Research report

Novel claustrum activation observed during a visuomotor adaptation task using a viewing window paradigm

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ABSTRACT

Previous literature has reported a wide range of anatomical correlates when participants are required to perform a visuomotor adaptation task. However, traditional adaptation tasks suffer a number of inherent limitations that may, in part, give rise to this variability. For instance, the sparse visual environment does not map well onto conditions in which a visuomotor transformation would normally be required in every-day life. To further clarify these neural underpinnings, functional magnetic resonance imaging (fMRI) was performed on 17 (6M, age range 20–45 years old; mean age = 26) naive participants performing a viewing window task in which a visuomotor transformation was created by varying the relationship between the participant's movement and the resultant movement of the viewing window. The viewing window task more naturally replicates scenarios in which haptic and visual information would be combined to achieve a higher-level goal. Even though activity related to visuomotor adaptation was found within previously reported regions of the parietal lobes, frontal lobes, and occipital lobes, novel activation patterns were observed within the claustrum – a region well-established as multi-modal convergence zone. These results confirm the diversity in the number and location of neurological systems recruited to perform a required visuomotor adaptation, and provide the first evidence of participation of the claustrum to overcome a visuomotor transformation.

1. Introduction

Under normal circumstances, we have few problems using sensory information to respond to our environment. In fact, much of our ability to acquire and maintain the motor skills utilized on a daily basis capitalize on the ability to integrate and transform sensory information into a motor response. It has been established that our sensorimotor system is able to adapt to a wide variety of visual and mechanical perturbations, however, there is still little agreement in the literature as to the amount and location of neurological areas implicated in the performance of this task [1]. The bulk of our knowledge regarding the neurological correlates of visuomotor adaptation comes from prism adaptation (e.g. [2–7]). Until recently, prism adaptation was largely held to be a function of the cerebellum. The cerebellum not only receives proprioceptive information from the limbs, but also receives visual information from cortical and subcortical areas, and is therefore a logical site for a discrepancy between these two information streams to be detected and corrected. Visual information projects from medial extrastriate regions to the dorsolateral region of the pontine nuclei [8,9], and it is known that experimental lesions in monkey cerebellar mossy-fibre, where input from the pontine nuclei is received, abolish prismatic adaptation in macaque [10]. Further bolstering the role of the cerebellum, human patients with cerebellar lesions may display adaptation impairments [11–13]. For example, Martin et al. [11] reported patients with damage to the inferior olive (the source of climbing fibres to the cerebellar cortex) were severely impaired when adapting to lateral displacement prisms.

Other prism work, utilizing functional neuroimaging, has implicated the parietal region's role in visuomotor adaptation [2–6]. For instance, Clower et al. [2] used positron emission tomography to directly examine brain activation during a pointing task while the participant wore lateral displacement prisms. Consistent patterns of brain activation were observed in the posterior parietal cortex (PPC) contralateral to the pointing limb on trials where vision was displaced. Providing further support for PPC involvement during visuomotor adaptation, Fernandez-Ruiz et al. [3] had participants wear left/right reversing prisms during a pointing task during functional magnetic resonance imaging, and found areas of PPC that typically respond to contralateral movement goals were responding to ipsilateral pointing movements during exposure to reversing prisms. This result was interpreted as providing evidence that the PPC does not function in strictly vision or movement coordinates,

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but rather encodes the spatial goal of the movement in retinal coordinates. In other words, the PPC works as an intermediary between visual and motor codes [3].

Even though visuomotor adaptation studies utilizing prisms are the most prolific in the literature, there have been alternative methods employed in the examination of the neurological mechanisms involved in correctly performing visuomotor transformation and/or adaptation. Many of these studies have had participants execute a pointing or tracking movement under normal visual conditions and compared the obtained activation to activation observed when a perturbation was introduced. Distortions have included simple rotations [14–18], magnification [18], lateral shifts of location [2], and axis reversals [19,20]. Interestingly, the adaptation related activity observed differed substantially between studies, not only in the anatomical locations of regions of activity, but also in the number of regions recruited. In a descending order of frequency, activity was observed within the posterior parietal lobe, the cerebellum, prefrontal cortex, basal ganglia, premotor areas, sensorimotor areas, temporal and occipital cortices, and the thalamus.

The present study utilizes a novel computer-based task, the viewing window, which presents participants with degraded pictures of objects and asks them to identify the objects using a small user controlled area (the "window"). Within the window, the underlying image is displayed with normal clarity [21]. Although aperture viewing paradigms are not new, dating back nearly 200 years [22–24], in order to be used as a tool to assess visuomotor performance a number of significant changes were made. The method of controlling the window, the size of the viewing region, and the information available in the transitional region between the window and the periphery are examples of some of the changes that were employed. This procedure has successfully demonstrated group differences in transformation ability using behavioural measures [25] and has a number of potential advantages over previously used visuomotor adaptation tasks including removing the focus of the task from the visuomotor distortion itself, providing multiple opportunities to compare a target foveal location and resulting movement, and providing a variety of ways to manipulate both the visual and motor information participants are exposed to. Perhaps most importantly, it is a substantially more complex task than those used in previous studies examining the neurological underpinnings of visuomotor adaptation, better replicating naturalistic task circumstances. For example, participants are presented with rich visual stimuli (greyscale images of an object) in a task that allows for a free range of motion across a visual scene. We believe this more naturally replicates scenarios in which visuomotor transformations are required in our day to day lives and may provide further insight into the cortical regions responsible for successfully performing goal directed visuomotor adaptations than those revealed through the use of simplistic centre-out pointing movements.

