NeuroImage 72 (2013) 55–68

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

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

Daniel E. Callan [a,*], Cengiz Terzibas [a], Daniel B. Cassel [a], Akiko Callan [b], Mitsuo Kawato [c], Masa-aki Sato [a]

[a] ATR Neural Information Analysis Laboratories, Kyoto, Japan
[b] NICT Multimodal Communication Group, Kyoto, Japan
[c] ATR Computational Neuroscience Laboratories, Kyoto, Japan

ARTICLE INFO

Article history:
Accepted 17 January 2013
Available online 26 January 2013

Keywords:
Action understanding
fMRI
Perceptual motor
Error-feedback
Mirror neuron
Tool use

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

* Corresponding author at: ATR Neural Information Analysis Laboratories, 2-2-2 Hikaridai, Seika-cho, Soraku-gun, Kyoto 619-0288, Japan. Fax: +81 774 95 1259.
E-mail address: dcallan@atr.jp (D.E. Callan).

1053-8119/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2013.01.028

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