A collaborative resource platform for non-human primate neuroimaging

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1 Abstract

Neuroimaging non-human primates (NHPs) is a growing, yet highly specialized field of
neuroscience. Resources that were primarily developed for human neuroimaging often need to
be significantly adapted for use with NHPs or other animals, which has led to an abundance of
custom, in-house solutions. In recent years, the global NHP neuroimaging community has made
significant efforts to transform the field towards more open and collaborative practices. Here we
present the PRIMatE Resource Exchange (PRIME-RE), a new collaborative online platform for
NHP neuroimaging. PRIME-RE is a dynamic community-driven hub for the exchange of practical
knowledge, specialized analytical tools, and open data repositories, specifically related to NHP
neuroimaging. PRIME-RE caters to both researchers and developers who are either new to the
field, looking to stay abreast of the latest developments, or seeking to collaboratively advance the
field.

13
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15 **Keywords**

16 Open science; Resource sharing; Toolbox; Pipeline; Structural; Functional; Diffusion

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Highlights

● PRIME-RE is a bottom-up open science platform for non-human primate neuroimaging.
● The website hosts a wiki and info about analytical tools and open data repositories.
● Specialized tools address structural, functional & diffusion-weighted analysis.
● Multiple templates & atlases for several non-human primate species are highlighted.
● Communication channels facilitate international conversation and collaboration
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27 **Conflict of interest:** The authors declare no conflict of interest.
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1. Introduction

When navigating an unfamiliar city, people orient themselves based on a few landmarks, use a map for detailed navigation, and take advice from locals and previous visitors about where to go and which areas to avoid. Navigating a highly specialized research field, such as non-human primate (NHP) neuroimaging, is conceptually very similar. In order to orient, access to basic information and support from knowledgeable peers is invaluable. Here we present the **PRIMatE Resource Exchange** (PRIME-RE, https://prime-re.github.io), a new community-driven platform that promotes communication among peers and facilitates the exchange of specialized knowledge and resources related to NHP neuroimaging.

Translational neuroimaging in animals bridges the gap between non-invasive imaging studies in humans and invasive neural recordings that are only carried out in animal models (and occasionally in neurosurgical patients). The approach is pivotal for our understanding of the neuronal basis of neuroimaging signals (Logothetis, 2003; Logothetis et al., 2001; Logothetis and Wandell, 2004), guides the selection of recording targets for invasive studies, and reveals the broader brain networks involved in particular cognitive functions or brain processes. Cross-species comparison of neuroimaging results can furthermore provide insight into the evolution of the brain and its capabilities (Friedrich et al., this issue; Heuer et al., 2019). Finally, combining neuroimaging in animals with invasive methods that influence neuronal activity makes it possible to draw causal inferences about brain function and test potential human therapies (Klink et al., this issue).

The NHP brain is similar to that of humans in many respects. Due to the evolutionary proximity of NHPs to humans, their ability to perform complex cognitive tasks, and the vast body of existing neuronal knowledge from invasive NHP studies, NHP neuroimaging is a crucial branch of translational imaging (Chen et al., 2012; Farivar and Vanduffel, 2014; Logothetis et al., 1999). However, the standard hardware and software used in human neuroimaging is generally not directly suitable for NHP neuroimaging, which requires highly specialized approaches. As a result, most research groups have developed their own in-house solutions that often require substantial further development for compatibility with other sites. These custom solutions often remain in-house and lack extensive documentation, which is far from ideal for peer review, collaboration, best practices, and reproducible science. In recent years, the international NHP neuroimaging community has begun embracing a culture of data-sharing, open science, and collaboration. These efforts led to the PRIMatE neuroimaging Data Exchange initiative (Milham et al., 2018), a

global workshop to discuss strategies for the future of the field (Milham et al., 2020), and this
special issue of NeuroImage on NHP neuroimaging.

Once NHP neuroimaging data are collected or shared, a new set of challenges presents itself.
Most neuroimaging software packages have been developed for use in humans and cannot be
easily applied to NHP data due to built-in assumptions, such as a larger field-of-view,
standardized voxel size, or a higher contrast between gray and white matter. The large number
of choices involved in neuroimaging data analysis is a hotly-debated issue in human
neuroimaging (Botvinik-Nezer et al., 2020). For NHP neuroimaging, these issues may be even
more pressing due to the custom-solutions that are often required to make existing software
compatible with NHP data. The field of human neuroimaging has started to address these issues
with initiatives for standardized, reproducible analysis pipelines (BIDS, Nipype, etc) (Gorgolewski
et al., 2011, 2016), data sharing (OpenfMRI, Zenodo, Neurovault, etc) (Gorgolewski et al., 2015;
Poldrack et al., 2013), and collaborative and open coding (GitHub, GitLab, etc). NHP
neuroimaging has been lagging behind in adopting such collaborative open science initiatives,
but people's willingness to share and be open about the resource solutions they developed is
steadily increasing (Balbastre et al., 2017; Tasserie et al., 2020) and new developments in
information technology promote these initiatives, while creating avenues to assign explicit credit
to developers. The global NHP neuroimaging consortium (Milham et al., 2020, 2018) aims to
facilitate this progress with the introduction and curation of the **PRIMatE Resource Exchange**
(PRIME-RE, https://prime-re.github.io), a community-driven online platform for the exchange of
knowledge and resources concerning the acquisition, analysis, and visualization of NHP
neuroimaging data.

PRIME-RE acts as an open hub where researchers from all countries and career stages can find
and contribute information and resources related to the challenges and advantages of NHP
neuroimaging. Dynamic collections of software tools are grouped by analysis-category to provide
an overview of existing solutions to common challenges. Links to communication outlets allow
researchers to meet international colleagues, discuss challenges and solutions, and start new
collaborations. Resources are maintained by their respective developers, with PRIME-RE serving
as an evolving access point with descriptions of the tools, their software requirements, a list of
authors, relevant citations, and links to the tools themselves.

2. Methods

This Methods section will offer a brief description of the main structure of the PRIME-RE platform,
including its main components, methods for people to contribute and interact, and possibilities for
future growth. The lightweight PRIME-RE website (https://prime-re.github.io/) is intended to be
dynamic and continuously evolve based on input from the research community. It can serve both
as a starting point for researchers that are new to the field of NHP neuroimaging and as a meeting
ground for more experienced researchers in the field. This initiative emerged from the Global
Collaborative Workshop 2019 of the PRIME-DE consortium and subsequent BrainHack (Milham
et al., 2020) and has since attracted a critical mass of active contributors dedicated to open and
collaborative NHP neuroimaging. The platform is hosted on GitHub, which greatly facilitates
community-driven contributions while also maintaining a complete version history of its content
and evolution.

Content-wise, PRIME-RE does not aim to host, curate and maintain all available tools and
documentation regarding NHP neuroimaging. Instead, it chooses an agile approach with
standardized listings of resources, categorized by the type of challenge they address. These
listings include a brief description, developer contact information, and a link to the developer-
maintained resource. This model furthermore ensures that the most recent version of a resource
will be found at its source and that developers receive credit for their efforts. The standardized
listings also make it easy for developers to submit their resource for inclusion on PRIME-RE
through a pre-formatted submission form in which they answer a few basic questions about their
resource (Table 1). These answers form the basis of a resource's listing on PRIME-RE. If the
developers are already hosting their resource online, a submission to PRIME-RE can be
completed in a few minutes.

Submissions to PRIME-RE are approved for inclusion through community-driven evaluation.
Once a submission form is submitted, a member of the community with access to PRIME-RE's
backend can opt to include it on the website. It is up to the community to evaluate a resource's
usefulness. A simple community support rating system has been implemented to allow anyone to
express support for a resource by 'liking' it. This system could help the users of PRIME-RE to
navigate the collection of resources and find tools that have accumulated a lot of community
support. If concerns arise, they can be discussed through any of the offered communication
channels. Direct community discussions are available through a dedicated "prime-re" chat-
channel on the Brainhack Mattermost server (https://mattermost.brainhack.org/brainhack/

channels/prime-re), and more conventional mailing-list or forum style discussion is available using

the Neurostars forum (https://neurostars.org) with the tag "prime-re". The Neurostars forum is

hosted by the International Neuroinformatics Coordinating Facility (INCF) and already has a broad

user-base of neuroscience researchers. It is also possible to submit a contact form with

comments, questions, or suggestions directly to PRIME-RE's backend, and often also to

individual developers of a resource through their provided communication information. To

facilitate collaboration among its users, PRIME-RE also partners with the BrainWeb initiative

(https://brain-web.github.io).

Name	*Name of the resource*
Authors	*Names of the developers or authors*
Description	*A brief description of the resource. What challenge was it developed for? What does it do?*
Documentation	*Provide a link to more extensive (external) documentation, e.g. on the developers' website.*
Link	*Where can the resource be found or downloaded?*
Language	*What kind of programming languages are used and/or required to use this tool?*
Publication	*If there is a publication associated with this resource you can mention it here.*
Communication	*How can (potential) users contact developers?*
Restrictions	*Are there any restrictions for using this resource? Does it only work on certain systems? Are users obliged to cite something?*
Category	*What would be the most suitable place on PRIME-RE to list this resource?*

Table 1. Standardized information table for the submission of a resource for inclusion on PRIME-RE. When developers
click a 'Contribute' button they are taken to a pre-formatted form where they can provide this information. Any member
of the community with access to the website's backend can then include the new resource under the correct website
category. In addition to this table, the submission form also has checkboxes with which the submitter can confirm that
resource development occurred in accordance with all applicable directives and guidelines.

At the moment, PRIME-RE has two main components, 1) the primary website with categorized

resource listings, and 2) an evolving wiki to document the challenges and best practices of NHP

imaging. The categories that are currently listed on the PRIME-RE website are: 1) Templates and

atlases; 2) Pipelines; 3) Data sharing; and 4) Software packages. The Pipelines section is further

subdivided into tools related to structural, functional, diffusion, and general NHP neuroimaging
analysis. The results section of this paper will present an overview of some of the tools listed
under these categories and subcategories at the time of writing. The Software Packages section
contains a list of commonly used neuroimaging packages that were not specifically developed for
NHP neuroimaging. Many of the specialized tools under the Pipeline sections integrate with some
of these packages or employ some of their subfunctions. The main website also provides links to
the above-mentioned communication channels and to the wiki. The wiki contains a primer on NHP
neuroimaging that documents common challenges and potential solutions. It has its own version
controlled back-end and is currently open for contributions for anyone with a GitHub account.
While the current wiki already constitutes a team effort, the document is presented as a starting
point that could potentially evolve into a 'best practices' guide with dynamic involvement of the
broader NHP neuroimaging community.

