, in-plane resolution of 64 × 64 pixels in a FOV of 24 cm). Each functional run began with four TRs during which no data were acquired to allow for steady-state tissue magnetization. The beginning of each trial and fixation-only interval was synchronized to the onset of acquisition for each EPI volume. A total of 128 EPI volumes were collected in each functional run, and a total of five functional runs were performed by each participant. High-resolution, T1-weighted axial images were also taken of each participant (TR = 25 ms, TE = 6 ms, bandwidth = 15.6 kHz, voxel size = 0.9375 × 1.25 × 1.2 mm). Data were processed and analyzed using SPM2 (http://www.fil.ion.ucl.ac.uk/spm). For each subject, the EPI images were corrected for motion (e.g., Friston et al., 1996) and then spatially normalized into MNI stereotaxic coordinates using the EPI template provided with SPM2 (e.g., Friston et al., 1995a). The normalized EPI images were then spatially smoothed using an isotropic 8 mm Gaussian kernel.

For each participant, the smoothed, normalized EPI data were analyzed via multiple regression using a fixed-effects general linear model (e.g., Friston et al., 1995b). In particular, the event-related responses to the onsets of the objects were examined, with each participant's model including six event-related regressors: one for each of the three objects on target absent trials (as effects of interest) and one for each of the three objects on target present trials (as effects of non-interest). Regressors were based on the canonical event-related hemodynamic response function, temporal derivatives of the event-related responses were included as additional regressors, and low-frequency scanner and/or physiological noise was modeled via linear, quadratic, and cubic regressors of non-interest. Group-level analyses were then based on a random-effects model using one-sample t tests. Mean β values reported for clusters identified in the group-wise data were extracted from the SPM2 data files using custom scripts implemented in MATLAB (The MATHWORKS Inc., Natick, MA); the group-wise cluster means were calculated by first determining each participants' mean β across all voxels in the given cluster. All reported voxel coordinates were converted to Talairach coordinates (e.g., Talairach and Tournoux, 1988) using a modified version of the mni2tal MATLAB script (www.harvard.edu/~slotnick/scripts.htm).

In terms of analyzing the fMRI data, our experiment was predicated on examining object-specific iVMRs as a function of object category—climbing hold, door knob, or car tire. Our operational definition of an iVMR followed from neuroimaging evidence showing that a number of different visuomotor-related areas in cortex may respond when a graspable object such as a tool comes into view (e.g., Johnson and Grafton, 2003; Rizzolatti and Matelli, 2003; Picard and Strick, 2001). Depending on conditions, these areas have included both dorsal and ventral premotor cortex (PMd and PMv), the region just anterior to PMd (prePMd), the supplementary motor area (SMA), the region just anterior to SMA (preSMA), and both the inferior and superior parietal lobules (IPL and SPL) (e.g., Jeannerod, 1997; Chao and Martin, 2000; Grafton et al., 1997; Grèzes and Decety, 2002; Grèzes et al., 2003). However, because graspable objects presented at fixation have consistently generated iVMRs lateralized to the left cerebral hemisphere (e.g., Chao and Martin, 2000; Grafton et al., 1997), fMRI data analysis was thus anatomically restricted a priori to those object-specific responses occurring in left hemisphere regions previously linked to visuomotor analysis (e.g., Johnson and Grafton, 2003; Rizzolatti and Matelli, 2003; Picard and Strick, 2001): the perimotor/premotor area (e.g., Chao and Martin, 2000; Grafton et al., 1997; Grèzes and Decety, 2002; Handy et al., 2003, 2005; Grèzes et al., 2003; Martin et al., 1995, 1996) and adjacent parietal and prefrontal regions (e.g., Battaglia-Mayer et al., 2003; Burnod et al., 1999; Caminiti et al., 1998; Culham, 2004; Marconi et al., 2001; Matelli and Luppino, 2001; Shikata et al., 2003). Accordingly, all group-level contrasts reported below were based on a threshold of $P < 0.001$ (uncorrected), with a minimum spatial extent (k) of 10 contiguous voxels. Voxel coordinates are given in the stereotaxic coordinates of Talairach and Tournoux (1988).

1.2. Results

1.2.1. *Behavior*

Mean reaction times (RTs) to the targets are shown in Table 1 (top) and were examined as a function of the object over which

Table 1 – Reaction times (in ms), by experiment (SD in parentheses)

	Object		
	Door knobs	Climbing holds	Car tires
Experiment 1 (Non-climbers)	802 (178)	795 (182)	794 (170)
Experiment 2 (Climbers)	601 (117)	600 (127)	607 (122)

Data are shown as a function of the object over which the target was superimposed.

the target was superimposed. A repeated-measures ANOVA with a factor of object category (3 levels) showed no main effect of object type on RT ($F(2,22) = 0.21$) (note: behavioral data from four subjects were not included in this analysis; see Materials and methods). Accuracy performance was at ceiling.

