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Detailed somatotopy in primary motor and somatosensory cortex revealed by Gaussian population receptive fields

Wouter Schellekens [a,b,*], Natalia Petridou [a,b], Nick F. Ramsey [a]

[a] Brain Center Rudolf Magnus, UMC Utrecht, The Netherlands
[b] Department of Radiology, UMC Utrecht, The Netherlands

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ABSTRACT

The relevance of human primary motor cortex (M1) for motor actions has long been established. However, it is still unknown how motor actions are represented, and whether M1 contains an ordered somatotopy at the mesoscopic level. In the current study we show that a detailed within-limb somatotopy can be obtained in M1 during finger movements using Gaussian population Receptive Field (pRF) models. Similar organizations were also obtained for primary somatosensory cortex (S1), showing that individual finger representations are interconnected throughout sensorimotor cortex. The current study additionally estimates receptive field sizes of neuronal populations, showing differences between finger digit representations, between M1 and S1, and additionally between finger digit flexion and extension. Using the Gaussian pRF approach, the detailed somatotopic organization of M1 can be obtained including underlying characteristics, allowing for the in-depth investigation of cortical motor representation and sensorimotor integration.

Introduction

Cortical sensorimotor areas in the human brain have been shown to exhibit somatotopic organizations at least at the macroscopic level between limbs. Perhaps best known is Penfield's homunculus (Penfield and Boldrey, 1937) which shows a coarse distribution of body part representations on both the precentral (i.e. primary motor cortex, or M1) and postcentral gyri (i.e. primary somatosensory cortex, or S1) in humans. It has also been demonstrated that S1 exhibits a somatotopic organization on a mesoscopic 'within limb' level for individual finger digits (Kolasinski et al., 2016; Martuzzi et al., 2014; Sanchez-Panchuelo et al., 2012). However, for M1 the existence of such a detailed orderly functional organization is still under debate. It has even been argued that M1 explicitly does not have an orderly somatotopic organization on the mesoscopic 'within limb' level (Sanes and Schieber, 2001; Schieber, 2001). It is argued that the human ability for acquiring new motor skills could require the brain to maintain a flexible attitude towards cortical motor organization. This poses several challenging questions, specifically how movement of body parts is represented within the human brain, and also how sensorimotor integration is accomplished if M1 is not somatotopically organized and could additionally change its organization over time depending on newly acquired motor skills.

Numerous studies have investigated the nature of M1 functionality in humans and animals over the past decades. Central to the investigation of the primary motor cortex is the issue of what its neuronal activity represents and how it relates to motor functioning. The first possibility is that M1 neurons directly send commands to specific motor units/muscle fibers (Kakei et al., 1999; Scott, 2012). However, with the use of viral tracers it has been shown that a single muscle receives input from a relatively large cortical region within M1 (Cheney and Fetz, 1985; Rathelot and Strick, 2009). Additionally, electrophysiological stimulation at single sites within M1 results in the display of complex movements, often accompanied by specific body and limb postures (Brown and Teskey, 2014; Graziano and Aflalo, 2007). It appears that individual neurons or even small neuronal populations do not send commands to individual muscles or motor units. Instead, M1 activity relates to complex motion behavior, where neuronal populations code for the building blocks of complex movements, or "muscle synergies", that together constitute a person's full motion repertoire (d'Avella et al., 2006; Ting and McKay, 2007). Such complex motion representation can arguably not be encapsulated in an orderly cortical topography, although a coarse categorization on the basis of related body parts or limbs could be computationally beneficial.

Recently, imaging studies have also engaged in the characterization

* Corresponding author. P.O. Box 85060, 3508 AB, Str. 4.205, Utrecht, The Netherlands.
E-mail address: w.schellekens@umcutrecht.nl (W. Schellekens).

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of M1 activity in humans. Several studies show that the movement of individual finger digits results in largely overlapping activity patterns, showing voxels that respond to all finger movements (Dechent and Frahm, 2003; Hlustík et al., 2001; Olman et al., 2012). A somatotopic organization of M1 at the level of individual finger digits is not immediately distinguishable and can primarily be appreciated after extended analyses, contrasting activity patterns of individual finger digits. Previous findings, thus, show that M1 might contain a somatotopic organization at the mesoscopic level of finger digits, while it simultaneously responds to a much larger range of bodily movements. The complexity of a neatly ordered somatotopy on the one hand, and a more diffuse activity pattern for many motor actions on the other hand, might well be characterized by a Gaussian function. Gaussian functions are able to describe the correspondence of (cortical) functioning with respect to measured neuronal activity patterns (Victor et al., 1994). Gaussian functions have been shown to successfully describe neuronal characteristics including topographies in research concerning sensory cortices, which has led in imaging studies to the population Receptive Field (pRF) approach to accurately assess the retinotopic organization in visual cortex (Dumoulin and Wandella, 2008; Harvey and Dumoulin, 2011).

