Extracting cognitive brain networks using machine-learning and information theoretical approaches

Research report - Etienne Combrisson

Abbreviations

iEEG = intracranial electroencephalography
EEG = electroencephalography
MEG = magnetoencephalography
fMRI = functional magnetic resonance imaging
CFC = cross-frequency coupling
PAC = phase-amplitude coupling
ML = machine-learning
IT = information-theory

Keywords

computational neuroscience, network, cognition, neurophysiology, anatomy, functional connectivity, structural connectivity, information theory, machine learning

Abstract

Our senses constantly sampled the environment and our brain integrates and processes this information in order to produce the appropriate behaviour in response. My research has focused on understanding and developing data-analysis frameworks that can characterize the dynamics of the modulations that occur in the **local neural activity** and **global brain area interactions** during complex cognition in humans. To do so, I first used machine learning models to examine how motor-related variables, such as hand directions, are represented in local neural computations. I then employed information theoretical measures to analyze the modulation of short and long-range cortico-cortical interactions during goal-directed learning. My findings were based on high-resolution neurophysiological recordings for fine-grained tracking of the dynamic of neural computations occurring during single-trial. To contribute to open science, I have shared neuro-oriented software for brain data analysis, statistics, and visualization. Overall, my work improved our understanding and provided the tools to depict how brain networks are perturbed during complex cognition in humans.

What's new in 2024?

- **Publications:**
  - The manuscript about the dissociation between reward and punishment learning using neural interactions has been accepted in *eLife*
  - The manuscript about decoding hand movement directions during motor planning is under review in *Communications Biology*
- **Supervision:**
  - I supervised a student during the 6 months of the *Google Summer of Code*. We worked on a software to estimate of Higher-Order Interactions on a GPU
  - With the Dr Bjørg Kilavik, we recruited a biomedical engineer on a project about the characterization of laminar travelling waves.
- **Software:**
  - Frites has been integrated in EBRAINS, a European open-research platform gathering tools and data for brain research

Introduction

The apparent simplicity behind having fun while playing pool actually relies on highly complex computations performed silently by the brain. Predicting trajectories and angles, power selection and movement execution up to the pleasant feeling of the dopamine shot released when the ball goes in. At any time, the orchestral activity of the brain propagates along highways and offers a vast functional repertoire, from sensing the environment, integrating complex information and acting on the world. Paradoxically, the brain can do all of that with a “fixed” wiring backbone (i.e. the anatomical connectivity). Modern theories suggest that this paradox can be disentangled once we consider that cognition and behaviour arise from the local activity of specialised regions (like the visual or motor cortices) but also, from the relationships between those regions.

My research involves understanding how the neural activity and neural interactions are modulated according to task variables (stimuli, feedback) or behaviours (actions, learning-rate etc.). Thus, I am exploring two different levels: at the **local domain** of the neural activity in isolated regions and also, at the **global domain** to understand **how interactions between regions are used** to produce cognition or behaviour in humans. To investigate both local and global domains, I have mainly used intracranial electroencephalography (iEEG). iEEG is an invasive recording used to localize the epileptic foci in pharmacoresistant patients in a presurgical context. iEEG is unique in that it offers the best compromise between spatial (millimetre) and temporal resolution (millisecond) to study complex cognition in humans in the cortical sheet and deep structures like the insula or some subcortical areas. However, analysing iEEG is challenging, mainly because the intracranial implantation depends on the localization of the epileptic zone and is unique to each patient, which complicates the statistical analyses especially to draw inferences on a population. Taken together, my research is lying at a crosspoint gathering neuroscience, statistics, theoretical work and efficient neuroinformatic tools to identify activity patterns and networks that are hallmarks of neuronal computations.

During my PhD and first postdoc at the university of Montréal, I investigated the local domain to understand how the rhythmic activity was modulated during a motor task involving both planning or executing movements with the hand. To do so, I was part of a rising generation discovering machine-learning (ML) approaches in neuroscience to extract local neural markers. Most of the literature was focusing on the modulation of amplitude and I shredded light on new features for decoding motricity (e.g. directions of movements or motor states), such as the instantaneous phase and cross-frequency coupling (CFC). Later, during my second postdoc in Marseille, I switched toward the global domain to understand how neural interactions change during learning. This time, I also switched from ML to metrics from the information-theory (IT) because of their popularity for measuring inter-areal interactions and for decomposing the information of a system. Throughout my career, I contributed to explain and demonstrate pitfalls in statistics and, inspired by advances in fMRI, I proposed statistical workflows dedicated to neurophysiological recordings such as iEEG, EEG or MEG. Finally, I shared with the community three open-source software used in several other publications.

