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Review article

Brain-mapping projects using the common marmoset

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ABSTRACT

Globally, there is an increasing interest in brain-mapping projects, including the Brain Research through Advancing Innovative Neurotechnologies (BRAIN) Initiative project in the USA, the Human Brain Project (HBP) in Europe, and the Brain Mapping by Integrated Neurotechnologies for Disease Studies (Brain/MINDS) project in Japan. These projects aim to map the structure and function of neuronal circuits to ultimately understand the vast complexity of the human brain. Brain/MINDS is focused on structural and functional mapping of the common marmoset (*Callithrix jacchus*) brain. This non-human primate has numerous advantages for brain mapping, including a well-developed frontal cortex and a compact brain size, as well as the availability of transgenic technologies. In the present review article, we discuss strategies for structural and functional mapping of the marmoset brain and the relation of the common marmoset to other animals models.

Contents

1. Introduction

There is an increasing interest in the common marmoset (*Callithrix jacchus*), a small New World primate, in brain-mapping projects in Japan and their international collaborations. Following an era of large-scale genome-mapping projects (Lander, 2011), an international movement has emerged directed towards large-scale brain-mapping projects (reviewed by Kandel et al., 2013), including The Brain Research through Advancing Innovative Neurotechnologies (BRAIN) Initiative project in the USA (http://www.whitehouse.gov/share/brain-initiative) and the Human Brain Project (HBP) in Europe (https://www.humanbrainproject.eu/). In Japan, a project titled Brain Mapping by Integrated Neurotechnologies for Disease Studies (Brain/MINDS) started in June 2014 (http://www.lifescience.mext.go.jp/files/pdf/n1332_07.pdf). Although the strategies of these three brain-mapping projects are somewhat different, all aim to map the structure and function of neuronal circuits and to ultimately understand the great

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complexity of the human brain, which would fundamentally contribute to the prevention, diagnosis, and treatment of brain diseases.

The USA and the European Union have adopted different approaches for their brain initiatives. The HBP is a centralized, large-scale enterprise with a computational focus, aimed at building detailed models of neural circuitry, along with a number of complementary sub-projects. In the USA, the Brain Initiative project is more distributed and closer to traditional investigator-driven neuroscience research, with different funding agencies (primarily the National Institute of Health (NIH), National Science Foundation (NSF), Defense Advanced Research Projects Agency (DARPA), Intelligence Advanced Research Projects Activity (IARPA), and private foundations) adopting coordinated yet differentiated strategies. An emphasis on the development of technologies to facilitate neuroscience research forms a basic theme of USA-led initiatives.

The NIH component of the BRAIN Initiative underwent a year-long planning process with a committee appointed by the NIH director, resulting in a final report outlining the NIH's efforts in this area (http://www.nih.gov/science/brain/2025/). Rather than focus on a single, centralized project, the report lays out seven major scientific goals ranging from the cellular/molecular to the systems/behavioral level, consistent with current research directions in neuroscience. The plan focuses on technology development for the first half of the decade, and on directing these technologies towards scientific and clinical questions in the second half. The NIH committed $40 M to the BRAIN Initiative for the 2014 fiscal year and plans to commit $100 M for 2015. The committee estimated that a yearly NIH commitment of $300–500 M would be required to meet the goals of the project.

The NSF component of the BRAIN Initiative (https://www.nsf.gov/news/special_reports/brain/) has centered on organizing a number of workshops (for example, http://news.sciencemag.org/physics/2014/05/brain-project-meets-physics), which also lead to investigator-driven funding opportunities. A focus on basic rather than clinical research typically characterizes NSF-funded work, and this remains true for the NSF component of the BRAIN Initiative.

BRAIN Initiative proposals funded by the DARPA focus on clinical applications with particular relevance to war veterans, for example, the Systems-Based Neurotechnology for Emerging Therapies (SUBNETS) program and the Restoring Active Memory (RAM) program (http://news.sciencemag.org/brain-behavior/2014/07/darpa-awards-40-million-restore-memories).