Previous research has provided a wide-range in the regions of reported activity, suggesting differences in methodology, or tasks may be leading to increased variability. Specifically, the superior and inferior parietal lobules (BA 40) [1,14,19], the precuneus (BA 7) [26], and the posterior cingulate gyrus (BA 23, 29, 31) [19] have all been implicated in the performance on visuomotor transformation and adaptation. Though less commonly reported in previous studies, additional regions of activity have been identified in areas of the occipital lobe, the cuneus (BA 17, 18) [26,27], and the lingual gyrus (BA 18, 19) [19]. Finally, regions of interest within the temporal lobes, include the temporo-parietal junction (BA 39, 40) [28], and the frontal lobes consisting of the anterior insula, and anterior cingulate (BA 24, 32) [19]. It was hypothesized that the viewing window would recruit similar neural networks to those reported above, however, due to the use of the viewing window

task, it was expected that the cortical regions involved in performing a goal directed visuomotor adaptation would display higher levels of activity than those previously reported.

## 2. Materials and methods

2.1. Participants

All experimental procedures received approval from the Psychology and Sociology Research Ethics Board of the University of Manitoba and the National Research Council's Research Ethics Board. All participants provided written informed consent before participating in any of the experiments and completed a pre-screening form to ensure it was safe for them to participate. Seventeen (6M, age range 20–45 years old; mean age = 26, SD = 6.8) participants were recruited from the University of Manitoba's introduction to psychology participant pool or through "word of mouth". Participants were right-handed, fluent in English, and had normal or corrected-to-normal vision as reported in pre-test screening, and reported their computer ability as "very proficient" on a Likert-type scale. Participants had no history of neurological disease and were naive to the objective of the study. All participants received $25.00 to cover travel expenses, with those recruited from the participant pool also receiving course credit.

2.2. The viewing window

The "window" was a circular region roughly corresponding with the size of useful foveal vision (2.98°), with a 51 pixel length radius, covering a total area of 8171 pixels. The outermost region of the window displayed the underlying image at full blur. The innermost regions displayed the image at normal clarity (see Fig. 1), with a smooth transition between these two regions. This gradient border was used to provide a more natural viewing experience. Participants were given both written and verbal instructions prior to beginning, and the correct use of the trackball and viewing-window was demonstrated by the experimenter. Participants were told that they could move a window around the screen, using the trackball, which would display the underlying object in perfect clarity. Participants were instructed to identify the presented object as quickly but as accurately as possible, and to signify their identification by pressing either of the buttons located on the trackball. Additionally, participants were told some of the trials would be difficult and that if they were unable to identify a given object, to take a "best-guess". Three visuomotor-flip conditions were created by varying how the participant's body movements affected the onscreen movement of the viewing window. During the No Flip condition, the movement of the window was matched to the participant's movements of the trackball. In each of the solitary x-axis and y-axis Flip conditions, only one dimension (horizontal or vertical) of movement was reversed. For example, in the x-axis Flip condition, leftward movements of the trackball resulted in the viewing window moving towards the right of the presented image.

2.3. Training

Participants were verbally instructed outside of the magnet as to how to perform the task, and were verbally reminded once inside the bore of the magnet. The first functional scan for all participants was used as a practice and was not included in the reported analyses. This ensured all participants were not only accustomed to the task, but also used to the auditory noise associated with the functional scan.
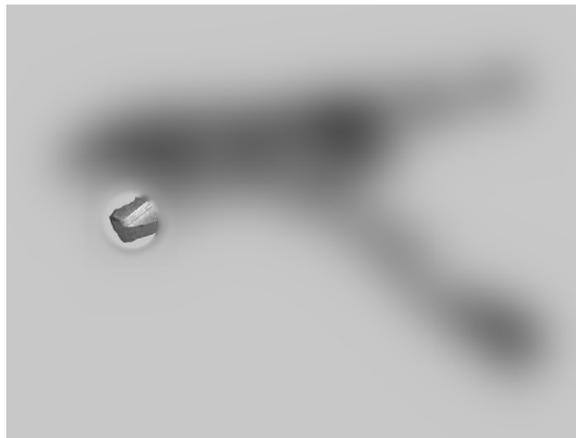
Fig. 1. Viewing window illustration. The circular viewing window displays the underlying image in normal clarity, while the remainder of the image is heavily blurred. The target item is a pair of vice-grips.

Table 1
List of stimuli used, and their associated foils.