1.2.2. *fMRI*

Initial analysis consisted of a set of three linear contrasts–one per object category–in order to identify voxel clusters in the anatomical region of interest (ROI) showing a significant increase in the event-related blood-oxygen-level-dependent (BOLD) response to any of the three object categories. The results of these contrasts are reported in Table 2 as a function of object type. While all three objects produced significant increases in the BOLD response in occipital cortex, only climbing holds were associated with an increased response in our parietal–prefrontal ROI (Fig. 2a). In particular, left ventral premotor cortex (PMv), left ventral motor cortex (M1v), and a region in the left anterior intraparietal sulcus (AIP) all showed a significant event-related response to the climbing holds.

Having identified three voxel clusters in the anatomical ROI manifesting a significant response to climbing holds, we then wanted to compare the response profile in each cluster across all three object categories in order to determine whether these regions were in fact differentially responding to climbing holds, relative to door knobs and/or car tires (Fig. 2b). Accordingly, an omnibus repeated-measures ANOVA was performed on the mean responses (or mean βs) within these clusters that had factors of cluster location (PMv, M1v, and AIP) and object type (climbing holds, door knobs, and car tires). This ANOVA revealed significant main effects of both cluster location ($F(2,30) = 5.05$; $P < 0.05$) and object type ($F(2,30) = 3.38$; $P < 0.05$), but no interaction ($F(2,30) = 1.01$). Given this main effect of object type, paired *t* tests between each object type within each voxel cluster confirmed that climbing holds had a consistently larger response relative to car tires (an object not expected to generate an iVMR) in all three voxel clusters (PMv: $t(15) = 4.46$, $P = 0.052$; M1v: $t(15) = 8.01$, $P < 0.05$; AIP: $t(15) = 4.64$, $P < 0.05$). In comparison, no *t* tests involving door knobs (vs. climbing holds or vs. car tires) approached significance (all Ps > 0.1).

Table 2 – Voxel cluster statistics for Experiment 1, by object

Object	Cluster			Anatomical locus	
	Coordinates	*t*	*k*	BA	Gyrus
Holds	28 −93 8	6.60	357	18	R middle occipital
	−24 −97 5	6.29	365	18	L middle occipital
	−36 −28 57	5.23	31	3	L postcentral
	−40 −17 41	5.03	11	4	L precentral
	32 −17 45	4.90	13	4	R precentral
	48 −57 25	3.61	11	39	R middle temporal
	−48 −3 26	4.35	12	9	L inferior frontal
Door knobs	40 21 25	5.58	21	46	R middle frontal
	24 −93 8	5.55	58	18	R middle occipital
	−24 −93 5	5.43	28	18	L middle occipital
Tires	28 −97 5	9.17	296	18	R middle occipital
	−32 −86 −6	8.40	336	18	L middle occipital

Reported coordinates and *t* values are for the cluster maxima. *k* = # of voxels in the cluster. BA = Brodmann's area, L = left, R = right.

1.3. *Discussion*

Two notable results were obtained in Experiment 1. First, the hemodynamic response generated by climbing holds in parietal and prefrontal cortex was consistent with an iVMR. As indicated by the initial contrasts, we found three clusters in the left cerebral hemisphere–PMv, M1v, and AIP–that manifest a significant increase in the event-related BOLD response for climbing holds. Not only were these clusters located in our anatomical region of interest, but each area showing this response has been previously tied to functions associated with visuomotor analysis. For example, it has been proposed that a circuit linking AIP and PMv underlies visuomotor transformations associated with grasping (e.g., Johnson and Grafton, 2003; Rizzolatti and Matelli, 2003; Binkofski et al., 1999; Frey et al., 2005). At the same time, M1–the primary motor region of the brain–has previously shown a sensitivity to both attention to action (e.g., Binkofski et al., 2001) and motor imagery itself (e.g., Hari et al., 1998; Schnitzler et al., 1997). While this does not mean that these functions are indeed manifest in the current data, given that participants had no prior experience with indoor climbing holds, the data are nevertheless consistent with the proposal that iVMRs do not depend on acquired motor experience with an object category. In short, this finding supports the hypothesis that iVMRs can be generated by an object conforming to a grasp-appropriate shape, even though the object may be unfamiliar to the observer and thus have no stored/learned motor representation.

Our second notable result concerned the response generated by door knobs. In particular, these objects were associated with well-learned motor associations acquired through a lifetime of repeated real-world experience opening doors, yet no apparent iVMR was observed. For example, while comparisons between mean responses (or βs) within left AIP, PMv, and M1v showed no significant differences between door knobs and climbing holds, door knobs also failed to show significant differences in these same comparisons made with car tires—an object category that did differ in mean response with climbing holds. These results suggest that door knobs had an intermediate and/or more varied level of response in the parietal and prefrontal clusters across participants, relative to climbing holds (which had a consistently larger response) and car tires (which had a consistently smaller response). Indeed, rather than generating the expected iVMR, the most salient characteristic of the response pattern observed for door knobs was that activity in visual cortex was limited to small bilateral regions of lateral occipital cortex. In comparison, both climbing holds and door knobs generated much more spatially extensive responses in visual cortex, extending from lateral occipital regions into ventral temporal areas bilaterally.

