Effect of visual feedback on brain activation during motor tasks: An fMRI study

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Abstract

This study examined the effect of visual feedback and force level on the neural mechanisms responsible for the performance of a motor task. We used a voxel-wise fMRI approach to determine the effect of visual feedback (with and without) during a grip force task at 35% and 70% of maximum voluntary contraction. Two areas (contralateral rostral premotor cortex and putamen) displayed an interaction between force and feedback conditions. When the main effect of feedback condition was analyzed, higher activation when visual feedback was available was found in 22 of the 24 active brain areas, while the two other regions (contralateral lingual gyrus and ipsilateral precuneus) showed greater levels of activity when no visual feedback was available. The results suggest that there is a potentially confounding influence of visual feedback on brain activation during a motor task, and for some regions, this is dependent on the level of force applied.

Keywords

fMRI; Motor Control; Visual Feedback

Introduction

A number of studies have used functional magnetic resonance imaging (fMRI) to examine the blood oxygenation level dependent (BOLD) response associated with the performance of motor tasks. These tasks have typically consisted of simple finger movements, such as finger tapping (Horenstein, Lowe, Koenig, & Phillips, 2009; Verstynen, Diedrichsen, Albert, Aparicio, & Ivry, 2005) or gripping exertions (Cramer et al., 2002; Dai, Liu, Sahgal, Brown, & Yue, 2001). Specifically, many of these studies utilized fMRI to identify the active neural centres during motor tasks that rely on visual feedback to control the force being produced by the participant (Dai, et al., 2001; Spraker, Yu, Corcos, & Vaillancourt, 2007; Thickbroom, Phillips, Morris, Byrnes, & Mastaglia, 1998). The use of visual feedback can help to ensure consistent motor output, facilitating comparisons of the BOLD response across a series of

exertions. However, the potentially confounding influence of visual feedback on brain activation during a motor task remains poorly understood. Relatively few neuroimaging studies have compared the performance of a motor task with and without visual feedback.

An elegant study was carried out by Vaillancourt, Thulborn, and Corocos (2003) to determine the functional activation associated with various components of a visuomotor task. In this study participants produced a pinch grip between their index finger and thumb for 30 s at 15% of their maximum voluntary contraction (MVC) under three conditions: with visual feedback, in the absence of visual feedback and with simulated visual feedback while producing no force. The authors used a subtractive whole brain analysis to determine the functional role of the brain activity. They found that the primary motor cortex generated the motor response with the influence of the premotor cortex, while activity within the occipital lobe was in response to the visual feedback. Integration of visual feedback and the motor response was found to occur in a subcortical network including the putamen, ventral thalamus, lateral cerebellum and the dentate nucleus of the cerebellum. Lastly, there was unique activation in the dorsolateral prefrontal cortex, the ventral premotor cortex and the anterior cingulate associated with the recall of the target force level. In contrast, Kuhtz-Buschbeck et al (2008) compared the BOLD response between different types of grips at 1% and 4% MVC and included conditions where visual feedback either provided or withheld. Their whole brain analyses showed that there was greater bilateral activation of occipital and posterior parietal areas during with visual feedback, when compared to a no feedback condition, regardless of the grip type used. Both the studies by Kuhtz-Buschbek et al (2008) and Vaillancourt et al (2003) showed higher levels of activity in occipital and posterior parietal areas when visual feedback was available at low forces (1% to 15% MVC). Kuhtz-Buschbeck et al (2008) found the effect of visual feedback to be similar between their two low force levels (1% and 4% MVC). Furthermore, both studies also showed increases in activity in the prefrontal cortex in conditions where no visual feedback was available to the participant, which was attributed to the recall of a motor memory regarding the response that was expected (Vaillancourt, et al., 2003).

