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## Chapter 9

# Techniques for Studying Brain Structure and Function

Erin Hecht and Dietrich Stout

**Abstract** Recent years have seen rapid improvement in neuroscience techniques for studying brain structure and function in humans and our primate relatives. These techniques offer new routes of inquiry into our evolutionary history. This chapter offers an overview of a collection of these methods, including discussion of each technique's strengths, weaknesses, and relevance to neuroarchaeology.

**Keyword** Neuroscience techniques · Comparative neuroanatomy · Neuroimaging

## Techniques for Studying Brain Anatomy

### *Structural MRI: Imaging Gray and White Matter*

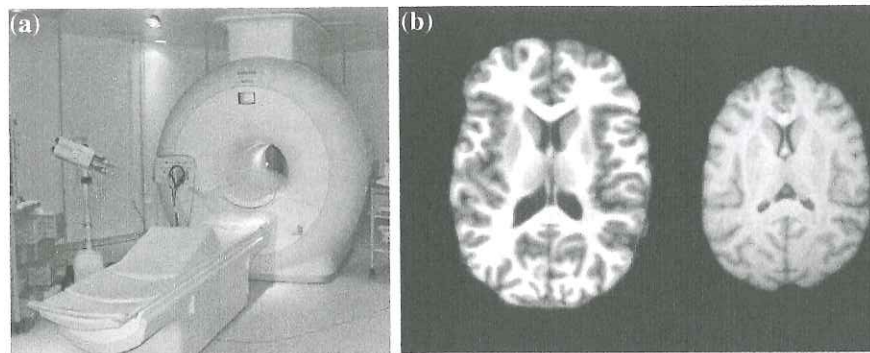
- *Description* Structural MRI allows visualization of two basic categories of brain tissue, gray matter and white matter (Fig. 9.1). MRI distinguishes between gray and white matter by taking advantage of the fact that these two types of tissue contain respectively more water and more fat, which have different magnetic properties. Gray matter contains the cell bodies and dendrites of neurons, which are responsible for information processing. White matter contains axons, which transmit electrical signals between neurons, and their myelin sheaths, which have a high fat content and act as insulation for axons. Various analysis methods are available to quantitatively compare differences in size, shape, and white/gray intensity between different scans. One of the most

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**Fig. 9.1** Structural MRI. **a** MRI scanner. Image credit Jan Ainali, Wikimedia Commons. **b** T1-weighted MRI scan of human brain (left) and chimpanzee brain (right)

common is voxel based morphometry, in which all scans are registered to an average template brain. The intensity of a given region is held constant, so that expansions or contractions required to align an individual subject with the template are associated with changes in voxel intensity. Intensity is then compared on a voxel-by-voxel basis across scans in order to identify volumetric changes.

- **Strengths** Structural MRI's main strength is that it is non-invasive, in contrast with other typical neuroanatomical techniques such as immunohistochemistry, which involves analysis of post-mortem tissue. It can be used safely in humans and other species without adverse health effects. Structural MRI also allows rapid collection of anatomical information from the entire brain and when performed post-mortem does not destroy the tissue sample, whereas processing an entire brain for immunohistochemistry would take far longer and would preclude use of the tissue for most other applications.
- **Weaknesses** The resolution of MRI has continued to increase steadily since its invention, but is still far coarser than histological techniques which allow resolution at a cellular scale. In vivo MRI suffers from motion artifact. Even if the subject is completely still, vibrations from the scanner and from the subject's own breathing and heartbeat introduce noise into the image. High-resolution post mortem scans take many hours (sometimes days) to complete, and scanner time is expensive. MRI scanners themselves are expensive and not all research institutions have a high-resolution scanner available.
- **Relevant uses for neuroarchaeology** Structural MRI can be used to detect neuroanatomical differences between groups of subjects, differences within subjects across time, or differences between species. High-resolution structural MRI images are typically acquired in conjunction with other neuroimaging techniques, such as fMRI, DTI, or PET, in order to provide a high-spatial-resolution anatomical map for interpreting results.

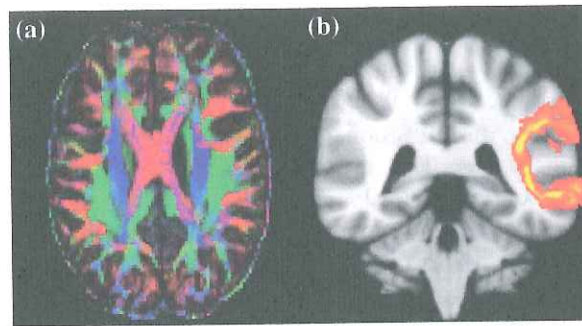
### DTI: Tracing White Matter Connections