Local domain: exploring neural markers using machine-learning approaches

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Local neural markers of motricity: decoding motor planning, execution and upper-limb directions using amplitude, phase and cross-frequency coupling features

- **Combrisson et al. (2017, *NeuroImage*) :** We found neural markers of motor planning, execution and movement directions using ML approaches on iEEG in humans during a center-out motor task
- **Combrisson et al. (*2020, PLoS Comp Biol*) :** We proposed an amplitude independent method for measuring cross-frequency coupling using the information-theory
- **Combrisson et al. (*Under review in Communications Biology*) :** We successfully inferred the direction of hand movements not only during execution but also, importantly, during planning.

Executing simple movement is associated with complex, yet reproducible, neural oscillatory patterns in the brain's activity. For example, both invasive and non-invasive brain recordings have shown that there is a relative increase in high-frequency power and a decrease in beta-band power in the motor cortex while executing hand movements (Pfurtscheller et al., 2006, 2003; Pfurtscheller and Berghold, 1989). BCIs (brain-computer interfaces) are devices that translate these neural patterns into commands, which can be used to restore communication or partial mobility to people with conditions such as locked-in syndrome (Birbaumer, 2006; Jerbi et al., 2007). Therefore, understanding and quantitatively characterizing these patterns not only contribute to our fundamental understanding of how the brain is functioning but also has direct clinical applications. However, our knowledge about the specific role of neural components such as amplitude, phase, or the coupling between the phase and the amplitude (PAC) was still limited (Canolty and Knight, 2010).

Neural markers distinguishing planning from executing a movement

I investigated this issue using iEEG recordings in patients performing a center-out motor task (*Figure 1A*). I used decoding approaches to identify neural markers of **motor states**, i.e. whether subjects were planning or executing hand movements (Combrisson et al., 2017a; Jerbi et al., 2013). We reached high-decoding performances (>80%) using classical power features in the motor and premotor cortex. However, the best decoding (~90%) was achieved using the phase in the very low-frequency band in the premotor cortex (*Figure 1C*). We replicated the existence of an alpha-gamma coupling (*Figure 1B*) in the premotor cortex (Yanagisawa et al., 2012) but we showed that it was **specific to the planning**. In addition to the well-known role of spectral power, this data-driven approach highlighted the significant contribution of low-frequency phase and CFC to the neural patterns associated with motor planning and execution, suggesting that BCI devices should explore phase and coupling features.

Predicting the direction of a movement before its actual execution

More ambitiously, we also demonstrated that we could accurately **predict the direction of a planned hand movement** (i.e. up vs. down vs. right vs. left) **before its execution** (Combrisson et al., 2024). For direction decoding, we found that amplitude features outperformed phase and CFC features. We found a predominance of alpha power features for decoding directions during planning and gamma power during execution (*Figure 1D*). Importantly, using the transfer learning temporal generalization approach (King and Dehaene, 2014), we showed that planning and executing a movement shared similar neural representations (*Figure 1E*). Finally, we used a feature-selection pipeline to identify synergistic features and maximize the decoding performance. This optimization strategy led to decoding accuracies of the four directions of ~75% and ~84% respectively during the planning and execution phases. However, we found that PAC was uniformly modulated across the direction of movements. Later, we introduced a method to estimate PAC using the Gaussian Copula Mutual Information (Combrisson et al., 2020; Ince et al., 2017) and we compared the impact of several filtering methods on the measure of PAC (Soto et al., 2018). Contrary to many other methods, our is amplitude independent, an essential feature for reliable PAC estimations (Aru et al., 2015) and does rely on an arbitrary number of bins.

To summarize, we were pioneers in the use of decoding approaches to extend the list of neural markers of motricity. We showed different patterns of amplitude activity, of phase and of cross-frequency coupling while planning or executing movements in different directions. Based on this experience in decoding from modulations of amplitude, I contributed to distinguishing wakeful consciousness from unconsciousness induced using sevoflurane (Thiery et al., 2018) or for decoding decision-making using iEEG (Thiery et al., 2020).

