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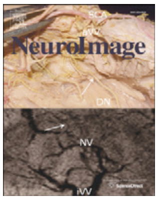

Differential activation of brain regions involved with error-feedback and imitation based motor simulation when observing self and an expert's actions in pilots and non-pilots on a complex glider landing task

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ABSTRACT

In this fMRI study we investigate neural processes related to the action observation network using a complex perceptual-motor task in pilots and non-pilots. The task involved landing a glider (using aileron, elevator, rudder, and dive brake) as close to a target as possible, passively observing a replay of one's own previous trial, passively observing a replay of an expert's trial, and a baseline do nothing condition. The objective of this study is to investigate two types of motor simulation processes used during observation of action: imitation based motor simulation and error-feedback based motor simulation. It has been proposed that the computational neurocircuitry of the cortex is well suited for unsupervised imitation based learning, whereas, the cerebellum is well suited for error-feedback based learning. Consistent with predictions, pilots (to a greater extent than non-pilots) showed significant differential activity when observing an expert landing the glider in brain regions involved with imitation based motor simulation (including premotor cortex PMC, inferior frontal gyrus IFG, anterior insula, parietal cortex, superior temporal gyrus, and middle temporal MT area) than when observing one's own previous trial which showed significant differential activity in the cerebellum (only for pilots) thought to be concerned with error-feedback based motor simulation. While there was some differential brain activity for pilots in regions involved with both Execution and Observation of the flying task (potential Mirror System sites including IFG, PMC, superior parietal lobule) the majority was adjacent to these areas (Observation Only Sites) (predominantly in PMC, IFG, and inferior parietal loblule). These regions showing greater activity for observation than for action may be involved with processes related to motor-based representational transforms that are not necessary when actually carrying out the task.

Introduction

Observing action of others as well as observing and imagining our own actions are behaviors used to support identification, imitation, and learning of various perceptual motor skills. Motor simulation is a key principle in the way in which observation of actions is processed and understood. Imitation learning and processing are thought to utilize a type of motor simulation that incorporates brain regions (premotor cortex PMC, inferior frontal gyrus IFG, superior temporal gyrus/sulcus STG/S, middle temporal cortex MT, and parietal cortex) responsive to both observation and execution of action (potential Mirror System sites) (Brass and Heyes, 2005; Caspers et al., 2010; Di Pellegrino et al., 1992; Gallese et al., 1996; Iacoboni et al., 1999; Molenberghs et al., 2009; Rizzolatti and Craighero, 2004; Rizzolatti et al., 1996, 2001). It is maintained that how a person observes an action is based on neural systems involved with production of that action (motor simulation) (Callan et al., 2004a, 2010; Calvo-Merino et al., 2005; Decety and Grezes, 1999; Gallese and Goldman, 1998; Iacoboni, 2008; Jeannerod, 2001; Mulder, 2007; Oztop et al., 2005; Raos et al., 2007; Skipper et al., 2007; Wilson and Iacoboni, 2006).

Another manner in which motor simulation is utilized during observation of action is in reference to error-feedback of control processes for various perceptual motor tasks such as visual tracking (Imamizu et al., 2003; Ogawa et al., 2006) which has been shown to involve the cerebellum (Diedrichsen et al., 2005; Grafton et al., 2008; Higuchi et al., 2007; Imamizu and Kawato, 2010; Imamizu et al., 2000, 2003; Miall and Jenkinon, 2005; Miall et al., 2000, 2001; Ramnani et al., 2000; Wolpert et al., 1998). Ongoing perceptual feedback is used to compare against the consequences of an internal motor simulation. The difference between the estimated and actual feedback constitutes error upon which prediction and subsequent learning can be achieved. Experiments have determined that the acquisition and instantiation of these error-feedback processing systems for the manipulation of various

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tools are modularly organized within the cerebellum (Higuchi et al., 2007; Imamizu and Kawato, 2010; Imamizu et al., 2003). Furthermore, acquisition and processes related to skill and expertise have also been determined to involve the cerebellum (Calvo-Merino et al., 2006; Higuchi et al., 2007).

Based on the computational architecture of neural circuitry in the brain it has been proposed (Doya, 1999) that the cortex is involved with unsupervised learning and the cerebellum is involved with supervised error-feedback learning. This distinction parallels the different types of motor simulation systems, one based on imitation processes involving cortical regions and one based on error-feedback involving the cerebellum.

Depending on the complexity of the action observed, experience and skill involved with that action is likely to be very important in terms of using motor simulation to process the observed action. The objective of this study is to determine whether these two hypothesized motor simulation systems are differentially activated by observation of a complex action when it is performed by an expert (differentially invoking imitation motor simulation in the cortex) or involves a replay of one's own previous action (differentially invoking error-feedback motor simulation in the cerebellum) as well as to determine how these differences may be a function of expertise on the observed task.

The complex perceptual-motor task we set out to investigate involves flying a glider. The same four degrees of freedom used to fly a glider in the real world (aileron, elevator, rudder, dive brake) were used to control a glider using a flight simulator while undergoing fMRI brain scanning. Even though such complex control is likely to use considerable independent and overlapping brain networks it is maintained that only by studying the brain under very closely simulated real-world conditions can we truly understand the processes carried out that are applicable to experience in the real world. This approach is in line with that of neuroergonomics (Parasuraman, 2003, 2011, 2012; Parasuraman and Rizzo, 2008), the study of brain and behavior at work in real world environments. This approach to investigating aspects of perception, action, and cognition in robust and more ecologically valid environments is also shared in the work of Calhoun and colleagues on driving simulation (Calhoun and Pearlson, 2012; Carvalho et al., 2006) and by experiments conducted by Maguire's group on spatial navigation and mentalizing (Pine et al., 2002; Spiers and Maguire, 2006) using fMRI as well as by aviation cerebral experimental sciences research (Callan et al., 2012).

The task involves landing a glider using the four flight controls as close as possible to a red + on the runway. The main focus of the study was the two replay conditions in which the subject passively observed the flight of the airplane. One replay condition was of an expert pilot's flight (Expert Replay). The other replay condition was of the subject's own previous trial flight (Previous Replay). There was also a baseline do nothing condition. All conditions were from the first person perspective of sitting in the cockpit of the glider and looking straight in front out of the canopy (Fig. 1).

In the case of flying a glider the view out of the cockpit is dictated by the roll, pitch, yaw, and sink (dive) rate in reference to the landscape (mainly the horizon) that have a direct correspondence to the movement of the aileron, elevator, rudder, and dive brake. From the first person perspective one does not perceive independent alterations in a landscape but rather perceives their body moving in an embodied sense in relation to a static landscape. Indeed it would be quite amazing if individuals perceived the vehicle as being static and the world moving independently around them. For a pilot, the percept of the roll, pitch, yaw, and sink (dive) rate is perceived in relation to the actions of the control surfaces by manipulating the control stick, rudder pedals and dive brake dictating the flight characteristics as seen from the cockpit, with the end-effector being the relation of the cockpit to the landscape. The foundations for the utilization of action observation by means of motor simulation have been established for situations in which biological motion of the articulators is not present in sensory stimulation such as in the case of perceiving speech (Callan et al., 2000, 2003a, 2003b, 2004b, 2006a, 2006b, 2010; Galantucci et al., 2006; Kent et al., 2000; Liberman and Mattingly, 1985; Liberman et al., 1967; Schwartz et al., 2012; Skipper et al., 2007; Wilson et al., 2004) and especially in the case of instrumental music (Bangert et al., 2006; Baumann et al., 2007; Lahav et al., 2007; Margulis et al., 2009). Just as the musician perceives music in relation to the action of the articulators responsible for producing the music on a specific instrument (even when the articulators cannot be directly viewed), a pilot perceives changes in the orientation of the landscape out of the cockpit of the airplane as resulting from the movement of their arms and legs manipulating the control surfaces of the glider (plane).

The objectives of this study are 1. To determine the extent to which the action observation network is differentially activated by imitation based motor simulation (observing an expert landing the glider) compared to error-feedback based motor simulation (observing one's own previous trial landing the glider), 2. To determine the similarities and differences that expertise (pilots versus non-pilots) has with reference to the above objective, 3. To determine, with reference to the replay conditions, the extent of the involvement of brain regions responsive to both execution and observation of action (Execution & Observation Sites: Constituting potential Mirror System sites), as well as brain regions selectively involved only in observation (Observation Only Sites) of a flying task in which the articulators responsible for action cannot be observed. Based on the results of previous studies several predictions can be made regarding the objectives of this study.

Consistent with the proposal made by Doya (1999) that the cortex is involved with unsupervised learning and the cerebellum is involved with error-feedback supervised learning (Objective 1), when pilots see an expert's flight they will process the information in part by relation to unsupervised imitation based motor simulation for action understanding and facilitating performance. A meta-analysis of action observation and imitation (Caspers et al., 2010) suggests that the imitation network involves the PMC, IFG, anterior insula, superior temporal gyrus/sulcus STG/S, visual motion processing area V5/MT, and the parietal cortex. Whereas, observation of one's own previous glider landing relative to an expert's glider landing is predicted to have greater activity in brain regions involved with motor simulation as it relates to error-feedback (cerebellum) (Imamizu et al., 2003; Ogawa et al., 2006). It is maintained that because the subjects know how far they were from landing on the target that this information can be used in a supervisory manner to evaluate observation of the previous trial in reference to visual tracking of the flight to guide error-feedback prediction based on motor simulation processes in the cerebellum.