- **Description** DTI allows visualization of the actual paths of connectivity taken by white matter tracts (Fig. 9.2). It takes advantage of the fact that within a white matter tract, the diffusion of water is largely constrained along the direction of the axons. This means that diffusion within an axon tract is anisotropic, or more probable along a given direction. Fractional anisotropy is thought to be related to the degree of axon myelination, the diameter of axons, and/or the density of a fiber tract. Comparative DTI/immunohistochemistry and dissection studies have confirmed that DTI can accurately retrace the actual routes taken by white matter tracts (Schmahmann et al. 2007).
- **Strengths** Non-invasive in living humans and great apes. It can be performed at high (~100–300 micron) resolution in fixed post mortem brains, which can be acquired after natural death from humans or great apes. Connectivity throughout the entire brain can be assessed from a single scan. When performed in fixed, post-mortem brains, scanning does not alter the tissue so it is still available for other forms of analysis (e.g., histology).
- **Weaknesses:** DTI has relatively lower resolution than injection tract-tracing. False positives and false negatives are likely without proper controls and analysis techniques. Tracking white matter connections through areas of crossing fiber tracts and into gray matter is problematic, but continuing increases in scanner technology and analysis algorithms are addressing this obstacle.
- **Relevant uses for neuroarchaeology** DTI is invaluable for studying brain anatomy in species in which the gold-standard technique, injection of axonal tracers followed by post-mortem histological examination of connectivity, is not possible (this technique is invasive and terminal). Because neuroarchaeology is concerned with the evolution of the human brain, DTI is an important technique for this field.

### Histological Analysis

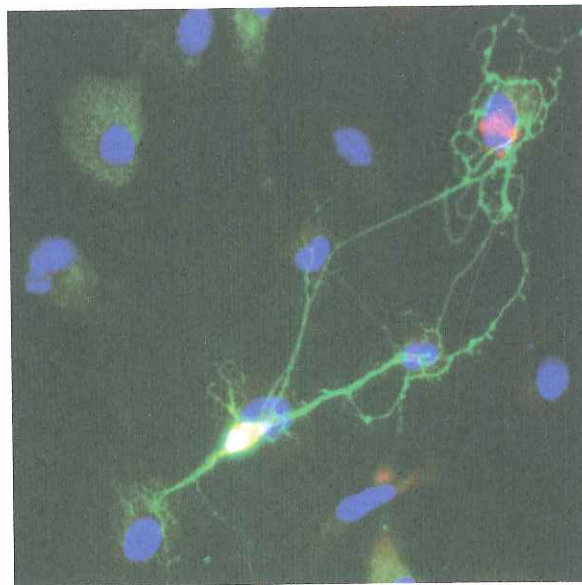
- **Description** Brain tissue is exposed to an agent that binds to or is taken up by a particular structure of interest (e.g., a particular neurotransmitter receptor type, such as 5HT1A serotonin receptors; cell type, such as interneurons or astrocytes; or cell compartment, such as axons or dendrites) (Fig. 9.3). This exposure can occur in fixed, post mortem brain tissue, or in vivo, as in the case of injection tract tracing, where a tracing agent is injected into an area of the brain, allowed to be transported along axons for a period of time. The animal is then sacrificed to obtain the brain, which now contains tracer along the axon pathways connected to the injection site. The brain then undergoes a series of processing steps to allow the location of the agent to be visualized in slices of tissue. Tissue is placed on slides and can be examined with either a light microscope or an electron microscope.





**Fig. 9.2** DTI. **a** Color map of a human brain. Colors correspond to the primary direction of diffusion (fiber tract orientation)—red, medial–lateral; green, anterior–posterior; blue, inferior–superior. **b** Tractography between anterior inferior parietal cortex and posterior middle temporal gyrus, a connection that may be important for tool use. This image shows combined results from 6 humans

**Fig. 9.3** Histology. Neurons in substantia nigra stained with a fluorescent agent that labels neurons with tyrosine hydroxylase, an enzyme involved in the production of dopamine and norepinephrine. Image credit D Feinstein, Wikimedia Commons



- **Strengths** Histological analysis is generally considered to be a “gold standard” which is more accurate and reliable than neuroimaging. It has very high spatial resolution. Light microscopy allows visualization at the level of cells and large cell compartments, such as dendritic arbors; electron microscopy allows visualization of even smaller features, such as synapses and synaptic vesicles. Many different reagents have been developed allowing high specificity for visualization of particular receptor classes, cell types, cell compartments, etc. These reagents can even be used in tandem on the same tissue, allowing for

visualization of co-localization of particular features, e.g., a particular neurotransmitter receptor on a particular type of cell. Different reactions can also be carried out on alternating slices of tissue, allowing for multiple experiments to be carried out in the same brain.