The use of visual feedback to ensure the appropriate force output also requires participants to attend to a moving target on the screen and adjust the force they are producing based on feedback, thus we expect brain areas associated with visual attention, including areas in the frontal, parietal and occipital lobes and the cerebellum will be activated when visual feedback is present (Johansen-Berg & Matthews, 2002). Attending to moving visual information and responding to visual input also alters activity in motor areas of the brain (Johansen-Berg & Matthews, 2002). Additionally, Vaillancourt et al (2003) showed differential brain activation when participants were simply observing simulated visual feedback bars as compared to when force modulations were made based on this feedback.

Since activities of daily living require force levels with the hand across a wide range, from very low forces to maximum exertions (Marshall & Armstrong, 2004), it is important to examine the neural control mechanisms at higher force levels. For example, common functional tasks such as writing, shaking hands and turning on a faucet require 20 to 40% MVC, while opening a jar or carrying groceries require 60–80% MVC (Marshall & Armstrong, 2004). Several brain areas have been shown to have greater levels of activation

at higher force levels, including cortical (Cramer, et al., 2002; Dai, et al., 2001) and subcortical regions (Dai, et al., 2001; Spraker, et al., 2007). It is not known how the additional activation that is required in these areas during the production of higher force levels would interact with brain activity associated with processing visual feedback. Therefore, the goal of the present study was to determine the effect of visual feedback (with and without) and force level (moderate 35% MVC and high 70% MVC) on the neural mechanisms responsible for the production of grip force. At high force levels, we postulated that the motor task would be more challenging without visual feedback, and thus, we hypothesized that some brain areas, particularly those involved in cognitive and memory processing (eg. the prefrontal cortex and the basal ganglia), would show greater activity during these conditions to recall the memory of the target force, since this task would be novel and it is unlikely that consolidation would take place in the short time frame of our study (Shadmehr & Holcomb, 1997). Thus, this should result in differential, force dependent patterns of activation between the two feedback conditions and result in an interaction effect between force and feedback conditions.

Method and Material

Participants

Nine healthy adults (aged 19–33 years; 5 male, 4 female) volunteered to participate. All were right handed, according to the Edinburgh Handedness Inventory (Oldfield, 1971) and had normal or corrected to normal vision. Each was screened to ensure that they were free of any neurological or other health conditions that would affect their performance. Informed consent was obtained prior to participation in this experiment following the local university and hospital institutional review boards requirements.

Force recording apparatus

A water based bulb system was used to measure the pressure of the squeeze produced with the hand. The device had a rubber squeeze bulb, held by the participants in their right hand, and connected to a pressure transducer via a PVC tube. Participants held the bulb with all four fingers of their right hand and were instructed to use all fingers and their thumb to squeeze the bulb, with the bulb resting in the palm of the hand. An investigator verified that the participants were using an appropriate grip at each session. The squeezes elicited with the device were near isometric, however due the deformation of the bulb with squeezing there was a small change in the aperture of the grip with exertion. During fMRI scanning the pressure transducer was located in the MRI control room. The signal from the pressure transducer was connected to a computer through a serial interface and was sampled by custom MATLAB software at a rate of 75 Hz. Prior to data collection, participants MVC with the squeeze bulb device was determined. To determine the MVC a series of three exertions were collected, and the peak pressure level across the three trials was used as the MVC for that condition. All of the following squeezes were then normalized to this value and expressed as a percentage of MVC. The same posture was employed across trials. The device showed a linear output within the range of pressures that were used in this study.

The computer display controlled the timing of the squeezes, via a back projected image on a screen visible to the participants in the MRI scanner. In the rest condition, the participants fixated on a cross at the centre of the screen. Two seconds before the go signal the fixation cross would double in size to alert the participant that they would shortly be required to squeeze. Two target pressure levels were used throughout the study, 35% and 70% of the participants' MVC. Participants were required to match the target force levels in conditions where visual feedback regarding the grip force they were producing was provided on the screen, and also when no visual feedback was available. Examples of the stimuli presented to the participants are shown in the lower right of Figure 1. The feedback bar was presented in real time and was updated with each sample of the force signal.