With regard to the second objective of this study it is predicted that expertise will be important in the extent to which the Expert Replay and Previous Replay conditions show differential brain activity. Studies investigating the effects of expertise on observation of dance (Calvo-Merino et al., 2005, 2006; Cross et al., 2006, 2009) and instrumental music (Bangert et al., 2006; Baumann et al., 2007; Lahav et al., 2007; Margulis et al., 2009) have identified differential brain activity as a function of skill on the task in brain regions involved with motor simulation primarily the PMC and parietal cortex. Based on these results it is hypothesized that pilots will have much greater differential activity between observation of an expert's glider landing and that of their own previous trial. Individuals (pilots) with real-world experience with flying gliders will have complex models in place that can simulate the complex transformations from observation to control of multiple degrees of freedom that will not be present in non-pilots.

Unlike previous studies investigating aspects of the action observation network involved with dance this study will be able to determine brain regions that are active both during observation as well as execution of the complex action (Execution & Observation Sites: Potential Mirror Neuron System sites) (Objective 3). Although investigating dance moves has been extremely informative in investigating neural processes underlying the action observation network especially with reference to issues related to expertise there are experimental limitations in being able to directly test the involvement of brain regions involved with both execution and observation of action (the Mirror Neuron system). This limitation arises from the inability to actually execute the dance moves while in the fMRI scanner. Based on the claims made in the studies concerning action observation of dance moves (Calvo-Merino et al., 2005, 2006; Cross et al., 2006, 2009) as well as instrumental music (Bangert et al., 2006; Baumann et al., 2007; Lahav et al., 2007; Margulis et al., 2009) it is predicted that brain regions involved with imitation based motor simulation will utilize brain regions concerned in both execution and observation of action (potential Mirror System sites). We also investigate activity that is greater during observation of action than during execution of action. It is predicted that additional neural processes are required to make perceptual-motor transformations (e.g. proprioceptive, kinesthetic, and haptic information) that are not necessary when one is executing the task because it is already present.

Methods

Ethics statement

All subjects gave written informed consent for experimental procedures approved by the ATR Human Subject Review Committee in accordance with the principles expressed in the Declaration of Helsinki.

Subjects

Thirty right-handed subjects participated in this study. Fifteen of the subjects were pilots varying in experience from 10 h to over 500 h. Fourteen out of the 15 pilots had experience flying gliders. The control non-pilot group all had experience with driving or flying related video games. The age and sex between the two groups were balanced. The pilots had a mean age of 22.6 years SE = 1.48 ranging from 19 to 42 years. The control non-pilot group had a mean age of 23.9 years SE = 1.46 ranging from 19 to 39 years. There was no significant difference between the age of the subjects in the pilot and control groups ($T = -.63$, $p = 0.53$). There were 13 males and 2 females in both the pilot and control groups.

Procedure

This experiment consisted of a flying condition, two replay conditions, and a baseline rest condition. The flying task was to land a glider (ASK-21) as close to a red + on the runway as possible to the left or right as instructed while keeping alignment with the runway and proper pitch, yaw, and roll on landing (See Fig. 1). The starting position of the glider was approximately 441 m perpendicular to the center of the runway between the left and right target marks (+), at an altitude of approximately 40 m. The starting speed was approximately 120 km per hour. The targets were spaced approximately 276 m from each other on the center of the runway. The runway used was that of Kobe Airport (RJBE). The X-plane (Version 9.31, Laminar Research) flight simulator was used for the experiment. The data for various flight parameters (yaw, pitch, roll, heading, speed, landing gear-forces, structural g-forces, latitude, longitude, altitude, etc.) were collected at a sampling rate of 100 Hz using a UDP Matlab interface. The experimental conditions could be controlled via Matlab by using the UDP interface to give commands to the flight simulator. Subjects utilized four degrees of freedom to fly the glider including a joystick used with right hand (aileron controlling roll and elevator controlling pitch), pedals used with both feet (rudder controlling yaw), and a dive break used with the left hand (air break controlling increased drag and increased steepness of glide slope) (See Fig. 2). The subject had to coordinate control of all four degrees of freedom to be able to properly land the glider on target while maintaining proper pitch, roll, yaw, and heading on landing without excessive g-force (A crash was signified by forces in excess of 9G, as well as a pitch or roll attitude on landing of greater than 25 degrees. Greater than a 10 degree deviation in pitch, roll, or heading upon landing incurred a 5 m penalty for each violation). The experiment consisted of two replay conditions. In one replay condition the subjects were presented with a video of their immediately previous flying trial (Previous Replay). In the other replay condition subjects were presented with a video of a landing made by an expert pilot (Expert Replay). The replay conditions were given with the same first person perspective as when they were flying the glider. The replay conditions essentially had the same visual information as the flying condition. Subjects were instructed to passively observe the two different replay conditions without making any movements. The experiment also consisted of a baseline control condition in which the subjects passively looked straight ahead at a static image of the runway. The trials were presented in blocks with instructions presented for 0.9 s on the center of the screen followed by a randomized time between 0.1 and 0.9 s before the start of the 20 s task (fly, passively watch replay or still screen). At the end of the task there is a randomized time between 0.7 and 0.9 s before the next trial begins. The instructions consisted of an arrow to the left < to designate landing to the left target on the flying condition, an arrow to the right > to designate landing to the right target on the flying condition, an up arrow ^ to designate Previous Replay, a square to designate Expert Replay, and an equals sign = to designate the baseline do nothing condition. The blocks were presented in a sequence of four trials in the following order: baseline, flying, replay, and flying. The target direction within each sequence is the same (either to left or right target +). This target direction was randomly determined and balanced for the 8 sequences in each session (4 to the left and 4 to the right). The type of replay either Previous or Expert for each sequence was also randomly determined and balanced (4 Previous and 4 Expert Replays for each session). Each subject completed 4 sessions. All subjects reported that they experienced the glider moving in relation to a static landscape rather than the landscape moving in relation to a static glider.

fMRI data collection and preprocessing

Visual presentation of the flight simulation was projected via mirrors to a screen behind the head coil that could be viewed by the subject by a mirror mounted on the head coil. An fMRI compatible control stick (NATA technologies) was used by the right hand of the subject to control the aileron deflection (roll left and right) and the elevator deflection (forward = pitch down and back = pitch up). The fMRI compatible rudder pedals (Current Design) were used by both feet of the subject to control the rudder deflections (yaw left and right). The fMRI compatible throttle quadrant (NATA technologies) was used by the left hand of the subject to control the dive brake (increases drag and increases steepness of glide slope). The flight simulator was controlled via an UDP interface (100 Hz) to a computer running the experimental protocol in Matlab. Trigger timing of the fMRI scanning was directly read into one of the flight parameters of the flight simulator by means of a National Instruments Hi Speed USB NI USB-9162 BNC analog to digital converter. Over 300 flight parameters of the airplane were collected at a rate of 100 Hz and included (latitude, longitude, altitude, roll, pitch, yaw, heading, landing gear forces, structural g-forces, control stick (aileron) and (elevator) deflection, rudder deflection, dive brake deflection). Given this information we could tell the location (distance to the target +) and the attitude of the glider on landing as well as the force of the landing (crash/damage) and whether there was a bounce on landing (landing defined after no bouncing).

The Siemens Trio 3T scanner was used for brain imaging at the ATR Brain Activity Imaging Center. Functional T2* weighted images were acquired using a gradient echo-planar imaging sequence (echo

Conditions

< Land Left
> Land Right
^ Expert Replay
☐ Previous Replay
= Do Nothing

Fig. 1. The task for the subject is to land the glider as close to the red + as possible. The instructions specified the conditions of the experiment which included: fly the plane to land on the left target (arrow pointing to left); fly the plane to land on the right target (arrow pointing to right); passively observe replay of Expert Replay (square); passively observe replay of Previous Replay (arrow pointing up); and a null condition in which subjects passively viewed a still screen of the starting position of the glider (equals sign).

