Neuropsychologia 51 (2013) 2690–2701

Contents lists available at ScienceDirect

Neuropsychologia

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

Is there a left hemispheric asymmetry for tool affordance processing?

Alice M. Proverbio *, Roberta Azzari, Roberta Adorni

Department of Psychology, University of Milano-Bicocca, Italy

ARTICLE INFO

Article history:
Received 13 May 2013
Received in revised form
10 September 2013
Accepted 14 September 2013
Available online 19 September 2013

Keywords:
Object perception
ERPs
Ventral stream
Affordance
Mirror neurons

ABSTRACT

The perception of tools vs. other objects has been shown to activate the left premotor and somatosensory cortex, which represents object affordance associated with tool manipulability (Proverbio, Adorni, & D'Aniello, 2011). The question of whether hemispheric asymmetry depends on right hand use or is linked to a hemispheric functional specialization for fine-grained precision movement is unclear. Thus, in this paper, ERPs were recorded from 128 sites in response to the visual presentation of bidimensional (2D) pictures depicting unimanual (e.g., a hammer) and bimanual (e.g., a handlebar) tools (Study 1). Central N2 and prefrontal N400 components were much larger for bimanual than unimanual tools (over the left hemisphere for N400). SwLORETAs performed for both components showed at first the activation of the left parietal cortex (BA39) and then of the right homologous (BA40) one, for both grips but stronger for the bimanual coordination. At all times and for both grips, the left premotor cortex (BA6) was involved in coding action affordance, while only unimanual tools activated the left postcentral gyrus (BA3).

In Study 2, unimanual tools were presented with an orientation congruent (standard) or incongruent to their interaction with the right hand (rotated), to manipulate affordance's quality. Standard objects elicited much larger ERP responses (namely: N1, N2, N400) than rotated tools (over the left hemisphere for N400). At the earliest stage (190–270 ms) the significant intracranial sources were of visual nature (mainly the contralateral precuneus). Regions representing motor information were not involved. Rotated tools induced a smaller activation in the STS and parahippocampal regions (possibly coding affordable biological motion and the spatial aspects of hand/object interaction), whereas rotated tools activated to a greater extent the dorsolateral prefrontal cortex (DLPF, BA9). In the later time window standard objects activated the left BA6 and the right BA40 more than rotated objects.

Overall, these data suggest that viewing tools automatically activates mental representations associated with their manipulation. The left premotor cortex was found to be involved with any kind of object and grip, as early as 200 ms post-stimulus, thus supporting the hypothesis of a LH asymmetry in the neural representation of grasping, within this region. The right supramarginal gyrus was also found to be crucially involved later in time.

1. Introduction

The motor/premotor and parietal cortices are commonly thought to be involved in the coding of both action execution and observation (Fadiga, Craighero, & Olivier, 2005; Grèzes & Decety, 2001; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Rizzolatti & Craighero, 2004; Turella, Canto, Brunelli, Allione, Andreasi, & Desantis, 2012) as parts of the so-called human mirror neuron system (MNS). In addition, it has been demonstrated that the posterior parietal and premotor cortex are specialized to convey information associated with the motor affordance of a tool or manipulable object, as these areas respond to the tool per se, without the performance of any action (Cardellicchio, Sinigaglia, & Costantini, 2011). For example, Grafton, Fadiga, Arbib, & Rizzolatti (1997), using PET, detected the activation of the left premotor cortex during tool observation, and Creem-Regehr and Lee (2005), using fMRI, demonstrated that viewing graspable tools activates motor-related regions of the cortex (namely, the posterior middle temporal gyrus, ventral premotor area and posterior parietal cortex), but not shapes. The ERP study of Proverbio et al. (2011) and the EEG study of Proverbio (2012) provided the time course of this activation and showed that the earliest neural tool/non-tool discrimination, in the form of an increased anterior negativity (210–270 ms) in response to tools, was preceded by an early (140 to 175 ms) μ desynchronization over centro-parietal sites (centered at approximately 10–12 Hz) during tool perception (Proverbio, 2012). The involved area might correspond to the anterior intraparietal sulcus (AIP). Overall, these findings support the hypothesis that there might be a temporal and functional relationship between rapid and transient μ suppression in the somatosensory cortex and successive increases in time-locked post-synaptic potentials (ERPs) in regions processing tool motor affordance. The LORETA inverse solution performed on the scalp potentials (Proverbio et al., 2011) showed that viewing