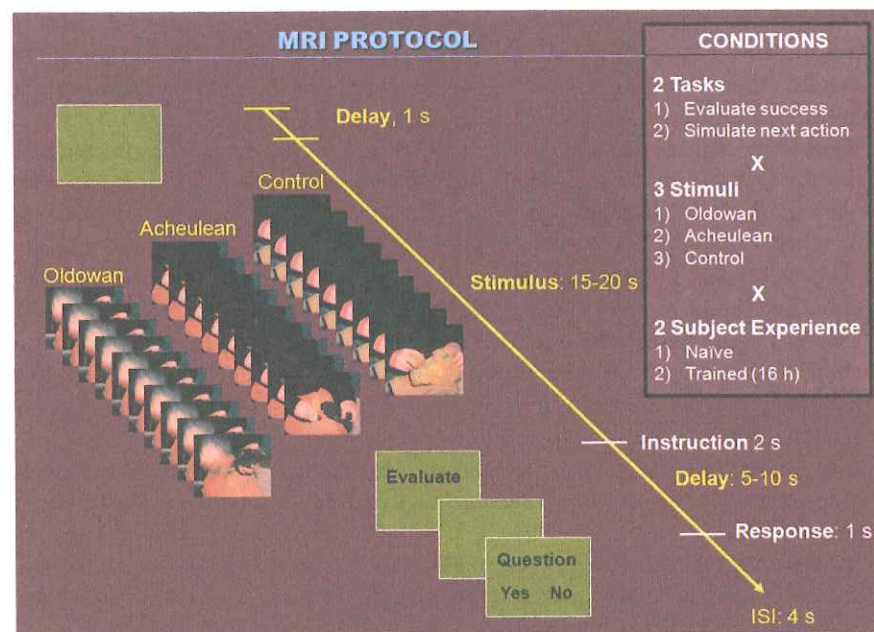
- **Weaknesses** Histological analysis requires brain tissue to be extracted and preserved immediately after death, which can be difficult to accomplish in great apes and humans, and histological experiments on connectivity involve in vivo injection of tracers, which is not ethically possible in great apes and humans. Well-preserved, high-quality human and great ape brain tissue is a rare and valuable resource, and histology studies in these species are relatively rare. Therefore, structural MRI and DTI provide important sources of information about brain anatomy in these species. Additionally, brain tissue shrinks after fixation, so volumetric measurements in preserved post mortem tissue may not accurately reflect the in vivo condition. Once tissue is processed, it is largely unavailable for other kinds of techniques. Histological processing is extremely time-intensive, so most experiments focus on only a small portion of a few subjects' brains.
- **Relevant uses for neuroarchaeology** This family of techniques is typically used in rodents and macaque monkeys. Injection tract tracing is not used in humans or other great apes, since it is invasive and requires the non-natural death of the subject. However, post mortem histological analysis has been used in brains from humans and other great apes that can be removed and preserved immediately after death. This type of research has identified uniquely human features in the cellular organization of several brain regions (e.g. Barger et al. 2012; Bryant et al. 2012).

## Techniques for Studying Brain Function

### fMRI: Mapping Neural Activation Using Blood Oxygenation

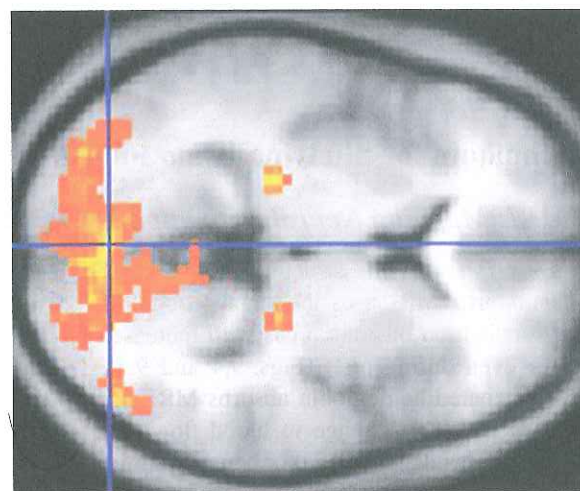
- **Description** While structural MRI and DTI both use MRI scanners to study anatomy, fMRI uses the same technology to study physiology. fMRI allows visualization of brain areas with increased blood flow during a functional task (or even during rest) (Figs. 9.4 and 9.5). It takes advantage of the fact that oxygenated hemoglobin absorbs MRI signal, while deoxygenated hemoglobin does not. This change in blood flow is referred to as the blood-oxygenation level dependent (BOLD) or hemodynamic response. This increase in blood flow is taken as a proxy for activity because blood flow is known to be closely related to neural firing; active cells require more blood to support their activity.
- **Strengths** Relatively greater spatial and temporal resolution than PET. New developments in scanner technology and analysis algorithms are improving fMRI's explanatory power. For example, event-related designs have improved researchers' ability to link the timecourse of activation to the timecourse of





**Fig. 9.4** fMRI task employed by Stout et al. (2011). Subjects viewed short videos of stone tool-making and then answered yes/no questions by pressing a button

**Fig. 9.5** fMRI functional neuroimaging data showing activation in visual cortex. Image credit Washington Irving, Wikimedia Commons



perception and cognition. Hyperscanning involves analysis of concordant brain activity between two individuals who are interacting with each other in real time while in separate scanners. Inter-subject correlation analysis uses the time course of activity in one brain to predict activity in other brains allowing

researchers to shared reactions to external stimuli. These new methods are enhancing the ability of fMRI to deal with the kinds of complex, naturalistic stimuli (e.g. Hasson et al. 2004) and tasks of interest to neuroarchaeologists.