At least two reasonable hypotheses appear to exist to explain this unexpected pattern of reduced activity for door knobs in both visual- and motor-related cortex, relative to

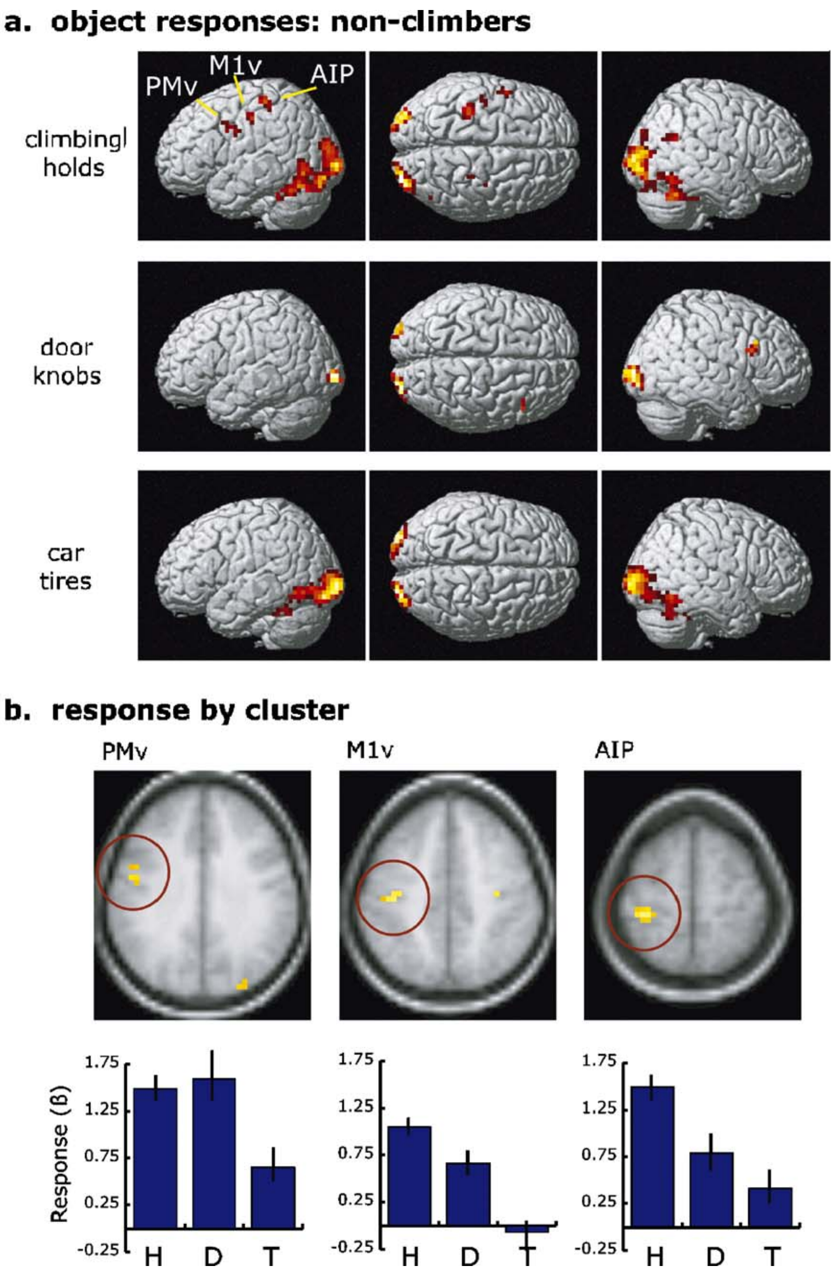


Fig. 2 – Results from Experiment 1. (a) Cortical regions showing significant increases in the event-related fMRI BOLD response for each of the three object categories. (b) The three clusters in left visuomotor cortex showing an iVMR to climbing holds, shown on a mean anatomical image averaged across the 16 participants from Experiment 1. PMv is shown at $z = 26$, M1v at $z = 41$, and AIP at $z = 57$. Below each cluster is plotted the mean response (or β) in the cluster for each of the three object categories, averaged across participants; H = holds, D = door knobs, and T = tires. Data shown were thresholded at $P < 0.001$ (uncorrected), with a minimum cluster size of 10 contiguous voxels.

climbing holds. First, the differential pattern may simply reflect between-object category differences in the low-level properties of the object images themselves. For instance, if there was an unequal distribution of image features–such as color, form, and/or spatial frequency–between the door knob and climbing hold exemplars, this could account for the differences in the extent of both visuomotor and occipitotemporal activity between conditions.

