Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research report

A distributed network critical for selecting among tool-directed actions

Christine E. Watson* and Laurel J. Buxbaum

Moss Rehabilitation Research Institute, Elkins Park, PA, USA

ARTICLE INFO

Article history:
Received 10 October 2014
Reviewed 4 November 2014
Revised 11 December 2014
Accepted 13 January 2015
Action editor Georg Goldenberg
Published online 24 January 2015

Keywords:
Action selection
Tool use
Inferior parietal lobe
Apraxia
VLSM

ABSTRACT

Tools pose a challenge to the need to select actions appropriate for task goals and environmental constraints. For many tools (e.g., calculator), actions for “using” and “grasping-to-move” conflict with each other and may compete during selection. To date, little is known about the mechanisms that enable selection between possible tool actions or their neural substrates. The study of patients with chronic left hemisphere stroke, many of whom are deficient in tool-use action (apraxic), provides an opportunity to elucidate these issues. Here, 31 such patients pantomimed or recognized tool use actions for “conflict” and “non-conflict” tools. Voxel-based lesion-symptom mapping (VLSM), lesion subtraction, and tractographic overlap analyses were used to determine brain regions necessary for selecting among tool-directed actions. Lesions to posterior middle temporal gyrus (pMTG) and anterior intraparietal sulcus (aIPS) tended to impair production of use actions similarly for both conflict and non-conflict tools. By contrast, lesions to the supramarginal gyrus (SMG), inferior frontal gyrus (IFG)/anterior insula, and superior longitudinal fasciculus (SLF) specifically impaired production of use actions for conflict tools. Patients' errors on conflict tools suggested inappropriate selection of grasping actions and difficulty selecting single actions. Use/grasp conflict had no effect on action recognition. We suggest that the SMG/SLF/IFG pathway implements biased competition between possible tool actions, while aIPS and pMTG compute the structure-based and skilled use actions, respectively, that constitute input to this competitive process. This is the first study to demonstrate a reliable link between a characteristic of single tools (i.e., their association with different use and grasp actions) and action selection difficulties. Additionally, the data allow us to posit an SMG-involved subtype of apraxia characterized by an inability to resolve action competition.

1. Introduction

A fundamental problem for the brain is the specification of potential actions and the need to select among these actions according to task goals. Substantial research indicates that the sensorimotor system prepares possible actions in parallel while awaiting additional information required to select between them (e.g., Cisek & Kalaska, 2005; Kim & Shadlen, 1999;

* *Corresponding author*. 50 Township Line Rd., Elkins Park, PA 19027, USA.
E-mail address: watsonch@einstein.edu (C.E. Watson).
http://dx.doi.org/10.1016/j.cortex.2015.01.007

Ledberg, Bressler, Ding, Coppola, & Nakamura, 2007; Pastor-Bernier & Cisek, 2011; see Cisek & Kalaska, 2010; Gold & Shadlen, 2007 for reviews). As evidence for each action accumulates, candidate actions compete with one another for selection, and selection is biased in favor of actions consistent with context and goals (Cisek, 2007).

For humans, interacting with tools poses a special challenge for action selection: many tools can be used with more than one skilled action (e.g., a knife can be used for slicing, stabbing, or spreading). Furthermore, for some tools, actions associated with skillful use differ from actions for transport. For example, a calculator is used with a non-prehensile "poke", but it is picked up and moved with a power grip. In fact, "grasp-to-move" and "use" actions are associated with different temporal dynamics of activation. While grasp-to-move actions are rapidly evoked but short-lasting, use actions show comparatively slower activation and decay (Jax & Buxbaum, 2010; Lee, Middleton, Mirman, Kalénine, & Buxbaum, 2012). Because of these differences in the time-course of their activation, grasp actions may interfere with use actions within single tools (Jax & Buxbaum, 2010; Osiurak, Roche, Ramone, & Chainay, 2013). For example, Jax and Buxbaum (2010) found that participants were slower to initiate use actions to tools associated with different use and grasp actions (e.g., calculator) than to tools associated with the same use and grasp actions (e.g., beer mug). These results indicate that an inconsistent grasp action can interfere with the production of a tool use action. However, no such effect was observed when participants initiated *grasp* actions (that is, a different use did not interfere with grasping), unless they had completed a use task prior to grasping. These and other related data (e.g., Lee et al., 2012) indicate that interference from use actions on grasping takes longer to emerge and may arise during the retrieval and processing of semantic knowledge of tools. In contrast, grasp actions are more quickly computed, based on currently–visualized structural properties of objects, and so grasp can interfere with use even on an individual trial, within single objects. In light of these data, a critical question is what mechanisms—and which brain regions—enable selection of appropriate tool-related hand actions.