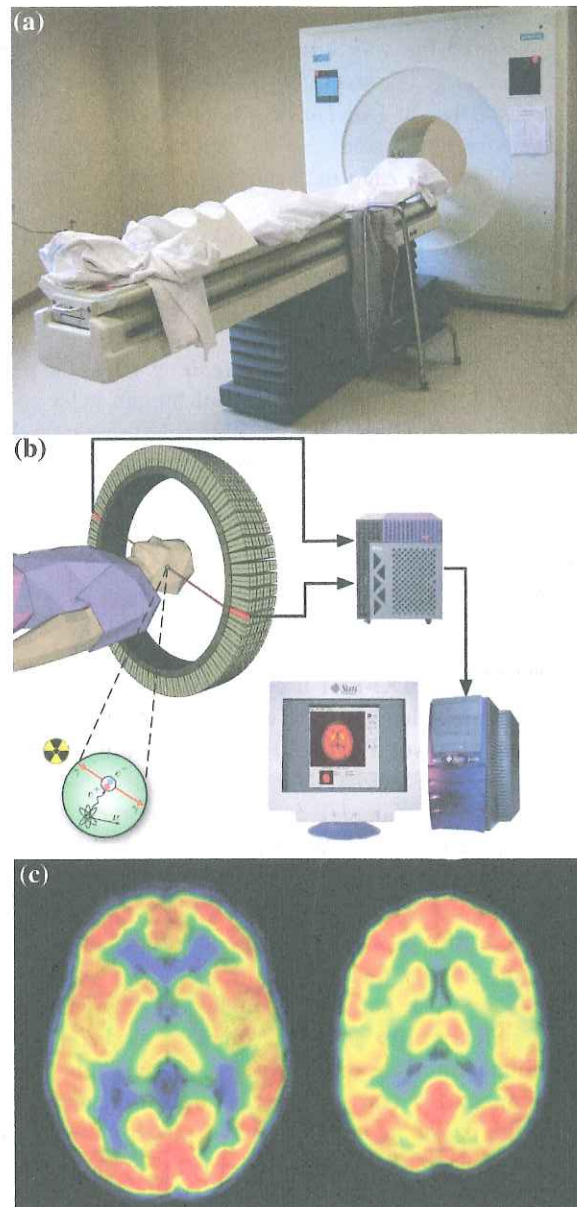
- **Weaknesses** In fMRI, images are acquired in a continuous stream during the behavior under study, so the behavior must be performed while the subject is immobilized inside the scanner. Therefore, behavioral tasks generally involve perceptual discrimination with a cognitive judgment indicated by a button press. This is not ideal for the study of some of the socially- and environmentally-situated behaviors of interest to neuroarchaeology, such as toolmaking. It also precludes the use of fMRI in unrestrained primates such as chimpanzees.
- **Relevant uses for neuroarchaeology** fMRI is the most common method of assessing functional correlates of human behavior in modern neuroscience. It has been used to study a variety of topics relevant to neuroarchaeology, including the neural correlates of tool use, action perception and imitation.

### FDG-PET: Mapping Neural Activation Using Glucose Metabolism

- **Description** FDG-PET uses fluorodeoxyglucose (FDG), which is glucose which is radio-labelled with  $^{18}\text{F}$ , which has a half-life of about 110 min (Fig. 9.6). The subject receives a dose of FDG, either orally or intravenously, and then begins a behavioral task. FDG is taken up by neurons as fuel as glucose would be, but the presence of the  $^{18}\text{F}$  causes it to become temporarily trapped inside cells. As the  $^{18}\text{F}$  decays, it releases positrons, which upon encounter with nearby electrons, release two photons that can be detected by a scanner. Therefore, regions of increased brightness in the PET scan correspond to regions of increased glucose metabolism during the task. Glucose metabolism is taken as proxy for neural activity (active cells need more glucose for energy). After decay, the FDG molecule is metabolised normally by the cell. Because FDG uptake drops off quickly after about 45 min, the subject's behavior after this point has a minimal effect on scan images. This means that subjects (including even awake chimpanzees) can perform naturalistic, unrestrained tasks during the FDG uptake period and be scanned afterward, and the scan images will still reflect brain activity during the earlier behavioral period
- **Strengths** FDG-PET scans collect data about task-related brain activity *after* the behavior to be studied has been performed, in contrast to fMRI, in which data are collected *during* the behavior. Therefore, unlike fMRI, FDG-PET does not require subjects to be inside the scanner while they are performing the behavior of interest. This has particular relevance for human and nonhuman primate behaviors relevant to archaeology, such as tool making. FDG-PET is also the only functional neuroimaging method that has been developed for safe use with great apes.



