Chapter 10
How Can iEEG Be Used to Study Inter-Individual and Developmental Differences?

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Abstract Inter-individual differences, including but not limited to those that distinguish children from adolescents and younger from older adults, are a hallmark of human cognition. As described throughout this book, intracranial electroencephalography (iEEG) affords unprecedented access to the human brain, permitting insight into the neurophysiology of human cognition with high spatiotemporal and single-trial precision. However, iEEG is also limited due to brain coverage that is sparse within one patient and variable across patients. This limitation poses a fundamental challenge for the use of iEEG in controlled investigations of inter-individual differences. In this chapter, we address this challenge and describe best practices for studies that aim to elucidate inter-individual and developmental differences in the neurophysiological mechanisms of human cognition using iEEG. We first briefly discuss how iEEG data are typically handled by minimizing sources of inter-individual variability. We then present best practices for the use of iEEG in controlled investigations of inter-individual differences and describe recent studies that used iEEG to reveal signatures of memory which differ across patients. We propose that iEEG be considered a gold standard in studies of inter-individual and developmental differences in the neurophysiology of human cognition.

10.1 Introduction

No two brains are identical, and inter-individual differences are a defining feature of the human experience. This chapter focuses on intracranial electroencephalography (iEEG) as a tool to investigate inter-individual and developmental differences in human cognition, understanding of which has been hindered by common neuroscientific approaches. First, because noninvasive imaging methods offer either spatial

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or temporal precision, reliance on techniques such as functional magnetic resonance imaging (fMRI) and scalp EEG has limited our ability to delineate human brain activity with both spatial and temporal precision. Second, because noninvasive imaging techniques offer relatively low signal-to-noise ratio [1], many studies have relied on group-level averaging of brain data and treated inter-individual variability as a source of noise [2–5]. Third, because invasive recording, which offers high spatiotemporal resolution and signal quality, has been traditionally performed in non-human animals, resulting data cannot explain factors that distinguish one person from another. This is especially relevant to developmental inquiry, as the maturational trajectory of the human brain is more protracted and qualitatively distinct from that of even our closest primate relatives [6–10]. iEEG addresses these hindrances by providing insight into the neurophysiology of human cognition with high spatiotemporal resolution and signal-to-noise ratio enabling single-trial precision [11–14]. With appropriate controls, iEEG studies offer immense potential to advance our understanding of inter-individual and developmental differences in human cognition.

Figure 10.1 illustrates two datasets in which responses such as behavioral performance or measures of brain structure or function differ between two experimental conditions [2]. In one dataset, most individual data are consistent with group averages and averaging reveals an omnibus pattern. However, some participants show opposite trends or higher responses that are masked by averaging. In the other dataset, group averages do not differ between conditions, but the underlying individual data could be divided into two groups of participants showing opposite trends. Here, averaging may mask a systematic pattern of inter-individual differences which reflects meaningful variability in the brain. Indeed, inter-individual variability in behaviors ranging from simple motor actions to complex executive functions have been linked to inter-individual variability in brain structure [2] and function [15, 16]. Neuroimaging measures provide better predictive power of inter-individual differences in cognitive and clinical outcomes than behavioral measures alone [16], and they explain relationships between factors like socioeconomic status and adolescent development [5]. Comprehensive models in human neuroscience must account for the fact that neural phenotypes and cognitive behaviors vary widely across the population and change over time within individuals across the lifespan [17].

Due to its unparalleled spatiotemporal and single-trial precision, iEEG investigations add crucial mechanistic insight to models in human neuroscience [11–14, 18]. However, despite the advantages of iEEG, surgical electrode placement is driven solely by clinical needs. Electrodes sample brain regions that are common sources of epilepsy, such that some regions tend to be over-sampled and others under-sampled, resulting in a "corticocentric bias" that pervades iEEG literature [12]. Further, electrodes should not be placed to sample more of the brain than is necessary to identify a patient's seizure focus and, in some cases, to characterize regions critical to motor and language functions to ensure they are spared from surgical resection [19]. Electrode coverage is therefore sparse within one patient and variable from one patient to another [11], which renders the exact placement of electrodes a potential source of noise. Individual electrode placement poses a fundamental challenge for the use of iEEG in investigations of meaningful inter-individual variability in brain function.