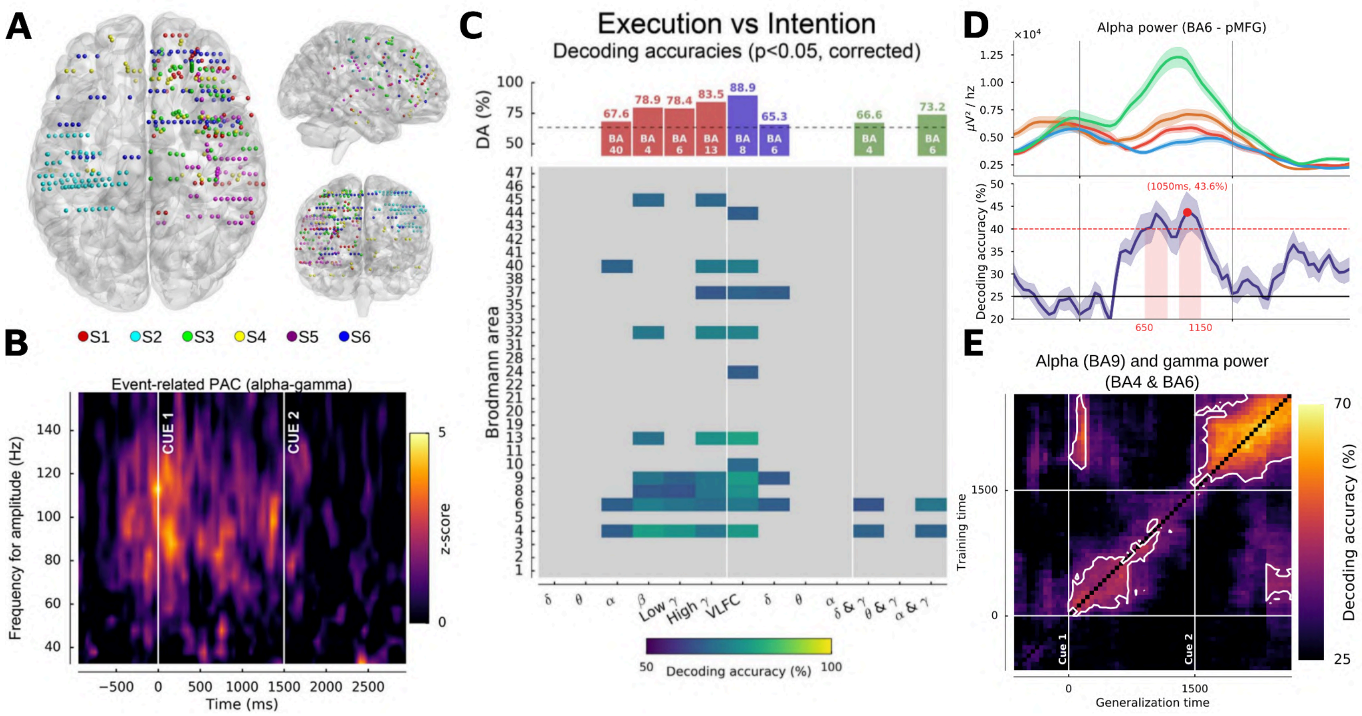

Figure 1. Decoding motor planning, execution and upper-limb directions using amplitude, phase and PAC neural markers extracted from human intracranial EEG
(A) Intracranial implantation of the six subjects *(B)* Event-related alpha-gamma PAC of a premotor site. The beginning of the planning and execution phases are represented by the two vertical white lines *(C)* Decoding performances of execution vs. planning. Non-grey indicates accuracies statistically above the chance level. The highest decoding achieved using the very low-frequency phase *(D)* top row represents the dynamic of the alpha power of a premotor site for the four upper-limb directions (up in red, down in blue, left in green and right in orange) and the two vertical lines delimit the three motor phases (i.e. rest, planning the movement and executing the movement). The bottom row represents the instantaneous decoding, with a maximum of ~44% reached during the planning phase (the theoretical chance level at 25%) *(E)* Temporal generalisation by combining alpha and gamma power features.