Item	Foil	Item	Foil
Practice items			
Clock	Ashtray	Telephone	Stereo
Typewriter	Computer		
Experimental items			
Apple	Banana	Paperclip	Ruler
Banana	Cucumber	Pen	Screwdriver
Binder clip	Wrench	Pencil	Tape measure
Camera	Ladle	Pencil sharpener	Nail
Clamp	Can Opener	Pepper	Tomato
Corkscrew	Gun	Pocket watch	Purse
Boot	Earring	Potato peeler	Pizza cutter
Dagger	Yo-Yo	Pumpkin	Lettuce
Ring	Hammer	Pushpin	Screw
Dice	Violin	Razor	Scissors
Drill	Magazine	Safety pin	Yarn
Guitar	Headband	Saw	Planar
Eyeglasses	Spoon	Scissors	Pliers
Diskette	Ruler	Screwdriver	Mallet
Fork	Paintbrush	Shoes	Boots
Frying pan	Sander	Spoon	Fork
Hairbrush	Pencil	Stapler	Hole punch
Highlighter	Blender	Stethoscope	Necklace
Hole punch	Pot	Strawberry	Kiwi
Hourglass	Strawberry	Tape dispenser	Stapler
Jug	Stool	Tape measure	Level
Kiwi	Lime	Teapot	Iron
Lamp	Orange	Toaster	Oven
Laptop	Typewriter	Tomato	Apple
Lemon	Knife	Toothbrush	Hairbrush
Light bulb	Perfume	Vice grips	Wrench
Lighter	Chisel	Walnut	Almond
Mallet	Toolbox	Watch	Bracelet
Notebook	Textbook	Watering can	Pail
Chair	Sofa	Wrench	Vice grips
		Yarn	Needle

2.4. Stimuli

Four lists of 16 items (totalling 64 items) were used, and can be seen in Table 1, with each list being used for one functional scan. Items were selected from a larger list of items used in previous experiments [21,25]. Response foils were chosen with a consideration of the objects overall shapes. Thirty percent of foil items were selected from the experimental items to reduce the likelihood of correct responses being selected based on item familiarity alone. Assignment of visuomotor condition was pseudo-randomized and counter-balanced, with all participants beginning Scan 1 with a normal non-flipped condition.

Each functional scan was 8 min in duration, and was run 4 times (with differing objects). Each trial began with a fixation point which lasted for a minimum time of 5 s. Participants were given up to a maximum of 20 s to explore the object before being presented with response options. Participants were then given a maximum of 5 s to choose a response. Any time remaining in either of the response or viewing window periods of the trial was added to the fixation period. These timings ensured a new trial was initiated every 30 s (see Fig. 2), and that there was a minimum of 10 s between the movement phases of each trial. All participants required less than the 20 s provided on 95% of trials, with the majority having 15–20 s of intervening time between movement phases (mean = 17.3, SD = 5.7).

2.5. Apparatus

Data were collected at the National Research Council – Institute for Biodiagnostics (NRC-IBD) using conventional Blood Oxygen Level Dependent (BOLD) imaging techniques using a 3-T whole-body Tim Trio scanner and integrated 12-channel birdcage RF coil (Siemens, AG). T2* weighted, contiguous single-shot blipped gradient-echo planar images were acquired with a 3 mm slice thickness (matrix size = 64 × 64, field of view = 240 mm, in-plane resolution 3.75 mm × 3.75 mm, TE = 40 ms, TR = 2000 ms, flip angle = 70°). Full coverage of the frontal and parietal lobes was achieved, with partial (superior) coverage of the occipital lobes. The cerebellum was not imaged. High resolution T1-weighted images were obtained after the functional scans for overlaying the acquired functional activation. Participants were lying supine in the bore, with their heads stabilized by memory-foam pillows. A plastic screen was placed at the head of the magnet, with participants' viewing of the screen accomplished through the use of a rear-ward facing single mirror box (11 cm × 9.3 cm) placed within the RF coil. Visual stimuli were back projected onto the translucent screen (122 cm × 91 cm) at a resolution of 1024 × 768, with a refresh rate of 60 Hz. The distance between the participant's head and screen was 2.4 m. This configuration maintained the size of the viewing window equal to the useful resolution of the fovea (2.98°). The viewing window was controlled by a MR-compatible trackball (Current Designs, Pittsburgh, PA) placed at participant midline at the level of the thigh stabilized on a fibreboard placed on the participant's lap. This placement ensured that the trackball was within easy reach, and also minimized participant movement within the bore of the scanner. Due to the use of a mirror when projecting the visual stimulus, the relationship between trackball movement and the resultant movement of the window on the screen was normalized.