fMRI Data Acquisition

All MRI data were acquired with a Philips Gyroscan Intera 3.0 T scanner (Philips, Best, the Netherlands) equipped with a 16-channel head-coil. Three functional runs were carried out where T2*-weighted echo-planar images (EPI) were acquired (matrix size = 128×128 , pixel size = 1.9×1.9 mm, TR = 2000 ms, TE = 3.7 ms, Flip Angle = 90°). Each functional run acquired a series of volumes consisting of 36 axial slices of 3 mm thickness, with a gap thickness of 1 mm. Each functional run lasted a total of 424 s (212 TRs). A high-resolution T1-weighted anatomical scan was also acquired for each participant (170 axial slices, matrix size = 256×256 , voxel size = $1.0 \times 1.0 \times 1.0$ mm, TE = 5 ms, TR = 24 ms, Flip Angle = 40°). In the MRI the participants laid in a supine position holding the squeeze bulb in their right hand. The participants' arm was positioned such that their elbow was flexed to 90° and their forearm rested across their chest in a pronated position. Head movement was minimized with a snug fitting memory foam pillow within the head coil.

Experimental Protocol

An event-related design was used in order to determine the combined effect of producing different force levels with the hand with or without visual feedback. A flowchart illustrating the experimental protocol is shown in Figure 1. Participants performed the functional task over three different fMRI runs. In each run the participants performed a total of 24 squeezes with the water-based squeeze bulb apparatus, with a total of six squeezes performed for each combination of target force level and feedback condition. There were four experimental conditions, which were presented in a random order: 35% MVC with visual feedback, 35% MVC with no visual feedback, 70% MVC with visual feedback and 70% MVC with no visual feedback. Each squeeze lasted 4s. The participants had a rest period of a random duration between 10–16s between each squeeze. A rest break of approximately five minutes was provided between each run. Thus, during the fMRI session participants performed a total of 18 squeezes in each of the four conditions across the three runs.

Prior to the fMRI scanning session all participants attended three orientation sessions to practice the force production task, with each orientation session lasting approximately 45 minutes. These sessions ensured that the participants learned to accurately produce grip exertions at the target force levels without visual feedback, in hope that any motor learning affects would be minimal in the fMRI session. In each of these orientation sessions the participants performed two different blocks of squeezes while sitting in front of a computer

screen. The first block was the experimental task, which was identical to that which was later performed in the MRI scanner. The second task was a practice block, where participants practiced performing squeezes with delayed visual feedback. For the practice block, visual feedback was absent for the first 2 s after the stimulus to squeeze, but then appeared for the final 2 s. Therefore, the participant was required to match the target force level based on their memory; after 2 s they could make corrections based on the visual feedback. There were 10 trials at each target pressure level (35% or 70% MVC) for each series of practice exertions. The duration of the squeezes and the rest periods were the same in the practice and experimental tasks. During the orientation sessions, electromyography was used to ensure that there were no mirror movements taking place with the contralateral limb.

During each orientation session, the participant first performed the experimental block of squeezes, then performed three runs of the practice block, and then performed the experimental block again. All participants were able to perform the task appropriately after the three orientation sessions. Participants took a break between each task to ensure that muscular fatigue would not affect their performance. The participants performed all three orientation sessions within 10 days of the MRI scanning session, with the last session occurring within 48 hours of the MRI session. The organization of the blocks performed by the participants in each session is summarized in Figure 1.

Data Processing

Behavioral Data—In order to determine how well the participants matched the target force level, the mean force level and the root-mean-square (RMS) error value were determined over the final 3 s of each squeeze. The first second of the squeeze was excluded because it included the increase in force to the target force level. The mean force levels and RMS error values were analyzed with a repeated measures analysis of variance (ANOVA). An alpha value of 0.05 was used.