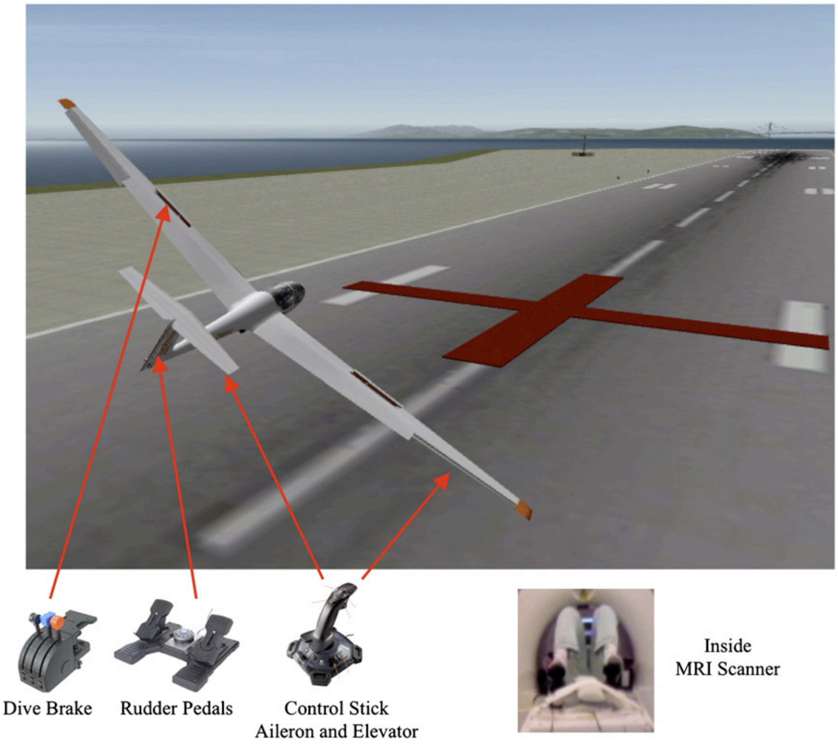

Fig. 2. The glider flight controls were the same as those used to fly a real glider. They consisted of the joystick, the dive brake, and the rudder pedals. The joystick was used by the right hand that controlled the defection of the ailerons (side to side motion–roll of the aircraft) and the elevator (front to back motion–pitch of the aircraft). The dive brake was used by the left hand (a single lever) to increase drag and increase steepness of glide slope without increasing speed (full up position the dive brake is not engaged, full down position the dive brake is fully engaged). The rudder pedals were used by both feet and controlled the deflection of the rudder (left foot yaw to the left, right foot yaw to the right). All controls had to be coordinated simultaneously to properly land the glider.

time 30 ms; repetition time 2500 ms; flip angle 80°). A total of 40 interleaved axial slices were acquired with a 4×4×4 mm voxel resolution covering the cortex and cerebellum. A single run consisted of 310 scans. The first 3 scans were discarded. T2 structural images, later used for normalization, were also collected using the same axial slices as the functional images with a 1×1×4 mm resolution. Images were preprocessed using SPM8 (Wellcome Department of Cognitive Neurology, UCL). Echo planar images EPI were unwarped and realigned. The T2 image was coregistered to the mean EPI. The T2 images were acquired during the same fMRI session as the EPI with the same slice thickness. Since the head was in approximately the same position it is thought that this will facilitate coregistration. The EPI were then spatially normalized to MNI space (3×3×3 mm voxels) using a template T2 image and the coregistered T2 image as the source. Normalization was done using the T2 image rather than EPI because we believe it gives better results due to better spatial resolution. The images were smoothed using an 8×8×8 mm FWHM Gaussian kernel. Regional brain activity was assessed using a general linear model employing a boxcar function convolved with a hemodynamic response function (block design experiment). High pass filtering (cutoff period 128 s) was carried out to reduce the effects of extraneous variables (scanner drift, low frequency noise, etc.). Auto-regression was used to correct for serial correlations. The 6 movement parameters were used as regressors of non-interest in the analysis to account for biases in head movement correlations present during the experimental conditions. Sessions with excessive head movement greater than 6 mm were removed from 11 of the 30 subjects (4 pilots and 7 controls). The results did not change significantly whether the sessions were removed or not.

For the purposes of this study it is maintained that a block design is sufficient to extract activation of the relevant brain networks involved with the glider task that are sustained throughout the 20 s duration of the block. However, one limitation is that a block design may miss out on transient short duration activity related to specific events. Although this may be the case, the dynamic continuous nature of the task does not lend itself well to an event-related design. If one were interested in specific events within the context of the glider-landing task such as activity during deployment of dive brake, activity on short final, activity after landing an event related design could be effectively employed. However, this was not the goal of this study. Rather, the goal of this study was to determine activity while viewing different types of replays as well as while carrying out the gliding task. Another method that would be advantageous in the case of finding neural correlates of specific dynamic continuous task variables is the use of independent component analysis ICA. This approach has previously been used to extract task related brain activity during simulated driving (Calhoun and Pearlson, 2012; Carvalho et al., 2006). One challenge in applying this ICA approach in this study is that it would be difficult to match up the same underlying components from the different groups especially in the case where corresponding components may be altogether absent for non-pilots.

fMRI analysis

Given the objectives of this article several contrasts between experimental conditions were carried out. Contrasts of interest between the various conditions were estimated for each subject using the general linear model. The parameter estimates of the analyses for each subject were used to conduct between subject random effects one-sample t-tests for these contrasts of interest that included: Fly–Baseline, Previous Replay–Baseline, Expert Replay–Baseline, Previous Replay–Expert Replay, and Expert Replay–Previous Replay. To determine the brain activity related to aspects of imitation that include Execution & Imitation sites an inclusive mask was made from a conjunction analysis of brain activity present for both the Fly–Baseline contrast and the respective replay contrast (Expert Replay–Baseline or Previous Replay–Baseline) threshold at $pFDR<0.05$ corrected for multiple comparisons across the entire brain. Observation Only Sites were assessed by the contrast of the respective replay (Expert Replay–Baseline or Previous Replay–Baseline) using a threshold of $pFDR<0.05$ corrected for multiple comparisons while excluding activity during the Fly–Baseline contrast using a lenient threshold of $p<0.05$ uncorrected. A comparison between the pilot and the control non-pilot group on how they differentially processes Expert and Previous Replays was assessed using a between subject t-tests. The anatomical coordinates reported in this study are given in Montreal Neurological Institute MNI units.

Region of interest analyses were carried out in brain regions thought to be involved with imitation and error-feedback processing. The MNI coordinates of brain regions involved with both observation and imitation of action as well as observation to imitate action as given in the ALE meta-analysis of action observation and imitation (Caspers et al., 2010) were used as sites for region of interest analyses. These sites include the PMC BA6 (54,6,40), the IFG BA44 (58,16,10) and (52,10,38), anterior insula (42,6,−2), STS/pMTG (54,−50,10), MT (52,−70,6). Two sites in the superior parietal lobule SPL were also included. One found to be involved with both observation and imitation of action (30,−62,63) and one involved with observing to imitate action (9,−63,64). Because our task included using both hands and feet we included both left and right side regions of interest for all search sites. The region of interest analyses at these sites was carried out using a small volume correction for multiple comparisons $p<0.05$ with a search radius of 10 mm. The cerebellum is thought to be a site of error-feedback learning (Doya, 1999; Imamizu et al., 2000, 2003; Miall et al., 2001; Wolpert et al., 1998). In our study visual feedback during the Previous Replay condition may be utilized as an error-signal because the performance of the trial is known. Experiments using visual feedback control suggest that the lateral cerebellum is involved with processing of dynamic error signals (Imamizu et al., 2003; Ogawa et al., 2006). The MNI coordinate for visually guided error processing in the cerebellum is given in Ogawa et al. (2006) at (−40,−74,−26). We conducted region of interest analyses using these coordinates to correct for multiple comparisons $p<0.05$ with a search radius of 10 mm on both left and right sides of the cerebellum. It should be noted that this area of the lateral cerebellum has been found to be involved with imagery of tool use (Higuchi et al., 2007). The flight controls of a glider can be thought of as a very complex tool.

Results

Behavioral results

Pilots were significantly better at landing the glider closer to the target mark (+) than non-pilots (between subjects $T=3.1$, $p<0.005$, $df=28$). The mean distance to the target (+) for pilots was 44.8 m ($SE=3.76$) and for non-pilots it was 69.6 m ($SE=7.39$). The number of crashes was significantly greater for non-pilots (mean = 1.62 trials per session of 16 trials, $SE=0.46$) than for pilots (mean = 0.58 trials per session of 16 trials, $SE=0.20$) (between subjects $T=2.1$, $p<0.05$, $df=28$).