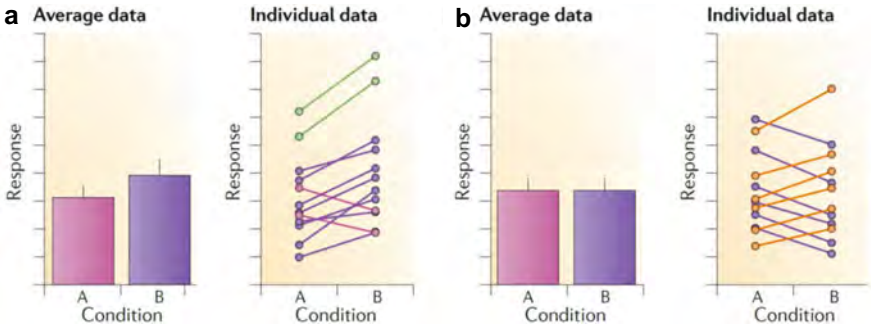

Fig. 10.1 Schematic examples of average and individual data in two experimental conditions. (**a**) The group average in condition B is larger than in condition A (left). Most individual data are consistent with the group averages (right; purple), however, some participants showed opposite trends (pink) or higher responses (green). Such inter-individual differences are masked by averaging. (**b**) Group averages do not differ between conditions A and B (left). However, the underlying individual data could be divided into two groups of participants showing opposite trends (right; orange vs. purple). Adapted from [2]

Here, we address this challenge and describe best practices for studies that aim to elucidate inter-individual and developmental differences in the neurophysiological mechanisms of human cognition using iEEG. We focus on aspects of iEEG studies that researchers can control to achieve high scientific rigor when examining systematic, generalizable patterns of inter-individual and developmental differences in the precise neurophysiology of human cognition.

10.2 Minimize Inter-Individual Variability in Study Design and Analysis

Most iEEG studies take considerable measures to minimize inter-individual variability and draw general conclusions about the neurophysiology of human cognition without considering the person to whom a brain belongs. In one common approach, patients are selected for a study based on electrode sampling of the same anatomical region-of-interest (ROI) and as few as 3-5 patients are included with results replicated per patient. This approach is akin to the standard two-sample procedure of non-human primate neurophysiology, and offers the advantage of replicability [20]. It is qualified by the high signal-to-noise ratio of intracranial data [1], which enables single-trial precision and single-subject reliability [11–14]. In another common approach, patients are selected for a study regardless of specific electrode sampling and electrodes from all patients are combined onto a population-template brain for analysis of all regions sampled. Larger sample sizes permit sampling of larger swaths of the brain [21]. These approaches are discussed in detail in Chap. 29. However, studies aiming to identify inter-individual differences cannot adopt approaches which ignore

the person to whom a brain belongs. For this reason, it is important to minimize inter-individual variability not related to effects of interest across subjects during study design and analysis.

At the design stage, experiments may be designed to promote statistical testing of iEEG effects of interest prior to analysis of inter-individual differences in those effects. Specifically, researchers should pay close attention to the appropriateness of the study design to test hypotheses, and ensure that any manipulation (e.g., of experimental condition) is successful. Such research design and strict theorizing should be considered a prerequisite to rigorous statistical testing [22]. Resulting data may then be divided trial-by-trial according to the study design, whether that is a condition manipulation [23, 24], participant-defined criterion (e.g., correct versus incorrect behavioral response [25–27]), or some other task-related component (e.g., post-stimulus versus pre-stimulus epoch [24, 25]). At the analysis stage, iEEG data may be analyzed trial-by-trial at the single-subject level according to the study design. Although these steps do not directly address the issue of electrode placement, they capitalize on the high signal quality of intracranial data and isolate iEEG effects of interest per patient while minimizing other sources of noise that vary from patient to patient (e.g., hospital testing environment). Applying these steps before analyzing inter-individual differences maximizes the likelihood that iEEG measures reflect meaningful factors with unambiguous interpretation of function.