Data were processed and analyzed using Brain Voyager QX 2.2 software (Brain Innovation, Maastricht, The Netherlands). The first functional scan was discarded as practice. The first two scans of each remaining functional block were omitted from the functional analysis to allow an equilibration of saturation effects, and were instead used to create pseudo-anatomical in-plane scans to assist in the alignment of the functional data to the high-resolution anatomical data collected. Cubic spline slice scan time correction, 3D motion correction using a trilinear/sinc inter-
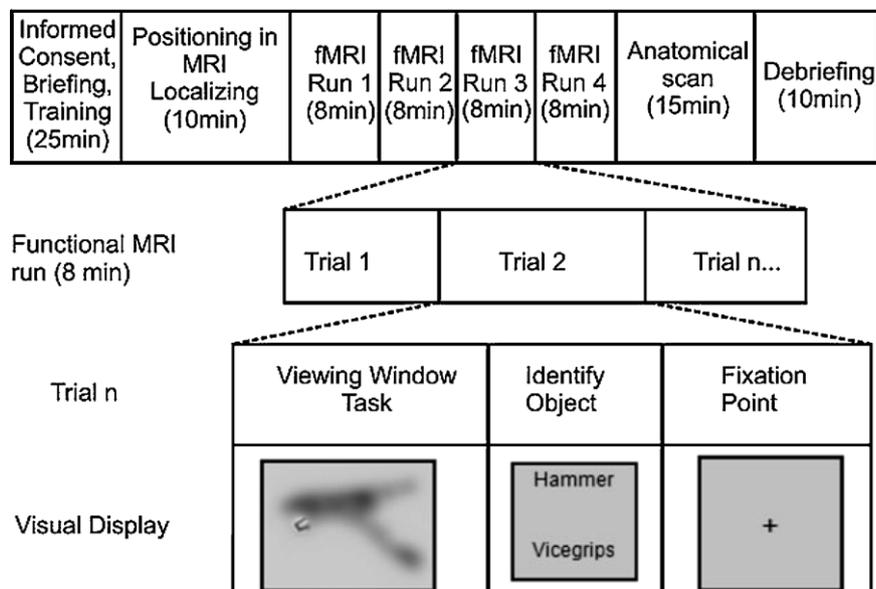
Fig. 2. fMRI protocol. One scanning session lasted approximately 90 min, consisting of training, four functional scans an anatomical scan and debriefing. Each trial consisted of performing the viewing window task, selecting the presented item following by a fixation point. A new trial was started every 30 s.

polation algorithm, and high-pass temporal filtering using a general linear model with Fourier basis set (including linear trend), with 2 cycles as the cut-off, were applied to each functional scan. Additionally, spatial smoothing using a Gaussian filter (full-width at half-maximum equal to 8 mm), was applied to the functional data. Following pre-processing, a multi-scan, fixed-effects GLM analysis with four predictors (fixation, response, normal movement, and flip in movement) was used to determine areas that were activated significantly more during a flip in the x-axis or a flip in the y-axis when compared to the normal condition (Contrasts of 0, 0, −1, and 1). A two-gamma hemodynamic response function (onset = 0; time to peak = 5 s; dispersion = 1; undershoot ratio = 6; time to undershoot peak = 15 s; undershoot dispersion = 1) was used to model the expected BOLD response. To correct for multiple comparisons, a cluster-threshold approach was taken [29].
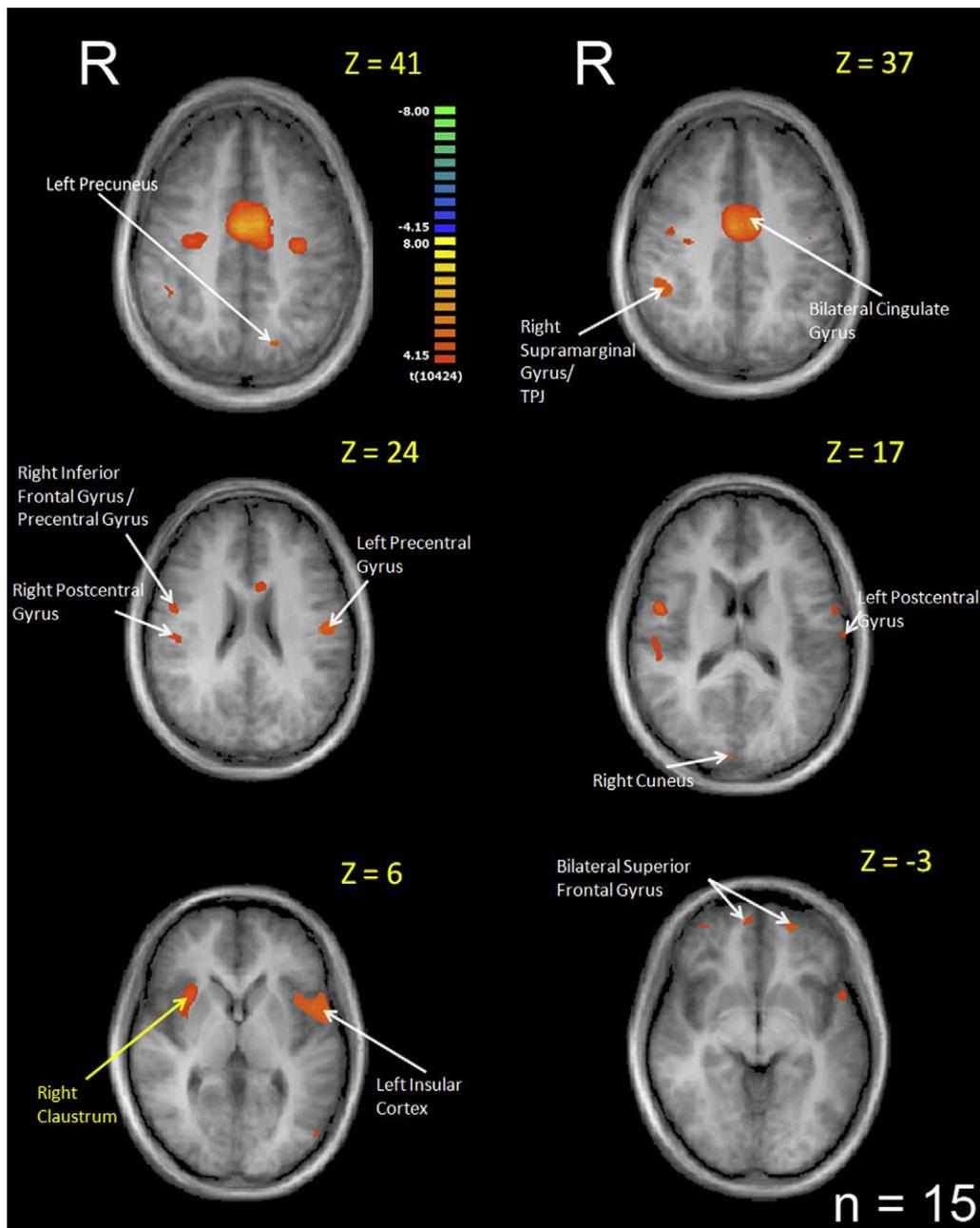
3. Results