Brain imaging results

The results of the fMRI random effects analyses for the pilots and non-pilot control subjects are shown in Fig. 3 for the Fly–Baseline, Expert Replay–Baseline, and Replay Previous–Baseline contrasts. Very similar patterns of activity across the brain are present for both pilots and non-pilot control subjects for all three contrasts. Activity is present in PMC, IFG, parietal cortex, prefrontal regions, occipital cortex, MT/middle superior temporal MST, and cerebellum for all three contrasts for both pilots and non-pilots (Fig. 3). For the fly condition activity is also present in the motor cortex that is not present in the replay conditions for pilots and non-pilots. While the replay conditions (Expert and Previous) look similar for the non-pilot subjects the pilot subjects show more overall activity for the Expert than for

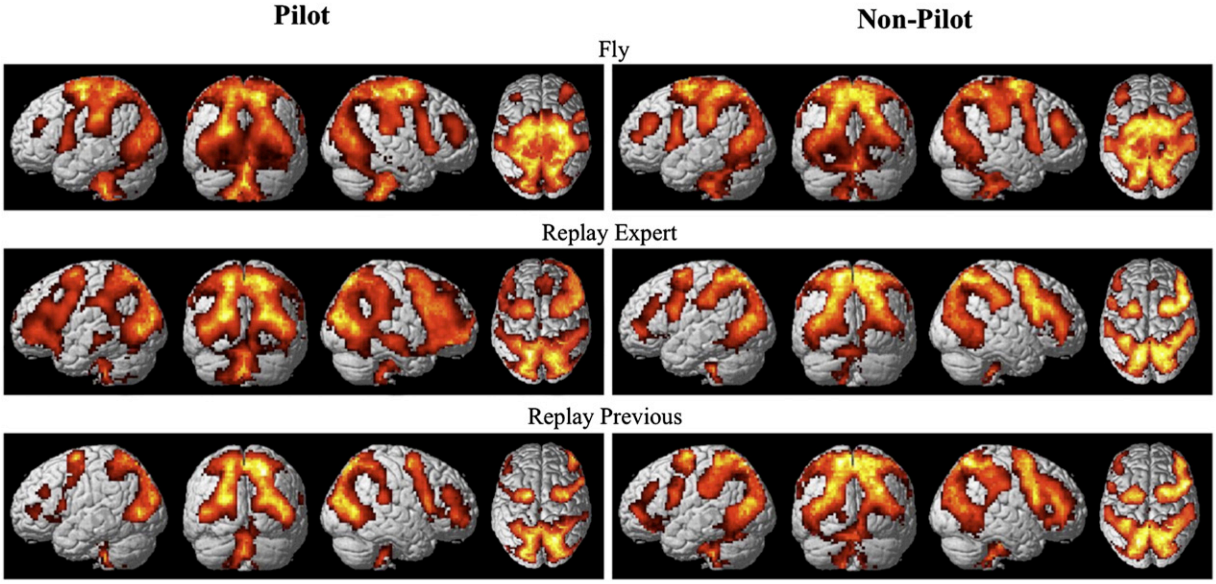

Fig. 3. Results of random effects analysis of differential brain activity rendered on the surface of the brain for pilots and non-pilots for various conditions relative to the baseline condition. The first row shows the Fly condition, the second row shows the Replay Expert condition, and the third row shows the Replay Previous condition. All results are shown with a threshold of pFDR<0.05 corrected for multiple comparisons.

the Previous condition. One can also see that most areas of the brain that are active for the Fly condition are also active for the Replay Expert and Previous conditions for both pilots and non-pilots with the exception of the motor cortex.

Regions found to be active during both execution and observation of action (Execution & Observation Sites) were determined by the conjunction of Fly with observation of Expert Replay and Previous Replay conditions and are shown respectively in Figs. 4a–b for pilots and non-pilots (pFDR<0.05 corrected for multiple comparisons). Widespread activity can be seen in PMC, IFG, SPL, as well as occipital cortex, MT/MST, prefrontal cortex, and cerebellum. Regions that were selectively active during the observation conditions (Observation Only Sites) were determined by the contrast of Previous (Expert) Replay relative to Fly for both pilots and non-pilots (pFDR<0.05 corrected for multiple comparisons) while excluding activity that is active for the Fly condition at a lenient threshold of p<0.05 uncorrected (Figs. 4c–d). These regions include PMC, IFG, middle frontal gyrus MFG, and inferior parietal lobule IPL (pFDR<0.05 corrected for multiple comparisons).

General Execution & Observation Sites for pilots and non-pilots were determined by taking the conjunction of significantly active voxels (pFDR<0.05 corrected for multiple comparisons) across the four analyses shown in Figs. 4a–b (brain regions active for both pilots and non-pilots for the Fly, Previous Replay, and Expert Replay conditions). Brain regions found to be conjointly active include predominantly the PMC, IFG, anterior insula, SPL, occipital cortex, and the cerebellum (Fig. 5a, Table 1). General Observation Only Sites for pilots and non-pilots were determined in a similar manner by finding the conjunction of significantly active voxels (pFDR<0.05 corrected for multiple comparisons) across the four analyses shown in Figs. 4c–d. These regions selectively responding only to observation of action include predominantly the PMC, IFG, MFG, and IPL.

The result of the contrast of the Expert Replay versus the Previous Replay conditions is shown for both pilot and non-pilot groups respectively in Fig. 6a, Table 2, and Fig. 6b, Table 3. For the pilot group extensive activity across the brain was present when using a threshold of pFDR<0.05 (corrected for multiple comparisons). Therefore, a threshold of pFDR<0.01 was used to focus on the regions showing the greatest differential activity. For the pilot group significant differential activity is present in Execution & Observation Sites including premotor cortex, IFG, SPL, and MT (Fig. 6a, Table 2). There was also considerable differential activity present in Observation Only Sites including PMC, IFG, MFG, dorsolateral prefrontal cortex DLPFC, anterior cingulate gyrus ACG, cingulate gyrus CG, STG, IPL, SPL, and precuneus (Fig. 6a, Table 2).

Using a threshold of pFDR<0.05 did not reveal any significant activity for the contrast of Expert Replay>Previous Replay for the non-pilot group therefore a region of interest analysis in imitation areas of the brain using a small volume correction for multiple comparisons was employed (see Methods section for selection of coordinates for region of interest analyses). Significant differential activity (p<0.05 small volume correction for multiple comparisons) was found in the right IFG (Fig. 6b, Table 3). To ensure that significance found in the region of interest analysis was selective and not a result of widespread activity across the entire brain the Expert Replay>Previous Replay contrast for the non-pilot group was conducted using a lenient threshold of p<0.005 uncorrected. It can be seen in Fig. 6b that activity is only present in the right IFG region found to show significant differential activity in the region of interest analysis.

Random effects analysis contrasting pilots relative to non-pilots for the Expert Replay versus Previous Replay contrast was conducted using a between subjects t-test. The analysis over the entire brain did not reveal significant activity at a threshold of pFDR<0.05 corrected for multiple comparisons. Region of interest analyses were conducted in imitation processing areas (see Methods section for selection of coordinates for region of interest analyses). Significant activity correcting for multiple comparisons (p<0.05) was present in the PMC, IFG, anterior insula, IPL/STG, and SPL, and MT/MST (Fig. 7, Table 4). To ensure that significance found in the region of interest analyses was not a result of widespread activity across the entire brain a lenient threshold of p<0.005 uncorrected was used to evaluate the same contrast. Fig. 7b does not show widespread activity across the entire brain but rather primarily only in regions involved with imitation processing.

The random effects analysis presenting differential brain activity for the contrast of Previous Replay relative to Expert Replay is given in Fig. 8 and Table 5. The analysis over the entire brain did not reveal significant activity at a threshold of pFDR<0.05 corrected for multiple comparisons for either the pilot or the non-pilot groups. However, region of interest analysis (see Methods section for selection of coordinates for region of interest analyses) in the right lateral cerebellum Crus I did reveal significant activity correcting for multiple comparisons (p<0.05) for the pilot group (Fig. 8, Table 5). The same contrast