Whereas the BRAIN Initiative has moved towards big neuroscience projects by focusing on investigator-driven neuroscience, the HBP, which preceded the BRAIN Initiative, is one of two Future and Emerging Technologies Flagship Initiatives (http://cordis.europa.eu/fp7/ict/programme/fet/flagship/) launched by the European Commission in 2013 with a funding goal of €1 B over a decade. The HBP is based at the Ecole Polytechnique Federale de Lausanne (EPFL) in Geneva, Switzerland, and is centered on the development of Information and Communication Technology (ICT) platforms, motivated by the need to integrate the large volume of data and literature generated by the neuroscience community. One of the primary goals of the HBP is to "develop ICT tools to generate high-fidelity digital reconstructions and simulations of the mouse brain, and ultimately the human brain" (https://www.humanbrainproject.eu/project-objectives). This goal has generated significant debate (http://blogs.nature.com/news/2014/07/baby-steps-towards-rescue-of-human-brain-project.html). The HBP has a number of sub-projects (https://www.humanbrainproject.eu/discover/the-community/subproject-leaders), as well as a large number of collaborative projects spanning several dozen institutions, primarily in Europe.

Considering these situations of brain mapping projects in USA and Europe, a community of Japanese brain scientists has made intensive brainstorming discussions what to do and what not to do in the brain mapping projects in Japan since 2013. As a conclusion of such discussions, it was decided that the structural and functional mapping of the brains of non-human primates, particularly, common marmoset should be one of major foci of in Brain/MINDS in Japan, since such strategies would have considerable implications for human brain science. The details on Brain/MINDS in Japan, particularly, structural and functional mapping of marmoset brain will be introduced in this review.

2. Brain/MINDS

In Japan, the brain-mapping project called Brain/MINDS started in June 2014 (http://www.lifescience.mext.go.jp/files/pdf/n1332_07.pdf). The major goals of Brain/MINDS include: (1) Understanding human higher brain function, (2) Improving diagnosis and treatment of psychiatric and neurological disorders, and (3) Establishing information technologies based on brain mechanisms. To achieve these goals in the most efficient fashion, one of the major foci of Brain/MINDS is the research on the non-human primate brain. This aspect of the project is unique compared to the BRAIN Initiative and the HBP. Brain science using non-human primates is essential for understanding the human brain and for developing knowledge-based strategies for the diagnosis and treatment of psychiatric and neurological disorders. The mouse brain is limited in the extent to which it can contribute to our understanding of the human brain due to differences in the structure of the neocortex, and the complexity of neuronal circuits and behavioral paradigms. Brain/MINDS has a strong focus on the common marmoset for the following reasons: (i) The frontal lobe is more developed than in other commonly used animals, including rodents, (ii) The brain is small (~8 g) and the neuronal circuits can be comprehensively analyzed, and (iii) Marmosets can be genetically modified and manipulated (Sasaki et al., 2009).

To understand the higher brain mechanisms that underlie human feelings and behaviors, researchers must integrate macro- and micro-level information from the whole brain. The marmoset shows human-like social behavior and can be genetically manipulated, and is thus a useful animal model to fill the gap between rodents and human. Through the development of cutting-edge technologies for brain imaging and manipulation, Brain/MINDS will use the marmoset model to reveal the structure and function of the brain, improve future diagnosis and treatment of psychiatric and neurological disorders, and establish new information technologies based on brain mechanisms.