Most of the tools that are currently listed on PRIME-RE were developed for macaque
neuroimaging, but the platform aims to be an inclusive place where resources for all non-human
primate species can be found. Several tools for marmoset neuroimaging are already listed, but
the species diversity is likely to further increase as PRIME-RE evolves.

3. Results

The first version of the PRIME-RE platform went live in November 2019. It currently describes
over 30 custom resources from contributors all over the world and houses an extensive primer on
NHP neuroimaging in the form of a wiki with references to the resources listed on PRIME-RE. It
also provides a comprehensive overview of neuroimaging tools that are not necessarily tailored
towards NHP neuroimaging (although some of these packages do offer built-in solutions to
facilitate working with non-human data). Here, we will present a synopsis of the wiki document
(https://github.com/PRIME-RE/prime-re.github.io/wiki) and an overview of some of the
specialized resources that are part of PRIME-RE at this time.

3.1. The wiki: A primer on NHP-MRI

The wiki-pages start with sections that address the various motivations for NHP neuroimaging
and some of the common challenges encountered in data collection (Farivar and Vanduffel,

2014). These sections include study preparation issues, such as obtaining ethical approval for
your study, responsible animal housing, handling, surgery, and transportation. The choice of coil
type is discussed and the consequences of using custom coils are clearly explained. Other
discussed challenges in data acquisition include non-standard body orientations, subject motion,
the use of anesthesia or contrast agents, variable fields-of-view, and a reduced signal-to-noise-
ratio (SNR) as a result of having to scan small NHP brains at higher resolution than human brains
at the same magnetic field strength.

The next section briefly addresses the topic of data organization. Standardization efforts in human
neuroimaging have yielded the Brain Imaging Data Structure (BIDS) standard, a widely adopted
file-naming and data-structure convention that facilitates data and resource sharing. Whereas a
range of tools on PRIME-RE understand data in BIDS format, the compatibility of NHP data with
the BIDS structure is not perfect, again due to some unique challenges in NHP neuroimaging that
are not present in human neuroimaging. There are, however, ongoing efforts to either expand the
BIDS format so that it can better incorporate the idiosyncrasies of NHP data, or create a derivative
NHP version that fulfills specific requirements to this research field.

The remainder of the wiki largely follows the categories that are also used in PRIME-RE's
resource listings. There are separate sections for structural, functional, and diffusion data
processing. The section on structural data processing includes data processing steps, such as
orientation correction, de-obliqueing, cropping, denoising and averaging multiple volumes or
images. It lists several options to handle bias-correction, brain extraction (skull-stripping), and
segmentation. It also links to several pipelines available from PRIME-RE that offer more or less
complete solutions to a range of these issues.

The section on functional data processing points out that this step is in fact not that different from
human neuroimaging since the same types of statistical models can be applied to different
species. One major difference that does exist is the extent to which data need to be pre-
processed. NHP data, especially data from awake NHP neuroimaging studies, tend to require a
lot more motion and distortion correction than the typical human dataset. The section on diffusion-
weighted imaging discusses the differences between *in vivo* and *post-mortem* (*ex vivo*) diffusion
MRI and their consequences for data analysis. Several caveats and solutions for tractography in
NHPs are also laid out.

The wiki ends with a section on cross-species comparison. While challenging, this is also one of
the most powerful uses of NHP neuroimaging since it has the potential to yield important

translational or evolutionary insights. The section explains the recently developed common
feature space approach (Mars et al., 2018a, 2018b), as well as comparisons based on activity
dynamics (Mantini et al., 2012), and brain matching based on homologous sulci (Auzias et al.,
2011). Several resources, suitable for the processing of NHP data, are suggested to implement
these approaches.

The PRIME-RE wiki is not meant as a definitive guide to NHP neuroimaging, but rather as a
community curated and dynamically updated collection of 'best' (or 'optimal') practices.
Improvements and additions from the community are highly encouraged.

3.2. PRIME-RE Resources

The resources that are currently listed on PRIME-RE are divided into a number of categories
based on their general purpose. Below we highlight these categories and a selection of tools from
each. Please consult the website for a complete and up-to-date overview of the available
resources (https://prime-re.github.io/resources). All resources listed on PRIME-RE, including
those described here, were developed and assessed with datasets collected in accordance with
locally approved guides and legislation concerning animal wellbeing, including the NIH Guide for
Care and Use of Laboratory Animals, the U.K. Animals (Scientific Procedures) Act, 1986,
European Directive 2010/63/EU, and the Australian Code for the Care and Use of Animals for
Scientific Purposes.

3.2.1. Templates & Atlases

Alignment of an individual's (f)MRI data to a standard template space provides several
advantages. Firstly, it provides a detailed anatomical image for evaluating and presenting
functional results or other maps. Secondly, it presents a standard orientation and coordinate
system for reporting findings, comparing results across subjects and labs, and aligning data for
group analysis. Thirdly, templates frequently include ancillary datasets such as brainmasks, tissue
segmentation masks, anatomical atlases, surfaces, morphometry, and data from other modalities
that put a variety of analysis tools at the user's disposal. These resources can eliminate time-
consuming manual processing and encourage the use of consistent and reproducible processing
streams. For example, a brainmask can be used for template-based brain extraction in the

subject's space or an atlas can be used for a region of interest (ROI) analysis in the template or
subject space.

The choice and adoption of a standard template space is becoming especially relevant now that
data sharing initiatives make it much more feasible to obtain larger sample sizes. For human
(f)MRI, the MNI152 template (Fonov et al., 2011) provides a widely adopted standard volumetric
space, while the fsaverage (Freesurfer average) (Fischl, 2012) template is a popular standard
space for surface-based analysis. For non-human primate (NHP) MRI, there are a variety of
templates. PRIME-RE currently lists several macaque and marmoset templates, as well as a
mouse lemur template. In addition to species, templates differ with regard to imaging modality, *in*
vivo versus *ex vivo* scanning, single subject versus population average, field strength, resolution,
etcetera. For the rhesus macaque, the NIMH Macaque Template (NMT) has been widely adopted
and has been incorporated in a number of the resources on PRIME-RE (Seidlitz et al., 2018). An
updated version of this *in vivo* population template (NMT v2) is presented in this special issue and
described below (Jung et al., this issue). The NMT v2 and its associated average surface (see
Section 3.2.2.5.1), together with their tissue segmentations and atlases, constitute a complete set
of complementary volumetric and surface spaces for representing macaque data.

Two novel macaque atlases are presented in this special issue and detailed below. Both are
defined on the NMT v2 and manually refined to this template. The first is an atlas of the cortex
(CHARM, Jung et al., this issue) and the second is an atlas of the subcortex, covering the
forebrain, midbrain, and hindbrain (Hartig et al., this issue). These complementary atlases are
arranged hierarchically, describing regions at various levels of granularity. Though these atlases
have been tailored to the NMT v2, they can be aligned to previous macaque templates already
used by some labs, and atlases in those templates can similarly be aligned to the NMT v2. The
RheMAP resource, which is described in the subsequent section on Structural MRI Tools (see
Section 3.2.2.2.2), stores nonlinear alignment warps between various macaque anatomical
templates to facilitate such conversions between template spaces (Klink and Sirmpilatze, 2020;
Sirmpilatze and Klink, 2020).

Two marmoset resources are also included in PRIME-RE. The Marmoset Brain Mapping Project
is a multimodal high-resolution template and atlas of the marmoset brain that includes white
matter maps based on diffusion MRI data. The most recent version is a population template based
on *in vivo* scans that includes surfaces (Liu et al., this issue). In addition, the Marmoset Brain
Connectivity Atlas (Majka et al., this issue) provides a large collection of anatomical tracer data
and histological material in an interactive platform, equipped with various analysis tools.

3.2.1.1. NIMH Macaque Template (NMT v2) and Hierarchical Atlas of the Cortex (CHARM)

A macaque template in stereotaxic coordinates with a multi-scale cortical atlas.

The National Institute of Mental Health (NIMH) Macaque Template (NMT) is an anatomical MRI

template of the macaque brain that serves as a standardized space for macaque neuroimaging

analysis (Seidlitz et al., 2018). The recently released NMT version 2 (Jung et al., this issue)

provides a complete overhaul of the NMT, including a fully-symmetric template in stereotaxic

orientation (i.e., in the Horsley-Clarke plane) (Horsley and Clarke, 1908). Coordinates in this

stereotaxic space are measured from ear bar zero (i.e., the intersection of the midsagittal plane

and a line through the interaural meatus). The adoption of stereotaxic orientation and coordinates

will assist users with surgical planning and facilitates reporting of coordinates commensurate with

those used with other techniques (e.g. electrophysiology, intracerebral injection).

The NMT was created by iteratively registering T1-weighted scans of 31 adult rhesus macaque

brains to a working template, averaging the nonlinearly registered scans, and then applying the

inverse transformations to bring the working template closer to the group average (Seidlitz et al.,

2018). The symmetric NMT was generated through the same process except that each subject's

anatomical was input twice, once in its true orientation and once mirrored about the midline.

Modifications to the scan averaging and postprocessing have improved template contrast and

spatial resolution. Brain masks, segmentations, and various other tissue masks are provided

(Figure 1A-C). The availability of symmetric and asymmetric variants of the NMT v2 allows users

to choose the version that best suits their analysis. Other template variants include an expanded

full head field-of-view and a lower resolution version for faster processing (0.5 mm isotropic,

down-sampled from 0.25 mm isotropic). Surfaces for NMT v2, generated using the new CIVET-

Macaque platform (Lepage et al., this issue), are provided for easy data visualization. For surface-

based group analysis, the NMT average surface, which comes with anatomical labels from the

D99 and CHARM atlases, can serve as a surface-based registration target for representing

cortical surfaces in a common framework regardless of the processing pipeline.

Atlases are an important aspect of group and ROI-based analyses. The NMT v2 package comes

with multiple anatomical atlases that have been manually tailored to the template's morphology.

These atlases include the D99 atlas (Reveley et al., 2017) and the new Cortical Hierarchy Atlas

of the Rhesus Macaque (CHARM; Jung et al., this issue). The latter is a novel anatomical

parcellation of the macaque cerebral cortex, where the cortical sheet is subdivided into six-levels

of increasingly fine-grained parcellation (Figure 1D-F). The broadest level consists of the four

cortical lobes and the finest level is based on the D99 atlas, with modifications that make the

regions more robust when applied to low resolution (e.g. fMRI) data. Different scales of CHARM

can be combined so that, for example, a tracer injection or the seed region for a resting state

analysis can be described using a fine scale, while the region's anatomical or functional

connectivity can be succinctly described on a broader scale. This way, whole brain data can be

characterized on a spatial scale that is most suitable to a study's findings. Users can also select

a CHARM level *a priori* based on how many regions it contains, and thus control the required

degree of multiple comparison correction for their analysis.

