Towards multi-modal, multi-species brain atlases: part two

Rogier B. Mars[1,2] and Nicola Palomero-Gallagher[3,4]

1Wellcome Centre for Integrative Neuroimaging, Centre for fMRI of the Brain (FMRIB), Nuffield Department of Clinical Neurosciences, John Radcliffe Hospital, University of Oxford, Oxford, United Kingdom
2Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, Nijmegen, The Netherlands
[3]Institute of Neuroscience and Medicine (INM-1), Research Centre Juelich, Germany, Juelich, Germany
[4]C. & O. Vogt Institute for Brain Research, Heinrich-Heine-University, Dusseldorf, Germany

Neuroanatomy is entering the era of big data. Advances in high throughput methods for gene expression, automated methods for histological investigation, and neuroimaging techniques mean that more data is available in more species than ever before. This abundance of new data allows for two types of inferences to converge, namely integration across levels or modalities (which we previously termed a vertical translations) and across different brains within a modality (which we previously termed a horizontal translation) (Mars et al., 2021). Together, these data allow us to test new hypotheses about principles of brain organization and how these translate across species.

However, researchers collecting and analyzing these data are often spread across a variety of subdisciplines. Many of the acquisition and analysis methods they use are highly specialized or consist of bespoke modifications of methods developed for the human brain. Brain atlases across species often use different methods, criteria, and terminology. This makes sharing of methods across labs difficult. The data themselves are often complex, because they involve rare species, specialized formats, or high initial investments. These problems are now well recognised by the community; a number of initiatives exist to share data (Milham et al., 2018; Tendler et al., 2022), standardize analysis pipelines (Grandjean et al., 2023; Markello et al., 2021), provide transformations between common atlases and templates (Seidlitz et al., 2018), and exchange information about new methods (Messinger et al., 2021). However, this endeavour is far from complete; there is still a lack of frameworks that formally integrate the many types of data, methods, and species now becoming available (but see Mars et al. (2021), Froudist-Walsh et al. (2023), Xu et al. (2020)).

These considerations prompted us to organize a special issue of *Brain Structure and Function* to bring together some of the researchers working on these issues. The first part of this special issue was published in 2023 (Mars and Palomero-Gallagher, 2023). The 14 remaining contributions are published here.

One framework for explicit inferences across species has been the comparison of connectivity blueprints. In the original study, the bodies of major white matter tracts in the human and macaque monkey were defined using recipes based on objective anatomical criteria (Mars et al., 2018). Tractography was then performed from the cortical surface, to create surface-based representations of homologous tracts across species. The surface by tract matrix was termed the connectivity blueprint. By comparing the rows of the human and macaque blueprints, each part of the brain could be compared across species in terms of its similarity in the profile of connections with the white matter tract. The tracts essentially formed a ‘common space’ across the species. This framework was subsequently implemented in the FSL analysis software as XTRACT (Warrington et al., 2020), and the current special issue presents two extensions to XTRACT. First, Assimopulos et al. (2024) extend the macaque recipes to a range of macaque templates. A series of templates are in use in the literature and by validating the tractography recipes for each of them, more labs can easily use the tool. This facilitates standardization across the literature, a major challenge in non-human primate imaging (Milham et al., 2022). The second XTRACT paper in this volume presents an extension of the tractographies to the *lar gibbon*, a species of lesser ape (Bryant et al., 2023). Complete or partial XTRACT libraries for a range of species are now available, including in great apes and in human infants, allowing increasingly large-scale comparisons of brain architecture across species and across development using the same standardized common space (Bryant et al., 2024; Warrington et al., 2022).

Whole-brain atlases of different species at a particular level of anatomy are constantly created and provide the important basis for comparisons. The relative availability and low costs of MRI mean that it is now increasingly used to study new species. Avelino-de-Souza et al. (2024) present a fine example of this, by providing the first whole brain description of the cetacean *Guiana dolphin*. Together with the descriptions of the night monkey (Ikeda et al., 2022) and silver fox (Rogers Flattery et al., 2023) from the first part of this special issue, this work shows the power of MRI as a tool for whole brain neuroanatomy. Advances in the use of MRI as a tool for comparative neuroscience, however, should always go hand in hand with developments using other approaches. A great example of whole-brain mapping of anatomy in detail is the contribution by Haghir and colleagues (2023), who present a new map of the rat isocortex and proisocortex, based on cell body and M_2 receptor distribution patterns. Comparing their work to existing atlases, they identify new subdivisions in the rat visual cortex. Zooming in on a specific part of the brain, Robertson et al. (2024) provide an example of the importance of histological work across species, quantifying myelin density in the feline auditory cortex. As the authors point out, the regional differences in myelin density they observed conform to the organizational structure that has been observed across mammalian auditory cortex, showing both an excellent example of evolutionary conservation and the use of myelin as a marker for segmentation in comparative studies. Along similar lines, the detailed analysis of the cytoarchitecture and connectivity of the Göttingen minipig subgenual region by Glud and colleagues (in press) reveals its translational value for studies on deep brain stimulation of area 25 for the treatment of depression. Finally, atlases of the nervous system do not have to be limited to the brain, as the neurochemical atlas of the spinal cord of the rabbit by Veshchitskii and colleagues (2024) demonstrates.