The objectives of Brain/MINDS can be categorized into the following three major subjects (see http://www.lifescience.mext.go.jp/files/pdf/n1332_07.pdf for details):

(1) Structure and functional mapping of the non-human primate brain (particularly the marmoset brain). *Leader, Hideyuki Okano (author of this article).*
(2) Development of novel, cutting-edge technologies that support brain mapping. *Leader, Atsushi Miyawaki (RIKEN Brain Science Institute).*
(3) Technology development for understanding psychiatric and neurological disease in humans. *Leader, Kiyoto Kasai (University of Tokyo).*

The integration of these subjects is essential for understanding diseases of the human brain. For example, in Brain/MINDS, researchers are highly motivated to identify the changes that take place in the brain of patients with mild cognitive impairment and very-early-stage Alzheimer's disease (AD) by using the transgenic marmoset model of AD. By using the transgenic marmoset AD

models, researchers aim to identify the earliest point of damage to neuronal circuits and the relation between pathogenic protein accumulation and cognitive impairment, with the ultimate aim of developing preemptive treatment for AD that can be implemented before the onset of cognitive impairments. In addition, Brain/MINDS plans to address the structural and functional changes that occur in the brain of patients with psychiatric diseases such as schizophrenia by concurrently characterizing the brains of human patients (*via* large-scale clinical imaging data sets) and marmoset models of psychiatric disease.

In this mini review article, we provide a more detailed description of the structural and functional mapping of the marmoset brain which will be performed as part of Brain/MINDS.

3. Structural mapping of the marmoset brain

The structural mapping will be performed at three different levels: macroscopic, mesoscopic, and microscopic.

3.1. Macroscopic structural mapping

Macroscopic structural mapping of the marmoset brain will be performed using magnetic resonance imaging (MRI), which is the most common method of visualizing human neuroanatomy (Bohland et al., 2009). Specifically, we will perform MRI-based diffusion tensor imaging (DTI), which will enable us to track and visualize the nerve fibers based on their anisotropy (Mori and van Zijl, 2002; Mori and Zhang, 2006; Fujiyoshi et al., 2013) and to identify long-range, region-to-region connections (inter- or intra-area mapping) in the marmoset brain. The current resolution of MRI/DTI-based mapping is far from the cellular level, with voxel size >1 mm^3 (Oh et al., 2014). However, in Brain/MINDS we aim to enhance the resolution of MRI/DTI-based mapping, reducing the voxel size to ~50 μm^3 for *ex vivo* analysis and ~200 μm^3 for *in vivo* analysis, by using ultra-high magnetic field MRI and developing a high-throughput radiofrequency (RF) coil for the marmoset.

We have already mapped several of the known tracts of the marmoset central nervous system, including the corticospinal tracts and the optic tracts (Fujiyoshi et al., 2007, 2013; Yamada et al., 2008) (Fig. 1). If DTI-based macroscopic mapping is performed in a quantitative fashion together with voxel-based morphometric analysis (Hikishima et al., 2011), it can be used to analyze structural MR images and identify differences in brain anatomy between control and experimental groups, or to detect longitudinal changes within groups. In Brain/MINDS, DTI-based macroscopic structural mapping will be performed not only for control adult marmosets, but also for wild-type and transgenic disease model marmosets of various developmental stages and ages. Data obtained from these analyses are expected to increase our understanding of the structural and functional bases of human brain disorders.

3.2. Mesoscopic structural mapping

Mesoscopic structural mapping will be used to obtain brain-wide connectivity maps and spatial gene-expression maps of the marmoset brain. The mesoscopic scale of analysis, which employs light microscopy, is intermediate to the macroscale defined operationally by MRI/DTI and the microscale defined by electron microscopy (EM). The scale of mesoscopic analysis corresponds to brain compartments defined in classical neuroanatomical atlases and is also defined operationally by injections of neuroanatomical tracers and subsequent light-microscopic analysis. Fortunately, marmoset brain histological images have been transformed into a modern stereotaxic atlas (Paxinos et al., 2012), which enables these tracer injections and subsequent histological analyses.

One of the authors of this review, Partha Mitra, led a study that mapped whole-brain connectivity in different model organisms at the mesoscopic level (Bohland et al., 2009; Pinsky et al., 2013). The basic methodology in Brain/MINDS uses anterograde and retrograde neuronal tracer injections on a systematic grid that spans the brain, analogous to the shotgun approach in genome sequencing (Bohland et al., 2009; Mouse Brain Architecture Project; http://mouse.brainarchitecture.org). An important recent milestone in this area is the publication of a whole-brain data set of anterograde injections in the mouse brain from the Allen Institute for Brain Science, using enhanced green fluorescence protein (EGFP)-expressing Adeno-associated virus (AAV) as an anterograde tracer (Oh et al., 2014). The Mouse Brain Architecture Project, currently ongoing, employs both anterograde and retrograde neuronal tracers. These two classes of neuronal tracers have complementary strengths and are employed jointly in classical neuroanatomical research.