While the NMT v2 works with any neuroimaging platform that accepts NifTI/GifTI format, the

template has been designed to have additional functionality within the AFNI ecosystem (Cox,

1996). Enhancements include support for the *NMT2* standardized space, recognition of the NMT

v2 in the @animal_warper alignment pipeline (see section 3.2.2.4.2) and the functional

processing pipeline generator afni_proc.py (see section 3.2.3.1), and downloadable demos

showing how AFNI can perform structural and functional analyses (task-based or resting state)

using the NMT v2. See the accompanying article by Jung et al. (Jung et al., this issue) for further

information.

3.2.1.2. Subcortical Atlas of the Rhesus Macaque (SARM)

A complete MRI atlas of the macaque subcortex suited for neuroimaging.

The Subcortical Atlas of the Rhesus Macaque (SARM) is an anatomical parcellation of the entire

subcortex tailored for magnetic resonance imaging (MRI) (Hartig et al., this issue). The regions-

of-interest (ROIs) are hierarchically organized, with grouping levels suited for both fine structural

and spatially broader functional analyses. SARM aims to facilitate the identification, localization,

and study of neural interactions involving subcortical regions of the brain.

A high-resolution structural MRI of an *ex vivo* rhesus monkey brain was segmented into 180

anatomical ROIs by matching distinctly contrasted structures with their histological counterparts.

ROIs followed the recently updated nomenclature and delineations of the Rhesus Monkey Brain

in Stereotaxic Coordinates atlas (Paxinos et al., in preparation). The *ex vivo* MRI was nonlinearly

registered to the symmetric population-level template of the rhesus macaque NMT v2 (see section

3.2.1.1 and (Jung et al., this issue). The SARM was warped using Advanced Normalization Tools

(ANTs; (Avants et al., 2008) and refined using AFNI (Cox, 1996). ROIs were delimited using the

tissue segmentation masks for the NMT v2, smoothed by computing the mode over neighboring

voxels, and individually refined by hand to match the average structural template. The SARM is

organized into 6 hierarchical levels. The finest level presents each individual ROI (Figure 1G),

whereas the broadest level corresponds to developmental subdivisions (i.e., tel-, di-, mes-, met-,

and myel-encephalon). The SARM was validated in 3 monkeys with a functional MRI (fMRI)

paradigm known to activate the lateral geniculate nucleus (LGN) (Logothetis et al., 1999).

The SARM offers neuroimaging researchers a complete subcortical segmentation of the rhesus

macaque brain. The atlas can be used for a range of structural and functional analyses and has

been specifically tailored to work with the CHARM and NMT v2 (Jung et al., this issue). The SARM

is also available to download via Zenodo, and has conveniently been incorporated with the atlases

available in AFNI. Additional information is available in the accompanying article (Hartig et al.,

this issue).

Figure 1. Macaque Templates. A) The NIMH Macaque Template v2 (NMT v2) comes in symmetric (shown here) and asymmetric variants, each with **B**) a manually refined brain mask, and **C**) 5-class tissue segmentations. **D-F**) Levels 2, 4, and 6 of the Cortical Hierarchy Atlas of the Rhesus Macaque (CHARM). **G**) The SARM in symmetric NMT v2 stereotaxic space. From left-to-right a representative sagittal, coronal and horizontal section is depicted with volumetric images (above) and corresponding surface views (below). Coordinates listed are in relation to the x(L), y(A), and z(S) dimensions.

3.2.1.3. Marmoset Brain Mapping Project (MBM)

MRI-based marmoset brain atlases and tools for neuroimaging and connectome studies

The Marmoset Brain Mapping Project (www.marmosetbrainmapping.org) includes three atlases

and templates:

1) Version 1 focuses on cortical parcellations (Liu et al., 2018). A 3D digital gray matter atlas was

constructed from high-resolution (150 μm isotropic) *ex vivo* MRI images, including magnetization

transfer ratio (a T1-like contrast), T2w images, and multi-shell diffusion MRI (dMRI). Based on the

multi-modal MRI contrasts, 54 cortical areas and 16 subcortical regions were manually delineated

on one hemisphere of the brain using a data-driven approach that was developed to minimize

manual drawing errors. The 54 cortical areas were then merged into 13 larger cortical regions

according to their locations to yield a coarse version of the atlas, and also subdivided into 106

regions using a dMRI connectivity-based parcellation method. A Paxinos-style cortical atlas

(Majka et al., 2016) was fused and refined into the high-resolution MRI template to provide

interoperability to other marmoset databases. The atlas set provides a readily usable multi-modal

template space with multi-level anatomical labels that can facilitate various neuroimaging studies

of marmosets.

2) Version 2 focuses on fine-detailed white matter pathways (Liu et al., 2020). In this version, *ex-*

vivo MRI data of the marmoset brain was collected with the highest spatial resolution available to

date, including 80 μm and 64 μm multi-shell dMRI, 80 μm MTR, and 50 μm T2w and T2*w images.

The data allowed building a fine-grained 3D white matter atlas, which depicts many fiber pathways

that were either omitted or incorrectly described in previous MRI datasets or atlases of the primate

brain. By combining dMRI tractography and neuronal tracing data (Majka et al., 2020), a detailed

fiber pathway mapping of cortical connections is provided. The white matter atlas, fiber pathways

maps and dMRI data, including both raw and processed data, are publicly available on the

project's website (Figure 2A,B).

3) Version 3 focuses on population standard templates and cortical surfaces (Liu et al., this issue).

While versions 1 and 2 were based on a few *ex vivo* brain samples, and lacked essential

functionalities for *in vivo* studies of large animal cohorts, version 3 is based on *in vivo* population

data. Standard templates are derived from multi-modal data of 27 marmosets, including multiple

types of T1w and T2w contrast images, DTI contrasts, and large field-of-view MRI and CT images.

Multi-atlas labeling of anatomical structures was performed on the new templates and highly

accurate tissue-type segmentation maps were constructed to facilitate volumetric studies. Fully

featured brain surfaces and cortical flat maps facilitate 3D visualization and surface-based

analyses with most surface analyzing tools. The population-based template will significantly aid a
wide range of neuroimaging and connectome studies that involve across-subject analysis.

3.2.1.4. Marmoset Brain Connectivity Atlas
Marmoset anatomical tracer data and connectivity analysis tools integrated with an atlas and
histological material.

The Marmoset Brain Connectivity Atlas (Majka et al., 2020) allows exploration of a growing
collection of data from retrograde tracer injections in the marmoset neocortex. At present, it
includes data from over 140 experiments covering almost 50% of currently recognized areas of
marmoset cortex, encompassing subdivisions of prefrontal, premotor, superior temporal, parietal,
retrosplenial and occipital complexes. Data from different animals are presented against high-
resolution images of the underlying histology, and registered to a template based on the Paxinos
et al. (Paxinos et al., 2012) stereotaxic atlas using an algorithm guided by an expert delineation
of histological borders. The portal (http://www.marmosetbrain.org) implements best practices
in terms of sharing the connectivity data. The resource provides access to primary experimental
results, as well as connectivity patterns that are quantified according to the currently accepted
parcellation of the marmoset cortex. To enable graph-based network analyses, the portal
incorporates   tools   for   data   exploration   relative   to   cytoarchitectural   areas
(http://analysis.marmosetbrain.org), including statistical properties such as the fraction of labeled
neurons, the percentage of supragranular neurons, and geodesic distances between areas
across the white matter. Importantly, it also provides the cellular connectivity data in a purely
spatial (parcellation-free) format, including the stereotaxic coordinates of ~2 million neurons
labeled by the tracer injections. These results can be downloaded in 3D volume format in
the template space (Majka et al., this issue), so they can be compared with MRI-based topologies.
The   portal   also   makes   data   available   in   a machine-mineable   way
(http://analytics.marmosetbrain.org/wiki/api) to facilitate large-scale models and simulations.

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Figure 2. Marmoset atlases. A-B) Example visualizations available on the website of the Marmoset Brain Mapping Project. **A**) 3D-viewer that demonstrates the connectivity profile of an area selected by clicking (here V4). **B**) Comparison with the weighted and directed connectivity graph based on the results of monosynaptic retrograde fluorescent tracer injections from the Marmoset Brain Connectivity Atlas (https://analytics.marmosetbrain.org/ graph.html). The graph view highlights the spatial relations between connected areas. Clicking a node reveals further information, including an average connectivity profile, interactive visualizations of the data for each injection, and metadata. **C-D)** Marmoset Connectivity Atlas**. C**) Locations of 143 tracer injections registered to a stereotaxic template illustrated in a 2-dimensional flat-map of the marmoset cortex (C). **D**) The main data layers of the histology-based average morphology of the adult marmoset brain showcasing the interoperability of this dataset with neuroimaging research (T2* MR signal).

Apart from the tracer-based connectivity data (Figure 2C), the portal hosts a collection of other

unique datasets typically inaccessible in non-invasive imaging, such as high-resolution images of

cytoarchitectural characteristics for each of the marmoset cortical areas, stained with a neuron-

specific antibody (Atapour et al., 2019) (http://www.marmosetbrain.org/cell_density). Moreover, a

unique histology-based average morphology of the adult marmoset brain provides the basis for

probabilistic registration of digital datasets to cytoarchitectural areas (Majka et al. this issue;

http://www.marmosetbrain.org/nencki_monash_template). Spatial transformations to other

marmoset brain templates are included to enable prompt integration with magnetic resonance

imaging (MRI) and tracer-based connectivity studies (Figure 2D).

3.2.2. Structural MRI Tools

3.2.2.1. Overview

Pre-processing of structural and functional MRI involves alignment of volumetric data across

scanning sessions or with a species-specific anatomical template/atlas in a standardized space;

segmentation (i.e., differentiation) of the brain from skull, muscle, and other tissues (a.k.a. "skull-

stripping"); segmentation of different tissue classes within the brain (e.g. gray and white matter).

Additionally, volumetric cortical data are sometimes represented on a flat map or surface map by

creating individualized surfaces or projecting data to a common surface. Here we briefly describe

some PRIME-RE resources for handling volumetric data. Typically, anatomical scans are

analyzed in detail and the results are then also applied to any functional data collected in the

same scanning session.

Some of the structural tools described perform a single pre-processing step, allowing them to be

flexibly used with other tools. Examples of dedicated alignment tools are Reorient, which does

rigid body alignment and cropping the borders of a scan, and RheMAP, which provides the non-

linear warps between various macaque templates. Dedicated segmentation tools include the

interactive Thresholdmann and the machine-learning based UNet, both of which generate binary

brain masks, and BrainBox, which is well suited for the collaborative development of binary or

multi-valued masks.