10.3 Define the Inter-Individual Factor(s) of Interest

As described above, factors reflecting the neurophysiology of cognition broadly may be tested on the single-subject level prior to analyzing inter-individual differences. These factors should be defined according to the study design [22], be they manipulations of experimental condition, participant-defined criteria, or other task-related factors. Inter-individual factors of interest, however, need not directly relate to the study design. Factors to consider include experimental task performance, demographic factors like age or sex, neuropsychological assessment data, and measures of brain structure.

Individual measures of task performance including accuracy and response time (RT) are straightforward to consider because they require no additional data collection. Here we describe two studies that used iEEG to reveal inter-individual differences in memory performance and addressed the issue of electrode placement in distinct statistical approaches. In one study, Sheehan and colleagues related individual iEEG effects to associative memory accuracy [26] (Fig. 10.2). iEEG data were analyzed for sample entropy, a measure of signal complexity posited to reflect the brain's ability to flexibly encode and process information, during the encoding of word pairs that were subsequently remembered. Individual signal complexity was found to correlate positively with associative memory accuracy across the sample of 43 participants. To address the issue of electrode placement, researchers included patients regardless of specific electrode sampling and applied spatial smoothing

around each 1 × 1 cm ROI to minimize noise related to exact sampling across patients. Although this procedure attenuated the spatial resolution slightly from the mm to cm scale, it balanced the spatial precision of iEEG with the need to maintain statistical power across patients. In another study, Brzezicka and colleagues related individual iEEG effects to RT in a task that manipulated working memory load [23]. Data were analyzed for load-related changes in power in three ROIs, and theta power in the dorsolateral prefrontal cortex (PFC), but not anterior cingulate or hippocampus, was found to correlate positively with RT across electrodes from 13 patients. To address the issue of electrode placement, researchers included patients with ROI sampling and used linear mixed-effects modeling with electrodes as random samples. Although this procedure limited the spatial precision to the ROI, it minimized noise related to specific electrode sampling and increased the sample size for enhanced statistical power.

In addition to task performance, demographic factors such as patient age and sex are often obtained as part of research without additional data collection, and the information is easily de-identified [19]. Studies which aim to study inter-individual differences as they relate to development may consider age as a factor of interest, or the interaction of age and performance. Ofen, Johnson, Yin, and colleagues pioneered this approach in the first published studies of memory development using iEEG [13,

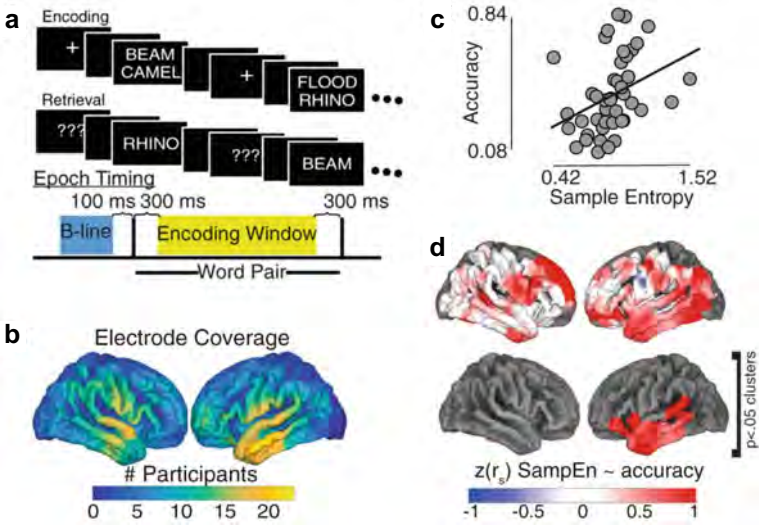

Fig. 10.2 iEEG signal complexity tracks inter-individual variability in associative memory performance. (**a**) Associative memory task in [26]. At study, participants encoded word pairs. At test, they were presented with single words and prompted to retrieve the other word in the pair. (**b**) Spatial distribution of electrode coverage color-coded by the number of participants with sampling of different regions. (**c**) Signal complexity, measured by sample entropy during the encoding window shown in (A), was positively correlated with associative memory performance across participants ($r = 0.51$, $p = 0.0007$). (**d**) Spatial distribution of correlations across all sampled regions, raw (top) and cluster-corrected for multiple comparisons at $p < 0.05$ (bottom). SampEn, sample entropy