One participant was excluded from the analysis due to head movements in excess of 5 mm of translation and/or 5° of rotation.

Additionally two functional scans from separate participants were excluded for having head movements in excess of 2 mm or 2°. One participant was released from the experiment early, due to investigator concern of claustrophobia. Data analyses were performed on the remaining 15 participants. All functional scans had a signal to noise ratio of 0.50 or greater.

3.1. Behavioural data

No significant differences in accuracy were observed in the visuomotor flip conditions. The overall accuracy rate across subjects was 90%, with no individual subject scoring below 70% (SD = 7%). Trials in which the target object was not correctly identified were omitted from further analysis. Data were separated by the associated functional scan (2, 3, and 4). An initial outlier analysis

Fig. 3. Observed activation. Whole brain axial slices of the average activation from all participants (n = 15) are shown. Multiple comparisons were corrected using False-Discovery Rate at the 0.001 level. Activations are the result of GLM predictor contrast of the normal (−), and flip in x (+), flip in y (+) conditions. At axial slice Z = 6, the novel claustrum activation can be easily observed (highlighted).

Table 2
Anatomical location of observed activation.

Anatomical location of peak voxel	Volume (voxel)	Voxel-level (t)	Talairach coordinates (x, y, z)	Corrected p-value
Right inferior frontal gyrus (BA 9)	755	5.54	50, 1, 18	<0.001
Right insula	1166	4.97	47, −20, 27	<0.001
Right supramarginal gyrus	1168	4.88	44, −41, 36	<0.001
Right inferior frontal gyrus (BA 47)	134	4.40	44, 13, −6	<0.001
Right claustrum	1661	4.87	29, 13, 6	<0.001
Right cingulate gyrus	13,693	7.08	−10, −5, 45	<0.001
Right inferior frontal gyrus (BA 47)	673	5.31	23, 22, −12	<0.001
Right cuneus (BA 18)	99	4.43	5, −89, 14	<0.001
Right superior frontal gyrus	103	4.68	9, 55, −3	<0.001
Left precuneus	90	4.44	−19, −68, 43	<0.001
Left superior frontal gyrus	106	4.47	−22, 53, −3	<0.001
Left superior temporal gyrus	3103	5.33	−52, 4, 3	<0.001
Left precentral gyrus	688	4.88	−51, −13, 28	<0.001
Left postcentral gyrus	85	4.16	−64, −17, 16	<0.001

Anatomical location of areas significantly more active during trials when a visuomotor flip was required (Flip vs. Normal). The amount of significant voxels, corresponding t-value, talairach coordinates, and p values.

was performed on the movement time data, excluding values 2.5 standard deviations from each participant's mean for that condition. No trials were excluded on the basis of the outlier analysis.

Analyses were conducted on the average movement time of the window required to identify the presented object, the number of reversals made in window movement, and average velocity for each trial. Only the velocity data revealed statistically significant differences (although all data were consistent with participants learning the presented visuomotor adaptation) with a main-effect of scan ($F(2,28) = 13.139$, $p < 0.001$) characterised by participants moving the viewing window faster in the later scans when compared to earlier scans. A significant Scan × Flip interaction ($F(2,88) = 5.578$, $p < 0.01$) was also observed, with the viewing window being moved at a lower velocity when a visuomotor distortion was introduced in scan 2, but at par with the no-flip condition by scan 4.