Other resources perform multiple steps within a single software environment or by calling on

various other tools. For example, Macapype uses several tools interchangeably to perform

alignment, normalization, and segmentation operations. Similarly, AFNI's @animal_warper

computes and applies a nonlinear alignment between a subject and a template and can warp the

template's masks to create a brain mask, tissue segmentation, and atlas parcellation for the

individual. For other tools, alignment and segmentation are precursors to additional steps such

as surface generation (e.g., CIVET-Macaque, PREEMACS) or functional analysis (e.g., C-PAC).

PRIME-RE offers four tools for generating surfaces from volumetric monkey data. The NHP-

Freesurfer, PREEMACS, and Precon_all tools all utilize the Freesurfer software package in

conjunction with several other tools. In contrast, CIVET-macaque is a novel adaptation of CIVET

for use with monkey data. It can be used to characterize surface morphology such as cortical

thickness (Lepage et al., this issue). All four programs require a T1-weighted anatomical scan.

Both CIVET-macaque and PREEMACS can take an optional T2-weighted scan as well, and both

provide quality control tools.

3.2.2.2. Alignment and registration tools

Having properly oriented MRI datasets is important for many neuroimaging workflows and often

crucial for further segmentation or registration across functional, anatomical and template images.

For non-human scans (both *in vivo* and *ex vivo*), orientations and field-of-views can vary

tremendously, which means that a correction through reorientation and cropping is often required

before any standard tools can be used. Group analysis of (f)MRI data is commonly performed in

a standard template space to which individual data are registered. Here we describe tools for

aligning datasets to a template or to each other as well as precalculated registrations between

templates (RheMAP). These tools include Reorient, which aids in visual rigid body alignment,

and nonlinear alignment tools such as macapype and @animal_warper (see Section 3.2.2.4).

3.2.2.2.1. Reorient

An intuitive web tool for reorienting and cropping MRI data.

Reorient (https://neuroanatomy.github.io/reorient) is an open source web application for the

intuitive manual alignment and cropping of MRI NifTI volumes. The MRI scan is dragged onto a

web interface and visualized in an interactive stereotaxic viewer. Users can then translate and

rotate the brain by simply dragging inside the three view planes. An adjustable selection box

determines the cropping of an image. Resulting affine matrices, selection boxes, as well as the

reoriented and cropped volume can be saved. The affine matrix and selection box can then be

used in scripted workflows to make these steps reproducible. Existing rotation matrices can also

be loaded or appended in the web interface. Reorient complements existing tools by providing an

intuitive approach for manual image reorientation and all components for a fully reproducible

workflow. It has been used extensively to reorient scans from many different vertebrate species,

including 60 different primate species.

3.2.2.2.2. RheMAP

Precomputed nonlinear warps between common rhesus macaque brain templates.

The generation of accurate nonlinear registrations between different brain images is a time-

consuming and computationally expensive operation. The RheMAP project was created to

generate a set of pre-computed nonlinear registration warps that allow the direct remapping of

(f)MRI data across different common macaque template brains. The non-linear warps were

generated using ANTs (Avants et al., 2008) and the Python code that was used in RheMAP to

compute the warps is available on GitHub (https://github.com/PRIME-RE/RheMAP) together with

documentation and example code that explains how to use the warps to remap data between

template spaces or register a single anatomical scan to one or more template spaces (Klink and

Sirmpilatze, 2020). The dataset of computed warps is freely available for download from Zenodo

(Sirmpilatze and Klink, 2020). Registration quality can be visually assessed with the help of

images that are distributed with the code and the dataset. RheMAP already includes a

comprehensive set of templates — NMT (Jung et al., this issue; Seidlitz et al., 2018), D99

(Reveley et al., 2017), INIA19 (Rohlfing et al., 2012), MNI macaque (Frey et al., 2011) and

Yerkes19 (Donahue et al., 2016) — but the provided code allows for easy inclusion of additional

template brains as well. Moreover, the general warp computation workflow can be easily adapted

for other animal species, since the underlying ANTs registration functions do not rely on prior

knowledge about brain size and shape.

3.2.2.3. Segmentation tools

Obtaining appropriate tissue masks (brain vs. surrounding tissue, or different tissue types within

the brain itself) can be particularly difficult in non-human brain imaging, as standard automatic

segmentation tools struggle with surrounding muscle tissue, the skull, and the strong intensity

gradients that are often present. PRIME-RE lists several tools that can facilitate segmentation of
NHP brain scans.

3.2.2.3.1. Thresholdmann
A web tool for interactively creating adaptive thresholds to segment NifTI images.

A simple intensity threshold can often provide a good initial guess for tissue segmentation, but in
the presence of strong intensity gradients, a threshold that works well for one brain region can
easily fail elsewhere in the same brain image. Thresholdmann (https://neuroanatomy.github.io/
thresholdmann) is an open source web tool for the interactive application of space-varying
thresholds to NifTI volumes. It does not require any software downloads or installation and all
processing is done on the user's computer. NifTI volumes are dragged onto a web interface where
they become available for visual exploration in a stereotaxic viewer (Figure 3A). A space-varying
threshold is then created by setting control points, each with their own local threshold value. The
viewer is initialized with one control point at the center of the brain. The addition of further control
points produces a space-varying threshold obtained through radial basis function interpolation.
Each local threshold can be adjusted in real time using sliders. Finally, the thresholded mask, the
space varying threshold and the list of control points can be saved for later use in scripted
workflows. Thresholdmann complements a variety of existing brain segmentation tools with an
easy interface to manually control the segmentation on a local scale. The resulting masks can
serve as starting points for more detailed manual editing using tools such as BrainBox
(https://brainbox.pasteur.fr) or ITK Snap (http://www.itksnap.org). The interactive approach is
especially valuable for non-human brain imaging data, where it has been successfully used to
create initial brain masks for a variety of vertebrate brains – including many NHP datasets (Heuer
et al., 2019) – as well as developmental data.

Figure 3. Segmentation tools. **A**) Thresholdmann interface (left). Control points (blue dots) are added by clicking at the desired position in the viewer. This adds a slider to the right, which can be used to locally adapt the threshold. If, based on the original control points, some part of the brain is not correctly segmented (right, top; ventral brain area excluded), additional points can be added to apply corrections (right, bottom). **B**) Brainbox interface. MRI page (left): Each MRI has its own page, centralizing the information provided by all the projects including it. Project settings (right): Users can collect datasets into projects, add collaborators, manage access rights, and add annotation layers. **C**) UNet brain extraction accuracy and example results. Local accuracy at each voxel estimated by the regional Dice coefficient (top). Three example results from PRIME-DE (bottom panels).

3.2.2.3.2. BrainBox

A web application for real time, collaborative visualization, annotation & segmentation

Automatic brain segmentations often need to be manually adjusted and in some cases a complete

manual segmentation is required. Manual segmentation can however be difficult, time consuming,

and it is often performed by researchers working in isolation, even for shared public data.

BrainBox (https://brainbox.pasteur.fr) is an open source tool for the visualization, collaborative

curation and analysis of neuroimaging data. BrainBox makes it possible for several researchers

to simultaneously work on the same dataset in a shared virtual working space. BrainBox can be

used to visualize and provide a layer of human annotation to any dataset available on the Web,

for example, to data stored in Zenodo, FigShare, Google Drive, Dropbox, Amazon S3, GitHub, or

the Open Science Framework. After providing the URL of a dataset, BrainBox presents an

interactive viewer, and a series of editing tools, e.g. for segmenting brain regions, erasing, or

building 3-D models (Figure 3B). Several datasets can be combined into "projects" and project

creators can invite collaborators. Access to the data can range from completely private to

completely open projects. Finally, BrainBox implements a RESTful API (Application Program

Interface) which allows programmatic access to all its data. For example, annotations and

segmentations can be queried by a local python script, or even a shared notebook running on

Google Colab.

BrainBox adds a layer of collaborative curation and analysis to shared neuroimaging datasets

using only a web browser, allowing users to incrementally improve each other's work. This

increases scientific efficiency, improves public data quality, and reduces redundant effort. All

PRIME-DE datasets (Milham et al., 2018) are already indexed in BrainBox projects, and ready for

collaboration.

3.2.2.3.3. UNet NHP brain extraction tool

A convolutional neural network model for skull-stripping of NHP images.

The UNet brain extraction tool provides a flexible brain labeling solution to facilitate the

preprocessing of NHP neuroimaging data, particularly for multi-site datasets with different scan

acquisition, quality, and surgical situations (e.g., with head-holder implants) (Figure 3C). The UNet

model was initially trained on a large sample of human neuroimaging data and transferred to the

NHP with additional macaque training samples from the PRIME-DE data repository (Milham et

al., 2018). In order to run the tool with the default model, a user only needs to specify the input

T1-weighted image. The full process requires ~20s on a GPU (NVIDIA GTX 1070TI, 700MB

graphics card memory) and ~2-15 min on a CPU, which means it can easily be run on a personal

computer. The current default model has been successfully applied to 136 macaque monkey

scans from 19 sites on PRIME-DE with good performance (https://github.com/

HumanBrainED/NHP-BrainExtraction). The tool also provides a module for the user to upgrade

the UNet model for a specific dataset (e.g., raw T1w from a highfield scan, MP2RAGE, etc.).

Unlike the traditional neuroimaging tools, no strong imaging background is required for the user

to adjust processing parameters for a specific dataset. Instead, the tool only requires a small

macaque image-set training sample (n=1-2) to upgrade the model and improve performance

accuracy for that specific dataset.

3.2.2.4. Alignment and Segmentation Pipelines

In addition to tools that specialize in a single step of structural analysis, there are also several

pipelines listed on PRIME-RE that can take care of multiple structural analysis steps.

3.2.2.4.1. Macapype

An open multi-software framework for non-human primate anatomical MRI processing

Macapype (https://github.com/Macatools/macapype) provides an open-source framework to

create customized NHP-specific MRI data processing pipelines based on Nipype (Gorgolewski et

al., 2011). Nipype is a widely-adopted Python framework for human MRI data processing, which

provides wrappers of various commands and functions from well-known neuroimaging software

(e.g., AFNI, FSL, SPM12, ANTs). In Macapype, custom scripts specific to NHP data processing

are also wrapped. These include a brain extraction tool (AtlasBREX; Lohmeier et al., 2019) and

a script for computing registrations between a subject brain and the NMT macaque template

(NMT_subject_align.csh; Seidlitz et al., 2018). Users can thus flexibly construct customized

pipelines by putting together various processing modules (and parameters) that are optimal for

their dataset.