Voxel-wise fMRI Analysis—All fMRI data were analyzed using publicly available open-source software-Analysis of Functional NeuroImaging (AFNI) (Cox, 1996). First, functional data for each participant were spatially aligned to eliminate head motion artifacts, co-registered to the same coordinate system and concatenated into a single series of volumes for data analysis. None of the participants had head motion that exceeded 2 mm in any direction. The skull was stripped and the anatomical image was aligned and registered to the concatenated functional data. For a first-level analysis, the functional data were analyzed with a General Linear Model (GLM) to produce impulse response functions (IRFs) on a voxel-wise level, for each participant. The regression matrix for the GLM consisted of four vectors, containing boxcar functions representing the timing of the stimuli to squeeze for each of force level, in both feedback conditions.

The results of the GLM analysis also provided baseline coefficients for each functional run, which defined the variation in baseline activity during the resting periods, for each participant. Percent signal change (PSC), which is an indicator of the intensity of the BOLD signal, was estimated on a voxel-wise level across the whole brain, for each participant, by

dividing the regression coefficient for each of the four conditions by the average of the baseline coefficients and multiplying by 100. The PSC value was calculated on a voxel-wise basis, for each participant.

All data was transformed to Talairach-Tournoux space (Talairach & Tournoux, 1988) by the AFNI software package using an automated process. The transformation was determined by the software package and applied to both the processed functional images and the anatomical image. To account for anatomical variability and allow for the application of statistical tests between participants a Gaussian blur (4 mm at full-width-half-maximum) was applied to each of the processed functional images containing the PSC values.

Because the primary goal of this study was to examine how visual feedback affected the performance of a visuomotor task across different force-levels a three-factor voxel-wise ANOVA, with a mixed effect model, was carried out as a second level analysis. The force and visual feedback conditions were fixed factors within the ANOVA, while each participant served as a random factor. Alpha was set to 0.005. To account for multiple comparisons, a clustering criterion was applied to find volumes greater than 200 voxels within the brain that demonstrated a significant force-by-feedback interaction effect, or a main effect of feedback condition. This analysis approach has been shown to be suitable for localizing significant differences and reducing the effect of multiple comparisons in fMRI data (Forman et al., 1995). The anatomical regions and Brodmann Area associated with the centre of mass of each cluster were determined with the use of the Talairach daemon (an online neuroanatomical atlas) (Lancaster et al., 2000). The mean PSC values within significant clusters were also analyzed with a post-hoc analysis that consisted of a comparison of Bonferroni corrected means in order to determine the nature of the significant interaction or main effect. In order to assess the appropriateness of the chosen clustering criteria a series of 1000 Monte-Carlo simulations were carried out with the AFNI software to determine the minimum clusters size to achieve a corrected alpha level of 0.05 (Forman, et al., 1995). This series of simulations revealed that a minimum cluster size of 146 voxels was required to achieve this desired alpha level. As the chosen clustering criteria were greater than this minimum threshold it can be confidently stated that the areas identified with the chosen clustering criteria represent a true difference between the conditions. To facilitate comparisons with the results from other studies, the Talairach coordinates were converted to MNI space in all figures and tables displaying the results of the current study.

Results

Behavioral Results

Participants were able to closely match the target force levels in all conditions. The average force level over the final three seconds of the squeeze, and the mean RMS error are shown in Table 1. An interaction effect between the feedback and force conditions was observed for the mean force produced during this period ($F(1,8) = 10.914$; $p = 0.0011$). The participants most closely matched the target force level when there was no visual feedback at the 35% MVC force level, where they were within 1% MVC. The participants were slightly less accurate in all of the other conditions, however they were within 5% MVC in all of the trials.