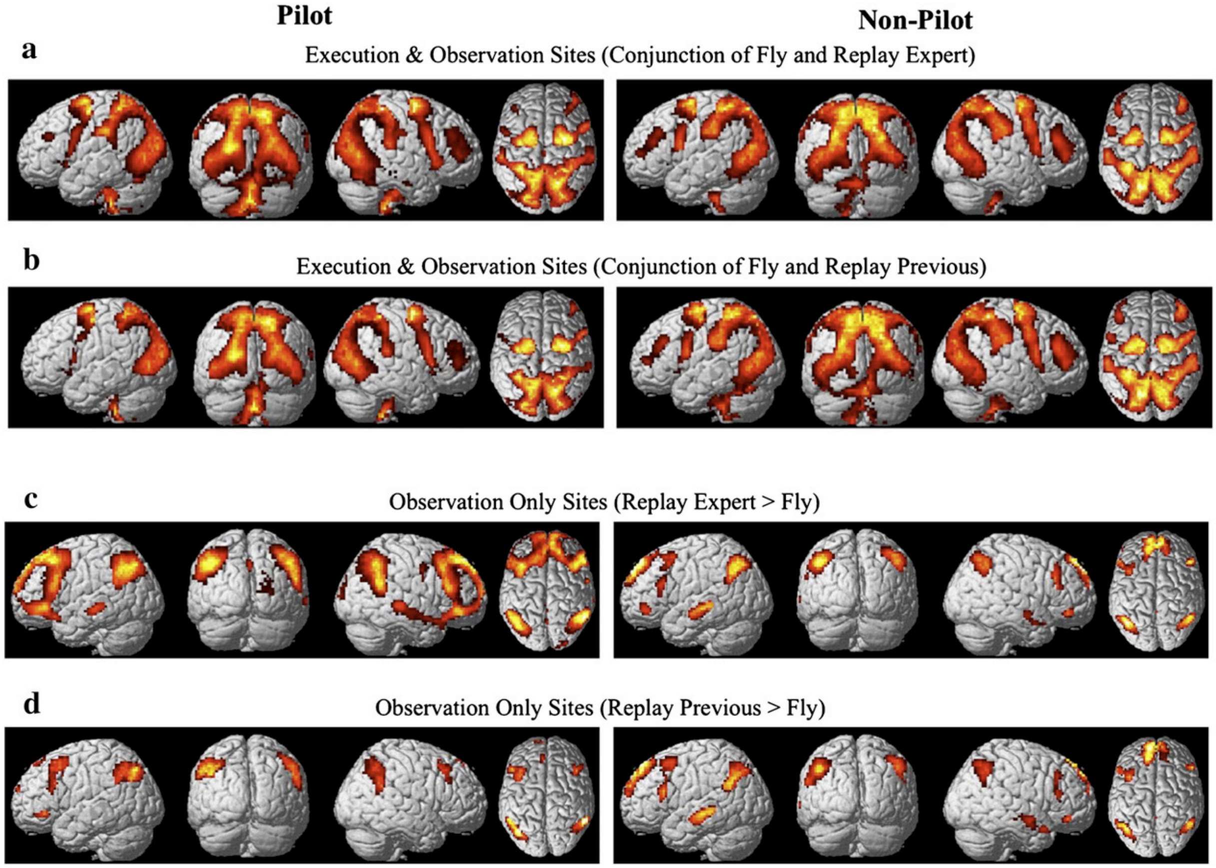

Fig. 4. Execution & Observation Sites and Observation Only Sites for the different groups and conditions. a–b: Brain regions responsive to both action execution (Fly) and action observation (Previous Replay and Expert Replay) for pilots and non-pilots. a. Conjunction of the Fly and the Replay Expert conditions b. Conjunction of the Fly and the Replay Previous conditions. All results are shown with a threshold of pFDR<0.05 corrected for multiple comparisons. c–d: Brain regions responsive during Observation Only (Previous Replay and Expert Replay) but not during action (Fly) for pilots and non-pilots. c. Contrast of the Previous Replay condition greater than Fly (pFDR<0.05 corrected for multiple comparisons) exclusively masking out activity present during Fly relative to Baseline at a lenient threshold of p<0.05 uncorrected. d. Shows the same but for the Expert Replay condition.

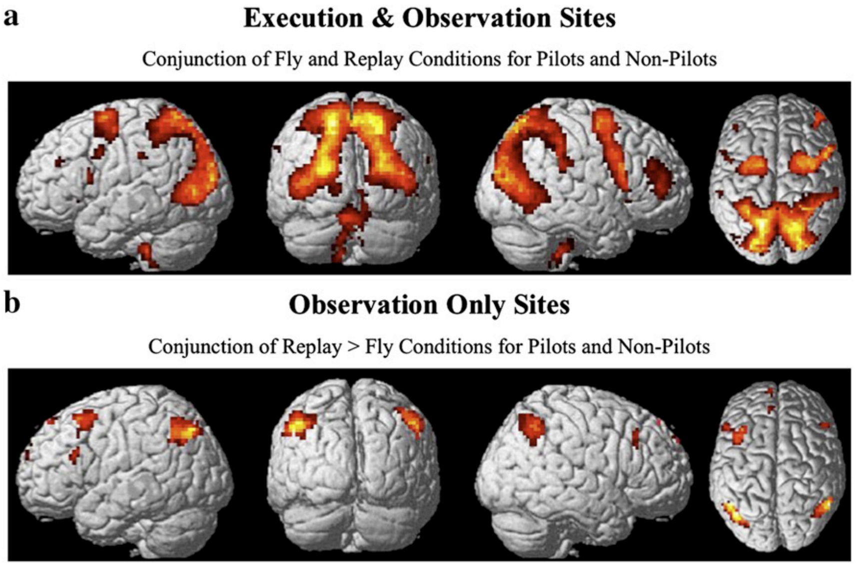

Fig. 5. Execution & Observation Sites and Observation Only Sites that generalize across pilots and non-pilots and conditions. a. Execution & Observation Sites: Brain activity in regions common to pilots and non-pilots taking the conjunction of the Fly, Replay Expert, and Replay Previous conditions using a threshold of pFDR<0.05 corrected for multiple comparisons (see Table 1). b. Observation Only Sites: Brain activity in regions common to pilots and non-pilots taking the conjunction of the Replay Expert relative to Fly and the Replay Previous relative to Fly contrasts (pFDR<0.05 corrected for multiple comparisons) while excluding activity present at a lenient threshold of p<0.05 uncorrected for the contrast of Fly relative to baseline (see Table 1).

Table 1
MNI coordinates for clusters of brain activity Execution & Observation Sites and Observation Only Sites.

Brain region	Action & Observation	Observation Only
	MNI x,y,z coordinates	MNI x,y,z coordinates
L PMC BA6	−24,−9,51 −51,3,39 −39,0 33	−39,9,60
R PMC BA6	36,−3,51 24,−9,51	
L SMA BA6	−18,0,63	
L IFG BA44,45	−51,12,21	−51,21,39 −54,24,27 −51,21,30
R IFG BA44,45	48,9,27 51,15,12 51,15,24	54,27,30
L IFG, Ins BA47,13	−30,24,0	
R IFG, Ins BA47,13	30,27,−3	
L MFG BA8,10		−36,21,51
R MFG BA8,10	48,48,15	45,27,45
L SFG BA8,9		−18,57,36
R SFG BA8,9		15,51,45
L DLPFC BA46	−45,39,30	
R DLPFC BA46	42,39,27 48,48,6	
L Medial Frontal Gyrus BA 8,10		−9,42,51 −6,63,21
L Middle Cing Cortex BA24	−9,−21,45	
L SPL BA7	−15,−63,57	
R SPL BA7	24,−69,54	
L Precuneus BA7	−18,−72,30	
R Precuneus BA7	15,−72,60	
L IPL BA7		−42,−75,45
R IPL BA7		42,−69,51
L IPL BA40	−60,−30,36	−51,−60,42
R IPL BA40	45,−39,36	51,−60,48
L S/MOG BA18,19	−21,−87,18 −39,−75,3	
R S/MOG BA18,19	24,−87,21	
R MT/MST	42,−69,3	
R Thalamus	21,−27,9	
L Globus Palidus	−15,−6,0	
L Brainstem	−6,−21,−24	
R Brainstem	6,−24,−27	
L Cerebellum IX,X	−12,−45,−45	
R Cerebellum IX, X	12,−48,−48	
L Cerebellum VIIIA	−21,−63,−51	

Corrected for multiple comparisons across entire brain $\text{pFDR}<0.05$.
R=Right; L=Left; BA=Brodmann Area; PMC=Premotor Cortex; SMA=Supplementary Motor Area; IFG=Inferior Frontal Gyrus; Ins=Insula; MFG=Middle Frontal Gyrus; SFG=Superior Frontal Gyrus; DLPFC=Dorsolateral Prefrontal Cortex; Cing=Cingulate; IPL=Inferior Parietal Lobule; SPL=Superior Parietal Lobule; S/MOG=Superior/Middle Occipital Gyrus; MT=Middle Temporal; MST=Middle Superior Temporal.

was assessed using a lenient threshold of $p<0.005$ uncorrected to assess whether there was widespread trends in activity across the entire brain or whether the activity was selective to the cerebellum. Fig. 8b shows that the only region showing activity using the lenient threshold of $p<0.005$ uncorrected is the right lateral cerebellum.

No significant differential activity in the cerebellum was present for the non-pilot group. However, between subjects analysis did not reveal significant differential activity in the lateral cerebellum for the contrast Previous Replay relative to Expert Replay for pilot versus non-pilot groups using a region of interest analysis (see Methods section for selection of coordinates for region of interest analyses).

Discussion

This research used a neuroergonomic approach in which visual and motor control aspects of the task are made to be similar to real-world experience. In reference to the objectives of this study our results show 1. That there are differential neural processes involved depending on the type of replay observed, 2. That activation is dependent on expertise, and 3. That the activity is in Execution & Observation Sites as well as Observation Only Sites. For pilots, brain regions involved with imitation based motor simulation were differentially activated for the contrast of observing an Expert Replay relative to Previous Replay (Fig. 6a, Table 2). This activity was in Execution & Observation Sites (Fig. 5, Table 1) as well as Observation Only Sites (Fig. 6a, Table 1; Compare with Figs. 4–5). For non-pilots, region of interest analyses (see Methods section for selection of coordinates for region of interest analyses) identified significant differential activity for this contrast only in the right IFG (Fig. 6b, Table 3). For the contrast of Replay Previous over Replay Expert, pilots showed significant activity in the cerebellum (Figs. 8a–b, Table 5), thought to be involved with error-feedback motor simulation. Differential activity was not present for the non-pilot group for this contrast (Fig. 8c).

The results of the pilot group (Fig. 6a, Table 2 and Figs. 8a–b, Table 5) are consistent with the hypothesis put forward by Doya (1999) proposing that the computational neurocircuitry of the cortex lends itself to unsupervised learning, whereas, the computational neurocircuitry of the cerebellum lends itself to supervised error-feedback based learning. This is suggestive of degenerate (Edelman, 1987) neural processes depending on contextual goals. When a pilot observes the flight of an expert it is thought that they attempt to reconstruct the manipulation of the flight controls through imitation motor simulation in order to understand the underlying actions that resulted in a successful landing. It is of note that associative type processes carried out in the cortex have been found to be sufficient to instantiate visuomotor imitation (Chaminade et al., 2008). On the other hand, when a pilot observes the flight of their own previous trial they already know how they performed and the observed replay of the flight can be compared with an internal motor simulation of the intended action goal, the difference of which constitutes error upon which supervised processing occurs (it should be noted that there is a delay between the error signal, distance to target, and the visual feedback of the replay but we maintain it serves as a supervisory signal). The use of visually very similar conditions Expert Replay and Previous Replay makes it unlikely that the pattern of brain activity found is a product of visual processing alone. Rather, it is more likely that differences in neural activity between the two conditions reflect differential activation of neural processes involved in the action observation network.