3.2. Functional data

False discovery rate thresholding was performed at the 0.001 level. Visuomotor adaptation-related neural activation was observed in a number of areas when the activity associated with both of the flip conditions was subtracted from the activity observed during the normal visuomotor condition. The peak location of each activation cluster can be seen in Table 2.

Within the parietal lobes, activation was observed within the bilateral post-central gyrus (BA 43), right supramarginal gyrus (BA 40) near the temporoparietal junction, right superior frontal gyrus (BA 10), and left precuneus. Additionally, activation was observed along the right parieto-occipital fissure encompassing both precuneus and cuneus. Substantial activation was also observed within the frontal lobes in bilateral cingulate gyrus, right inferior frontal gyrus (BA 9 and 47) extending into precentral gyrus (BA 6), left precentral gyrus (BA 4) and left superior frontal gyrus (BA 10). Within the occipital lobe, activation was observed within the right cuneus. Within the temporal lobe, significant activation was found within left insular cortex. Finally, an area of activation was observed within the right claustrum (see Fig. 3).

To further examine the novel claustrum activation, a number of region-of-interest analyses were conducted. Overall, a significant difference between the parameter estimates of activity (beta weights) in the right claustrum was found. When data were split across the three successive scans, significant differences in activity were only present during the final scanning session (see Fig. 4). When examining the time course of the claustrum activation, a significant overall difference between visuomotor condition was found. When the data were split across scans, differences in both
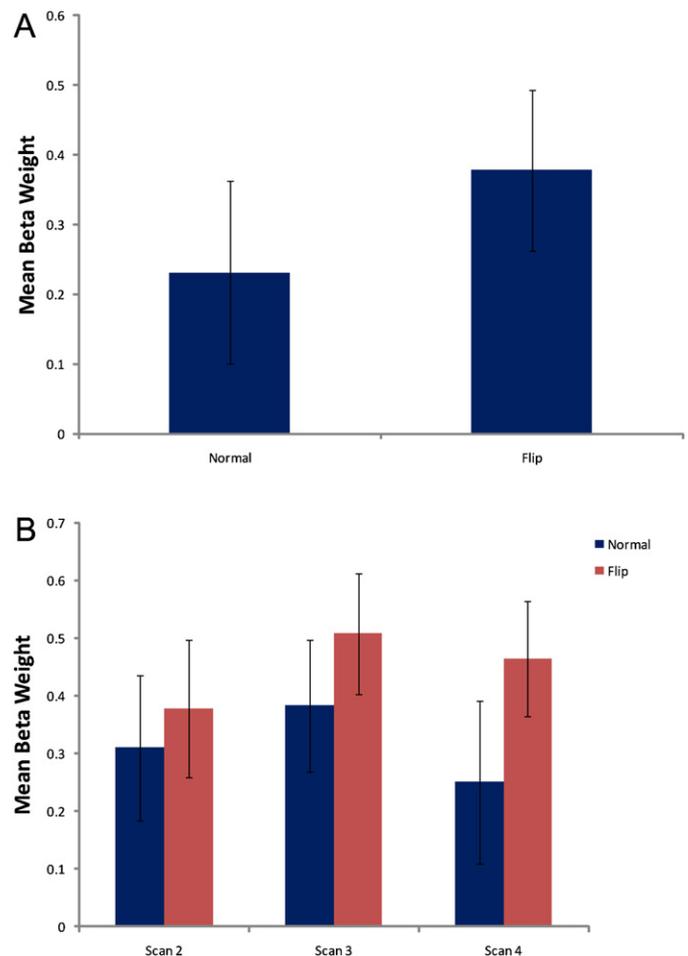

Fig. 4. Parametric modulation of claustrum activation during the viewing window task. (a) Overall, a significant difference between the level of claustrum activation during trials which required a visuomotor transformation (flip) and those that did not (normal) was found. (b) When the data were separated by functional scan, statistically significant differences in the parametric modulation were only visible in the final block of trials. *Significance at the $p < 0.05$ level, error bars represent the ± standard error of the mean.

the level of activation and onset of divergence were found to increase as a function of time (Fig. 5).