Comparison of atlases across levels allows an assessment of how principles of brain organization translate across levels (Eichert et al., 2020; Froudist-Walsh et al., 2023). As the macaque is still the most often studied non-human primate and both MRI and histological techniques are used, this is the animal in which most modalities are available, including various MRI templates, histological atlases, neurotransmitter receptor maps, and registered combinations of two or more of these modalities (Reveley et al., 2016). Luo and colleagues (2024) add a sagittal cytoarchitectonic atlas in the cynomolgus macaque. Their emphasis is on the use of the macaque as a model species for neurodegenerative diseases, which they argue benefit more from the sagittal plane, rather than the commonly used coronal plane. The macaque is also still studied at increasingly detailed levels, providing a better understanding of how principles of structural organization can influence behavior. A fine example of this is the contribution of May and colleagues (2024), who attempt to better understand the anatomical basis for communication of visual error signals between the superior colliculus and cerebellum.

The availability of large volumes of MRI data in different species has provided the community with unique opportunities, such as facilitating the development and validation of methodologies. The primacy of the macaque in neuroscience research, means that it is also a useful target for validations of different methodological approaches. Charbonneau and colleagues (2024) provide and excellent example of this, by leveraging a number of MRI scans collected at the California National Primate Research Center and comparing manual and automatic segmentation of macaque MRI scans. Another opportunity provided by MRI databases is the ability for researchers to study animals that would otherwise be inaccessible to them. Hathaway and colleagues (2023) exploit the National Chimpanzee Brain Resource (chipmanzeebrain.org) to compare the frontal cortex of the chimpanzee and the human using a different anatomical feature, that of sulcal morphology. They test for the presence of tertiary sulci in the chimpanzee brain, based on their pattern in the human. The results show that, while tertiary sulci are identifiable in both species, some occur more frequently in the human. These results extend the increasingly detailed mapping of cortical species across the primate order (Amiez et al., 2019) and directly inform debates about relative cortical expansion across species, where the presence of sulcal markers is often taken as a prime feature.

Imaging-based comparisons of connectivity are also the focus of two other contributions. Again exploiting the National Chimpanzee Brain Resource, Chauvel et al. (2024) compare superficial structural connections between the human and one of its two closest animal relatives. Similar to the methods discussed above, they create comparable atlases across the two species, allowing a direct comparison across species. They show differences in superficial white matter geometries, perhaps associated with the differential gyrification patterns in humans and chimpanzees. Since diffusion MRI tractography of major white matter bundles is not feasible in the mouse brain, Van Hout and colleagues (2024) use resting state functional connectivity to compare the organization of the cingulate cortex across the mouse and the human brain. Their choice of species was motivated not because of the closeness of the two species, but because the mouse is now the most used mammalian model species in neuroscience. Formal comparisons between its brain organization and that of the human are vital for translational neuroscience.

Perhaps the greatest advantage of the increasing availability of data from many species using the same modalities is that this allows one to search for evolutionary patterns of diversity of brain organization. An excellent example of this approach is provided by the contribution of Stimpson and colleagues (2023). They created a dataset consisting of five neurostructural markers in each of three frontal cortical regions in 14 different primate species. This allows them perform analysis of the evolutionary rate of change of these markers. They report that neuropil fraction, i.e. the fraction of space between the somata of the neurons and the glia, showed a lower rate of evolutionary change that the other markers. Importantly, neuropil fraction in the orbitofrontal cortex was correlated with between-species measurements of behavioral control. Such work demonstrates how principles of evolutionary change and difference in species' traits can be unified within a single framework. It provides a powerful level of inference beyond the use of a single or a few 'model species' (Manger et al., 2008; Preuss, 2019). Another example of this approach is provided by Bonfanti and colleagues (2023) who review the literature on adult neurogenesis across mammalian species to provide a hypothesis regarding the existence of a trade-off between various forms of brain plasticity that coexist during brain evolution.

Together, these contributions highlight both the variety of anatomical data currently available, their ability to elucidate principles of brain organization beyond the mapping of single areas in a single or a few species, and the emergence of frameworks to analyse these data in a coherent fashion. We hope the contributions in this special issue will provide further inspiration for researchers to reach out across the boundaries of their own labs and subfields, to create a new, large-scale but highly detailed, comparative neuroanatomy.

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