**Fig. 9.6** FDG-PET. **a** PET scanner. *Image credit* Liz West, Wikimedia Commons. **b** Diagram of PET data acquisition. Radioactive decay of the tracer causes emission of two photons that are emitted at approximately 180°. Temporally coincident photons at these locations are detected by the scanner, allowing reconstruction of the spatial source of the photons in an image. *Image credit* Jens Langner, Wikimedia Commons. **c** FDG-PET images from a chimpanzee (*left*) and human (*right*). These images represent glucose metabolism during the observation of object-directed grasping actions



- **Weaknesses** The entire ~45-min uptake period is averaged down to one datapoint, limiting statistical power and analytic approaches. For example, FDG-PET precludes investigation of temporal dynamics (the timecourse of brain activation to a stimulus or during a behavior).

- **Relevant uses for neuroarchaeology** FDG-PET is generally used in situations where it is not possible or desirable to constrain the experiment to performance inside an fMRI scanner. For example, it has been used in humans to study stone tool making (Stout and Chaminade 2007; Stout et al. 2008). It has also been used relatively extensively in chimpanzees because sedation and anesthesia can occur at the completion of the uptake period and the scan will still reflect brain activity during the uptake period, even if scan acquisition occurs when the subject is unconscious. Chimpanzee FDG-PET studies have examined neural responses at rest, during the production of communicative gestures and vocalizations, and during the production and observation of grasping actions (Hopkins et al. 2010; Parr et al. 2009; Rilling et al. 2007; Tagliabattola et al. 2008, 2009, 2011).

### $H_2^{15}O$ -PET: Mapping Neural Activation Using Blood Oxygenation

- **Description** Like FDG-PET,  $H_2^{15}O$ -PET uses a scanner that detects photons emitted after radioactive decay. In this case, though, the tracer is water which is radio-labeled with  $^{15}O$ , which has a half-life of only about 2 min. Therefore, it is injected throughout the uptake process, as images are being acquired. Regions of greater brightness in the resultant images represent regions of greater blood flow, which is taken as a proxy for neural activation.
- **Strengths**  $H_2^{15}O$ -PET has higher temporal resolution than FDG-PET. It is non-invasive.
- **Weaknesses** Like fMRI,  $H_2^{15}O$ -PET cannot be used to study awake behavior in unrestrained primates because it requires that the subject perform the behavior while inside the scanner. It also has poorer spatial and temporal resolution than fMRI.
- **Relevant uses for neuroarchaeology**  $H_2^{15}O$ -PET has similar applicability as fMRI. Because fMRI has surpassed  $H_2^{15}O$ -PET in spatial and temporal resolution, this technique is rarely used anymore.

### PET with Other Ligands

- **Description** PET tracers can also image the activity of a particular class of neurotransmitters. A variety of tracers, or ligands, exist, and more are continually being developed. The ligand is labeled with a radioisotope (commonly  $^{18}F$  and  $^{11}C$ ) and binds to a specific class of neurotransmitter receptor or neurotransmitter transporter. Neurotransmitter receptors receive chemical signals from other neurons with neurotransmitters bind to them; neurotransmitter transporters transport neurotransmitters from one neuron to another across the synapse.



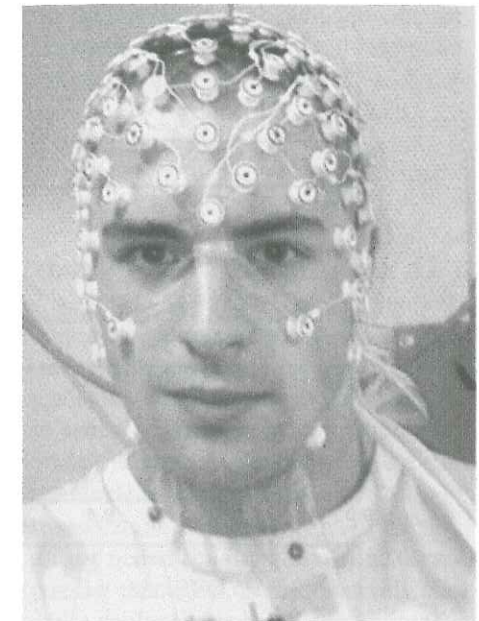
Isotope decay causes the emission of photons which are detected by the PET scanner. The spatial distribution of particular receptors or transporters throughout the brain can be detected by binding of the ligand; regions of increased brightness in the scan correspond to regions with increased density of that class of receptor or transporter. Endogenous neurotransmitter release can be detected via displacement of the ligand. In this case, regions of decreased brightness in the scan correspond to increased endogenous neurotransmitter activity.