The substantially greater activity for the Expert over the Previous Replay conditions for pilots may be accounted by processes other than just that of imitation motor simulation. One potential reason for the greater differential activity may be that pilots are paying attention more to observing Experts flying the glider than to their own previous trial. We do not believe that the results can entirely be accounted for by this potential confound because there was also differential activity in the lateral cerebellum involved with error-feedback motor imitation for the opposite contrast of Previous Replay over Expert Replay. This area of the lateral cerebellum is involved in instantiating processes related to tool use (Higuchi et al., 2007). It is possible that the results reported reflect paying attention to aspects of the visual scene that are relevant for imitation versus paying attention to aspects of the visual scene that are relevant for detecting error in flight control.

In our study we assessed similarities and differences between pilots and non-pilots for observation of an expert landing a glider and that of one's own previous trial of landing the glider. Both pilots and non-pilots showed greater differential activity in the right IFG (Figs. 6a–b, Tables 2–3) in sites involved with imitation (Caspers et al., 2010). The right lateralized activity is consistent with the hypothesis that the right cortical hemisphere is dominant for spatial processing whereas the left is dominant for non-spatial processing (Schubotz and von Cramon, 2003). One would expect a great deal of spatial

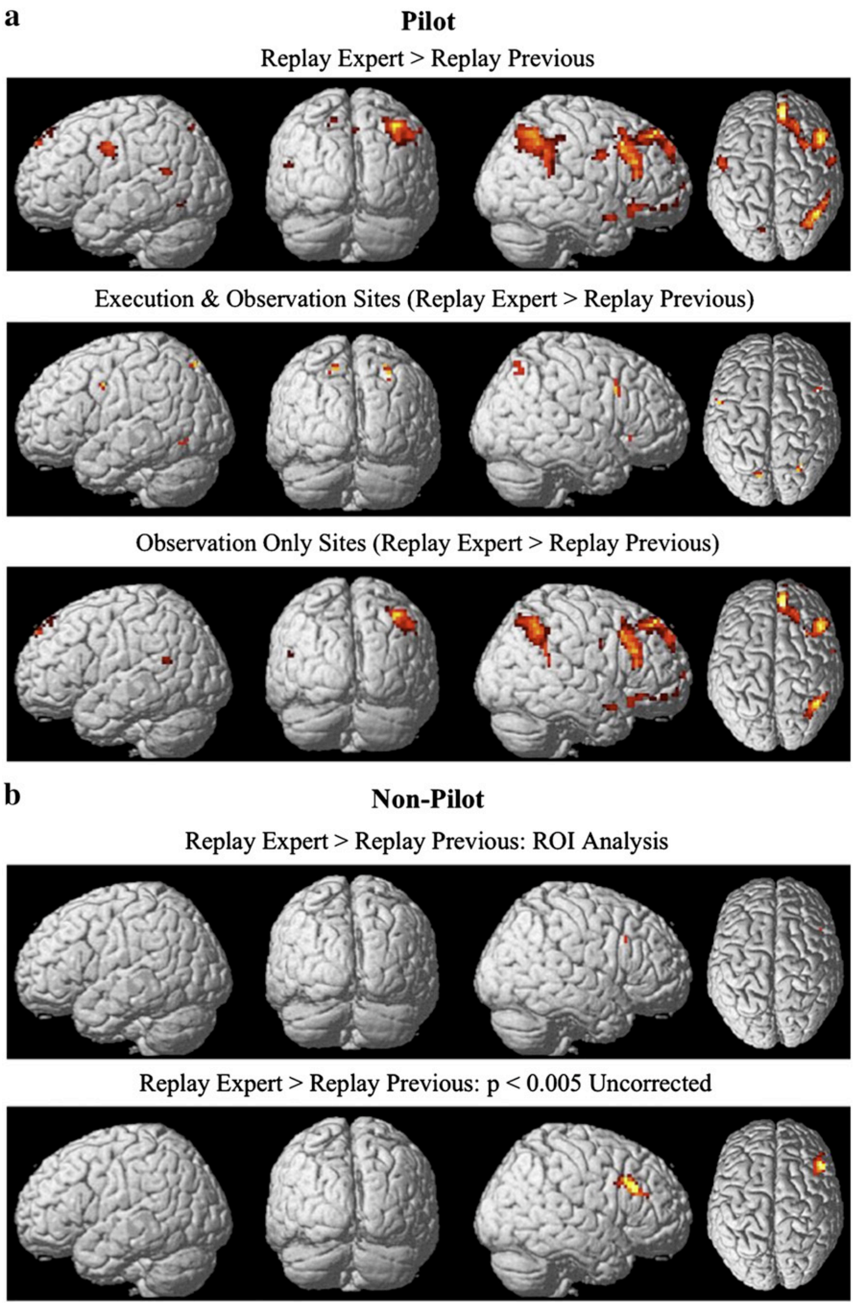

Fig. 6. Results of random effects analysis of differential brain activity rendered on the surface of the brain for pilots and non-pilots for the Expert Replay versus the Previous Replay conditions. The results for Pilots are given in a (also see Table 2). The first row shows overall differential activity throughout the brain with a threshold of $pFDR<0.01$ corrected for multiple comparisons. The second row shows the differential activity that overlaps with brain regions responsive to both Fly and Expert Replay conditions (Execution & Observation Sites). The third row shows differential activity overlapping with brain regions that are selective for observation of Expert Replay over Fly (exclusively masked by Fly over Baseline at $p<0.05$ uncorrected) (Observation Only Sites). b. No significant activity was found for the non-pilot condition when correcting for multiple comparisons across the entire brain so region of interest analyses (see methods for sites) using small volume correction for multiple comparisons were employed. The first row shows significant activity ($p<0.05$ small volume corrected for multiple comparisons) in the right IFG (see Table 3). The second row shows activity at a lenient threshold of $p<0.005$ uncorrected only in the right IFG region. Confirming that the activity found in the region of interest analysis was not a result of distributed widely spread activity across the brain.

processing to be involved with observing piloting of a glider for landing. These results are consistent with the hypothesis that to some degree both pilots and non-pilots utilize imitation based motor simulation when observing an expert's landing over their own previous trial landing. This may be somewhat at odds with the results of the dancing observation studies in which it was shown that observation by non-experts did not activate these regions of the action observation network (Calvo-Merino et al., 2005, 2006). One reason for the finding of activation of these regions in non-pilots in our study may be because although they did not have any real-world piloting experience they all had experience with first person perspective video games such as driving simulators. From this experience it is likely that non-pilots also have established generalized neural processes involved with visual-motor transformation necessary to utilize a joystick to control a plane. This is not to say that the differential brain activity between the two observation conditions was the same for pilots and non-pilots.

One of the goals of this study was to assess the extent that experience is important in how one observes action and how it is processed. While there was no significant difference between pilots and non-pilots for the

Table 2
MNI coordinates for clusters of brain activity pilots (Replay Expert > Replay Previous).

Brain region	MNI x,y,z coordinates	T-value
Execution & Observation Sites		
L PMC BA6	−54,0,39	5.79
R IFG BA44,9	48,12,42	5.58
	48,15,33	5.2
R IFG BA47,13	33,24,−6	5.35
L SPL BA7	−15,−75,54	5.0
	−12,−72,60	3.6
	−33,60,54	3.79
R SPL BA7	30,−66,51	5.35
R Precuneus BA7	9,−54,48	5.75
L MT/MST	−42,−63,−9	4.8
Observation Only Sites		
R PMC BA6	60,−3,33	5.42
R IFG BA44,9	48,18,42	6.1
R MFG BA45,46	51,21,42	6.6
R DLPFC BA46	51,27,24	5.62
R IFG, Anterior Insula BA47,13	33,21,−15	6.43
R SMedG BA9	9,51,39	8.85
R ACG BA32	6,48,6	5.37
CG BA31	9,−39,36	5.14
L STG SMG BA22,40	−48,−51,18	5.28
L STG SMG BA22,40	−48,−51,18	5.28
L STG SMG BA22,40	−48,−51,18	5.28
R STG SMG BA22,40	48,−45,24	6.76
R IPL BA40	42,−57,51	7.33
R SPL BA7	33,−66,54	5.25
Precuneus BA7	6,−57,45	4.89
Other brain regions		
L PMC BA6	−57,−3,36	6.1
R PMC BA6	57,0,3	5.26
R MFG BA8	24,30,45	6.21
R SMed FG BA8	9,42,48	6.57
L IPL BA40	−36,−57,45	4.4

Corrected for multiple comparisons across entire brain pFDR < 0.01.
R = Right; L = Left; BA = Brodmann Area; PMC = Premotor Cortex; IFG = Inferior Frontal Gyrus; SPL = Superior Parietal Lobule; MT = Middle Temporal; MST = Middle Superior Temporal; MFG = Middle Frontal Gyrus; DLPFC = Dorsolateral Prefrontal Cortex; SMedG = Superior Medial Gyrus; ACG = Anterior Cingulate Gyrus; CG = Cingulate Gyrus; STG = Superior Temporal Gyrus; SMG = Supramarginal Gyrus; IPL = Inferior Parietal Lobule.