However, a second possibility is that the magnitude of analysis in these cortical areas may negatively covary with object-specific motor experience as participants in the experiment were well-practiced at grabbing door knobs but not climbing holds. That is, motor experience with an object may simplify or reduce the amount of implicit cortical processing generated by that object. Indeed, several converging lines of evidence support this possibility: the cortical representation of motor skills will change as object-specific actions become automatic or overlearned (e.g., Grafton et al., 1992, 1995; Passingham, 1996), familiar objects tend to generate less analysis in cortex–and less overall fMRI BOLD activity–relative to objects that are novel or unfamiliar (e.g., Habib and Lepage, 1999), and, finally, activity in visual cortical areas is reduced under conditions where object processing is more holistic or shape-oriented (e.g., Murray et al., 2002).

To distinguish between these two possibilities, we thus performed a second experiment that was identical to Experiment 1, with the exception that the participants were selected for having a year or more of experience with indoor rock climbing. If the data pattern obtained in Experiment 1 was based solely on between-category differences in the low-level properties of the object images, it predicted that we should replicate the results from our initial experiment across all three object categories. Conversely, if the differences observed between climbing holds and door knobs were due to a difference in real-world motor experience with these objects, it predicted that (1) a similar response pattern should be observed for door knobs and climbing holds, and (2) the pattern should resemble the pattern of BOLD activity observed for door knobs in Experiment 1—a reduction in the spatial extent of activity in occipitotemporal cortex (relative to car tires) and an absence of significant activity in left parietal and prefrontal cortices.

2. Experiment 2

Sixteen right-handed volunteers were paid to participate in Experiment 2 (12 male, 4 female, age 18–29 years old, mean = 21.8 years). All had normal or corrected-to-normal vision, and all self-reported over 1 year of consistent experience climbing indoors on artificial rock climbing holds, defined as climbing indoors at least once a week, on average. The mean number of years of experience climbing indoors was 3.6, and the range was 1.5–7 years. All other stimuli, procedures, and analysis protocols were identical to Experiment 1.

2.1. *Results*

2.1.1. *Behavior*

Mean reaction times (RTs) to the targets are shown in Table 1 (bottom) and were examined as a function of the object over which the target was superimposed. A repeated-measures ANOVA with a factor of object category (3 levels) showed no main effect of object type on RT ($F(2,26) = 0.21$) (note: behavioral data from two subjects were not included in this analysis; see Experiment 1). Accuracy performance was at ceiling.

2.1.2. *fMRI*

As with Experiment 1, all group-level contrasts were again based on random-effects models thresholded at $P < 0.001$ (uncorrected), a minimum spatial extent (k) of 10 contiguous voxels, with voxel coordinates given in the stereotaxic coordinates of Talairach and Tournoux (1988). Initial analysis again consisted of a set of three linear contrasts in order to identify all voxel clusters showing a significant increase in the event-related blood-oxygen-level-dependent (BOLD) response to any of the object categories. The results of these contrasts are reported in Table 3 as a function of object type. All three objects produced significant increases in the BOLD response in occipitotemporal cortex, but the spatial extent of this activity was numerically greater for car tires, relative to climbing holds and door knobs (Fig. 3a). Notably, however, no areas of significantly increased BOLD activity were found in left visuomotor-related cortex for any of the object types.

Table 3 – Voxel cluster statistics for Experiment 2, by object

Object	Cluster			Anatomical locus	
	Coordinates	t	k	BA	Gyrus
Holds	−40 −70 3	5.74	17	37	L middle occipital
	44 −82 1	5.62	51	18	R middle occipital
	−32 −89 4	5.19	25	18	L middle occipital
Door knobs	12 −94 −9	6.60	19	17	R lingual
	28 −66 3	6.08	39	18	R middle occipital
Tires	20 −89 8	8.70	645	18	R cuneus
	−32 −78 −13	8.57	613	19	L fusiform
	48 −3 22	6.45	12	9	R precentral
	48 39 −2	6.41	16	10	R inferior frontal
	48 −33 46	6.37	54	40	R IPL
	28 −52 43	6.16	29	7	R SPL
	44 10 47	5.03	13	6	R middle frontal

Reported coordinates and t values are for the cluster maxima. k = # of voxels in the cluster. BA = Brodmann's area, L = left, R = right, IPL = inferior parietal lobule, SPL = superior parietal lobule.

Because one purpose of Experiment 2 was to determine whether or not an iVMR to climbing holds would be observed in left parietal and/or prefrontal cortex, we performed several additional analyses to more closely consider possible hold-specific responses in these regions. To assess whether increased activity was present but perhaps occurring just under the $P < 0.001$ threshold, we re-examined the event-related BOLD response to the climbing holds at two successively less-restrictive thresholds. At a value of $P < 0.005$ (minimum $k = 10$ voxels), clusters emerged in bilateral superior parietal cortex (maxima at 44/−52/44 and −32/−52/44). At a value of $P < 0.01$ (minimum $k = 10$ voxels), two additional clusters emerged, both in left frontal cortex (maxima at −32/32/−4 and −52/32/32). However, neither contrast showed evidence of increased BOLD activity in the left hemisphere regions that were associated with climbing hold-specific responses in Experiment 1—PMv, M1v, and AIP (Fig. 2b).