The current study investigates whether a detailed, yet complex, somatotopic organization of cortical area M1 can be obtained through the implementation of a Gaussian pRF approach during finger movements. The Gaussian pRF approach is novel to the modeling of cortical motor activity for both motor and somatosensory cortex, and is here implemented analogously to the pRF approach in visual cortex. Note that this means that the Gaussian function is not to be fitted across spatial cortical activity patterns, but instead on functional features of neuronal populations. Functional features of motor cortex are in fact control over and/or information processing of certain limbs, i.e. finger digits in the current experiments, which can be probed by means of a simple finger movement task. Based on previous research, neuronal populations in M1 are expected to respond to a wide variety of functional features, which is described by a Gaussian fit with a center feature corresponding to a population's preferred finger digit and a Gaussian spread corresponding to the degree of response to adjacent finger digits. In sensory cortices the Gaussian spread is often referred to as a neuron's receptive field (RF), or the average neuronal population receptive field (pRF). Through the Gaussian pRF approach, we show that an orderly somatotopic organization of preferred finger digits is present in M1. Additionally, we reveal differences as well as similarities in properties of population receptive fields between flexion and extension of finger digits and across separate cortical areas in the contralateral hemisphere.

Materials & methods

Subjects and task

Eight healthy volunteers (mean age = 24, female = 4) were recruited from the Utrecht University. All participants gave written informed consent before entering the study. The protocol was approved by the local ethics committee of the University Medical Center Utrecht, in accordance with the Declaration of Helsinki (2013).

All participants performed a simple finger movement task with their right hand. The primary task objective was to isolate movements of individual finger digits as well as movement type, i.e. dissociate flexion from extension. Task instructions were projected on a screen in the bore of the scanner, which participants viewed using prism glasses and a mirror. The instruction onsets were triggered by the scanner. During the experiment, the participants viewed 5 rectangles on a grey background that together resembled the shape of the 5 finger digits of a hand. Each rectangle represented the instruction for its respective finger digit, which was denoted by the rectangle's contrast. During the entire experiment, when a rectangle was displayed having a white contrast, that respective finger digit was to be flexed. Finger digit extension was cued when the contrast changed to black. The rectangles were only displayed having a black or white contrast, meaning that each finger digit was always flexed or extended and there was no separate rest condition. The order of rectangle contrast change occurred in a sequential manner. Initially, all 5 rectangles started out having a black contrast, which meant that the participant assumed a fully extended hand position. Then one by one, the rectangles became white starting from either the thumb or the little finger, moving its way across all finger digits and ending with a fully flexed hand (i.e. all white rectangles). Afterwards, all 5 rectangles became black again in sequential order from thumb to little finger or vice versa, resulting in the sequential extension of each finger digit. By doing so, we obtained separate flexion and extension runs, which were both repeated 8 times (4x starting from the thumb and 4x starting from the little finger). The time between two sequential movement cues was 4.8s, except for the last of the 5 digits and the first of the next run, which had an interval of 14.4s allowing the Blood Oxygen Level Dependent (BOLD) signal to return to baseline prior to the new sequence of movements. Making the cue interval shorter than approximately 5 s (4.8s was chosen as a multiple of the TR of 1.6s, see scan protocol) would result in the inability to effectively distinguish BOLD signals following a movement cue, while making it longer would increase the risk of decreasing attention and task performance.

Thus, the BOLD signal is expected to increase following a movement cue only, rather than during the maintaining of finger positions (Branco et al., 2017). Keeping digits flexed or extended, therefore, serves as the baseline for digit movement. Finger digits that maintain their position might cause neuronal activity, but not specifically at the time-locked events of the motor cues. Finally it is worth mentioning that the participants were explicitly instructed to disregard any co-occurring movements. Some finger digits are enslaved in the movements of others (e.g. due to tendon connections). Participants were expected to only perform the cued motor command and not to correct for any co-occurring movements. Compliance with the task instructions was tested using a MR-compatible data glove (5DT Inc.)

Scan protocol

Scanning was performed on a 7 T Philips Achieva scanner (Philips Healthcare, Best, Netherlands) with a 32-channel receive headcoil (Nova Medical, MA, USA). Functional MRI (fMRI) measurements were obtained using an echo-planar imaging (EPI) sequence with the following parameters: SENSE factor = 3.0, TR = 1600 ms, TE = 27 ms, flip angle = 70°, axial orientation, interleaved slice acquisition, FOV (AP, FH, LR) = 208.8 × 41.6 × 208.8 mm^3. The acquired matrix had the following dimensions: 132 × 26 x 132, voxel size: 1.6 × 1.6 × 1.6 mm^3. The functional images were acquired from the superior 42 mm of the brain, covering the majority of the frontal and parietal lobes. During the functional image acquisition, 8 flexion runs and 8 extension runs were performed by each participant, where a single movement run took 21 images to complete (4 × 4.8s + 14.4s). Also a rest block of 9 images (14.4s) was acquired at the start of the experiment, resulting in a total of 345 functional images per participant. A T1-weighted image of the whole brain (0.49 × 0.49 × 0.8 mm^3, FOV = 512 × 512 x 238) and a whole-brain proton density image (0.98 × 0.98 × 1.0 mm^3, FOV = 256 × 256 x 190) were acquired at the end of the functional sessions.

Image processing

The T1-weighted image was corrected for macroscopic field inhomogeneities by dividing it by the proton density-weighted image (Van de Moortele et al., 2009). Grey/white matter surfaces were constructed on the basis of the corrected T1-weighted image using Freesurfer (http://surfer.nmr.mgh.harvard.edu/ (Dale et al., 1999),). The reconstructed brain surfaces are triangulated surface meshes, where each triangle consists of 3 nodes (sometimes called vertices), while the entire surface mesh contains over 100,000 nodes per hemisphere. All reconstructed surface meshes were flattened using Caret (Van Essen et al., 2001) and