Previous Replay over the Expert Replay contrast, only the pilot group showed significant activity for this contrast using a region of interest analysis in the cerebellum (involved with error-feedback motor simulation). Furthermore, the lack of activity anywhere in the brain for the non-pilot group using a lenient threshold ($p < 0.005$) and the presence of activity only in the cerebellum for the pilot group using this lenient threshold suggest that experience is important in error-feedback motor simulation utilized during observation of one's previous action. Region of interest analyses in imitation areas (Caspers et al., 2010) identified significant differential activity (Fig. 7, Table 4) for pilot over non-pilot groups for the Expert Replay relative to the Previous Replay contrast in PMC, IFG, anterior insula, SPL, IPL/STG, and MT/MST. This result is consistent with the hypothesis that pilots, to a greater extent than non-pilots, have well established models for the visuomotor transforms involved with the 4 degrees of freedom of flight control based on real-world experience. These models are differentially utilized for imitation based motor simulation when observing an expert flying a glider over that of one's previous trial. It is unlikely that these findings are a result of differential visual characteristics of the Previous and Expert Replays between pilots and non-pilots because there was much greater variability between video types for the non-pilot group than the pilot group. One would therefore predict that just based on dynamic visual characteristics of the stimuli there would be greater differential activity between the two different types of observed replays for the non-pilot group. However, this was not the case.

Table 3
MNI coordinates for clusters of brain activity non-pilots (Replay Expert > Replay Previous).

Brain region	MNI x,y,z coordinates	T-value
R IFG BA44,45	48,18,36	3.41

Small volume corrected for multiple comparisons pFWE < 0.05 using pre-specified regions of interest (see Methods section). R = Right; BA = Brodmann Area. IFG = Inferior Frontal Gyrus.

Greater differential brain activity while observing Expert Replays over Previous Replays for pilots over non-pilots (Fig. 7, Table 4) (especially the PMC and parietal cortex) is consistent with studies investigating the effects of expertise on observation of dance (Calvo-Merino et al., 2005, 2006; Cross et al., 2006, 2009) and instrumental music (Bangert et al., 2006; Baumann et al., 2007; Lahav et al., 2007; Margulis et al., 2009). Observation of an action that one is skilled at shows much greater activity in brain regions involved with motor simulation (imitation) than actions one is not skilled at. These brain regions include but are not limited to the premotor and parietal areas thought to compose the 'Mirror Neuron' system that is a subpart of the more general action observation network. It is believed that these neural processes may underlie in part our ability to learn how to imitate another person's actions through observation (Calvo-Merino et al., 2005, 2006; Caspers et al., 2010). It has been shown that brain regions involved with motor simulation (imitation) including the premotor cortex and parietal areas are activated to a greater extent when dancers watched videos of others performing their own dance style compared to that of a different dance style (Calvo-Merino et al., 2005). It was further demonstrated in an experiment in which gender specific ballet moves (of which a dancer is familiar with both but performs only one) were shown to ballet dancers that the gender specific moves that the subject performed showed greater activity in brain regions involved with both execution and observation of action (potential Mirror System sites) (PMC, parietal cortex, as well as the cerebellum) than the opposite gender moves that they are familiar with observing but not performing (Calvo-Merino et al., 2006). These results suggest that observation of actions that one is skilled at is not just visual representations of actions but is understood motorically (by motor simulation). It has further been shown that dancers who physically learned new dance moves had increases in activity in PMC and parietal regions as a function of training and rating of their skill to perform these moves (Cross et al., 2006). However, it should be noted that passive observation alone was sufficient to show increased activity in similar premotor and parietal regions as physical training (Cross et al., 2009). These results were conjectured to be the product of observational learning utilizing processes related to imitation based motor simulation (Cross et al., 2009). In a study similar to that of Calvo-Merino et al. (2005) investigating motor simulation of trained and untrained dance styles, the study by Margulis et al. (2009) shows that experience with a specific instrument differentially activates the IFG to a greater extent when listening to music produced by the instrument they play (violin or flute). All of the above studies suggest that action observation may rely to some extent on motor simulation that is a function of expertise with the observed action.

In this study we investigated brain regions having potential Mirror System properties by a conjunction analysis of the Fly and the Replay conditions. We refer to regions having potential Mirror System properties as Execution & Observation Sites (Figs. 4–6, Tables 1–2). The extraction of articulatory gestures from the observed action in this experiment may differ somewhat from experiments involving observation of articulation of the hands during grasping (Caspers, et al., 2010) or of articulation of the body during dancing (Calvo-Merino et al., 2005, 2006; Cross et al., 2006, 2009). When observing the action of the glider from the first person perspective, in which the flight controls and flight surfaces are not visible, it is necessary for the observer to reconstruct the actions made on the stick controlling the ailerons

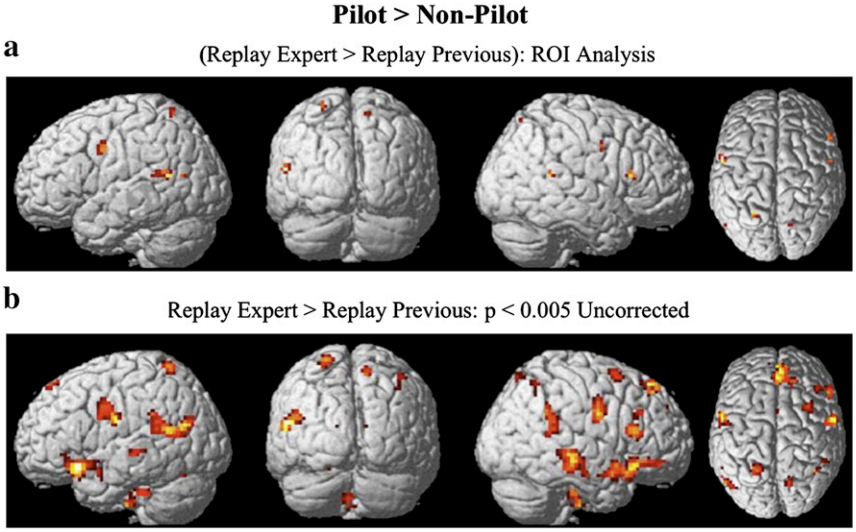

Fig. 7. Differential brain activity related to expertise for pilots over non-pilots for the contrast of Replay Expert over Replay Previous. No significant activity was found when correcting for multiple comparisons across the entire brain so region of interest analyses were conducted (see methods for sites) using small volume correction for multiple comparisons. a. Significant activity ($p<0.05$ small volume corrected for multiple comparisons) is present in several of the regions of interest (see Table 4). b. Activity is shown using a lenient threshold of $p<0.005$ uncorrected. Activity is present primarily in regions involved with imitation processing (PMC, IFG, anterior insula, STG/IPL, SPL, and MT) and is not distributed widely across the brain, suggesting that the region of interest analysis is not a result of noise.

and elevator, the rudder pedals controlling the yaw, and the dive brake controlling the steepness of descent from the visual changes in the attitude of the glider. There is a direct relationship between changes in attitude and manipulation of the controls.

While the Mirror Neuron system has been to a large part associated with observation of action of the articulators (e.g. hand grasping) (Caspers et al., 2010) the use of the Mirror Neuron system for action observation has also been extended to include the use of complex tools. Arbib et al. (2009) argue, drawing on the idea of a dynamical multi-sensory body representation introduced by Head and Holmes (1911), that action observation and execution (involving Mirror System Areas) includes extension of the body schema to incorporate complex tools. The size and shape of the tool do not matter, rather it is the action of how the end-effector interacts with the environment that is important (Arbib et al., 2009). One example of the extension of tool use to incorporate Mirror System regions (area F5 corresponding to ventral premotor cortex in humans) is given in the study of Ferrari et al. (2005) where they show that observation of pliers by monkeys activate these regions. In an fMRI study conducted by Jacobs et al. (2010) it was found that the same grasping circuit involving the anterior intraparietal sulcus and the ventral premotor cortex (composing the Mirror System) was used for grasping actions involving the hand or a novel tool.

Table 4
MNI coordinates for clusters of brain activity pilots > non-pilots (Replay Expert > Replay Previous).

Brain region	MNI x,y,z coordinates	T-value
L PMC BA6	−57,−3,36	4.0
R PMC BA6	57,−3,36	3.35
R IFG BA45	54,24,15	3.41
L IFG, Anterior Insula BA 47,13	−39,9,−9	3.2
R IFG, Anterior Insula BA47,13	36,9,−9	3.2
	45,9,−9	3.16
L SPL BA7	−24,−57,66	3.37
R SPL BA7	12,−72,60	3.30
L IPL,STG BA40,22	−48,−51,18	3.82
R IPL,STG BA40,22	51,−45,15	3.33
L MT/MST	−54,−66,15	3.41

Small volume corrected for multiple comparisons pFWE<0.05 using pre-specified regions of interest (see Methods section). R = Right; L = Left; BA = Brodmann Area; PMC = Premotor Cortex; IFG = Inferior Frontal Gyrus; STG = Superior Temporal Gyrus; IPL = Inferior Parietal Lobule; SPL = Superior Parietal Lobule; MT = Middle Temporal; MST = Middle Superior Temporal.