To confirm this data pattern, we then compared the mean response (or mean β) in each of these three clusters using a between-groups approach (Experiment 1 or E1 vs. Experiment 2 or E2). In all three clusters, a significant between-group effect was observed such that the mean response was larger for non-climbers (E1) relative to climbers (E2): PMv (mean response E1 = 1.48, mean response E2 = 0.46; $F(1,30) = 5.80$, $P < 0.05$), M1v (mean E1 = 1.05, mean E2 = −0.12; $F(1,30) = 12.23$, $P < 0.005$), and AIP (mean E1 = 1.49, mean E2 = 0.22, $F(1,30) = 11.81$, $P < 0.005$). Together, these analyses support the conclusion that the anatomical regions in the left hemisphere that generated a response to climbing holds in the non-climber participants in Experiment 1 did not generate a response to climbing holds in the climber participants of Experiment 2.

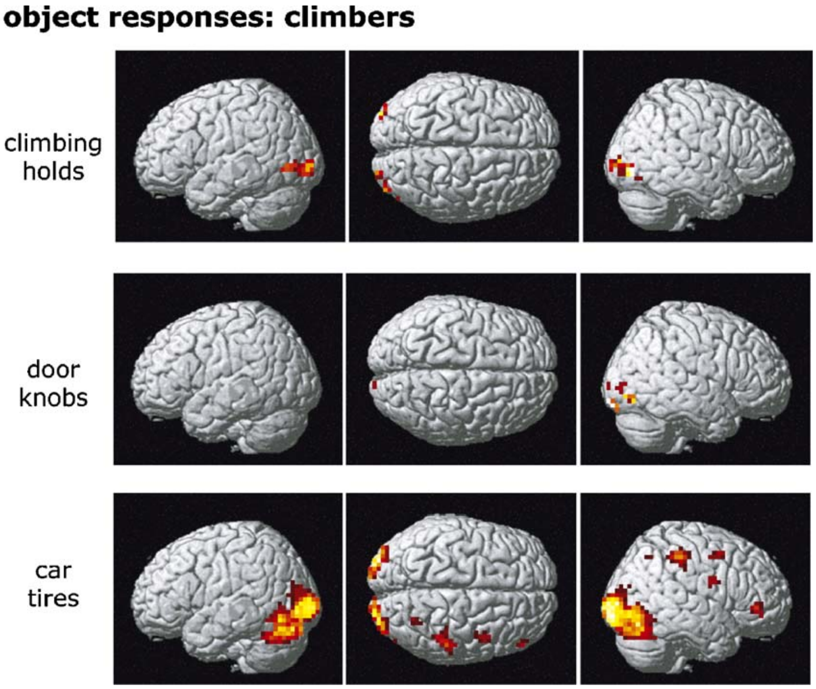


Fig. 3 – Results from Experiment 2. Cortical regions showing significant increases in the event-related fMRI BOLD response for each of the three object categories. Data shown were thresholded at $P < 0.001$ (uncorrected), with a minimum cluster size of 10 contiguous voxels.