Macapype consists of several configurable modules for: 1) Data preparation steps, such as image

reorientation, deoblique-ing, cropping, and the registration and averaging of multiple images; 2)

Anatomical preprocessing steps like bias-correction with ANTs N4BiasCorrection; Tustison et al.,

2010) and/or T1w x T2w bias field correction (Rilling et al., 2012), denoising using the adaptive

non local means filter (Manjón et al., 2010), brain extraction (e.g. with AtlasBREX), and brain

segmentation (e.g. using AntsAtroposN4 or SPM Old Segment).

Two examples of modular anatomical pipelines are already implemented in the distributed version

of Macapype. They are customized for the preprocessing, brain extraction and segmentation of

macaque anatomical data, and have performed robust segmentations on different datasets. The

first pipeline creates a high quality segmentation in native space for surface reconstruction.

Briefly, the pipeline takes the T1w and T2w images as inputs, and first applies cropping, bias-

correction (via T1w x T2w and N4 intensity bias correction), and denoising (adaptive non-local

means filtering) to improve image quality. Next, brain extraction is performed using AtlasBREX.

For segmentation, transformations between the subject skull-stripped image and the NMT

macaque template are first computed using the NMT_subject_align.csh script (Seidlitz et al.,

2018), and then applied to register the NMT tissue segmentations to the subject image. Finally,

segmentation is performed using AntsAtroposN4.sh to segment the subject image in native

space, with the template segmentation as priors. The second pipeline reaches the same goal with

different packages. This pipeline provides an iterative sequence for normalization (source to

template space) of T1w and T2w, and provides segmentation with both SPM12 (OldSegment)

and FSL FAST.

A docker file is included in the package to allow users to get a fully embedded version of the

pipelines working on any computer without previous installation of MRI processing software. Both

pipelines are compatible with BIDS (Gorgolewski et al., 2016) formatted datasets. The two

pipelines have been demonstrated to achieve robust skull-stripping and segmentation on

anatomical data from different primate species: Pipeline 1 was tested on both macaque (Milham

et al., 2018) and marmoset datasets, while Pipeline 2 was tested on both human and macaque

datasets. Documentation and an extensive description of the segmentation results from the

macaque and marmoset brain extraction and segmentation are available on Github

(https://macatools.github.io/macapype).

3.2.2.4.2. @animal_warper

AFNI program that aligns structural data to a template.

@animal_warper is a bidirectional alignment program made for animal neuroimaging. While
human neuroimaging has typically required a standard template, many animal researchers may
prefer to keep their data in the native acquisition space and move atlas regions and tissue
segmentations into the native space of the subject. Alternatively, data can be transformed to a
standard template space to allow voxelwise group analysis and have the advantage of a
standardized coordinate reporting system.

The @animal_warper program proceeds in a series of alignment steps. First, the center of the
input dataset is moved to match the center of the template. Then, an affine alignment uses a 12-
parameter transformation to match translation, rotation, shear and scale. Finally, a nonlinear warp
is computed to align structural details to the template. The inverse warps and inverse affine
transformations are computed and applied for the reverse direction of template to native space.
"Follower" datasets, like ROIs drawn in the native space, can also be transformed into a target
space. Datasets and ROIs typically follow from native to template space; templates, atlases and
segmentations follow from template to native space.

The widely varying kinds of data used in animal imaging require different cost functions for
alignment to flexibly deal with the voxel resolution and with the kinds of tissue contrast in each
imaging modality. Several features of @animal_warper address some of the idiosyncrasies of
animal alignment. First, the user can specify a "feature size" that controls blurring and cost
functions. For many macaque MRI datasets, a value of 0.5 mm, which roughly matches the
apparent voxel resolution, is a useful feature size. Other species, such as mouse, marmoset, and
rat, may require a feature size that accommodates the finer voxel resolution typically used with
these animals. Animal brain sizes can vary dramatically from each other and from any particular
template, so a "supersize" option allows for up to a 50% difference in size. The program applies
a kind of spatial regularization for ROI and atlas regions that goes beyond the typical nearest
neighbor interpolation; a modal smoothing is applied to all transformed ROIs. This kind of
smoothing assigns to each voxel the most common voxel value in a user-specified radius around
it.

@animal_warper is developed within the larger AFNI software ecosystem. The computed
transformations serve as input to a general fMRI processing pipeline implemented with
afni_proc.py (see section 3.2.3.1). Output datasets in native space are viewable in the AFNI GUI

and marked with the appropriate space. Data that have been transformed to a standard space

have all the functionality of the "whereami" atlas command line and GUI. While NifTI datasets are

marked as being in a scanner, Talairach, MNI or other space, @animal_warper adds an

identifying space to the data. Atlas regions are generated in the native space both as volumes

(Figure 4A) and as individual surfaces in GifTI format. Every region can be shown by itself or with

any or all other atlas regions along with a simple surface rendition of the template in the native

space of the subject. Quality control reports are generated as simple png images.

The program has been tested with a wide variety of the macaque data available on the PRIME-

DE website (Milham et al., 2018). The AFNI website hosts the D99, NMT v1 (Seidlitz et al., 2018),

the stereotaxic NMT v2 templates as well as the D99 atlas and the CHARM (see section 3.2.1.1

and Jung et al., this issue) and SARM (see section 3.2.1.2 and Hartig et al., this issue) hierarchical

atlases.

Figure 4. Anatomical MRI pipelines. **A**) D99 atlas transformed to native space of a macaque subject with @animal_warper. **B**) CIVET-macaque results for the D99 subject. Top row (left to right): anatomical scan, brain mask, tissue classification (CSF in dark blue, cortical GM in green, portions of non-cortical GM in white, WM and other non-cortical GM in yellow), and cortical surfaces overlaid on the anatomical scan (WM surface in red, pial surface in green). Bottom row (left to right): white and pial surfaces; cortical thickness (1.0 mm in light blue to 3.5 mm in red) and D99 surface parcellation viewed on the pial surface. **C**) PREEMACS results. Top row, brainmask created by a Deep Learning convolutional neural network model (left) and volumetric tissue segmentation (right). Middle row, white matter and pial surface estimation (left) and white matter surface (right). Bottom row left, surface registration to the PREEMACS Rhesus parameterization template to obtain vertex correspondence between subjects. Bottom row (right), individual cortical thickness estimation. The resulting surfaces can be analyzed in the geometric space of the PREEMACS average surface.

3.2.2.5. Surface generation pipelines

Surface visualizations offer a rich view of cortical fMRI activity. The generation of surface
visualizations for non-human brains can however be rather involved. The pipelines below were
specifically designed to facilitate this process.

3.2.2.5.1. CIVET-macaque
A pipeline for generating surfaces and cortical thickness maps from anatomical MRIs

The CIVET pipeline for automated reconstruction of cortical surfaces from *in vivo* human MRI has
been extended for processing macaque brains. CIVET-macaque requires only a T1-weighted MRI
image to generate high resolution cortical surfaces, capable of intersubject surface-based
coregistration with per-vertex correspondence between gray and white matter surfaces.
Preprocessing and surface reconstruction were customized for macaques to address species
related issues such as variations in head size and brain morphology (Lepage et al., this issue).

The pipeline features registration to the NMT v1.2 population template (Seidlitz et al., 2018), brain-
masking, tissue classification, cortical surface reconstruction, and calculation of cortical
morphometrics (thickness, surface area, and curvature). Surface-based registration to the NMT
average surface allows for group analysis and regional analysis based on either the D99 or
CHARM anatomical parcellations (Jung et al., this issue). Figure 4B illustrates a typical CIVET
run with the preprocessing stages (top row: registration, brain-masking, tissue classification) and
the generation of the cortical surfaces (bottom row). The preprocessing stages, which can be
generated without cortical surfaces, can serve as the foundation for the analysis of other *in vivo*
modalities (fMRI, qMRI, PET, EEG, MEG, sEEG, etc.) as well as *post-mortem* histological and
genetic data. Images of the outputs from various viewpoints are provided for quality assessment.

The full pipeline was successfully run on the *in vivo* scans from the 31 subjects that were used to
make the NMT and on the *ex vivo* scan of the D99 subject. The preprocessing stages of the
pipeline were run on 95 PRIME-DE subjects from 15 sites that provided scans in the sphinx
position with complete sex and age information (Milham et al., 2018). Efforts have also begun to
further extend CIVET to the marmoset and, using archived data, the chimpanzee. The pipeline
thus has the potential to make it possible to study surface-based morphometry across a range of
primate species.

3.2.2.5.2. NHP-Freesurfer

Creating Freesurfer surfaces of macaque brain scans

Freesurfer (Fischl, 2012) is one of the most widely used software packages for the creation of

surfaces from volumetric MRI data in humans. While it can also be used to process non-human

brains, its convenient recon-all pipeline that automates most of the processing steps cannot be

readily applied to macaque brains due to its differences in size and contrast. NHP-Freesurfer

offers a pipeline that does work for macaque brains. It is based on Freesurfer tools and a number

of additional workarounds. All these steps are explained and pre-coded in annotated Jupyter

Notebooks based on the bash-kernel that allow the user to run the code directly from the

notebook. Unlike recon-all, which is mostly automated, creating high quality surfaces of macaque

brains requires some manual adjustments that can be difficult to figure out for novice users. NHP-

Freesurfer provides a full guide starting with one or more T1-weighted anatomical scans and

ending with surfaces and flatmaps. To facilitate this process, NHP-Freesurfer uses freely available

tools from the NMT template brain (Seidlitz et al., 2018), ANTs (Avants et al., 2008), and AFNI

(Cox, 1996). In addition to the core Freesurfer functionality, NHP-Freesurfer also explains how to

project volumetric statistical results to the Freesurfer surfaces with Freesurfer tools, but this

workflow has been superseded by the NHP-pycortex package (see 3.2.3.5) that uses an adapted

version of PyCortex (Gao et al., 2015) to obtain similar results with a much more flexible approach

based on the Python programming language.

3.2.2.5.3. Precon_all

An automated Freesurfer and HCP compliant surface pipeline for preclinical animal models

Precon_all is a surface reconstruction pipeline inspired by Freesurfer's recon-all and adapted for

use with non-human brains (Fischl, 2012). The great success of Freesrufer's recon-all is in part

due to the ease of use for the end user as well as the automation of surface generation from

volumetric data. Precon_all aims to export this ease of use and automation to the animal imaging

community. In order to achieve the flexibility that makes the precon_all pipeline work with a large

range of species, a set of 5 easily drawn masks are required as input. Guidelines for drawing

these masks are provided in the precon_all documentation. Once they are made, they can be

used for an individual subject or added to the precon_all standards directory and used to automate

surface reconstruction for a new species. Currently, precon_all comes preloaded with standards

for the NMT v1.2 (Seidlitz et al., 2018) and a pig template.