For the RMS error a significant difference was observed between the two force levels ($F(1,8) = 55.255$; $p < 0.001$) and the two feedback conditions ($F(1,8) = 11.564$; $p = 0.009$). Because both factors in the ANOVA showed a significant main effect, post-hoc comparison of Bonferroni corrected means were used to determine differences between the conditions. It was found that the participants made smaller errors at the 35% MVC level, and when visual feedback was available respectively. Conversely, the participants made the largest errors in conditions without visual feedback in the 70% MVC condition.

fMRI results

The primary analysis consisted of a mixed model ANOVA, with the two fixed factors of the force and feedback conditions. Two regions were found to demonstrate a significant interaction effect between the force and feedback conditions (Figure 2). The first region was the left precentral gyrus (MNI coordinates: $X = -51$ $Y = -6$, $Z = 19$, $BA = 6$), which corresponds functionally with the rostral premotor cortex. The second area was the left putamen (MNI coordinates: $X = -22$, $Y = -2$, $Z = 3$). In both of these clusters there were no differences in the PSC values between the forces conditions when visual feedback was available, however there was a significant increase in the observed PSC value at the 70% MVC force level when there was no visual feedback (Figure 3). The voxel-wise analysis of the feedback main effect identified a total of 24 clusters that showed a significant difference between the two feedback conditions. Higher activation when visual feedback was available was found in 22 of the 24 clusters (Table 2 and Figure 4). The two clusters that showed higher activation without visual feedback were the left lingual gyrus and the right precuneus.

Discussion

The primary objective of this study was to utilize fMRI to determine whether force-dependent patterns of brain activation occur between visual feedback and no feedback conditions in exertions with the hand at force levels that might be used during activities of daily living. We discovered that two regions demonstrated an interaction effect between force and feedback conditions, indicating that visual feedback was processed differently between these two force levels in these areas. In both of these regions, a similar level of activation was observed across the two force levels when visual feedback was available, however when visual feedback was removed, a statistically greater level of activity was observed at the higher force level.

The regions that demonstrated the force-visual feedback interaction involved the basal ganglia, specifically the ipsilateral putamen, as well as the rostral premotor cortex. Vaillancourt et al. reported that the putamen was involved in the visuomotor transformation process (Vaillancourt, et al., 2003), as well as during the selection of force levels during motor tasks (Vaillancourt, Yu, Mayka, & Corcos, 2007). Further, it has been hypothesized that the rostral premotor cortex acts as a gateway between cognitive and motor processes within the brain (Hanakawa, 2011). Given the necessity of updating the motor plan based on the available visual information it may be that the activity we noted in rostral premotor cortex represented the neural interface between cognitive and motor systems in the brain for our force control task.

One possible explanation for the force-feedback interaction noted in the putamen and rostral premotor cortex is that the higher force condition represented a more challenging motor task especially when visual feedback was absent. We postulate that the higher force condition without visual feedback required greater dependence on the memory of the target level, and hence, higher activation in these regions. This explanation is supported by our observance of greater RMS errors during the higher force condition, particularly when there was no visual feedback. Greater RMS error indicates that there was more variability in force production at the target of 70% MVC, which likely required additional neural resources to recall the target and sustain a high force output. This greater challenge likely resulted in higher activation throughout the brain (Cramer, et al., 2002; Verstynen, et al., 2005), but particularly in the basal ganglia, which has been shown to exhibit increased levels of activity where there is variability in force production (Floyer-Lea & Matthews, 2004). In addition, activation of the rostral premotor cortex may be necessary as this region uses context-dependent information to link cognitive resources, which would be required for the recall of the target force level with the recruitment of motor resources (Hanakawa, 2011). Recent animal work in primates work has shown that there are direct neural connections between the striatum, including the putamen, and the rostral premotor cortex (Saga et al., 2011). It has been hypothesized that this connection facilitates interaction between subcortical resources, motor planning and cognitive processing (Hanakawa, 2011; Saga, et al., 2011).

Our results contrast with Kuhtz-Buschbeck et al (2008), which is the only prior study to investigate the effect of visual feedback and force control. They found that there was increasing activation in regions of the cerebellum, and the occipital and parietal lobes that were correlated with force when visual feedback was available. The difference in findings is likely due to the low range of force (1–4% MVC) utilized by Kuhtz-Buschbeck et al (2008) as compared to our study (35 and 70% MVC).