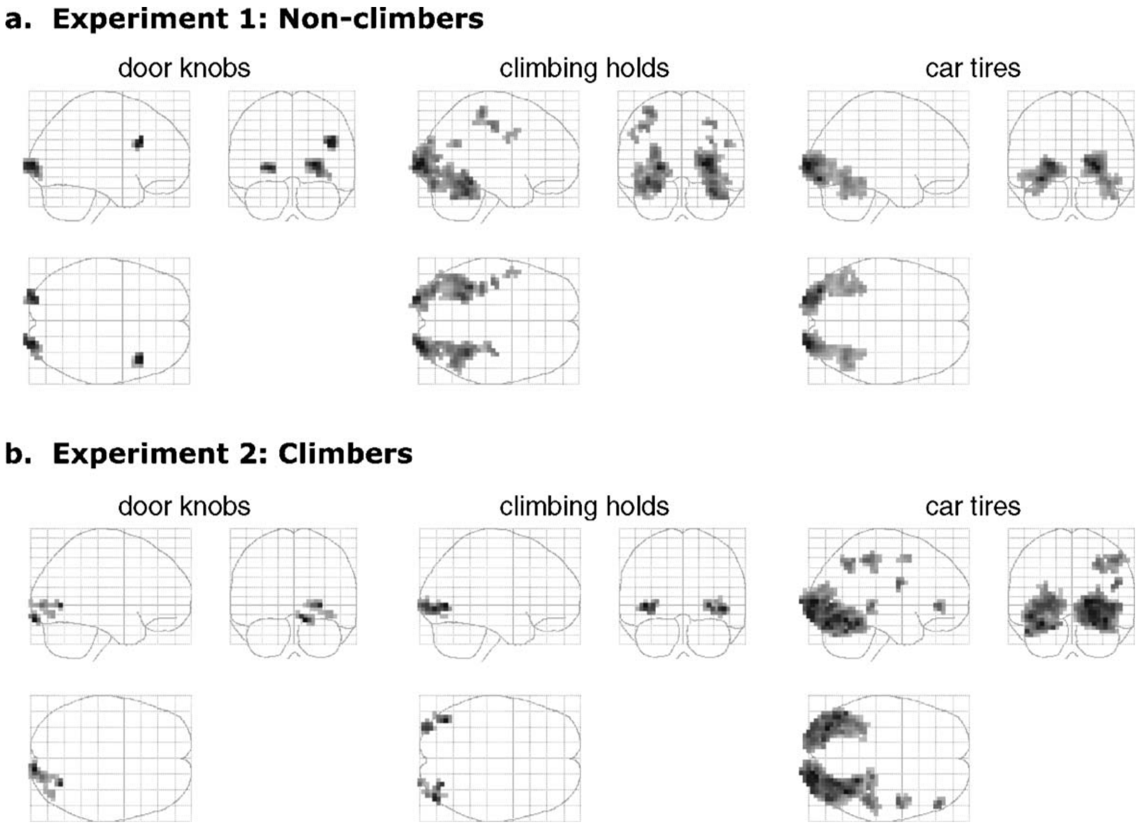
2.2. *Discussion*

Experiment 2 was designed to distinguish between two competing hypotheses regarding the data pattern found in Experiment 1, where reduced BOLD activity was observed for door knobs in both visual- and motor-related cortex, relative to climbing holds: (1) could this differential pattern be attributed to between-object category differences in the low-level properties of the object images themselves, or (2) does the magnitude of analysis in these cortical areas negatively covary with object-specific motor experience? Towards answering this question, we found that, when the same object images from Experiment 1 were presented to participants having extensive real-world experience grasping climbing holds, the fMRI BOLD response generated by these objects then paralleled the response generated by door knobs in both Experiments 1 and 2: spatially reduced activity in visual cortex relative to car tires and an absence of increased activity in left visuomotor-related cortex. The results thus support the proposal that the extent to which a graspable object generates activity in visual- and motor-related cortex may depend on the degree to which an observer has had real-world motor experience with the graspable object being viewed.

The basis for this conclusion is highlighted in Fig. 4, which emphasizes how the object-specific pattern of response across occipital and temporal cortex appears to track with motor experience. That is, for object categories associated with repeated real-world motor experience (door knobs in Experiment 1 and both door knobs and climbing holds in Experiment 2), there is a systematic pattern of visual activity limited to comparatively small regions of lateral occipital cortex. In contrast, for object categories not associated with repeated real-world motor experience (climbing holds and car tires in Experiment 1 and car tires in Experiment 2), there is a much more spatially extensive visual response that extends from lateral occipital cortex well into the ventral temporal region.

While the broader implications of this data pattern are discussed below, two additional points are considered here. The first concerns the degree to which the response to climbing holds found in Experiment 1 can be ascribed to a novelty response, as participants were unfamiliar with these objects at not just a motor level, but at a semantic level as well. On the one hand, Fig. 4 underscores how the BOLD response in occipital and temporal cortex covaries directly with motor experience rather than object novelty. That is, if the response in these regions for climbing holds in Experiment 1 was due solely to novelty at a semantic level, it would not explain why a similar occipital–temporal response was observed for car tires in both Experiments 1 and 2—objects that were semantically familiar to both participant cohorts. On the other hand, the responses observed in left AIP, left M1v, and left PMv for climbing holds in Experiment 1 were in fact unique to the one object category across both experiments that was semantically unfamiliar to participants. However, the difficulty of a novelty interpretation of the AIP/M1v/PMv responses is that it would not necessarily explain why visuomotor-related regions of left parietal and prefrontal cortices were specifically manifesting the novelty response. Rather, this anatomical specificity suggests that the implicit object-specific activity in these regions reflects a form of visuomotor analysis that–at least in the current study–was idiosyncratic to graspable objects unfamiliar to the motor system.

A second point concerns the pattern of behavioral performance observed in the two experiments, with participants in



a. Experiment 1: Non-climbers

b. Experiment 2: Climbers

Fig. 4 – Comparison of whole-brain activations from Experiments 1 and 2. Shown are "glass-brain" representations from the left–right, anterior–posterior, and superior–inferior perspectives for non-climbers (a) and climbers (b), by object category. This figure highlights that activity in occipital and temporal cortex appears to be reduced for graspable objects associated with motor experience—door knobs in both (a and b), as well as climbing holds in (b). In comparison, the one graspable object unfamiliar to the motor system–climbing holds in (a)–had visual activity extending into ventral temporal cortex; this latter pattern was also observed for those objects not associated with motor experience—car tires in both (a and b).