- *Strengths* This type of imaging offers a non-invasive, non-terminal way to study the distribution and activity of different neurotransmitter systems. Comparable studies in common neuroscience model species, such as macaque monkeys and rats, would use techniques that either require a well-preserved post-mortem brain or involve invasive experiments, which makes this class of PET methods a better choice for humans and great apes.
- *Weaknesses* Spatial and temporal resolution are relatively low relative to the comparable invasive or post-mortem techniques. Many ligands exist, but radiolabelled ligands able to cross the blood-brain barrier have not yet been developed for all neurotransmitter systems.
- *Relevant uses for neuroarchaeology* To our knowledge, this type of imaging has not yet been used in a neuroarchaeological context. However, it could be used to investigate the neurochemical correlates of archaeologically relevant behaviors—for example, dopamine receptor displacement studies could address whether making symmetric tools activates neural reward systems to a greater extent than making non-symmetric tools. This class of PET imaging could also be used to identify potential human adaptations in receptor distribution or neurotransmitter activity that may be linked to the development of uniquely human behaviors or cognitive abilities.

## EEG

- *Description* Electroencephalography (EEG) uses small electrodes to detect voltage fluctuations at the scalp which are caused by the aggregate electrical activity of large numbers of neurons close beneath the scalp (Fig. 9.7). When neurons fire together in synchrony, voltage fluctuations at the scalp have higher power; when they fire asynchronously, voltage fluctuations at the scalp have lower power. Oscillations can be filtered into different frequency bands, and the relative power of these different bands can be compared for different stimuli. Different frequency bands are associated with different aspects of perceptual, motor, and cognitive function. For example, mu is an 8–12 Hz oscillation originating from sensorimotor cortex that becomes suppressed during either the performance or observation of manual or facial movements; this suppression is thought to occur due to input from frontal mirror neurons (Muthukumaraswamy et al. 2004; Pineda 2005). EEG data can also be time-locked to the presentation of a stimulus or to the subject's response and then averaged across many trials;

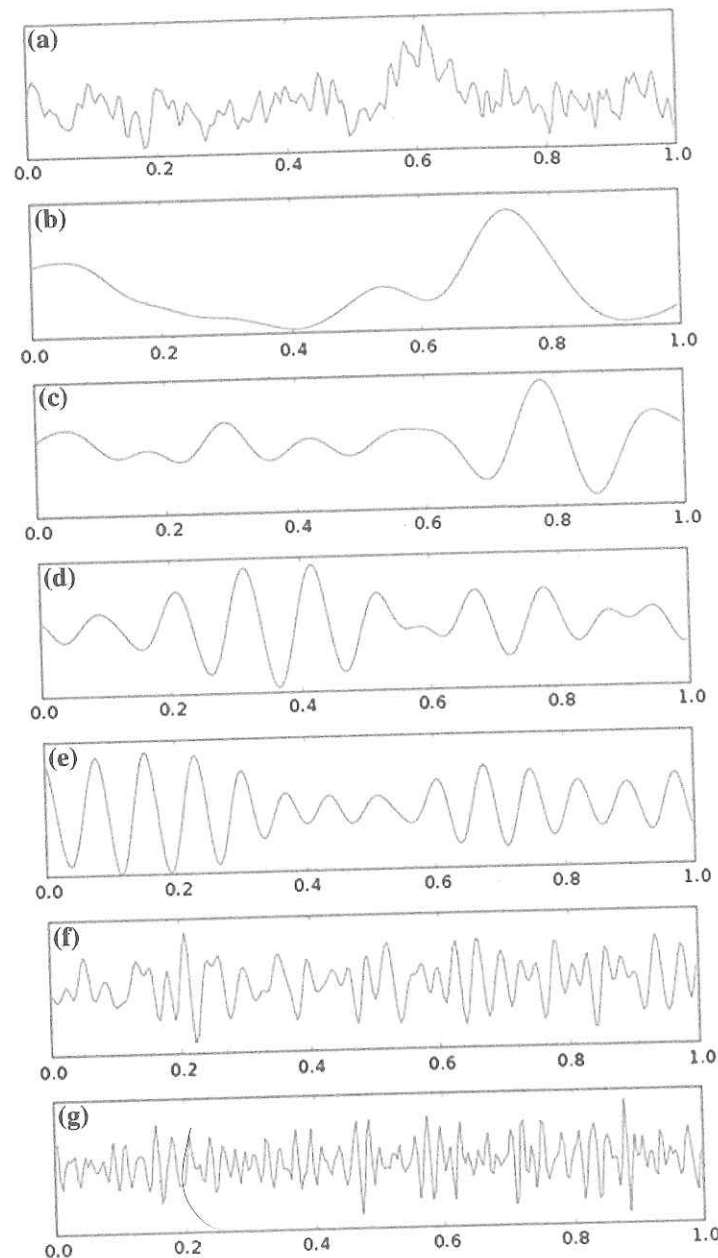
**Fig. 9.7** Subject undergoing EEG data collection. *Image credit Douglas Myers, Wikimedia Commons*



the resultant averaged waveforms are referred to as evoked potentials (EPs) or event-related potentials (ERPs) (Fig. 9.8). A number of characteristic ERPs have been identified and linked to specific perceptual, motor, and cognitive phenomena. For example, the error-related negativity (ERN) is a negative voltage fluctuation originating from frontal electrode sites that peaks 80–150 ms after a subject commits an error in a task.