The principal advance of these current projects over the previous era of neuroanatomical research is the digitization and computational analysis of whole-brain data sets with a spatial resolution at the level of light microscopy. Prior to this, visual examination by expert human neuroanatomists was the gold standard for extracting science from these kinds of microscopic images. However, this approach is not scaleable. Whole-brain digital imaging for mesoscale connectivity mapping generates petabyte-scale data sets, and thus requires new computational tools for automated processing, quantitative analysis, and visualization (Helmstaedter and Mitra, 2012). In Brain/MINDS, a close collaboration between the RIKEN Brain Science Institute in Japan and the Cold Spring Harbor Laboratory in USA will enable the system integration procedures and computational methodology developed for mesoscale circuit mapping of the mouse brain to be applied to the mesoscopic structural mapping of the marmoset brain.

A major advance of the structural mapping performed in Brain/MINDS over previous structural-mapping studies of the mouse brain is the creation of high-resolution MRI/DTI data sets. This gives rise to an additional opportunity to combine the high-resolution MRI/DTI data sets with the whole-brain light-microscopy data sets. Mitra's group recently developed a new methodology that enables the co-registration of high-resolution whole-brain Nissl-stained sections from the same animal from which MRI/DTI was scanned. This procedure permits a finer correspondence between light-microscopic histological data and MRI/DTI data than has previously been available and will be utilized for marmoset brain mapping in Brain/MINDS.

An important aspect of mesoscopic structural mapping is gene-expression mapping at the brain-wide level (Lein et al., 2006). The spatial co-expression of genes reflects the underlying spatial distribution of cell types (Grange et al., 2014) and provides a complementary data set to combine with a mesoscale connectivity map. As a first step in investigating the spatial co-expression of genes in the marmoset brain, we examined the expression of 26 genes that are known to play an important role in cortical development by performing *in situ* hybridization in the marmoset brain (Mashiko et al., 2012) using anatomical terminology of the common marmoset brain (Tokuno et al., 2009a,b). More comprehensive gene-expression database atlases will be constructed through Brain/MINDS and international collaborative interactions.

Transgenic methods developed for the common marmoset, including the lentiviral vector (Sasaki et al., 2009) and genome editing (Kishi et al., 2014), will greatly contribute to the mesoscopic structural brain mapping of particular subtypes of neurons (such as dopaminergic neurons, parvalbumin-positive neurons and serotonergic neurons) by enabling Cre/loxp-mediated labeling. These are crucial studies that will be performed as part of Brain/MINDS.