Our study also identified a total of 22 areas that showed significant differences in activation depending on the feedback condition. Further analysis revealed that 20 of these 22 areas showed greater levels of activity in conditions where visual feedback was available to the participants. Most of these areas are consistent with areas that have been identified in previous studies of visually guided force production (Kuhtz-Buschbeck, et al., 2008; Vaillancourt, et al., 2003). However, it was interesting to note that some identified regions (e.g., precentral gyrus, cingulate motor areas and caudate) that were additionally activated with visual feedback are primarily known for their motor functions. These areas may be involved in the processing of visual feedback and subsequently used to alter motor output based on visual feedback. Given that past work has largely relied on motor control tasks with a visual feedback element, it is possible that these regions display a differential pattern of activity when vision is not available. That is, if only a visual guided task is performed, it is difficult to determine the contributions of the brain activation to the motor task itself versus the visual requirement of the task. It must also be stated that based on the methods used in this study that we cannot separate brain activity required to perform the visual task of observing the moving feedback bar from the attentional task of making motor decisions based on the feedback. In order to achieve this there would need to be additional conditions where the participants simply observe the moving feedback bar as was done by Vaillancourt et al (2003). Future work should differentially employ motor tasks with and without visual

feedback and include conditions with simulated visual feedback to further elaborate the roles of these brain regions in force control, response to visual feedback, or both.

We also identified two regions that showed greater activation in conditions when visual feedback was not available. Specifically these areas were the left lingual gyrus and the right precuneus. Both of these areas are involved in the processing of visual information. The lingual gyrus has been shown to have higher levels of activity when the global visual field must be evaluated (Fink et al., 1996). In the conditions where no visual feedback was available to the participants, only the global visual stimuli would have to be evaluated (leading to activity within the lingual gyrus) as the screen presented the participant with a static view of the target force. In contrast, in conditions where visual feedback was available, processing of a dynamic local feature of the visual field would be required (hence, deactivating the lingual gyrus) as the screen presented the participant with a responsive target level. The precuneus is typically thought to be involved in basic visual processing and has been identified as being involved in behavioral engagement, such as making a decision to start or stop a task based on visual information (Ogata, Horaguchi, Watanabe, & Yamamoto, 2011; Zhang & Li, 2012). The precuneus has also been linked with the recall of memories based on visual information (Cavanna & Trimble, 2006; Spraker, et al., 2007), which would be consistent with the greater activity that was observed when no visual feedback is available to the participants in this study, and thus, memory recall of the target was required.

While the participants were able to closely match the target force level in all conditions, it is interesting that the closest match to the target force level occurred with no visual feedback at the 35% MVC force level. Based on observations of time-series data of individual subjects' data we postulate that this finding is related to an overshoot when the participants were first provided with the visual feedback at the 35% MVC condition. At the lower force level, when the participant had visual feedback they would often overshoot the target force level and then release force to attempt to match the target force level. This often resulted in periods during the middle of the squeeze where the force produced was below the target force level. This pattern was not observed when the participants were not provided with visual feedback in the 35% MVC condition, nor was it evident in either feedback conditions at the 70% MVC level.

It is possible that the neural areas showing higher levels of activity at the higher force-levels may be associated with other aspects of the control of the gripping action. Empirical work and analytical models suggest that the aperture of the grip may be a factor that is controlled during gripping exertions (Pilon, De Serres, & Feldman, 2007). The aperture used during the higher force level in the present experiment would be smaller than that used at the lower force level, due the slight deformation of the bulb that occurred with each squeeze.

A limitation of this study is that only two target force levels were examined. While some other studies have used fMRI to examine the neural control of muscle force with a greater number to target force levels, it is difficult to have participants learn to produce more than two distinct force levels when visual feedback is not available. Given that past work in this field has not considered the impact of higher force production on the brain we believe that our choice of 35% and 70% MVC allowed us to begin to disentangle the relationships

between force level, visual feedback and motor control. Another limitation may be the fact the postures of the participants were different between the practice sessions, where the participants were seated in front of a computer screen, and the experimental session within the MRI, where the participant was supine. While this difference in posture may introduce some novel task components once the participant was in the MRI, the differences were likely negligible as participants were still able to match the target force levels without visual feedback with little difficulty.