24, 25, 27]. In these studies, researchers employed an established subsequent memory task where pediatric patients studied scenes in preparation for a recognition test [13] (Fig. 10.3A). iEEG data were analyzed per patient based on the participant-defined criterion of subsequent memory (i.e., scenes that were later remembered or forgotten at test) and then analyzed for inter-individual differences related to age and overall accuracy. The first study investigated the latency of PFC responses in 17 patients aged 6–19 years [25] (Fig. 10.3B–C). Response latency was defined as the time of peak high-frequency broadband activity, a partial proxy for multi-unit neuronal activity [28–31], and individual latency was quantified in four ROIs. The onset latency of high-frequency responses in inferior frontal gyrus was found to predict behavioral RT and explain age-related gains in recognition performance. The second study investigated alpha oscillations in the primary visual cortex of 24 patients aged 6–21 years [24] (Fig. 10.3D–E). Decreased alpha activity, which is posited to reflect increased information processing similar to signal complexity [11, 26, 32], was found to explain age-related gains in the recognition of visually complex scenes. To address the issue of electrode placement, both studies included patients with ROI sampling and used linear mixed-effects modeling with patients as random samples (see also Chap. 36 for a detailed description of this approach). Although this procedure limited the spatial precision to the ROI, it reduced noise related to specific electrode sampling across patients.

The third study, published in 2022, investigated patterns of inter-regional connectivity between medial temporal lobe (MTL) and PFC in 21 patients aged 6–21 years [27] (Fig. 10.4). Functional connectivity was assessed separately at slow and fast theta frequencies using both phase- and amplitude-based measures [33, 34]. Importantly, these analyses were performed using individually defined frequencies to capture oscillatory phenomena of interest while controlling for inter-individual differences in these phenomena. Both increased slow theta amplitude correlations [35] between MTL and inferior frontal gyrus and fast theta phase-locking values [36] between MTL and middle frontal gyrus were found to explain age-related gains in recognition performance. Patients were again included based on ROI sampling and inter-individual differences were assessed using linear mixed-effects models with patients as random samples. Finally, to identify potential underlying brain structures supporting functional connectivity effects, the researchers incorporated diffusion tractography data that had been obtained as part of the presurgical workup of 11 patients in the sample. Specifically, they tested whether distinct functional connectivity mechanisms in top-performing adolescents were more likely to reflect maturation of the same white matter tract or distinct tracts. They focused a priori on the two major white matter tracts connecting MTL and PFC, the cingulum and uncinate. Bayesian analysis provided an initial test due to limitations of the small sample [37] and suggested that age-related differences in both functional connectivity mechanisms reflected maturation of the cingulum. The high spatiotemporal precision of iEEG, combined with measures of brain structure, supported a mechanistic proposal about how brain maturation supports memory development and addressed major outstanding questions in theoretical models of memory [13].