An important opportunity to examine this issue is afforded by studying the determinants and neuroanatomic substrates of errors in patients with limb apraxia, a disorder of skilled action characterized by spatiotemporal and postural hand action errors. Patients with apraxia after left hemisphere stroke (LCVA) exhibit slowed activation of "use" actions (Lee, Mirman, & Buxbaum, 2014), and, relative to control participants and non-apraxic patients, erroneously grasp (and subsequently erroneously use) tools when asked to use them but not when asked to transport them (Randerath, Li, Goldenberg, & Hermsdörfer, 2009). Furthermore, patients with apraxia have particular difficulty producing hand actions for tools associated with *conflicting* use and grasp actions, like a calculator ("conflict" tools) (Jax & Buxbaum, 2013). Even so, these patients perform normally when reaching and/or generating grasping actions based on object shape and size (Buxbaum, Johnson-Frey, & Bartlett-Williams, 2005; Buxbaum, Sirigu, Schwartz, & Klatzky, 2003; Haaland, Harrington, & Knight, 1999). In contrast to patients with limb apraxia, patients with optic ataxia exhibit impairments when grasping objects but can often correctly pantomime object use actions (Karnath & Perenin, 2005; Perenin & Vighetto, 1988).

This pattern of data suggests that functionally and/or neuroanatomically distinct cognitive systems subserve skilled use of tools and prehensile grasping. In addition, neuroimaging studies of healthy participants reveal different patterns of activation for these two kinds of actions with objects (Buxbaum, Kyle, Tang, & Detre, 2006; Creem-Regehr, Dilda, Vicchrilli, Federer, & Lee, 2007). Although visually-guided control of action relies on brain regions in the dorsal processing stream (Goodale & Milner, 1992; Goodale, Milner, Jakobson, & Carey, 1991), several researchers have proposed further divisions of the dorsal stream for different kinds of object-directed actions (Binkofski & Buxbaum, 2013; Buxbaum & Kalénine, 2010; Fridman et al., 2006; Johnson-Frey, 2004; Rizzolatti & Matelli, 2003; Vingerhoets, Acke, Vandemaele, & Achten, 2009). Specifically, a bilateral dorso-dorsal "Grasp" system is specialized for prehensile actions based on object shape, size, and orientation, while a left-lateralized ventro-dorsal "Use" system mediates skilled object use actions that cannot be inferred from object structure.

The decision to use a tool or grasp it to move depends on context and task goals. Moreover, everyday actions often entail both moving and using in relatively rapid succession (e.g., when selecting a tool from a drawer or storage container, performing a task with the tool, and then clearing it from the workspace) and likely require coordination between Use and Grasp systems (Binkofski & Buxbaum, 2013). Yet, little is known about how different actions specified by these two systems compete for selection. Many important questions remain, including which regions within the left hemisphere normally select between tool-directed actions, the impact of deficient selection on apraxic errors, and the stage of cognitive processing at which such errors arise.

Neuroimaging studies implicate left inferior gyrus (IFG)/ventral premotor cortex (vPMC), inferior parietal cortex (IPL), and posterior middle temporal gyrus (pMTG) as key nodes in the network subserving skilled tool use (Lewis, 2006), and lesions to each of these regions are associated with apraxia (Buxbaum, Shapiro, & Coslett, 2014; Randerath, Goldenberg, Spijkers, Li, & Hermsdörfer, 2010). Two of these regions—IFG and IPL—may play a role in selection, broadly defined. On many accounts, IFG resolves competition that arises when selecting between incompatible representations (e.g., Thompson-Schill & Botvinick, 2006). Similarly, anterior parietal cortex/supramarginal gyrus (SMG) is activated during response competition (Hazeltine, Poldrack, & Gabrieli, 2000) and may update or suppress prepared but incorrect actions (Hartwigsen et al., 2012). However, studies of response conflict typically examine simple and/or arbitrary actions (e.g., button presses) with questionable relevance to tool actions.

In the present study, we used voxel-based lesion-symptom mapping (VLSM) with LCVA patients to test the hypothesis that within the key nodes of the tool-use network, IFG and SMG (but not pMTG) enable selection between different hand actions naturally associated with the same tool. While apraxia is apparent in actual tool use (e.g., Poizner, Mack, Verfaellie, Gonzalez Rothi, & Heilman, 1990), object structure constrains the degrees of freedom of movements (see Buxbaum,