* Correspondence to: Department of Psychology, University of Milano-Bicocca, piazza dell'Ateneo Nuovo 1, U6 Building, 20126 Milan, Italy. Tel.: +3902 6448 3755.
E-mail address: mado.proverbio@unimib.it (A.M. Proverbio).

0028-3932/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.neuropsychologia.2013.09.023

manipulable objects significantly activated the left somatosensory and premotor cortices, as these regions are the neural generators of the synchronized surface electrical activity recorded in the 210–270 ms time window.

The left hemispheric asymmetry in the activation of brain areas involved in object affordance has been frequently described (Proverbio et al., 2011; Proverbio, 2012, Grafton et al., 1997; Rushworth, Johansen-Berg, Göbel, & Devlin, 2003; Johnson-Frey, 2004). However, it is not known whether the visuomotor neurons coding action affordance are somewhat left lateralized or whether the left lateralization is associated with manual dexterity in the use of unimanual tools/manipulable objects.

The available literature does not provide data to address this issue, as typically, only right hand actions are considered. For example, Turella et al. (2012) studied corticospinal facilitation during the observation of graspable objects. In their study, TMS was administered over the left motor cortex, and motor-evoked potentials (MEP) were recorded from the right hand. Similarly, Valyear, Gallivan, McLean, and Culham (2012) performed fMRI while participants grasped and used tools with their right hand. Parietofrontal activations were observed bilaterally, although with clear left hemisphere prevalence, which is consistent with the fact that participants performed actions using their right hand.

Regarding the representation of the motor action per se, the left hemisphere appears to be dominant in unimanual grasping (Davare, Duque, Vandermeeren, Thonnard, & Olivier, 2007; Ehrsson et al., 2000; Gonzalez, Ganel, & Goodale, 2006), but it remains unclear whether bimanual grasping involves the same areas as unimanual grasping, as subjects described in the literature have been scanned during either reaching or grasping actions performed with their (dominant) right hand (e.g., Tunik, Frey, & Grafton, 2005; Tunik, Ortigue, Adamovich, & Grafton, 2008). However, all of the aspects relative to the movement kinematics of bimanual movements have been deeply investigated (e.g., Castiello, Bennett, & Stelmach, 1993; Corbetta & Thelen, 1996; Tresilian & Stelmach, 1997).

In the comprehensive review "The neuroscience of grasping" by Castiello (2005) there is no reference to studies involving manual actions performed with left hand, thus leaving the matter of a possible hemispheric asymmetry in the neural representation of grasping an unresolved issue. But there is for example this one paper (Castiello, Bennett, Eganc, & Tochonc, 1999), in which different kind of grips were considered: a precision grip action towards a sweet with the right hand, grasping with the mouth, and imagining grasping with the mouth. The results showed an extensive hand-grasping network, including the left precentral and postcentral gyri and the IPL bilaterally. Specifically, mouth grasp was associated with PET activation over the left and right pre-central gyrus, the left post-central gyrus, and the right inferior parietal lobule (IPL). Finger grasping with the right hand was associated with the activation of the left and right IPL and the left precentral and post-central gyrus, while the imagined mouth grasp activated the left hemispheric brain regions only (left AIP, left post-central gyrus, and left IFG). Overall, the grasp modality (real or imaginary) was only activated in the left hemisphere and not the right post-central gyrus, providing evidence for left hemispheric asymmetry in the neural representation of grasping.