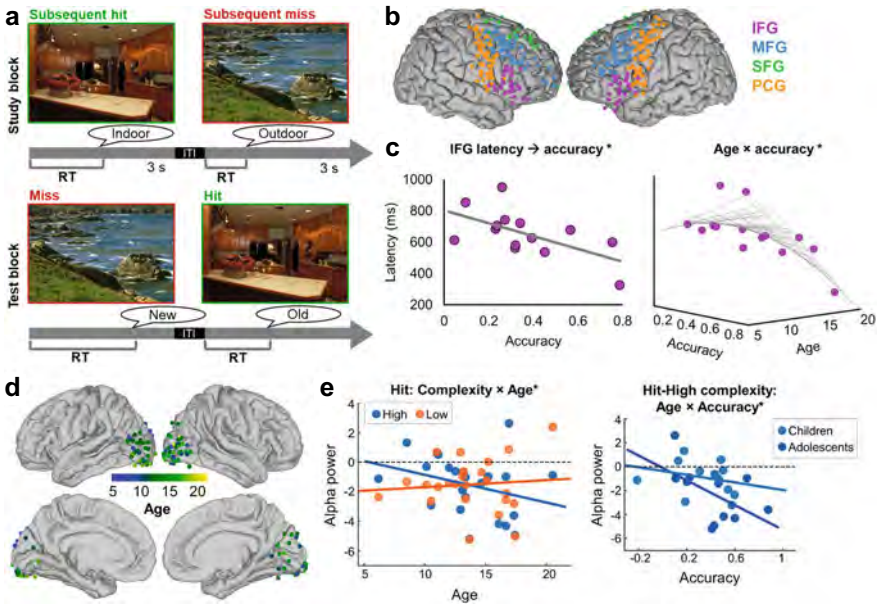

Fig. 10.3 iEEG spectral activities track age-related variability in recognition memory performance. (**a**) Recognition memory task. At study, participants encoded pictures of scenes and classified each scene as 'indoor' or 'outdoor'. At test, they were presented with studied scenes inter-mixed with new scenes and prompted to indicate whether each scene was 'old' or 'new'. (**b**) Frontal electrode coverage across participants color-coded by region of interest in [25]. IFG, inferior frontal gyrus; MFG, middle frontal gyrus; SFG, superior frontal gyrus; PCG, precentral gyrus. (**c**) The latency of peak IFG high-frequency broadband activity during encoding was negatively correlated with recognition memory performance across all participants (left; r = –0.60, $p = 0.0004$). The negative relationship between peak high-frequency activity latency and performance explained superior performance in adolescents (right; $p = 0.00004$). (**d**) Occipital electrode coverage across participants color-coded by participant age in [24]. (**e**) Occipital alpha power differed by age during the encoding of high- (≥5 object categories) and low-complexity (≤3 object categories) scenes that were subsequently recognized (left; FDR-corrected $p < 0.05$). The negative relationship between alpha power and age during the encoding of high-complexity scenes explained superior performance in adolescents (right; $p < 0.05$).

Developmental iEEG research is a burgeoning field which poses additional challenges. In studies that consider age and performance as factors, for instance, it is important to demonstrate whether patients in the sample exhibit the expected pattern of performance for their age. This may be accomplished by comparing the behavioral data from patients to a larger sample of data on the same task from non-clinical participants [11]. In the memory development studies described above [24, 25, 27], researchers related the pattern of performance by age in iEEG patient samples to larger samples of data from non-clinical participants [13]. Alternatively, researchers may present normative data from neuropsychological assessments, which may be obtained as part of routine clinical care. If patients do fall in the range of expectations, iEEG findings of inter-individual and developmental differences may generalize to