Global domain: neural interactions during goal-directed learning

Beyond local activations: neural interactions involved during goal-directed learning, information-flow, redundant and synergistic codings

- **Combrisson et al. (*in prep*):** Large-scale cortico-cortical interactions during visuomotor mapping relies on both redundant and synergistic coding
- **Combrisson et al. (2023, *eLife*):** Interactions between prefrontal and insular regions better discriminate reward and punishment learning than local activations

Goal-directed learning is a form of learning involved in instrumental conditioning where agents learn to associate the motor responses with the resulting outcomes (Staddon and Cerutti, 2003). Evidence are suggesting that goal-directed learning emerges from the coordinated activity of neural populations distributed over the associative fronto-striatal circuit (Balleine, 2019; Dolan and Dayan, 2013). Most of what we know about goal-directed learning comes from neurophysiological recordings in animals or from the fMRI literature, with a high spatial resolution but a poor temporal resolution. Consequently, very little is known about the dynamic in humans and about how core learning-related regions are interacting.

Update of internal cognitive map supported by redundant and synergistic cortico-cortical interactions

Goal-directed learning critically depends on the update of internal representation, or "cognitive map" representing the causality between actions and their consequences on the environment (Behrens et al., 2018). Using MEG recordings, we investigated whether the update of a cognitive map encoding the relationships between stimuli, actions and outcomes supporting exploration and exploitation is supported by large-scale cortico-cortical interactions (Combrisson et al., in prep). To this end, we used the interaction information and measures of higher-order to reveal the nature of the cortico-cortical interactions i.e. distinguish between redundant and synergistic interactions (Ince et al., 2017; McGill, 1954). Preliminary results are suggesting that the update of the internal cognitive map requires strongly redundant within lobe interactions (segregated within the occipital and prefrontal cortices) superimposed with long-range fronto-occipital synergistic interactions (*Figure 2A*).

Reward and punishment learning disentangled by neural interactions

Reward seeking and punishment avoidance are two driving strategies used by humans to learn. fMRI meta-analyses revealed that reinforcement learning primarily involves subcortical (ventral striatum), prefrontal (orbitofrontal and dorsolateral cortex) and insular regions (Bartra et al., 2013; Fouragnan et al., 2018; Garrisona et al., 2013; Yacubian et al., 2006). However, it is currently debated whether both strategies are supported by a single set or regions that activate differently or by anatomic divide learning systems (Gueguen et al., 2021; Palminteri and Pessiglione, 2017; Pessiglione and Delgado, 2015). We tested a more modern hypothesis suggesting that instead, learning could emerge from the interactions between those regions (Hunt and Hayden, 2017). 17 subjects implanted with iEEG electrodes participated in a reinforcement learning task that consisted in choosing the stimulus to maximize reward incomes or minimize punishments. Preliminary results are suggesting that prefrontal and insular regions were all involved in various degrees during both reward and punishment learning. However, interactions between those core learning regions were more specific than local activations suggesting that strategy selection could be more precisely achieved through neural interactions

(Combrisson et al., 2023). Importantly, we found a driving role of the anterior insula during punishment learning and from the ventromedial prefrontal cortex during reward learning (*Figure 2B*). Interestingly, we already showed earlier the leading role of the anterior insula toward the anterior cingulate cortex for trials followed by error answers, suggesting an important implication for error monitoring (Bastin et al., 2016).