Precon_all makes use of commonly used software packages, including FSL, ANTs, Freesurfer,

and Connectome Workbench (Avants et al., 2008; Fischl, 2012; Glasser et al., 2013; Jenkinson

et al., 2002). Written as a set of shell scripts, precon_all is called from the command line and, like

Freesurfer's recon-all, it can be run in stages for manual editing and correction of surfaces. These

stages include brain extraction, segmentation via FAST or ANTs, cutting and filling, surface

generation, and optional surface down-sampling. Outputs are contained within a subject directory

similar to that of recon-all, allowing Freesurfer users to easily transition from human to animal

imaging. Final outputs include Freesurfer and Human Connectome Project compatible cortical

surface models, as well as all required NifTI images and transforms created in the surface

reconstruction process. A set of scripts is provided to easily generate group average surfaces and

registration templates which can then be used to create a custom FSaverage for individual

species.

3.2.2.5.4. PREEMACS

Brain surfaces and cortical thickness from raw structural data

PREEMACS (pipeline for PREprocessing and Extraction of the MACaque brain Surface) is a set

of common tools, customized for Rhesus monkey brain surface extraction and cortical thickness

analysis. Some of the advantages of using PREEMACS are: 1) it avoids manual correction, 2)

the pipeline was developed in the standard MNI monkey space, 3) it provides visual reports in

each module as quality control, and 4) its highly accurate surface extraction with vertex

correspondence between subjects. PREEMACS has a modular design, with three modules

running independently. These modules perform the canonical workflow for MRI preprocessing

(Alfaro-Almagro et al., 2018; Esteban et al., 2019; Glasser et al., 2013) using different previously-

available functions from FSL (Jenkinson et al., 2002), ANTs (Avants et al., 2008), MRtrix (Tournier

et al., 2012), MRIqc (Esteban et al., 2017), DeepBrain (https://github.com/ iitzco/deepbrain), and

FreeSurfer (Fischl, 2012). Inputs to the pipeline should be one (or preferably more) T1- and T2-

weighted volumes per animal from the same session. Module 1 prepares the raw volumes for

initial preprocessing in six steps: volume orientation, conformation, image cropping, intensity non-

uniformity correction, image averaging, resampling and skull-stripping. Module 2 is the quality

control module. It was adapted from the MRI Quality Control tool (MRIqc) (Esteban et al., 2017)

for humans to obtain image quality metrics and provide a visual report from the results of Module

1. Module 2 uses these quality control metrics to provide a classification of image quality that

allows PREEMACS to estimate whether the input will yield an appropriate surface reconstruction.

Finally, Module 3 obtains cortical thickness measures based on the brain surfaces using an NHP-

customized version of Freesurfer v6. To evaluate the generalizability of this procedure,

PREEMACS was tested on two different NHP datasets: PRIME-DE (Milham et al., 2018) (57

subjects) and INB-UNAM (5 subjects). Results (Figure 4C) showed accurate and robust automatic

brain surface extraction for both datasets. PREEMACS thus offers a robust and efficient pipeline

for the automatic NHP-MRI surface analysis.

3.2.3. Functional MRI Tools

Functional MRI (fMRI) uses time-series data in an attempt to model the fluctuations in the imaging

signal with some type of event structure. These events can be external stimuli (i.e., task-based

fMRI), or the time series of activity in another brain area (i.e., functional connectivity).

Conceptually, the analysis of fMRI data is not radically different across species, but the checks

required at each analysis step do differ. For example, animal scanner setups may produce

different kinds of B0 inhomogeneity and distortions, due to customized coils or the use of other

specialized equipment during acquisition. Both the potential use of anesthesia and contrast

agents can furthermore impact processing choices such as hemodynamic response modeling

and noise filtering. Importantly, pre-processing steps like motion correction and alignment to a

high resolution anatomical scan or template brain often require different options and parameters

compared to what one would choose for human data. For awake animals, body motion can cause

distortions in the magnetic field resulting in slice-specific nonlinear deformations that can be

especially difficult to correct. Proper head-fixation and extensive training will keep such problems

to a minimum, but EPI distortion and brightness artifacts can still occur, requiring post-acquisition

amelioration. The resources below contain several NHP specific solutions to deal with pre-

processing and alignment correctly.

3.2.3.1. afni_proc.py

AFNI program that generates a complete fMRI processing script from a list of data files and the

desired processing steps and options.

AFNI's afni_proc.py program (Cox, 1996) allows a researcher to create a complete fMRI

processing pipeline for individual subjects, from raw inputs, through alignment to standard space,

and regression modeling. To use it, one specifies input datasets (e.g., EPIs, anatomicals, tissue
masks), major processing blocks (motion correction, warping to standard space, blurring,
regression, etc.), and detailed choices for each block (e.g., what kind of alignment, the blur radius,
order of the polynomial for baseline modeling and types of motion regressors). Thus, one can
plan the processing hierarchically, for conceptual clarity and organization. The command
generates a full, commented processing script, which is then executed to carry out single subject
processing. In practice, a typical afni_proc.py command contains 20-25 options, which is a very
compact way to specify a full pipeline.

For convenience and assured mathematical correctness, afni_proc.py automatically takes care
of several aspects of the processing. For example, all warps (motion correction, B0 distortion,
alignment to anatomical and to standard space) are concatenated before being applied to the EPI
dataset to minimize smoothing due to regridding. This allows the user to focus on the parameter
choices in processing, rather than on the technical programming aspects, which greatly reduces
the number of bugs in an analysis stream, particularly if one updates or tweaks existing code.
Because the processing script itself is explicitly created and saved, researchers can check exactly
what steps are occurring in their analysis, and the whole process is documented, which increases
reproducibility.

While afni_proc.py was mainly developed in conjunction with human brain researchers, it is fully
compatible with animal data and has been applied in animal studies. For example, it integrates
directly with AFNI's @animal_warper command (see 3.2.2.4.2) and its list of possible
hemodynamic response functions includes a stimulus response shape for MION (monocrystalline
iron oxide nanoparticle), a contrast-agent that is commonly used in animal neuroimaging studies.
When performing EPI-anatomical alignment, one can furthermore set the minimum "feature size"
of structures to match to a value that is relevant for smaller animal brains.

There are currently two demos available in AFNI for macaque fMRI processing with afni_proc.py:
one for task-based data (visual stimuli, MION contrast), and the other with resting state data from
PRIME-DE (Milham et al., 2018). Each dataset uses the stereotaxic NMT v2 as its standard space
and demonstrates nonlinear warp estimation with @animal_warper (see sections 3.2.1.1,
3.2.2.4.2, and Jung et al., this issue). AFNI is freely available, and most programs are written in
C (as well as Python, R and shell), for generality and computational efficiency.

3.2.3.2. C-PAC

A flexible pipeline for performing preprocessing and connectivity analyses with various tools.

The Configurable Pipeline for the Analysis of Connectomes (C-PAC) is an open-source platform

that allows users to configure their own analysis pipeline for structural and functional MRI data. It

is designed and tested for use with human, non-human primate, and rodent data. One of the key

strengths of C-PAC is its ability to perform different processing strategies on the same dataset.

Multiple tools can be specified for the same type of operation (for example, brain extraction or

registration to a template), with the different results getting saved in separately-labeled output

directories. This allows users to compare a set of methods and evaluate what type of

preprocessing decisions may be best for their data.

A web-based pipeline editor is available (http://fcp-indi.github.io), but pipeline configuration files

can also be edited with any text editor for quick and easy modifications. C-PAC also features a

visual quality control interface which allows users to inspect the quality of brain extraction,

segmentation, and registration outputs.

C-PAC is available as a Docker or Singularity container, allowing users to quickly get started. It

is cloud-compatible through Amazon Web Services (AWS), and a machine image is available with

a ready-to-use C-PAC Docker container for users who wish to run large-scale analyses. Finally,

users can also point directly to a data directory that is hosted on the AWS cloud storage service

(S3), and C-PAC will download and organize the data automatically.

3.2.3.3. NeuroElf

Versatile Matlab-based tool for visualization and (pre-)processing of fMRI data.

Active development of NeuroElf has ceased since its developer is no longer active in

neuroscience. This makes NeuroElf slightly outdated in some respects, as it relies on SPM8, an

older version of the SPM package (Penny et al., 2004). Several components of the resource can

however still be useful for the neuroimaging community. These components include the ability to

import subject-level regression maps into a "GLM" format to rapidly test hypotheses and visualize

bar and scatter plots of extracted regions, as well as some data export utilities, and its scripting

capabilities.

3.2.3.4. NHP-BIDS

A BIDS-compatible Nipype-based pipeline for non-human primate fMRI data.

NHP-BIDS is a pipeline for (pre-)processing of non-human primate fMRI data based on Nipype
(Gorgolewski et al., 2011) and the BIDS (Gorgolewski et al., 2016) conventions for data storage.
It is developed and maintained at the Netherlands Institute for Neuroscience (NIN). The
accompanying Wiki-pages contain instructions to process data from scanner generated dicom
images through to statistical results. The NHP-BIDS pipeline is available in fully configured form,
set up for compatibility with the site where it was developed. However, NHP-BIDS is almost
entirely written in Python and due to its implementation of the Nipype framework, it offers the user
great flexibility in adapting the code-base to implement their own behavioral logging strategies or
preferred choice of image processing modules. The first steps of NHP-BIDS deal with data-
preparation and the creation of BIDS-compatible data structure. Shell scripts are offered that can
easily be adapted to different data curation strategies to ensure automated data handling. Further
data-processing steps are organized in Nipype workflows that can either be run on a local
machine or offloaded to a cluster computing service. Instructions on how to use a SLURM-based
job-scheduling system are included in the wiki.

The NHP-BIDS pipeline is modular and saves the intermediate results after every processing step
for quality control. Standard modules used in the NIN-configuration are: 1) a minimal processing
step that reorients the data to correct for the awake NHPs being scanned in sphinx position in a
horizontal scanner; 2) a resampling step to ensure all data has isotropic voxels; 3) extensive
preprocessing that includes non-rigid slice-by-slice realignment based on AFNI tools (Cox, 1996)
and FSL-based motion correction (MCFLIRT) (Jenkinson et al., 2002); 4) registration to NMT
template-space (Seidlitz et al., 2018); and 5) statistical analysis using FSL-FEAT (Woolrich et al.,
2004, 2001). The resulting data can be visualized using standard software packages, or further
processed for projection to the cortical surface using the packages NHP-Freesurfer and NHP-
pycortex that are also made available by the NIN (see sections 3.2.2.5.2 and 3.2.3.5).

3.2.3.5. NHP-pycortex

Projecting volumetric statistical maps to macaque brain surfaces.