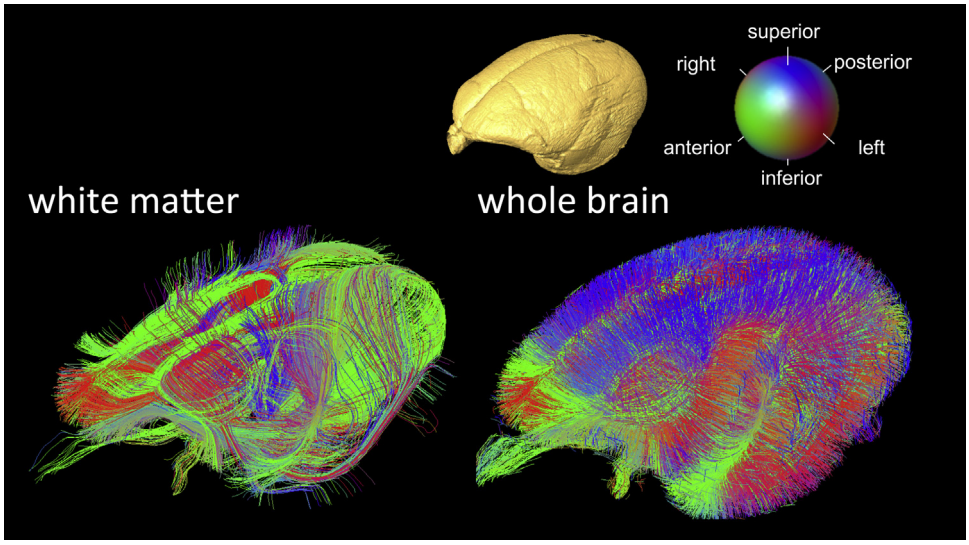

Fig. 1. Fiber structures of white matter and whole-brain regions using diffusion MRI tractography in marmoset brain. Each fiber structure was virtually reconstructed from diffusion MRI data and is color-coded for local direction. White matter fibers contained many long tracts connecting different regions within the brain. Fiber structures in the whole brain also showed short connections within cortex. The data shown in this figure were kindly provided by Dr. Keigo Hikishima.

3.3. *Microscopic structural mapping*

A new method of serial EM, developed by Prof. Jeffery Lichtman's laboratory at Harvard University (http://www.hms.harvard.edu/dms/neuroscience/fac/lichtman.php) will be used to map neural connections (connectomes) at nanometer resolution. This and similar EM-based technologies have enabled researchers to quantitatively map the precise location of cells, synapses and even organelles in a certain micro-domain of the brains (Bock et al., 2011; Briggman et al., 2011; Chklovskii et al., 2010). However, quantification of the EM-based micro-connectome for the entire marmoset brain is not realistic within the limited time period of Brain/MINDS. Thus, Brain/MINDS will focus on mapping the brain regions that are intimately involved in higher brain functions or associated with disease. It is important to develop new technologies that connect and integrate the EM-based microscopic mapping with the light-microscopy-based mesoscopic mapping.

4. Functional mapping of the marmoset brain

The structural map of the marmoset brain should be considered alongside a map of functional connectivity. Functional mapping of the marmoset brain will be conducted using functional MRI (fMRI), positron emission tomography, and electrophysiological recordings such as electrocorticography. fMRI-based functional connectivity has been studied using task-based imaging and, increasingly, using task-free imaging (resting-state fMRI) (Castellanos et al., 2014). Resting-state fMRI is particularly attractive for functional mapping of the human brain in healthy individuals and patient populations (Anderson et al., 2013; Dennis and Thompson, 2014). However, the relation between anatomical connectivity and functional connectivity derived from resting-state fMRI remains largely unsolved. This issue will be clarified in the marmoset brain in the Brain/MIND projects. The method for fMRI of the marmoset brain has recently been improved so that awake animals can be monitored according to the method of Afonso Silva (Papoti et al., 2013).

To increase the spatial and temporal resolution, functional mapping will also be performed by monitoring neuronal activity more directly *via* the expression of a calcium-sensitive reporter such as G-CaMP (Tian et al., 2009) or an ultrafast fluorescent voltage sensor (Accelerated Sensor of Action Potentials 1) (St-Pierre et al., 2014) in a particular region of interest in the marmoset brain and using viral vectors or transgenic lines together with a miniature (<2 g) integrated fluorescence microscope in freely behaving animals (Ghosh et al., 2011). These functional mapping approaches will also be adopted for marmoset disease models, including AD, psychiatric disease, and autism, which will be generated through transgenic technologies.

5. Conclusion and perspectives

Mapping the brain of the common marmoset is an ambitious project that requires extensive technological innovations. Detailed information on the structural and functional connectivity of the entire marmoset brain will enormously advance our understanding of the human brain and its diseases. Extensive international collaboration will be required to achieve the goals of the project.

Competing financial interests

H.O. is a scientific consultant for San Bio, Co. Ltd., and Daiichi Sankyo Co. Ltd.

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