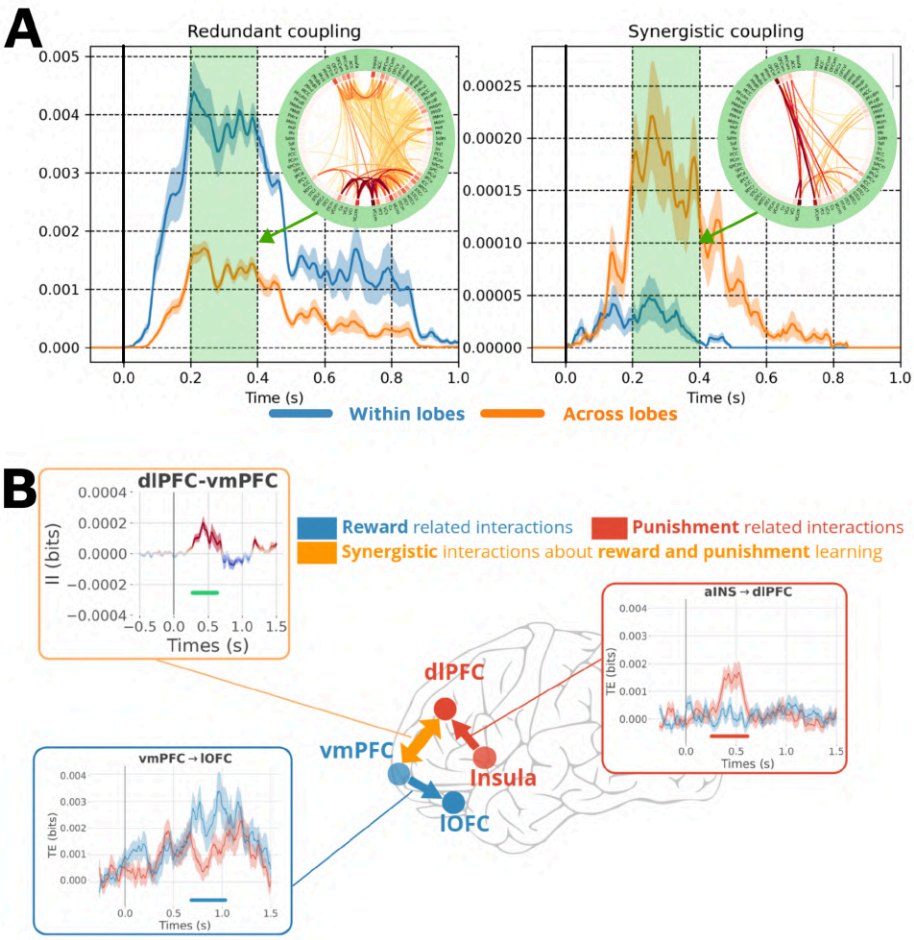

Figure 2. Cortico-cortical interactions during goal-directed learning
(A) MEG recordings during a visuomotor mapping learning task revealed that updating the internal cognitive-map ([200, 400]ms) required local redundant interactions mostly within lobes (occipital and prefrontal cortex) superimposed with long-range synergistic interactions (fronto-occipital)
(B) iEEG recordings during a reinforcement learning task revealed clearly dissociated interactions between the vmPFC→lOFC about reward only (blue), and between the aINS→dlPFC about the punishment only (red). Decoding both reward and punishment learning required synergistic interactions between the dlPFC-vmPFC (yellow) (*aINS = anterior insula; vmPFC = ventromedian prefrontal cortex; dlPFC = dorsolateral prefrontal cortex; lOFC = lateral orbitofrontal cortex*)

Non-parametric statistics on measures of information

We use statistics to evaluate whether an effect (e.g. decoding, a quantity of information etc.) is reliable or not. Non-parametric statistics can be used for significance testing and it consists of estimating if the effect obtained could have been reached by chance or not. To this end, we slightly destroy the data structure (e.g. by shuffling across conditions) and recompute the measure of information. By doing this enough, we can sample the chance-level distribution of the considered measure and quantify the likelihood of our true effect. Non-parametric statistics do not require assumptions about how the data are distributed (e.g. normally distributed, equal variance etc.) however, those methods are computationally cumbersome. I contributed to promoting and democratising non-parametric statistics combined with measures of information, especially one applied to neurophysiological data as intracranial EEG.

Statistical analyses at the subject- and population-level by combining non-parametric approaches and measures of information (information-theory, machine-learning etc.) for neurophysiological data

- **Combrisson and Jerbi (2015, *J. of Neuroscience Methods*):** We recalled to neuroscientists that when using ML approaches, the decoding chance-level depends on the number of samples (>580 citations)
- **Combrisson et al. (2022, *NeuroImage*):** I introduced a statistical framework to perform group-level inferences using powerful measures of information

Empirical estimation of the chance level in machine-learning

For a standard two classes problem, the theoretical chance level i.e. the decoding achievable by chance is 50%. This theoretical threshold is reachable with an infinite number of samples however, in practice, the decoding chance level depends on the number of samples and high decoding can be observed with a few samples. The ML community was already aware of this dependence on the number of samples, but several neuroscientific studies used this theoretical threshold as statistical proof of significant decoding. We took this opportunity to raise a red flag by showing this phenomenon (Combrisson and Jerbi, 2015). To this end, we classified simulated noise and resampled MEG data with a varying number of samples. As expected, we showed that high decoding could be reached by chance in the presence of a few samples and the more samples there are, the closer the empirical threshold is to the theoretical one (*Figure 3A*). To conclude, we insisted on the use of non-parametric permutations as a data-driven estimation of the chance level. Recently, we reused this simple data simulation approach to compare the performance of standard classifiers in the case of imbalance classes (Thölke et al., 2022).