Of considerable importance to our study is the literature on perception of music in individuals trained to use the instrument in which the music was performed (Bangert et al., 2006; Baumann et al., 2007; Lahav et al., 2007; Margulis et al., 2009). Just as in the case of piloting a glider in our experiment observation of action and that of direct observation of biological motion are uncoupled yet the perceptual stimulation resulting from the operation of the complex tool (in this case a musical instrument) has been shown to activate brain regions involved with action execution (potential Mirror Neuron sites). In studies investigating both observation and execution of music by skilled pianists and non-musicians it was found that the premotor cortex (Bangert et al., 2006; Baumann et al., 2007) as well as IFG including Broca's area (Bangert et al., 2006) were activated by both conditions and were greater for the skilled pianist group (Bangert et al., 2006; Baumann et al., 2007). Lahav et al. (2007), further demonstrate that perception of aurally presented music activates areas of the brain involved in playing the instrument (Broca's area, PMC, intraparietal sulcus, and the inferior parietal region) as a product of motoric experience with the music. Based on the results of these studies involving perception of instrumental (complex tool) music it has been argued that neural processes involved in action observation (localized primarily in PMC and IFG, as well as parietal regions) involve motor simulation and are consistent with Mirror System properties (Bangert et al., 2006; Baumann et al., 2007; Lahav et al., 2007; Margulis et al., 2009). It is interesting to point out that the IFG activity found in these studies is similar to that found in our study (Fig. 5, Table 1). While there are considerable differences between observation of manipulation of a tool and that of the articulators of the body one of the key arguments for the evolution of the 'Mirror System' in humans and its relevance for language is through the use of tools and imitation thereof (Arbib et al., 2009; Higuchi et al., 2009; Stout and Chaminade, 2012).

In this study we determined brain regions common to pilots and non-pilots for both types of replay conditions involved with action Execution & Observation (Fig. 4a, Table 1). While a considerable amount of this activity can be ascribed to visual information that is the same in the observation and flying conditions (e.g. superior/middle occipital gyrus

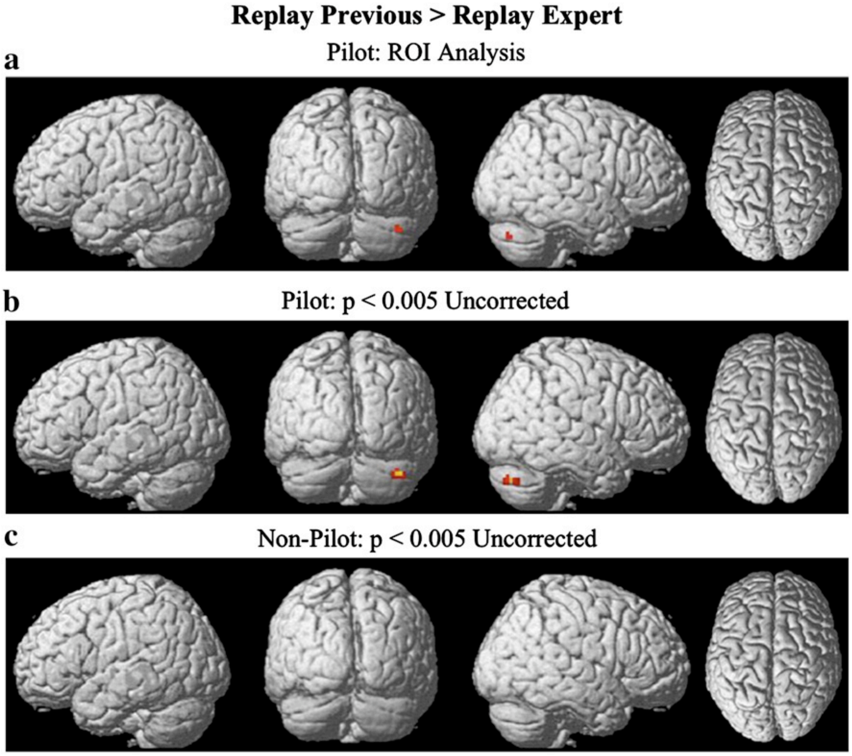

Fig. 8. Results of random effects analysis of differential brain activity rendered on the surface of the brain for pilots and non-pilots for the Previous Replay versus the Expert Replay conditions. No activity was present using a threshold of pFDR<0.05 corrected for multiple comparisons over the entire brain. a. Region of interest analyses (see methods for sites) using a small volume correction for multiple comparisons in the revealed significant activity ($p<0.05$ small volume corrected for multiple comparisons) in the right lateral cerebellum (see Table 5). To ensure that activity was restricted to the cerebellum a lenient threshold of $p<0.005$ uncorrected was used for analysis across the entire brain. b. Only the right lateral cerebellum shows activity even when using this lenient threshold. c. No significant activity was found for the non-pilot condition using a lenient threshold of $p<0.005$ uncorrected or the region of interest analysis in the cerebellum.

S/MOG visual processing regions and MT/MST visual motion processing regions), there are a considerable number of regions involving the action recognition network predominantly in PMC, IFG, and parietal regions such that understanding of action may be made in reference to execution (potential Mirror System sites). Some of these regions (PMC, IFG, SPL areas) are active regardless of experience with the tool under control (in this case the glider) as can be seen for non-glider and glider pilots (Figs. 4a–b, 5a, Table 1). The observation and manipulation of a complex tool, in this case a glider, activate the same cortical regions found in other studies (Brass and Heyes, 2005; Caspers et al., 2010; Di Pellegrino et al., 1992; Gallese et al., 1996; Iacoboni et al., 1999; Molenberghs et al., 2009; Rizzolatti and Craighero, 2004; Rizzolatti et al., 1996; Rizzolatti et al., 2001) involved with observation and execution of the articulators (hands, feet, etc.) to be part of the Mirror System suggesting perhaps that at least in part they may be mediated by the same processes.

It is likely that action understanding through observation of a complex tool involves regions with Mirror System properties as well as other regions involved in transformations that are not necessary when one is actually controlling the glider. This point for action understanding has been made for grasping (Oztop et al., 2005; Raos et al., 2007) as well as for flying planes (Callan et al., 2012). In this experiment we determined areas that are Observation Only Sites (predominantly IFG and IPL) that show greater activity than the flying condition and are not active during the flying condition (Figs. 4c–d, 5a, Table 1). It is interesting to point out that these regions are adjacent to Execution & Observation Sites. These areas may be involved in processing of a model of the tool or apparatus under control that is not necessary when one is actually controlling the object and getting feedback based on actions. They may also be utilized when observing the complex actions of other individuals in attempting to simulate these actions in terms of control as a type of imitation training. The large amount of differential activity in these Observation Only Sites for the contrast of Expert Replay over Previous Replay (Fig. 6a, Table 2) is consistent with this hypothesis.

Our experiment utilized complex real-world tasks to determine brain activity in a neuroergonomic manner that is relevant to how the brain works when interacting in the actual environment. The primary focus of the study was to determine if there are differential neural processes related to observation of two types of replays that are visually very similar and how experience is related to this processing. Consistent with predictions, the results showed for pilots over non-pilots, greater differential activity in brain regions involved with imitation based motor simulation when viewing a replay of an expert pilot landing a glider and greater activity in brain regions involved with error-feedback based motor simulation when viewing a replay of one's own previous trial. While it has been conjectured that the way we understand observed action is by utilizing brain regions involved with carrying out the action, (the Mirror System theory), our results showed considerable differential activity related to expertise in brain regions that were not active when actually carrying out the task. It is maintained that these regions are involved with aspects of imitation

Table 5
MNI coordinates for clusters of brain activity pilots > non-pilots (Replay Previous > Replay Expert).

Brain region	MNI x,y,z coordinates	T-value
Cerebellum Crus I	39, −78, −33	4.77

Small volume corrected for multiple comparisons pFWE<0.05 using pre-specified regions of interest (see Methods section).

based motor simulation concerned with representational transformations that are not necessary when actually carrying out the task because the information is readily available to the motor system. While this study did not investigate how observation of different types of replays may influence learning and performance future studies will be designed to investigate the role of motor simulation systems as they relate to learning and performance on piloting tasks utilizing optimal scheduling (Callan and Schweighofer, 2010) and various types of reward feedback (Callan and Schweighofer, 2008). Additionally, fMRI is limited in its temporal resolution to be able to discern the time course of activation of different brain regions in a given network (e.g. unsupervised imitation processing networks and supervised error-feedback processing networks) involved with dynamic continuous perceptual and motor control properties of landing a glider. In the future, MEG and/or EEG can additionally be utilized to obtain better spatiotemporal resolution to discern the dynamic neural correlates underlying these task related properties as has been done in previous research (Callan et al., 2010; Ortigue et al., 2009).

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