Experiment 1 manifesting RTs to targets that were approximately 200 ms longer in latency, relative to participants in Experiment 2. In particular, how should this between-group difference in mean RT be interpreted? That the two participant groups showed a similar pattern of BOLD response to both door knobs and car tires suggests that, other than the systematic effect of motor experience on the response to climbing holds, there were no gross strategic differences in how task-related materials were being processed. Instead, the more likely explanation is that, in the active rock climbing participants, we also had a group self-selected for physical fitness and novelty-seeking in high-threat situations. Both of these factors may have contributed–either directly and/or indirectly–to overall faster responses in the fMRI setting, where participants often manifest delayed task responses relative to when the same tasks are performed outside the scanning environment.

3. General discussion

When people passively view images of graspable objects, regions of parietal and prefrontal cortices will implicitly respond to that object regardless of the observer's intention to act (e.g., Chao and Martin, 2000; Grafton et al., 1997; Faillenot et al., 1997; Grèzes and Decety, 2002; Handy et al., 2003, 2005). In a study designed to examine whether these implicit iVMRs depend on prior motor-related experience with the object being viewed, we found that not only does motor experience appear to play a critical role in their generation, but it does so in a manner that was unexpected in two different ways. First, rather than depending on motor experience with a graspable object, it appears that implicit iVMRs under passive viewing conditions may be more strongly associated with a *lack* of direct real-world motor experience. Second, in addition to this reduced visuomotor-related activity, motor experience with a graspable object also appears to reduce activity in visual cortex. In short, graspable objects unfamiliar to the motor system (climbing holds in Experiment 1) generated responses in left parietal and prefrontal cortex that were consistent with an iVMR, as well as activations in visual cortex that extended from lateral occipital regions into ventral temporal areas. Conversely, graspable objects familiar to the motor system through repeated real-world experience (door knobs in both Experiments 1 and 2 and climbing holds in Experiment 2) failed to generate iVMRs and had activity in visual cortex that was limited to lateral occipital regions only. The collective evidence thus suggests that motor experience with an object may simplify or reduce the amount of implicit cortical processing generated by that object when passively viewed. What follows is a discussion of several key questions and issues arising from this proposal.

3.1. *Relation to prior evidence*

For one, how can the current data–suggesting that iVMRs may be preferentially generated by graspable objects unfamiliar to the motor system–be reconciled with prior studies showing iVMRs when clearly including objects familiar to the motor system? One possible explanation concerns appreciating how object categories are defined and familiarity is controlled. In particular, earlier studies investigating how cortex responds to graspable objects have typically included a wide variety of different object types (e.g., cups, pliers, pencils) under the category of "graspable", while controlling for familiarity at a semantic level between "graspable" and "non-graspable" object categories (e.g., Chao and Martin, 2000; Grafton et al., 1997; Faillenot et al., 1997; Grèzes and Decety, 2002; Handy et al., 2003, 2005). In comparison, here, the aim was to compare between "familiar graspable" and "non-familiar graspable" object categories, with familiarity defined in relation to motor experience, not semantic knowledge (see also the Discussion section of Experiment 2). Given this emphasis in our study, what it stresses is that efforts to control familiarity in prior related studies have not focused on equating (or controlling) the motor familiarity of graspable objects within that object category itself. As a consequence, "graspable" object categories may have included any number of items that, although perhaps familiar at a semantic level, were nevertheless objects not strongly associated with actual real-world motor experience—for example, many people may be semantically familiar with watering cans or pliers, but rarely if ever use them. If so, iVMRs reported in prior studies under comparable viewing conditions could be explained as having been primarily driven by the subcategory of graspable objects less familiar to participants motor-wise.

A second, related explanation for reconciling the current data with prior studies concerns appreciating the different kinds of motor programs that may be activated or primed by a graspable object. In particular, a distinction can be made between the grasping affordance of an object (i.e., the manual engagement characteristics of the object itself) and the action associated with the actual use–if any–of the object once it is in hand (e.g., Bub et al., 2003). Moreover, the pattern and extent of activity generated in cortex by a graspable object are sensitive to both of these factors (e.g., Creem-Regehr and Lee, 2005; Kellenbach et al., 2003). Given this background, the current study employed only two kinds of graspable objects, with one having no overt action once grasped (climbing holds) and one having a relatively simple action once grasped (door knobs). For studies having a more diverse set of objects in the graspable category, it may be possible that–in addition to motor familiarity effects–the presence of iVMRs may also be influenced by the implicit priming or activation of more complex action programs. Notably, this possibility also speaks to a key caveat of the current data: while motor experience with graspable objects requiring relatively simple actions may reduce the implicit motor responses those objects generate, objects associated with more complex action programs (e.g., scissors or chopsticks) may show different effects of motor familiarity.