Group-level statistics on measures of information

I recently introduced a statistical framework to identify both task-related local and network modulations (*Figure 3B*) i.e. local activity and interactions between regions modulated according to variable of the task or following the behaviour (Combrisson et al., 2022a). To this end, this framework is combining powerful measures of information from popular fields like the information-theory, machine learning models or measures of distances (Cover and Thomas, 1991; Glaser et al., 2019; Kriegeskorte et al., 2006; Kriegeskorte and Douglas, 2019; Panzeri et al., 2017; Vu et al., 2018) with non-parametric statistics (Maris and Oostenveld, 2007; Nichols and Holmes, 2002). The framework supports both spatially uniform recordings like M/EEG such as sparse intracranial EEG. Importantly, it allows us to take into consideration inter-subjects variability by using fixed- and random-effects models (Penny and Holmes, 2007). We recently applied my framework to show that the beta power extracted from local field potential recorded in monkeys' striatum encodes reward prediction error (Basanisi et al., under review).

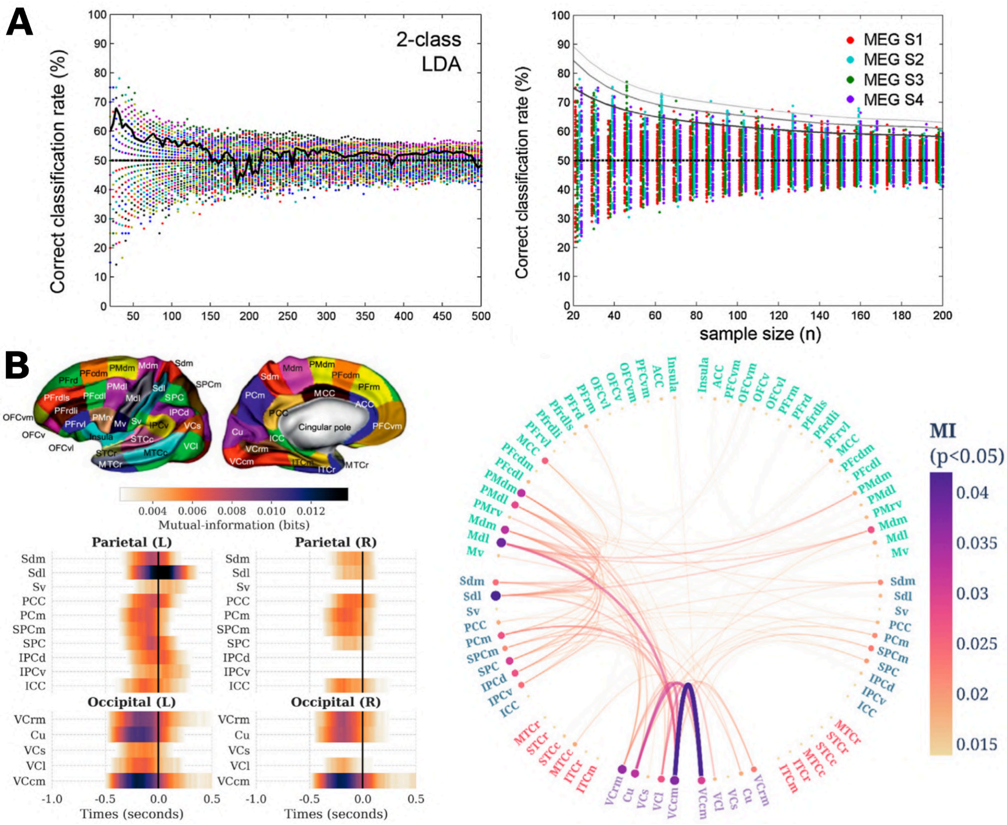

Figure 3. Non-parametric statistics on measures of information
(A) Dependence of the decoding on the number of samples using simulated and resampled MEG data. The larger the sample size, the more the empirical chance level gets closer to the theoretical one (50% for two classes) (Combrisson and Jerbi, 2015)
(B) local regions and pairwise interactions modulated during visuomotor learning revealed by our statistical framework (Combrisson et al., 2022a).

Neuroinformatics

Throughout my career, I have always made this extra effort for sharing my neuroinformatic developments in coherent packages and make them accessible to non-expert through illustrated examples and tutorials. I have also contributed to neuroinformatic events gathering all sorts of scientists around neuroinformatic questions and issues.