- *Strengths* EEG has higher temporal resolution than PET or fMRI, and data can be precisely time-locked to stimuli and responses on a millisecond scale. The behavior under study must be performed while the subject is wearing the electrodes, but EEG analysis systems are fairly flexible and portable, so behavior is not as constrained as it is inside a scanner and can be semi-naturalistic.
- *Weaknesses* EEG has lower spatial resolution than PET or fMRI. It is mainly limited to detecting cortical activity near the surface of the skull and is generally not useful for studying deeper structures that are far from the scalp surface. Movement of the subject's eyes or body causes electrical artifacts that have historically posed significant challenges for EEG data analysis, so most EEG tasks were designed to minimize these with on-screen display of stimuli and simple button-press responses. However, recent technical advances are producing hardware and software that can accommodate more eye and body movement, allowing for more naturalistic stimuli and responses, although EEG is still not as naturalistic as FDG-PET.





**Fig. 9.8** Event-related potentials. *Image credit* Albert Kok, Wikimedia Commons. **a** One second of raw EEG data **b** Delta waves **c** Theta waves **d** Alpha waves **e** Mu waves **f** Beta waves **g** Gamma waves

- *Relevant uses for neuroarchaeology* Mu oscillations are of particular interest because of their link to mirror neurons. Because of its high temporal resolution, EEG can also be used with eye tracking to identify neural correlates of perception of specific aspects of a stimulus.

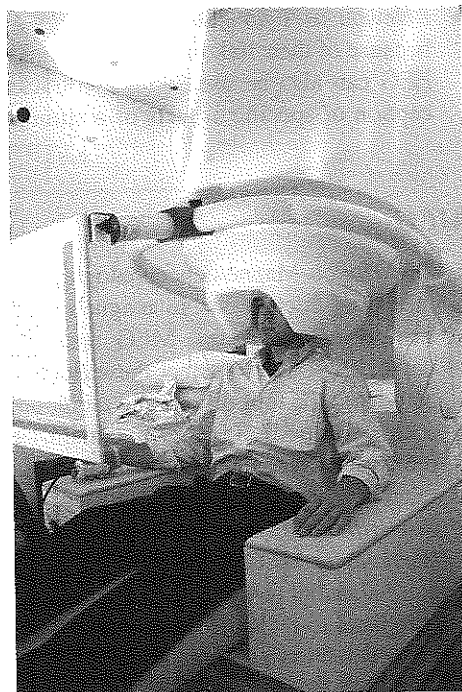
## MEG

- *Description* Magnetoencephalography (MEG) is similar to EEG except that it measures fluctuations in magnetic fields instead of electric fields (Fig. 9.9). Instead of electrodes, MEG uses a superconducting quantum interference device (SQUID) to detect these fluctuations. EEG is sensitive mainly to neural activity at the tops of gyri and the floors of sulci (cortical surfaces parallel to the scalp), while MEG is sensitive mainly to neural activity originating within sulci (cortical surfaces perpendicular to the scalp). Magnetic oscillations and event-related waves have been identified, comparable to those in EEG.
- *Strengths* MEG has very high temporal resolution, like EEG.
- *Weaknesses* MEG is not useful for measuring neural activity beneath the cortex, and its spatial resolution, while slightly better than EEG, is still relatively poor compared to fMRI. Because MEG detection equipment is more substantial than EEG detection equipment, behavior is more constrained and less naturalistic than with EEG.
- *Relevant uses for neuroarchaeology* MEG has been used to study neural activity related to the mirror system in humans (Hari 2006). It could conceivably be used to address other neuroarchaeologically-relevant topics, but MEG equipment is fairly rare.

## TMS

- *Description* Trans-cranial magnetic stimulation (TMS) is different from the other techniques described above because it involves not the passive observation of neural activation that is related to a particular stimulus or behavior, but rather the *active manipulation* of neural activity with measurements of subsequent changes in perception, cognition, or behavior. This is achieved by the application of a rapidly changing magnetic field to the surface of the scalp, which induces currents in the underlying neurons. Single-pulse TMS uses individual stimulation events to evoke action potentials in underlying neurons. Application of single-pulse TMS to motor cortex causes muscle twitches in the corresponding part of the body; application to occipital cortex causes the subject to perceive flashes of light. In contrast, repetitive TMS uses a stream of pulses to suppress neural activity. This can be used to experimentally, temporarily disable a part of the brain in order to assess its role in perception, cognition, or behavior.
- *Strengths* TMS provides a way to assess whether a brain area is necessary for a given function. This is an alternative to lesion studies, which are used in

Fig. 9.9 MEG equipment



macaques and rodent species to address the same question, but are not used in humans or great apes because they are invasive. TMS has high temporal resolution, on par with EEG and MEG. It is also highly portable and can be used while the subject is behaving naturalistically.