Projecting fMRI activity dynamics or statistical maps on surface renderings of the cortex allows a
much richer view of their spatial characteristics than can be obtained with static 2D slice image
renderings. Creating surface renderings and projecting volumetric data to it can however be

challenging, especially for non-human data. The Pycortex package (Gao et al., 2015) is a very
flexible python-based toolbox designed to work with human brain surfaces that are generated with
Freesurfer (Fischl, 2012). NHP-pycortex is an adapted version of the pycortex package that is
compatible with the macaque brain surfaces generated with Freesurfer based tools (it is
specifically tailored to the output of NHP-Freesurfer, see section 3.2.2.5.2). Jupyter Notebooks
are provided to guide the user through the process of importing the Freesurfer surfaces into the
Pycortex database and project data to it.

3.2.3.6 Pypreclin
A workflow pipeline dedicated to macaque functional and anatomical MRI preprocessing

Pypreclin (Tasserie et al., 2020) was originally developed to face the challenges of artifacts
induced by intracranial implants and body movements during awake fMRI acquisition. The
pipeline development was further extended to a greater panel of experimental parameters such
as BOLD-fMRI, CBV-fMRI (MION contrast agent), anesthesia with different pharmacological
agents, or different RF coil configurations. Pypreclin is a Python module that is available on an
open source repository (https://github.com/neurospin/pypreclin) with HTML documentation.

Pypreclin development aimed at including state-of-the-art algorithms to allow the automatic
preprocessing of raw fMRI data. The diversity of acquisition conditions and hardware in the
PRIME-DE database (Milham et al., 2018) was used to validate Pypreclin's versatility and
robustness across a large range of magnetic field strengths (1.5, 3, 4.7 and 7T), for data acquired
with both single loop or multi-channel phased-array coils, with or without iron-oxide contrast agent,
in awake and anesthetized animals, and both with or without intracranially implanted electrodes
(Figure 5).

Compared to a previously used macaque fMRI preprocessing pipeline at the developer's site
(NeuroSpin Monkey), Pypreclin returned more accurate anatomical localization of neural
activations in the gray matter in the awake state where body movements are often a major issue.
The pipeline supports different brain templates for both *macaca mulatta* (Rhesus macaque) and
macaca fascicularis (cynomolgus macaque) and can easily be customized, for instance with
additional templates.

Figure 5. Functional MRI pipeline Pypreclin. The Pypreclin pipeline has been validated with a range of input data (left), a broad set of template brains (middle) and auditory task data.

3.2.4. Diffusion-Weighted MRI Tools

Diffusion-weighted MRI is a technique to visualize the organization of the brain's white matter

structure. Although tracer data are generally considered to be the gold standard for connectivity

analysis, their invasive nature and high costs restrict their applicability. Diffusion MRI, however,

can be performed both *ex vivo* and *in vivo* to obtain high quality, repeatable images that can be

compared across species.

Several MRI software packages contain sets of diffusion processing tools that can be applied to

either human or non-human datasets. The diffusion data processing and probabilistic

tractography functions in FSL (Behrens et al., 2007; Jenkinson et al., 2002) were recently

expanded with the Xtract tool to facilitate explicit comparison of fiber tracts across species. Xtract

contains tractography libraries for humans and macaques derived from the same protocols

(Warrington et al., 2020) and is currently being extended to include more species, including the

chimpanzee (Bryant et al., 2020). AFNI (Cox, 1996) and TORTOISE (Pierpaoli, et al., 2010) have

several diffusion processing tools and integrated features for distortion correction (Irfanoglu et al.,

2015), deterministic and probabilistic tractography (Taylor and Saad, 2013), tensor-based

morphometry (Hutchinson et al., 2018; Irfanoglu et al., 2016), and network-based structural

analyses (Taylor et al., 2016b). Additionally, Dipy is a Python-based software toolbox for diffusion

processing (Garyfallidis et al., 2014), and DSI-Studio contains tools for tracking and statistics with

a particular focus on high angular resolution diffusion imaging (HARDI) techniques (http://dsi-

studio.labsolver.org). These and other software solutions provide a wide range of functionalities

that are often either complementary or integrable and facilitate analysis for various acquisition

and study paradigms.

3.2.4.1. Mr Cat

Pipelines for processing of structural, functional, and diffusion non-human MRI data.

The MR Comparative Anatomy Toolbox (Mr Cat; www.neuroecologylab.org) specializes

predominantly in processing *post-mortem* data of a wide variety of brains, which are preprocessed

using adaptations of FSL tools implemented in the 'phoenix' module. A number of post-processing

modules are furthermore aimed at providing quantitative comparisons of brain organization across

species. These are often based on connectivity measures, including matching of areal

connectivity fingerprints across species (Mars et al., 2016) or comparisons of 'connectivity

blueprints' of the cortex with the whole brain that allow the description of different brains in terms

of a common connectivity space (Mars et al., 2018b). Recent extensions of this approach focus

on the comparison of brain organization measured by multiple modalities, testing in effect whether

the relationship between distinct aspects of brain organization differs across species (Eichert et

al., 2020).

3.2.4.2. Diffusion-MRI

Pre- and postprocessing steps for diffusion-weighted imaging

The Diffusion-MRI repository hosts Jupyter notebooks in Python and bash that guide users

through multiple pre- and post-processing steps in the analysis of diffusion-weighted imaging

(DWI) data. A step-by-step example analysis is provided of macaque DWI data from PRIME-DE

(Milham et al., 2018). While the workflows were developed and tested with macaque data, they

can easily be adapted for other primate brains. The workflow, which is based on tools from the

Nipype (Gorgolewski et al., 2011), Dipy (Garyfallidis et al., 2014), FSL (Jenkinson et al., 2012)

and MRtrix3 (Tournier et al., 2012) software libraries, requires single-shell or multi-shell DWI data

in NIfTI file format as input, with reverse phase-encoding acquisition containing at least one non-

diffusion-weighted image. Preprocessing includes denoising (Veraart et al., 2016), correction for

susceptibility distortions, eddy current distortions, and subject movement artifacts using TOPUP

(Andersson et al., 2003) and EDDY (Andersson and Sotiropoulos, 2016). Post-processing

includes standard and advanced DWI models to fit the diffusion signal, including Diffusion Tensor

Imaging (DTI) (Basser et al., 1994), Diffusion Kurtosis Imaging (DKI) (Jensen et al., 2005), Neurite

Orientation Dispersion and Density Imaging (NODDI) (Zhang et al., 2012), Single-Shell 3-tissue

Constrained Spherical Deconvolution (SS3T-CSD) (https://3tissue.github.io), and Multi-Shell

Multi-Tissue Constrained Spherical Deconvolution (MSMT-CSD) (Jeurissen et al., 2014). The

outputs are parametric maps extracted from the various model fits. The DTI model results in maps

of axial, radial, and mean diffusivity, as well as fractional anisotropy. The DKI model – an

extension of the DTI that captures diffusion non-gaussianity – also outputs axial, radial, and mean

kurtosis. The three-compartment NODDI is fitted using Accelerated Microstructure Imaging via

Convex Optimization (AMICO) (Daducci et al., 2015) and computes maps of Intra-cellular Volume

Fraction (a measure of neurite density), cerebrospinal fluid (CSF) volume fraction, and fiber

orientation dispersion. SS3T- and MSMT-CSD are used to estimate the multi-tissue orientation

distribution function followed by whole-brain tractography (Figure 6A).

3.2.4.3. FATCAT and TORTOISE

DWI processing, distortion correction, tractography and various group analyses

Diffusion-based imaging provides a great deal of structural information about the brain, with a

particular emphasis on WM properties. It also presents particular processing and quality control

(QC) challenges for limiting the effects of distortions due to subject motion, eddy currents and EPI

inhomogeneity. AFNI's FATCAT (Taylor and Saad, 2013) and the TORTOISE toolbox (Pierpaoli,

et al., 2010) provide a full set of programs for processing and visualizing diffusion data, from

DICOM conversion through distortion correction to group analysis, including quality control.

FATCAT contains validated deterministic and probabilistic tracking tools (Taylor et al., 2012) that

can be used for DTI- and HARDI-based modeling. Examples of tractographic output for a high-

resolution macaque dataset are shown in Figure 6B. These tools can be useful in performing

network-based comparisons of structural properties (Taylor et al., 2016b), possibly in conjunction

with functional network studies. TORTOISE provides methods for group analysis based on

separate comparisons of structural properties from diffeomorphic registrations (DR_TAMAS;

(Irfanoglu et al., 2016). Study design is important for all aspects of analysis, but the DWI

acquisition method particularly affects how well distortion artifacts can be reduced. Acquiring sets

of DWIs with opposite phase encoding has been shown important in reducing EPI inhomogeneity

distortions (Irfanoglu et al., 2019, 2015), especially in the presence of subject motion (Taylor et

al., 2016a). A T2-weighted structural volume with fat suppression can furthermore act as a useful

reference for further reduction of geometric distortions. TORTOISE's tools have been designed

to take advantage of such acquisitions.

Multiple demos for TORTOISE and AFNI's FATCAT are available. The FATCAT_DEMO2

illustrates full single subject processing of a dual-phase encoded DWI dataset, including

probabilistic tractography on gray matter parcellation. Each step of processing automatically

generates QC images to help evaluate the data. These include alignment images, subject motion

plots, directionally encoded color (DEC) maps, thresholded FA maps, and ROI overlays. The

FAT_MVM_DEMO provides an example of combining FATCAT tractography results from a

network of target ROIs with multivariate modeling (MVM) for a hierarchical group analysis: first,

at the "network level" with an omnibus F-statistic, and then zooming in at the "ROI level" with post

hoc t-tests. The techniques in each of these demos can be applied directly to other human or

animal studies.

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Figure 6. Diffusion-weighted MRI. **A**) Result from the Diffusion-MRI resource using macaque data. Fiber orientation distributions (left) and tractography (right). **B**) Examples of DTI-based tractographic output in a high-resolution macaque dataset in AFNI, following distortion correction with TORTOISE. Both images show a (frontal) coronal view of whole brain tracking using AFNI's 3dTrackID: the left panel shows the results of deterministic tracking (as tract fibers), and the right panel shows the results of probabilistic tracking (as WM volume surfaces). Coloration reflects the orientation of the local structure relative to the coordinate frame, where red, blue and green are parallel to the x-, y- and z-axes, respectively. In the probabilistic panel, the FA value modulates the brightness (higher FA is brighter). The images are displayed using SUMA.