Python open-source software

Open-source Python softwares for brain data visualization, cross-frequency coupling, statistical analyses and functional connectivity estimations

- **Combrisson et al. (2017, 2019, *Frontiers in neuroinfo.*):** we shared with the community a Python software called *Visbrain* dedicated to efficient brain data visualization, oriented toward intracranial EEG
- **Combrisson et al. (2020, *PLoS Comp. Biol.*):** we introduced a method for assessing cross-frequency coupling using mutual-information and wrapped it inside a Python package called *Tensorpac*
- **Combrisson et al. (2022, *JOSS*):** we opened *Frites*, a Python library for group-level analyses and functional connectivity estimations using cutting-edge metrics from the information-theory
- **Vinchhi*, Neri*, ..., Marinazzo*, Combrisson* (*in prep*):** in 2023, I supervised a student during the 6 months of the *Google Summer of Code*. We worked on a solution to estimate Higher-Order Interactions on a GPU. We are preparing the manuscript.

Intracranial EEG offers both exceptional temporal and spatial resolution. However, the implantation of the electrodes depends on the localization of the epileptic zone, which means that at the population level, the number of unique subjects per brain region changes. I started a software called Visbrain[1] (236 stars - 65 forks) (Combrisson et al., 2019, 2017b) dedicated to solving my visualisation issues related to intracranial EEG (*Figure 4A*). The software has then been extended to support parcel-based representations, functional connectivity, M/EEG data etc. During my PhD, I implemented and compared several existing methods for measuring cross-frequency coupling and benchmarked them aginst the one I proposed based on the Gaussian Copula Mutual Information (Ince et al., 2017). I gathered together all of those methods in an open-source Python package called Tensorpac[2] (76 stars) (Combrisson et al., 2020). The package also included methods for simulating cross-frequency coupling and non-parametric statistics for significance testing (*Figure 4B*). More recently, I shared with the community the statistical pipeline I introduced inside a Python package called Frites[3] (68 stars) (Combrisson et al., 2022b). Since then, Frites has been integrated in EBRAINS, a European open-research platform gathering tools and data for brain research. In total, the three software represent almost 40000 lines of code. I did several workshops and tutorials to form students on programming and statistics in Lyon (in Lyon, Marseille and Rome) and I presented my neuroinformatic tools during the NeuroFrance 2023 conference. All three come with tests to certify that they work as expected, online documentation and a gallery of examples mainly dedicated to students. I also contributed to several other packages for processing neurophysiological data (Lajnef et al., 2017; Meunier et al., 2020).

[1] https://github.com/EtienneCmb/visbrain
[2] https://github.com/EtienneCmb/tensorpac
[3] https://github.com/brainets/frites

Finally, in 2023 I proposed a project for the *Google Summer of Code* (GSoC) aimed at estimating Higher-Order Interactions (HOI). HOI seeks to go beyond pairwise interactions by examining the type and quantity of information conveyed by groups of *3, 4, ..., N* variables. However, computational challenges arise in estimating HOI due to the substantial number of multiplets compared to pairwise interactions. For instance, with 20 brain regions, there are 190 undirected pairwise links and over 1 million possible multiplets. To address this challenge, I supervised a student for six months to develop a method for computing HOI using the Jax library on a GPU (or CPU). Together, we implemented ten different metrics into a single package, still under development, named hoi[4].

