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Brain Research

Research Report

Functional somatotopy revealed across multiple cortical regions using a model of complex motor task

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ARTICLE INFO

Article history:
Accepted 29 July 2013
Available online 3 August 2013

Keywords:
Somatotopy
Representation
Motor map
Motor control
Movement
Posterior parietal cortex
Primary motor cortex or M1
Functional MRI or fMRI

ABSTRACT

The primary motor cortex (M1) possesses a functional somatotopic structure—representations of adjacent within-limb joints overlap to facilitate coordination while maintaining discrete centers for individuated movement. We examined whether similar organization exists across other sensorimotor cortices. Twenty-four right-handed healthy subjects underwent functional magnetic resonance imaging (fMRI) while tracking complex targets with flexion/extension at right finger, elbow and ankle separately. Activation related to each joint at false discovery rate of 0.005 served as its representation across multiple regions. Within each region, we identified the center of mass (COM) for each representation, and the overlap between the representations of within-limb (finger and elbow) and between-limb joints (finger and ankle). Somatosensory (S1) and premotor cortices (PMC) demonstrated greater distinction of COM and minimal overlap for within- and between-limb representations. In contrast, M1 and supplementary motor area (SMA) showed more integrative somatotopy with higher sharing for within-limb representations. Superior and inferior parietal lobule (SPL and IPL) possessed both types of structure. Some clusters exhibited extensive overlap of within- and between-limb representations, while others showed discrete COMs for within-limb representations. Our results help to infer hierarchy in motor control. Areas such as S1 may be associated with individuated movements, while M1 may be more integrative for coordinated motion; parietal associative regions may allow switch between both modes of control. Such hierarchy creates redundant opportunities to exploit in stroke rehabilitation. The use of complex rather than traditionally used simple movements was integral to illustrating comprehensive somatotopic structure; complex tasks can potentially help to understand cortical representation of skill and learning-related plasticity.

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http://dx.doi.org/10.1016/j.brainres.2013.07.050

1. Introduction

Traditionally, the primary motor cortex (M1) was known to be organized with a point-to-point layout of cortical representations of joints and muscles, a feature known as discrete somatotopy (Foerster, 1936; Grafton et al., 1993; Kawashima and Fukuda, 1994; Penfield and Boldrey 1937; Penfield 1950; Rao et al., 1995; Woolsey et al., 1979). A more recent concept of M1 organization, instead, demonstrates that cortical representations of adjacent joints overlap while maintaining distinction between their centers (Beisteiner et al., 2001; Dechent and Frahm, 2003; Plow et al., 2010). Evidence of organization within M1, thus, suggests a balance between discrete and distributed structure, an organization that is now termed functional somatotopy. We have previously discussed (Plow et al., 2010; Plow and Carey, 2012), along with others (Beisteiner et al., 2001; Hlustik and Mayer, 2006; Kleinschmidt et al., 1997; Molina-Luna et al., 2008; Nudo and Milliken, 1996; Pascual-Leone et al., 1996), that such a structure may afford flexibility to M1, where sharing of cortical substrates may create opportunities for coordinated movements involving within-limb joints (such as index finger and elbow in reaching to grasp), while disparate centers may allow discrete control for individuated movements at the respective joints. It remains unclear, however, whether other cortices that participate in movements, such as higher motor areas, primary sensory and associative areas, demonstrate similar somatotopic structure.

To define the somatotopic structure across cortical networks, it is critical to first choose an ideal motor task. Somatotopy within M1 has been routinely studied using simple volitional flexion–extension movements during functional magnetic resonance imaging (fMRI) (Kapreli et al., 2006; Lotze et al., 2000; Luft et al., 2002). However, to define somatotopic structure across comprehensive cortices, complex movements may offer a better model because (1) complex movements, unlike simple, are associated with greater task preplanning, error-detection and correction, thereby eliciting widespread fMRI activation (Beisteiner et al., 2001; Carey et al., 2006; Dechent and Frahm, 2003; Hlustik et al., 2001; Kleinschmidt et al., 1997; Luft et al., 2002) and (2) complex movements are more strongly applicable to motor skills, and learning such movements initiates adaptive plasticity across representations in M1 (Kleim et al., 1998; Nudo and Milliken, 1996; Plautz et al., 2000). Thus, by defining the organization of representations based on complex motor tasks, we can more accurately deduce a region's role in motor skill and motor control.