Also classical neuropsychological observations of brain-damaged patients (Fisk & Goodale, 1988) support the notion of left hemispheric asymmetry in motor-programming execution and representation. Again, ipsilateral motor deficits (e.g., externally paced fast tapping, limb apraxia, ballistic movements, and planning sequences) are more commonly observed after left hemisphere damage than after right hemisphere damage (Haaland & Harrington, 1989), suggesting that the left hemisphere is more dominant for controlling most cognitive aspects of movement, at least in right-handers. In particular, Haaland and Harrington (1989) reviewed the various patterns of motor deficits after unilateral hemispheric damage and described bilateral deficits after left hemisphere damage only. In addition to that, it has been shown that the left inferior parietal cortex (BA40) (as compared to the homologous right counterpart) has a crucial role in action representation, in that its lesion is associated with apraxia deficit, which is the inability to execute or carry out learned purposeful movements despite having the desire and the physical ability to perform the movements (Heilman & Rothi, 1999; Goldenberg & Spatt, 2009).

Despite evidence supporting the existence of hemispheric specialization for grasping and particularly, precision grasping or tool-related handling and manipulation with both hands, little is known (except for Proverbio et al., 2011; Proverbio, 2012, Grafton et al., 1997) about the similar existence of homologous asymmetry in object affordance representation involving the action observation system and the MNS in humans.

The present study aimed to compare the brain processing of unimanual tools (i.e., objects that recalled a specific motor pattern for the right hand) vs. bimanual tools (e.g., objects that recalled a specific motor pattern for both hands, such as handlebars) to determine whether the pattern of brain activation and its time course differed as a function of the hands involved in action processing in right-handed viewers.

In the first study, hundreds of tools of both types that were balanced for all perceptual characteristics (size, color, luminance, spatial frequency distribution, and familiarity) were presented in central visual field. It was assumed that any difference in the amplitude of the ERP components elicited by tools graspable with different grips/hands would therefore depend on the way the brain represented their motoric properties. Based on a previous study on unimanual tools (Proverbio et al., 2011), we also expected to observe the first neural sign of action affordance processing at about 250 ms. In a second study neural processing of easy-to-grasp vs. hard-to-grasp tools was compared by means of ERP recordings and swLORETA reconstructions.

2. Study 1

2.1. Materials and methods

2.1.1. Participants

A total of 18 Italian university students aged between 20 and 31 years (23.7, SD = 2.74), including 11 females between the ages of 20 and 31 years (23.27, SD = 3.38) and 7 males between the ages of 22 and 25 years (24.43, SD = 1.14), participated in this study. The subjects obtained university credits (CFU) for their participation. All participants reported a preference for the right side/hand, as estimated using the Italian version of the Oldfield Inventory on lateral preference and two practical tests for eye dominance. All participants had normal vision or corrected vision through the use of glasses, and all subjects were in good health and did not have any previous neurological disturbances. Two participants were excluded from analysis due to excessive EEG artifacts. The experiments were conducted with the understanding and written consent of each participant according to the Declaration of Helsinki (BMJ 1991; 302: 1194), with approval from the Ethical Committee of the University, and in compliance with APA ethical standards for the treatment of human volunteers (1992, American Psychological Association).

2.1.2. Stimuli and procedure

2.1.2.1. Stimuli. The stimuli were 2D color pictures depicting familiar manipulable tools or objects selected from an initial set of 250 stimuli that were evaluated by a group of 20 judges for their perceived manipulability on a 3-point scale. A randomly mixed PowerPoint presentation of all of the pictures was administered to 20 volunteers between the ages of 22 and 55 years (M = 33.65, SD = 11.91), including 12 females between the ages of 22 and 55 years (M = 34.58, SD = 12.54) and 8 males between the ages of 23 and 50 years (M = 32.25, SD = 11:58). The depicted objects (of which some examples are shown in Fig. 1) might recall a specific motor pattern for the right hand (unimanual) or for both hands (bimanual), e.g., via a handle, wheel, or button/key/knob. The set of images was balanced between classes (unimanual vs. bimanual) based on their physical characteristics (e.g., elongated handle vs. short) and the action purpose (e.g., work tools, kitchen utensils, and handles to open/close something). Each image was assessed according to the instructions reported in legend of Fig. 2. All of the pictures were evaluated, and on average, scores below 0.75 were considered fully unimanual (unimanual objects