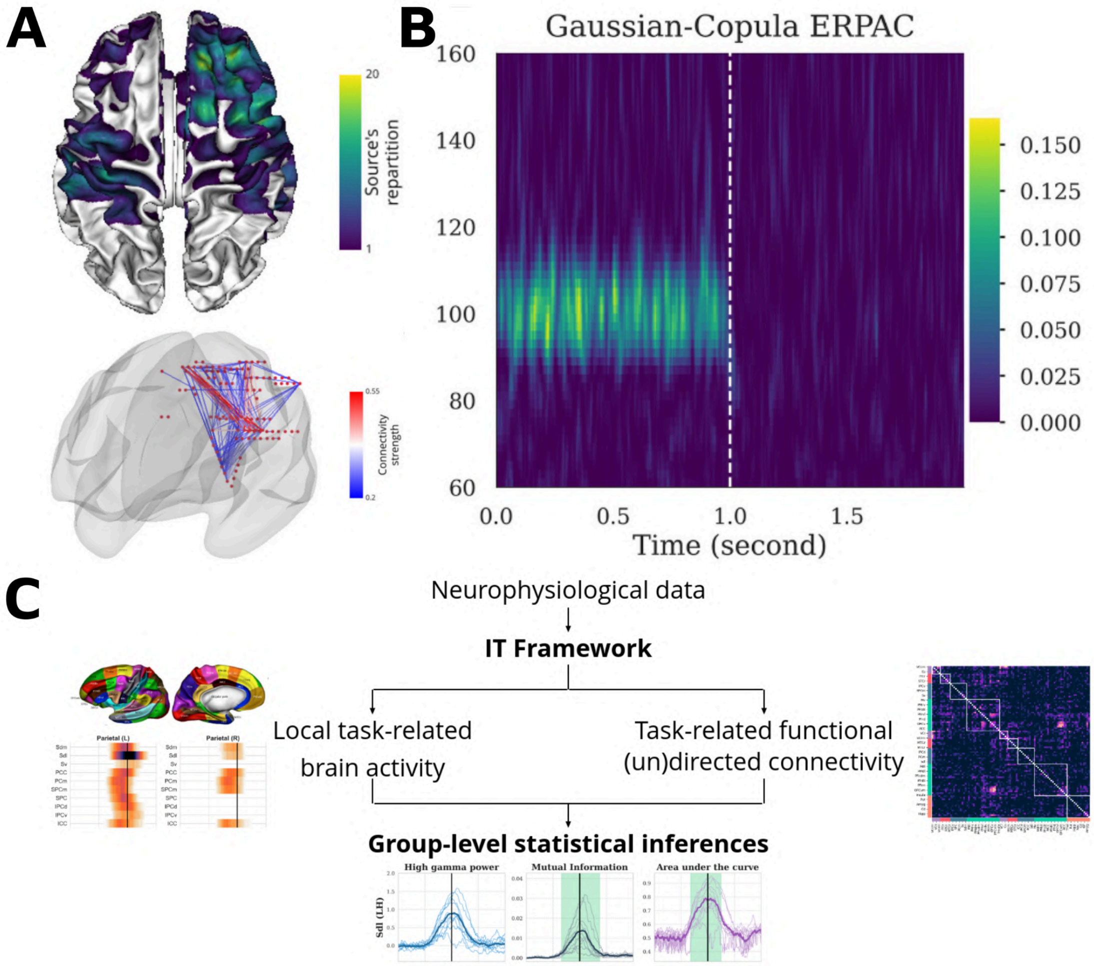

Figure 4. Open-source Python software

(A) Brain data visualization of intracranial EEG, using *Visbrain* to plot the cortical repartition of the number of unique subjects and the functional connectivity between intracranial recording contacts (Combrisson et al., 2019, 2017b)
(B) Dynamic phase-amplitude coupling on simulated data using our method embedded inside the *Tensorpac* package (Combrisson et al., 2020)
(C) Statistical framework included inside the *Frites* Python package applied on local activity and functional connectivity to relate both of them with behavioural variables at the population-level (Combrisson et al., 2022b)

[4] https://github.com/brainets/hoi

Community-driven projects

Bringing neuroinformatic knowledges to the non-expert community

- **Gau, Combrisson et al. (2021, *Neuron*):** three years in a row, I contributed to the organization of BrainHack events gathering neuroinformatic experts and non-experts
- **Niso et al. (2022, *NeuroImage*):** I was invited to contribute to the statistic and software sections of a collective initiative

Since my arrival at the INT in 2019, I have been co-organising BrainHack events (Gau et al., 2021). This event gathers students and researchers from many disciplines for collaborating on neuroinformatic problems. I have been leading projects for four years in groups of 5-8 people (mainly PhD students and postdocs), from pure informatic optimization problems to the understanding of the math behind higher-order interactions. I was also invited to contribute to the software and statistics sections of a collective initiative for gathering the best practices with neurophysiological recordings (Niso et al., 2022).

Supervision and integration in the INT

I co-supervised the internships of three master's students in 2021, 2022, and 2023. One of them was awarded a PhD scholarship this year. I will continue to co-supervise his PhD, particularly focusing on the data analysis component. Additionally, this year, I supervised a student from India during the six-month Google Summer of Code program. Lastly, together with Dr. Bjørg Kilavik, we recruited a biomedical engineer for a project focused on characterizing laminar traveling waves. She commenced her project in February.

This year, I joined a working group within the INT focusing on the ethics of publication. The group aims to clarify internal rules regarding authorship, especially for technicians and engineers as well as experimentalists. I am representing the postdoctoral researchers of the INT in this group. Finally, I am one of the organizers of a workshop on transient activity (TRANSint[5]).

[5] https://conect-int.github.io/transint.github.io/

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