The purpose of the present study was to explore the somatotopic structure across cortical substrates besides M1 using complex movements with fMRI. We employed joint tracking involving flexion/extension to precisely follow moving target waveforms (Bhatt et al., 2007; Carey et al., 2002, 2006) because this task maximally elicits the activation of higher cortical substrates besides M1 (Bhatt et al., 2007; Carey et al., 2002), more so than simple movements (Carey et al., 2006). Furthermore, training upon joint tracking initiates comparable mechanisms of plasticity of representations in M1 (Plow and Carey, 2012) as described with learning of skill in animal studies (Kleim et al., 1998; Nudo and Milliken, 1996; Plautz et al., 2000).

Subjects performed joint tracking at index finger, elbow and ankle, simultaneous with fMRI. We defined activation related to these individual joints as their movement representations. Within each active cortical region, we identified centers of and calculated overlap between representations of within-limb (finger and elbow) and between-limb (finger and ankle) joints. In doing so, we investigated whether the somatotopic structure for a region resembled that which is now established for M1 (Beisteiner et al., 2001; Carey et al., 2006; Dechent and Frahm, 2003) 'functional somatotopy' containing overlapping

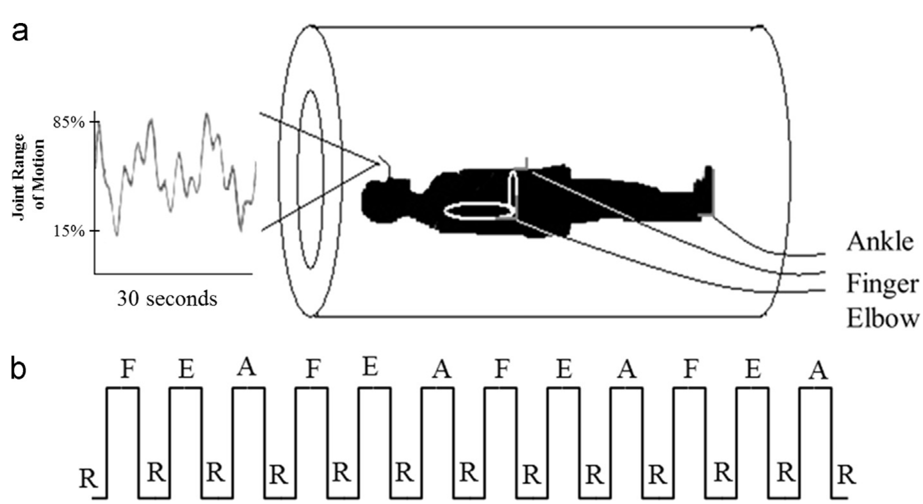

Fig. 1 – Experimental description: (a) schematic depicting a subject performing a tracking task in the MRI. Task is performed separately at differing joints, right index finger, elbow and ankle, using flexion/extension. Movement at the joint is recorded via special sensors (see Section 4.2). Subject uses flexion/extension at the designated joint to follow a moving target waveform presented on a projection screen that is viewed through a rear-projection mirror attached to the MRI head coil. Prompts at the bottom of the screen indicate the block—rest or finger, elbow or ankle tracking. Accuracy of tracking is emphasized as subjects can view their response and its relation to the moving target waveform in real-time. (b) Repeating sequence of blocks for finger (F), elbow (E), ankle (A) tracking and rest (R).