4. Discussion

The aim of the present experiment was to explore and further clarify the neural areas affected by adaptation to a visuomotor dis-
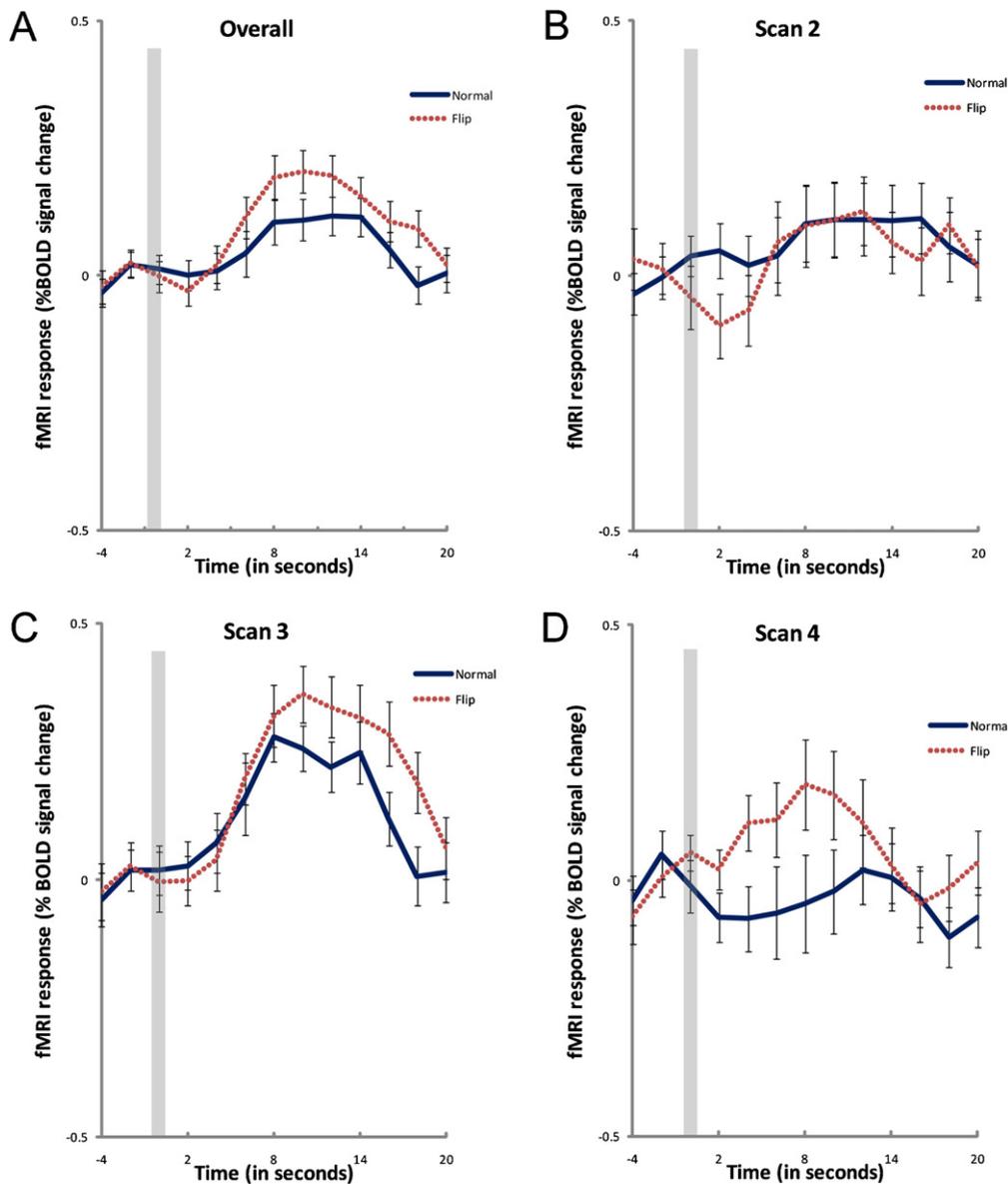
Fig. 5. Time course of changes in neural effects of the claustrum during the viewing window task. (a) Overall, a significant difference in time course signals was observed approximately 7 s after stimulus onset. (b–d) When grouped by blocks of trials, the divergence between the two signals increased as a function of time.

tortion using a complex, goal-directed task. This study provides the first evidence of participation of the claustrum to overcome a visuo-motor transformation. Based on the time course of this activation, it would appear that claustrum activity increases as a function of task proficiency, however, further study examining this signal in more detail is required. Specifically, an attempt to correlate behavioural measures of proficiency with claustrum activity would be of benefit.

The claustrum is a thin sheet of grey matter located between the insula and the outer surface of the putamen. The claustrum of primate species consists of a diverse network of bi-directional connections to many parts of cortex including motor cortex, pre-frontal cortex, and posterior parietal cortex [30,31]. Functionally, the claustrum has long been known to become active during cross-modal processing [31,32], especially when integrating tactile and visual representations [33], and is a substantial multi-modal con-vergence zone within primates [34]. Taken together, the anatomy and functional activation of the claustrum has led to theories that posit the claustrum may play a substantial role in multisensory integrative processing [35–37]. Though speculative at this time,

it is possible that the increased activation observed within the claustrum is a result of the integration of information obtained hap-tically (the proprioceptive information associated with the use of the trackball) with information obtained from vision in an attempt to minimize performance detriments associated with the required visuomotor adaptation. Activation within the claustrum has not previously been observed in other visuomotor fMRI tasks. One plau-sible reason could be that the viewing window task is one of object explorations, in addition to visuomotor adaptation and more natu-rally replicates scenarios in which haptic and visual information would be combined to aid in object identification. In compar-ison, most previous studies have utilized ballistic pointing and centre-out tasks that may not evoke the same necessity to combine multi-modal sensory information. Additionally, simple centre-out pointing tasks typically require well under 1 s to complete. It is possible that such a limited time frame does not allow for a robust BOLD signal increase related to the adapted movement within the claustrum. In comparison, the viewing window task had, on aver-age, over 10 s of movement during adapted trials. Finally, imaging work using viewing window type tasks has also shown patterns

of additional activation when compared to whole-viewing conditions [38], suggesting the increased demand of spatial and temporal integration, and the necessity to differentially allocate attentional resources may also play a role in the activity observed.