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3.2.5. Data sharing

As an extension of the PRIME-DE consortium, which was established to openly share NHP
neuroimaging data (Milham et al., 2020, 2018), PRIME-RE also maintains a list of NHP
neuroimaging data-sharing initiatives. Similar to the analytical resources described above,
anyone can submit a (link to a) data resource for inclusion on PRIME-RE using a simple
submission form. The data sharing section of PRIME-RE currently lists PRIME-DE, OpenNeuro,
and NeuroVault. The PRIME-DE initiative (Milham et al., 2018) specifically focuses on NHP data
and comprises data from 22 different sites all over the world. The database contains structural,
functional and diffusion data; BOLD and contrast-agent data; awake and anesthetized scans;
resting-state and task-based fMRI. OpenNeuro, previously known as OpenfMRI (Poldrack et al.,
2013; Poldrack and Gorgolewski, 2017) hosts MRI, MEG, EEG, iEEG, and ECoG data. Most of
the data are from human subjects, but OpenNeuro is not restricted to human data and some NHP
data-sets are now available as well. Neurovault (Gorgolewski et al., 2015) specializes in sharing
un-thresholded statistical maps, mask files, parcellation maps, and any other voxelwise data.
Originally restricted to human imaging data, the framework was recently extended to allow non-
human data as well (Fox et al., this issue). For NHP data, volumetric data should be registered to
the NMT, a processing step that can easily be done using several of the tools listed on PRIME-
RE (see section 3.2.2).

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1032 4. Discussion

Neuroimaging with non-human primates requires highly specific experimental and analytical
expertise. Recent initiatives such as PRIME-DE (Milham et al., 2018) have made a wealth of
shared NHP neuroimaging data openly available, but the analysis of these datasets demands
appropriate analytical expertise, tools, and workflows. To facilitate the study of NHP neuroimaging
data, PRIME-RE was established as an infrastructure for knowledge and resource sharing,
collaboration and communication. The PRIME-RE website serves as a central knowledge hub for
the NHP neuroimaging community. It is home to a structured dynamic overview of relevant
analytical resources, and a continuously evolving wiki that describes the challenges and potential
solutions of all facets of NHP neuroimaging. Both these knowledge bases are collectively curated
by community-driven practices. This content makes PRIME-RE a NHP-specific complement to
more broadly oriented sites, such as the Neuroimaging Tools and Resources Collaboratory
(NITRC, https://www.nitrc.org) (Kennedy et al., 2016; Luo et al., 2009) that catalogues data, tools

and pipelines for all general aspects of neuroimaging. A common data structure to reference

research resources, such as the RRID (Research Resource Identifier) (Bandrowski et al., 2016)

might allow seamless integration of the resources in PRIME-RE and NITRC in the future.

It is common for development teams of broadly used neuroimaging packages to organize courses

focused on the use of their specific package (e.g., AFNI[1], FSL[2], or SPM[3]). In recent years, open

science initiatives such as Brainhack (Craddock et al., 2016) and the NeuroHackademy, have led

to a boost in the creation of tutorials, courses, demos and workshops that more generally cover

different aspects of neuroimaging and open science practices. While this content is often spread

over various websites, some efforts are being made to curate this information (e.g, https://learn-

neuroimaging.github.io/tutorials-and-resources). Besides its community-curated wiki and links to

tutorials and documentation for individual resources, PRIME-RE also hosts a list of links to

external tutorial and resource collections that may be useful for the NHP neuroimaging

community.

The PRIME-DE/RE initiatives follow on prior large-scale human neuroimaging resources, such as

the 1000 Functional Connectomes Project (Biswal et al., 2010), ADHD-200 (Brown et al., 2012)

or ABIDE (Di Martino et al., 2014). In these projects, data sharing was complemented by open

source pipelines for preprocessing and analyzing the data (Configurable Pipeline for the Analysis

of Connectomes) (Craddock et al., 2013). While these accompanying tools may be limited in

resolving all potential issues, their early release lowers the barrier for users to engage with the

shared data, and accelerates the development of novel analysis solutions. By focusing on

community building, PRIME-RE aims to provide a broad dynamic framework to channel the efforts

of the NHP neuroimaging community and evolve together. In the future, PRIME-RE may be

expanded to include an even broader spectrum of resources involved in NHP neuroimaging, such

as blueprints for hardware, electronic schematics, models for 3-D printing or laser cutting, or

protocols for data acquisition (e.g., sequences), animal care, training and handling.

PRIME-RE supports best practices of open science at every step from data acquisition, through

data organization, to code structure and analysis. Contributors and users are encouraged to

adhere to the FAIR principles (Wilkinson et al., 2016) and both communicate and document their

tools and data. Compared to human neuroimaging, NHP neuroimaging has been lagging behind

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[1] https://afni.nimh.nih.gov/pub/dist/doc/htmldoc/educational/bootcamp_recordings.html
[2] https://fsl.fmrib.ox.ac.uk/fslcourse
[3] https://www.fil.ion.ucl.ac.uk/spm/course

in adopting such collaborative open science initiatives, and we can only speculate about the

reasons why. It is conceivable, for instance, that due to the large amount of work involved in

overcoming the challenges of NHP neuroimaging, the researchers involved might be a bit more

protective of their solutions. In many cases, these solutions are furthermore developed by early

career researchers that tend to get judged on their research output and not necessarily on the

tools they develop for use by others in the field. Systems neuroscience and translational

neuroimaging are strongly multidisciplinary in nature, combining elements of biology, psychology,

physics, engineering and more. Researchers involved in the field cannot be expected to be an

expert in all these disciplines and a substantial proportion of them may not have extensive formal

training in mathematics, physics, or programming which could make them reluctant to share their

custom-written code for outside scrutiny. Another possibility is that such sharing initiatives do

actually exist but that they are rather difficult to find for outsiders. For instance, because they

reside on a laboratory's internal servers or personal websites. However, people's attitudes

towards openly sharing the resource solutions they have developed appears to be improving

(Balbastre et al., 2017; Tasserie et al., 2020) and new developments in information technology

promote such initiatives while simultaneously creating avenues to assign explicit credit to

developers.

A collaborative open approach to NHP neuroimaging will not only foster collaboration in the short

term, but also guide future development efforts, enhance reproducibility, and benefit the whole

community in the long term. The contribution template for PRIME-RE requires a minimum set of

metadata to ensure a consistent and comprehensive resource index (see Table 1). The website

provides a graphic interface that simplifies database navigation and makes it easy for researchers

to discover relevant tools, data, and learning material. PRIME-RE's agile governance structure is

decentralized and open (hosted on GitHub) with clear guides to help researchers integrate into

the community and contribute to it. The original resources listed on PRIME-RE are maintained by

their respective developers and indexed in a completely community-driven way. Acting as a

community-based curation layer on top of open resources reduces processing bottlenecks that

could be encountered if a small single team were responsible for maintaining and updating the

system, while simultaneously facilitating scalability, and inclusiveness.

The maintenance of experimental and analytical code is a challenge in academic research. The

adoption of code development best practices, such as version control, comment inclusion, testing,

coding style, and continuous integration (Eglen et al., 2017), accelerates the continuous

improvement of tools and assists in the swift detection and fixing of bugs. Unfortunately, these

practices are not yet common in academia. We strongly advocate for their adoption and are
hopeful that open and informal communication between researchers and developers at all levels
of NHP neuroimaging research, as facilitated by PRIME-RE, can accelerate this process.

What makes a neuroimaging resource suitable for use with NHPs or other non-human species?
While toolboxes that were primarily developed for use in humans sometimes generalize to, or
contain options for use, in non-human imaging, more often such packages require substantial
customization for use in non-human species. Built-in assumptions that, while valid for most human
neuroimaging data, are not met by animal data include subject orientation in the scanner, signal
quality (contrast), brain size, and field-of-view. An open conversation about such limitations
between developers and researchers could help the development of tools that are innately
capable of processing data from a range of different species (and developmental stages). Such
tools are invaluable for cross-species comparisons that inform our understanding of brain
evolution and development. Software customizations that are often required to make a package
compatible with NHP data can make it difficult to assess data quality and intermediate results of
analytical steps in more comprehensive pipelines. Such quality control is underutilized in
neuroimaging in general but it is even more crucial for non-human data that is analyzed with tools
that were not developed for this type of data or extensively tested on it.

Finally, because NHP-specific analysis tools are often developed by a single team for one
particular research environment, local dependencies could make it difficult for research teams
elsewhere to employ such tools in their own research, even if they are openly shared. The
increasing popularity of modular pipelines (Gorgolewski et al., 2011; Mourik et al., 2018; Tasserie
et al., 2020) is an important improvement for cross-site compatibility and reproducibility and some
of the broader software packages on PRIME-RE contain functionality that specifically addresses
this challenge. Packages like AFNI have modularity built-in, while others, like FSL, integrate with
'notebook-style' scripting modules. A wealth of Python-based tools developed by the NIPY
community (https://nipy.org) furthermore provides access to functions from many different
analytical toolboxes through standardized wrapper modules that can be used as building blocks
for analysis and visualization pipelines. The sharing of tools in pre-packaged containers that
include all dependencies (e.g., Docker or Singularity images) can also make it easier for users to
try a particular piece of software. Standardization of tools and quality assessment methods benefit
from predictable data structures and file formats. While PRIME-RE does not host any data itself,
it does promote the use of standardized data structures like BIDS and platform-neutral data
formats (e.g. NifTI/GifTI/CifTI).

5. Conclusion

With PRIME-RE, we introduce a collaborative platform to address the experimental and analysis
needs of the NHP neuroimaging research community. By allowing the community to curate
relevant resources, disseminating and encouraging open science practices, and strengthening
communication and interactions among researchers and developers, we aim to accelerate
reproducible discovery, minimize redundant efforts, and maximize efficiency of this invaluable
form of translational and comparative neuroscience.

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CRediT authorship contribution statement

AM, PCK: Conceptualization, Methodology, Project administration, Data curation, Writing,
Software, Resources, Visualization, Supervision.
NS, JuS, BC, KH: Conceptualization, Writing, Software, Visualization
DSM: Writing, Project administration, Supervision
KKL, RM, TX, DG, BJ, JaS, PT, RT, EAG-V, CS, XW, RAB, RD, HCE, PG-S, SG, RH, CIL, CiL,
PM, HM, MM, MGPR, JT, LU: Writing, Software, Visualization

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Code and data availability

Both the code for the PRIME-RE website (https://prime-re.github.io) and its Wiki pages are
available on GitHub (https://github.com/PRIME-RE/prime-re.github.io). All resources described in
this paper and listed on PRIME-RE are freely available from their respective developers or
maintainers. Every listing on PRIME-RE comes with a link to the actual resource and a brief
statement on possible usage restrictions (e.g., citing a specific paper). The list of more common
software packages may contain packages that require users to purchase a license, but most are
freely available as well.

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A collaborative resource platform for non-human primate neuroimaging

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Figure 1

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