Conclusion

We discovered that the brain regions active to control force production for the hand differ depending on whether or not visual feedback is available to the participant. Further, for some brain regions, this finding depends on the level of force applied with higher forces invoking a distinct set of brain activity when visual feedback is absent. These regions likely represent brain areas responsible for the interaction between cognitive planning associated with recalling the memory for the desired target force level and the required motor output. Given that we discovered differential patterns of activity for varied force and visual feedback conditions, these factors may be important to consider when examining brain networks associated with motor control of hand function.

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Figure 1.

Outline of the sessions and the blocks of squeezes that participants performed in this experiment. Sample visual stimuli provided to the participants in each condition are also shown.

Figure 2.

Clusters that showed significant interaction effects are highlighted in white. The MNI coordinates of each clusters' CoM are indicated in the figure.

Figure 3.

Average ($N = 9$) PSC values in the clusters that showed significant interaction effects in each force and feedback condition. The error bars represent the standard deviation.

Figure 4. Clusters that showed significant differences between the feedback conditions are highlighted in white. The MNI coordinate of each axial slice is shown in the figure.

Table 1

Mean (N=9) Force Levels and RMS error values for each feedback condition, at each target force level.

		35% MVC		70% MVC	
		Feedback	No Feedback	Feedback	No Feedback
Relative Pressure (%MVC)	Average	32.10	35.30	66.60	65.97
	SD	2.80	6.32	3.20	7.58
RMS Error (% MVC)	Average	4.94	6.15	9.36	11.47
	SD	1.95	1.26	2.31	2.19

Table 2

Clusters showing significant differences between visual feedback conditions

Cluster Size(mm ³)	MNI Coordinates			Z	Location	Brodmann Area
	X	Y	Z			
A. Clusters greater than 200mm ³ that show greater activity with Visual FB (<i>F</i> > 14.74; <i>P</i> < 0.005).						
4830	-39.2	76.4	-2.6		R. Inferior Occipital	19
4454	42.7	72.8	-1.2		L. Inferior Occipital	19
2469	-0.6	81.0	24.6		L. Cuneus	18
1193	-24.0	59.1	51.5		R. Superior Parietal	7
776	-28.6	50.2	-21.5		R. Culmen	
731	39.8	7.4	59.2		L. Precentral Gyrus	6
707	33.3	46.4	53.6		L. Superior Parietal	7
684	22.6	-57.8	-34.7		L. Superior Frontal	11
666	-6.0	74.8	-9.6		R. Declive	
630	-23.1	76.5	35.2		R. Precuneus	31
577	5.4	73.7	-26.1		L. Pyramis of Vermis	
535	-26.8	-31.7	17.9		R. Anterior Cingulate	32
486	10.6	25.3	42.9		L. Cingulate Gyrus	31
406	16.2	-23.6	-0.2		L. Caudate	
321	25.5	58.7	52.6		L. Superior Parietal	7
305	21.0	72.1	17.2		R. Cuneus	30
288	18.9	9.4	61.8		L. Middle Frontal	6
271	-17.6	-47.0	-4.1		R. Anterior Cingulate	10
247	32.5	78.6	-17.3		L. Declive	
238	-39.4	50.7	18.7		R. Superior Temporal	22
232	-19.2	-25.8	6.3		R. Caudate	
218	-11.5	27.0	45.4		R. Cingulate Gyrus	31
B. Clusters greater than 200mm ³ that show greater activity without Visual FB (<i>F</i> > 14.74; <i>P</i> < 0.005).						
611	12.7	64.5	7.6		L. Lingual Gyrus	
482	-43.3	75.1	41.1		R. Precuneus	19