- *Weaknesses* Using the subject's structural MRI scan and a stereotaxic positioning system, it is possible to reliably target a brain region on the order of, say, ventral premotor cortex or anterior intraparietal sulcus, but the spatial precision of TMS is not as high as the spatial resolution of fMRI or PET. TMS can only be used to stimulate regions of the brain close to the skull, and is not useful for deeper structures.
- *Relevant uses for neuroarchaeology* To our knowledge, TMS has not yet been used in any archaeologically-motivated experiments, but its ability to be used during unrestrained, naturalistic behavior make it a good candidate for assessing cortical regions involved in neuroarchaeologically-relevant behaviors like tool use.

### Single-Cell Electrophysiology

- *Description* In common neuroscience model species (monkeys and rodents), electrodes are inserted into the brain to measure voltage fluctuations immediately adjacent to a neuron. This reflects the electrical activity of that neuron

(i.e., its action potentials). Data can be collected in different conditions to study particular aspects of perception, cognition, or behavior. Intracranial recordings can be collected from one neuron at a time or from many neurons at a time, and can be combined with techniques to electrically or chemically stimulate neuronal activity so that resultant neural or behavioral changes can be measured. Different classes of neurons can be recognized by their firing patterns or response properties. For example, mirror neurons were identified using this technique in macaques and are defined as cells that fire both during the execution and observation of similar actions (Rizzolatti et al. 1996).

- *Strengths* This technique is considered a "gold standard" for assessing neural function. It has very high spatial and temporal resolution.
- *Weaknesses* Its invasiveness precludes its experimental use in humans and other great apes. Intracranial recordings are occasionally performed opportunistically in humans, with the subject's consent, during already-scheduled neurosurgery, such as resection of a tumor or epileptic focus. These experiments are rare, though, and necessarily involve a non-normal brain.
- *Relevant uses for neuroarchaeology* Several lines of research in monkeys are directly relevant to archaeology. In addition to mirror neurons, this technique has also been used to study cells that are active during tool use in experimentally trained macaques. This led to the finding that learning to use a tool extends the body schema to incorporate the tool (Iriki et al. 1996).

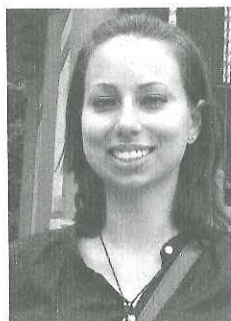
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### Authors Biography



**Erin Hecht** received a B.S. in Cognitive Science from the University of California, San Diego in 2006 and a Ph.D. in Neuroscience from Emory University in 2013. In 2013, she performed postdoctoral research in the Department of Anthropology at Emory University with Dietrich Stout. As of 2014, she is a postdoctoral researcher in the Department of Psychology at Georgia State University. She studies the evolution of social cognition. Her research has involved comparative structural and functional neuroimaging studies in humans and nonhuman primates.



**Dietrich Stout** is an Assistant Professor of Anthropology at Emory University. He received his Ph.D. in Paleoanthropology in 2003 from Indiana University, Bloomington, where he studied with Nicholas Toth and Kathy Schick. He served as a Visiting Assistant Professor in Anthropology at George Washington University for one year and as a Lecturer (equivalent U.S. Asst. Prof.) in Paleolithic Archaeology at the University College London Institute of Archaeology for 4 years before relocating to Emory in 2009. His research focus on Paleolithic stone tool-making integrates methods ranging from lithic analysis to experimental archaeology, ethnoarchaeology, and brain imaging.

## Chapter 10 A Digital Collection of Hominoid Endocasts

José Manuel de la Cuétara

**Abstract** The major focus of this book is to provide the researcher or student with a general overview of the recent advances and updated knowledge regarding human paleoneurological research. In this context, the objective of this chapter is to provide the reader with a series of plates showing endocranial casts of several well-preserved and relevant fossil specimens representing different extinct hominid species, as well as some examples from living modern humans and great apes. Each plate depicts the external aspect of the cranium and its spatial relationship with the endocranial cavity in lateral norm, as well as a general view of each endocast viewed from all six norms. Additionally, some basic taxonomic notes collected from the literature are also provided (Groves 2001; Holloway et al. 2004; Isler et al. 2008; Wood and Lonergan 2008). With this material in hand, the reader may look at the evolutionary changes discussed in the present book regarding the evolution of the human endocranium and brain. It is worth noting that this chapter is not intended to give a detailed description of any particular specimen. For that purpose, we recommend to consult Holloway et al. (2004) extensive monograph on hominid endocasts. All specimens depicted here were digitally reconstructed from computed tomographic (CT) sections following the principles of digital anatomy (Zollikofer and Ponce de León 2005; Weber and Bookstein 2011). Missing parts of fossil crania were estimated using sliding semi-landmarks and thin-plate spline techniques as proposed elsewhere (Gunz et al. 2005, 2009). The only exception to this procedure is the Asian *Homo erectus* specimen Zhoukoudian XII, which consisted of surface scans of a reproduction of the original endocast made by Weindereich (1943) as well as a cast of the cranial reconstruction made by Tattersall and Sawyer (1996).

**Keywords** Endocasts • Fossil hominids • Modern humans • Great Apes

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