It is interesting to note that activity within the claustrum was only observed within the right hemisphere. The right claustrum is largely connected to unilateral cortical structures, however, contralateral connections are also present [31]. Therefore, it is possible, though entirely speculative at this time, that the unilateral activity observed is a result of the dominant status of the right-hemisphere in the performance of visual remapping in humans [39].

Although not all regions of interest previously identified in imaging studies showed significant levels of activation, one must consider the variability in both the number and location of activation observed in previous work. With this in mind, it is not surprising there was only partial overlap with the patterns of activation previously reported. Importantly, significant activation was observed in a number of parietal regions previously identified as being involved in visuomotor transformations and adaptation. First, activation within the parietal lobe has been previously observed in both the ipsilateral and contralateral hemispheres in relation to the hand used in studies examining visuomotor adaptation [1,2,14,16]. Additionally, similar to what was observed in this experiment, precuneus activation is often reported during visuomotor adaptation tasks [14], especially those of a complex nature [26]. The final areas of activation observed within the parietal lobes were bilateral activation of the post-central gyri. Of the four a priori regions of interest identified by a survey of previous literature, the present study demonstrated significant levels of activation in three of those regions. Activation was not observed within the posterior cingulate gyrus, as may have been expected. When taken as a whole, the presented results demonstrate that when participants are forced to adapt to a visuomotor motor "flip" to successfully complete a complex, free-range task, additional parietal resources are required than when compared to the same task completed under a normal visuomotor relationship. One might be surprised that when performing an object identification task, participants did not display significant activation within traditional object processing areas, such as the fusiform and inferior temporal gyri [40–45]. However, the contrasts utilized in the present analysis involved subtracting the activity observed in the normal condition from that observed in the flip condition. In both conditions, explicit visual object recognition was required, resulting in the removal of object identification related activation.

The frontal regions of activation observed, including bilateral cingulate gyrus, frontal gyrus, and primary motor areas have also been reported as active during similar tasks requiring a re-mapping of motor movement as related to movements within a visual scene [15,18,19] or during prismatic adaptation [46]. Within the occipital lobe, cuneus activation was observed. Cuneus activation has previously been reported in similar adaptation tasks [26,27], however, it should be noted that although the peak voxel of the activated cluster was within the cuneus, this region of activation extended into parietal (crossing the parieto-occipital fissure) regions as well, making the precise location of the activation difficult to determine. Validating these additional cortical regions is reassuring, and suggests that although the viewing window task is substantially different from those that have been used previously, it is still recruiting many of the same neurological regions as the simpler tasks.

A discussion about what the pattern of activity actually represents is prudent. As fMRI uses contrasts to determine areas of significantly increased BOLD signal change, the employment of proper comparison conditions is crucial to ensure the observed activation is a result of the variable of interest. Although much effort was put into the present study to ensure this was the case, the use of the normal movement condition as a baseline for subtraction has some drawbacks. First, we are unsure if the pattern of activity observed is related to the visuomotor distortion itself, regions of cortex that are associated with error monitoring and corrections, or mechanisms involved in switching from an easier task to a more difficult one, as all of these confounds would be present in the subtractions used. The current methodology serves the intended purpose of examining areas of activation for the successful completion of a trial in which a visuomotor remapping is required, it does not clarify which areas of activation are associated with the different components of the task. For example, the posterior parietal cortex is known to be involved in error corrections [47–49], and may therefore be involved in more than one single function, with the present data highlighting an amalgam of this processing. It important to note that although previous studies have identified areas of activation that may be solely related to performing visuomotor adaptation (for example, see an elegant solution offered by Diedrichsen et al. [49]), none of these studies have demonstrated activation within the claustrum. Therefore, it is more likely that this new area of activation is specifically related to the use of the viewing window paradigm, rather than secondary processes involved in successfully adapting to the distortion identified by others. Second, though it is unlikely based on the regions of activation, that differences in the programming of eye-movements, or that eye-movements themselves, are responsible for the different patterns of activity observed. These alternative possibilities cannot be ruled out with the presented data. Based on pilot data using eye-tracking obtained during a visuomotor distortion trial using the viewing window, it is known that there are more eye-movements made while adaptation is taking place. Future studies should attempt to quantify this difference by performing eye-tracking during the fMRI task, or should control for eye-movements within the experimental design.

In conclusion, in addition to the typical areas of activation observed during performing a task requiring visuomotor adaptation such as the parietal lobe, frontal lobe and occipital lobe, a new site of activation was found. Within the right claustrum, a significant BOLD response was observed during conditions of visuomotor adaptation when compared to the performance of the viewing window task under normal movement conditions. These results confirm the diverse nature of the systems recruited to perform a required visuomotor adaptation, and offer a new area requiring further research targeting its role in this essential skill.

Acknowledgements

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