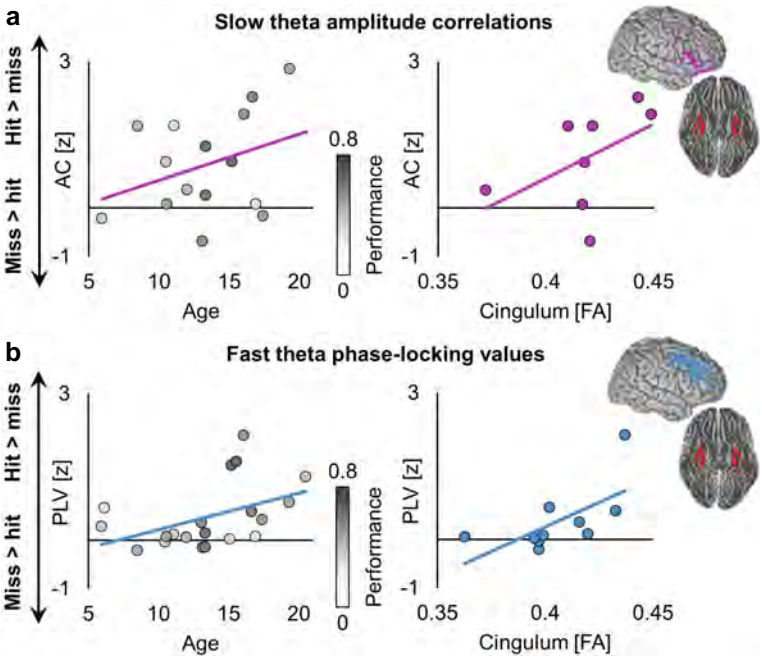

Fig. 10.4 iEEG functional connectivity tracks age-related variability in recognition memory performance and maps to brain structure. (**a**) Subsequent memory effects in slow theta amplitude correlations (AC) between MTL and inferior frontal gyrus differentiated top-performing adolescents from both low-performing adolescents and children (left; $p = 0.011$). AC subsequent memory effects correlated with individual differences the strength of the cingulum tract (right; $r = 0.50$, $BF_{10} = 1.48$). (**b**) Subsequent memory effects in fast theta phase-locking values (PLV) between MTL and middle frontal gyrus differentiated top-performing adolescents from both low-performing adolescents and children (left; $p = 0.0006$). PLV subsequent memory effects correlated with individual differences the strength of the cingulum tract (right; $r = 0.64$, $BF_{10} = 4.31$). FA, fractional anisotropy. Adapted from [27]

the population. If they do not, it is a limitation of the study sample and findings should be interpreted and acknowledged as such.

10.4 Understand (and Increase) the Sample Size

In all studies described above [23–27], analyses of inter-individual differences minimized noise related to specific electrode sampling and maintained statistical power across patients by reducing spatial precision. This illuminates a tradeoff between statistical power and spatial precision in group-level analysis of iEEG data. Because research in clinical samples is inherently constrained by the availability of patients who fit study criteria, many iEEG studies are based on few patients and examine

effects in single trials, making the sample size constrained by the number of trials in an experiment as opposed to number of patients who participated. This approach capitalizes on the single-trial precision of iEEG data and, although it ignores the person to whom a brain belongs, it is relevant here as it demonstrates the reliability of the data in single subjects. The single-subject reliability of iEEG data is especially advantageous in inter-individual differences analysis because it means few patients are needed at different levels of a factor, for example, task performance for a given age. It is therefore feasible to investigate inter-individual differences in fewer participants than might be needed to achieve comparable reliability using noninvasive measures with lower signal quality [1].

Nonetheless, iEEG investigations of inter-individual differences are subject to the same rules of statistics as any other investigation and the availability of patients who fit study criteria limits the sample size, limiting statistical power [38]. For instance, samples of approximately 20 participants achieve 80% power to detect large effects and are likely to miss smaller effects (i.e., Type II error) [39]. It is likely that initial iEEG investigations of inter-individual differences [23–27] missed not only the potential to detect meaningful variability within ROIs due to spatial smoothing, but also smaller effects due to sample size constraints. This is especially relevant in developmental iEEG studies examining interactions among multiple factors. Future iEEG investigations of inter-individual and developmental differences may address both limitations by increasing sample sizes. Substantially increasing sample sizes would also permit cross-validation analysis, which is recommended over correlation to demonstrate the generalizability of findings to the population [16, 40]. As more researchers apply iEEG to examine inter-individual and developmental differences in human cognition, they may seek to increase sample sizes through multi-site collaboration and data sharing [13, 41]

10.5 Discussion

Intracranial EEG affords unprecedented access to the human brain, permitting insight into the neurophysiology of human cognition with high spatiotemporal and single-trial precision and single-subject reliability. However, because iEEG sampling is sparse within one patient and variable across patients, the technique poses a fundamental challenge in investigations of inter-individual differences. Here, we address this challenge and describe best practices for studies that aim to elucidate inter-individual and developmental differences in human cognition using iEEG. We focus on aspects of iEEG studies that researchers can control to achieve high scientific rigor when examining systematic, generalizable patterns of inter-individual and developmental differences. First, researchers should pay close attention to the appropriateness of the study design to test hypotheses and ensure that iEEG measures reflect meaningful factors with clear interpretation of function before analyzing inter-individual differences. Second, researchers should define inter-individual factors of

interest based on what is feasible given sensitive, potentially identifiable patient information, and ensure that group-level analysis of inter-individual differences controls for noise in electrode sampling across patients. In developmental studies, researchers should also demonstrate whether the study sample represents the population based on non-clinical or normative data and interpret findings accordingly. Third, researchers should understand the statistical power achieved given the sample size and seek to increase the sample size when possible. With appropriate controls, we propose that iEEG be considered a gold standard in studies of inter-individual and developmental differences in the neurophysiology of human cognition.

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