3.2. *Motor and visual object representations*

Regardless of how best to characterize the context of the current results, if real-world motor experience with an object can reduce the extent of analysis that object receives in visual- and motor-related cortex, what can be inferred about the nature of this analytic change? In terms of motor-related cortex, recent evidence from both humans and monkeys has linked grasp-related functions to an AIP–PMv circuit, where AIP codes the shape and size of an object as it relates to grasping (e.g., Shikata et al., 2003; Frey et al., 2005; Binkofski et al., 2001) and then–based on that coding–PMv selects a motor schemata appropriate for manually interacting with the object of interest (e.g., Johnson and Grafton, 2003; Rizzolatti and Matelli, 2003; Johnson-Frey et al., 2003). What this implies is that AIP and PMv appear to play a central role in evaluating the manual engagement characteristics of a viewed object. At the same time, M1 has been shown to activate during motor imagery tasks (e.g., Hari et al., 1998; Schnitzler et al., 1997), a finding consistent with possible M1v involvement in similar grasp-oriented object evaluation. Taken together, such evidence would suggest that one potential consequence of object-specific motor familiarity may be to reduce the need to perform such on-line analysis of an object's engagement characteristics. Indeed, not only is the cortical representation of an object-specific motor skill known to change as the object-specific action becomes over-learned (e.g., Grafton et al., 1992, 1995), but studies of visuomotor learning–where arbitrary associations are generated between a sensory stimulus and a motor response–have demonstrated that activity in a number of parietal and prefrontal regions is strongly modulated by the degree of sensory–motor associations involved (e.g., Eliassen et al., 2003; Deiber et al., 1997; Passingham et al., 2000; Grafton et al., 1998; Toni et al., 2001).

In terms of motor experiencing also altering visual cortical activation, this too may not be a surprising result in hindsight. In particular, perceiving the shape of an object can lead to increases in the visual activation of lateral occipital cortex while simultaneously reducing activity in earlier visual areas, relative to when perceiving the elementary features or constituent elements of an object (e.g., Murray et al., 2002). Taken in this light, that we found lateral occipital cortex to be the sole visual area showing significant increases in BOLD activity for objects familiar to the motor system suggests that perhaps one visual consequence of motor experience is to shift visual object analysis towards a more pragmatic, shape-based assessment. Interestingly, not only is this possibility congruent with the observed reductions in activity in object recognition areas of ventral temporal cortex for motor-familiar objects, but object-specific perceptual expertise has been shown to produce systematic changes in object-related processing in the ventral visual pathway (e.g., Gauthier et al., 1999, 2000; Tanaka and Curran, 2001). In short, what the collective evidence points towards is that visual- and motor-related regions of cortex may systematically analyze how to manually interact with an unfamiliar object, but once the visuomotor association is learned, these analytic processes may no longer be activated by the object category—at least to the same degree. Rather, there may be a qualitative shift in the nature of the cortical representation generated.

3.3. *Behavioral performance*

As a final consideration, although no behavioral effect was associated with the iVMR from Experiment 1, this null result is perhaps not surprising in that recent fMRI studies have shown a consistent absence of RT and accuracy effects associated with iVMRs (e.g., Handy et al., 2003, 2005). What explains this dissociation between measures? Investigations of visual illusions have demonstrated that, if an illusion arises from processing in the visuoperceptual pathway, then the illusion will affect behavior in a visuoperceptual task but not a visuomotor task (e.g., Dyde and Milner, 2002; Milner and Dyde, 2003). Given that the iVMR measured here via fMRI reflects visuomotor processing, while task performance itself–target detection–reflects visuoperceptual processing, a similar dissociation is likely at play in our data. That is, while the visuomotor system may manifest an iVMR to an unfamiliar object, this response in the dorsal pathway would not necessarily translate into an effect observable in manual behavior driven by the visuoperceptual system (e.g., Bonfiglioli et al., 2002; Ganel and Goodale, 2003).

3.4. *Conclusions*

In closing, we stress that the apparent effects of motor experience reported here may be idiosyncratic to situations where observers are not explicitly instructed to think about or engage in visuomotor-related functions. Whether motor experience can modulate more controlled or deliberate aspects of visuomotor-related processing (e.g., Creem-Regehr and Lee, 2005; Gerardin et al., 2000; Rushworth et al., 1997, 2001a,b; Schluter et al., 2001) remains an open question. Nevertheless, what our data support is the possibility that iVMRs in parietal and prefrontal cortices do not necessarily depend on prior motor-related experience with the object being viewed. Rather, such experience appears to reduce or diminish the degree of analysis that takes place not just in motor-related cortex, but in visual cortex as well.

Acknowledgments

We thank Michael Hamilton for his assistance with digital photography and computer programming, and two anonymous reviewers for constructive comments on an early version of this work. This study was supported by grants from NSERC (to T.C.H.) and NIH (to T.C.H. and to M.S.G.).

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