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► **To cite this version:**

Guillaume Dumas. Neural dynamics of synchronous imitative interaction. Neuroscience. UPMC, 2011. English. NNT: . tel-01123458

HAL Id: tel-01123458

<https://hal.science/tel-01123458v1>

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Ecole Doctorale ED3C : Cerveau, Cognition, Comportement

THÈSE DE DOCTORAT

Discipline : Neurosciences Cognitives

présentée par

Guillaume DUMAS

**Dynamiques neuronales de
l'interaction imitative synchrone**

**Neural dynamics of
synchronous imitative interaction**

dirigée par Jacqueline NADEL et Jacques MARTINERIE

Soutenue le 3 Octobre 2011 devant le jury composé de :

Prof. Philippe GAUSSIER	Univ. de Cergy-Pontoise	rapporteur
Dr. Jean-Philippe LACHAUX	INSERM	rapporteur
Prof. Fabio BABILONI	Univ. de Foggia	examinateur
Dr. Julie GRÈZES	INSERM	examinateur
Prof. Lionel NACCACHE	Univ. Paris 6	examinateur
Prof. Olivier OULLIER	Aix-Marseille Univ.	examinateur
Dr. Jacqueline NADEL	CNRS	directrice
Dr. Jacques MARTINERIE	CNRS	directeur

Institut du Cerveau et de la Moelle épinière
47 boulevard de l'hôpital
75 651 Paris Cedex 13

École doctorale ED3C
4 place Jussieu
75 252 Paris cedex 05

*Cette thèse est premièrement dédiée à Line Garnero,
qui fut et restera un exemple humain et scientifique.*

Je dédie également ce travail à mes parents.

*"If everybody would agree that their current
reality is A reality, and that what we essentially
share is our capacity for constructing a reality,
then perhaps we could all agree on a
meta-agreement for computing a reality that
would mean survival and dignity for everyone
on the planet, rather than each group being
sold on a particular way of doing things."*

Francisco Varela

Remerciements

Mes pensées vont en premier lieu vers Line Garnero qui était à l'origine même de cette aventure. Je la remercie de m'avoir fait confiance et donné la chance de travailler sur ce sujet passionnant. Je n'ai cessé de penser à elle et à ses nombreux conseils bienveillants. Les mots me manquent pour rendre hommage à cette belle personne qui nous a tous marqué et continuera à nous manquer.

Je souhaite remercier ma famille pour leur compréhension et leurs encouragements. Ils m'ont fourni les possibilités de faire ce à quoi j'aspirais et je leur en serais toujours reconnaissant.

Mes remerciements vont également aux deux rapporteurs ainsi qu'aux examinateurs de cette thèse. Le fait qu'ils aient accepté de prendre de leur temps pour l'évaluer est autant un honneur qu'un encouragement.

Je suis profondément reconnaissant envers Jacqueline Nadel et Jacques Martinerie pour l'encadrement qu'ils ont su me donner. A eux deux, ils ont fourni de manière complémentaire l'environnement idéal à ma formation à la fois par leur grande érudition et leurs qualités humaines. Tout en me laissant explorer en autonomie ce moment de métamorphose qu'est la thèse, ils ont toujours été là pour me guider. Chacun incarne des valeurs nécessaires à l'épanouissement du scientifique. Jacqueline m'a montré l'importance de conserver sa force morale ainsi que de tenir un discours légitime. Jacques a su me montrer par sa sérénité et son humour qu'il faut toujours rester humble face à la connaissance. Il a réussi également à cultiver de façon bienveillante mon goût pour la sérendipité.

Ce projet n'aurait pas été possible sans toutes les personnes qui y ont contribué : Robert Soussignan par son aide en analyse comportementale et ses conseils, Laurent Hugueville ainsi que Pierre Canet pour leur expertise technique et leur disponibilité, et Florence Bouchet pour son aide lors des expériences et sa gentillesse. Je tiens également à remercier chaleureusement Mario Chavez pour ses nombreux conseils méthodologiques et sa bonne humeur si encourageante.

Merci également à Michel Le Van Quyen, Jean Lorenceau, Anne-Lise Paradis, Nathalie George et Catherine Tallon-Baudry pour les discussions scientifiques que nous avons pu avoir.

Une pensée pour tous les amis du *LENA* : Olivier, Yohan, Karim, Rémi, Guillaume, Benoît, Anaël, Julien, Frederic, Valentin, Claire, Mario, Lionel, Jean-Didier, Christophe, Denis et Antoine.

Une mention spéciale pour Charles avec qui j'ai partagé ces trois ans entre le laboratoire et notre colocation. Cela a offert maintes occasions de discussions sur le plan scientifique et au delà.

Luc Halard a également été un excellent partenaire de discussions entre philosophie et science. Nos projets artistiques furent autant une source d'inspiration que de plaisir.

Je ne peux omettre Alexandre Lehmann et Luc Foubert qui m'ont accompagné amicalement de ma découverte des sciences cognitives jusqu'à leurs frontières. Ils ont une grosse part de responsabilité dans le fait que je sois "tomber dans la marmite".

Par avance toutes mes excuses à l'ensemble des personnes que je n'ai pas nommé ici. Cette thèse, à l'image de son sujet, émane d'une myriade d'interactions sociales, bon nombre de personnes de multiples horizons y ont contribué sans même le savoir.

Enfin, je tiens à exprimer ma gratitude à la DGA pour le support financier de cette thèse.

Résumé

Depuis 2002, une nouvelle technique de neuroimagerie appelée hyperscanning permet d'enregistrer plusieurs participants simultanément et ainsi d'étudier l'interaction sociale dans un contexte réciproque et spontané. Parallèlement, les approches neurodynamique et sensorimotrice ont suggéré d'appréhender l'interaction sociale de manière plus holistique en considérant les deux individus en interaction comme un seul système, et en donnant autant d'importance au comportement qu'à leur activités cérébrales.

Cette thèse présente l'étude de paires de participants enregistrés simultanément, lors d'imitations spontanées du mouvement de leurs mains, par un système de double-vidéo combiné à un dispositif d'hyperscanning-EEG. Une analyse comportementale fine de leurs interactions a permis de procéder à une caractérisation neurodynamique des différents aspects de l'interaction, à la fois à l'échelle inter- et intra-individuelle. La première étude a démontré que les épisodes de synchronie interactionnelle étaient accompagnés de l'émergence de synchronisations de phase inter-cerveaux dans plusieurs bandes de fréquences. La seconde étude a montré à l'échelle neurale une différenciation entre l'agentivité attribuée à soi ou à l'autre et a découvert une signature de la co-appropriation de l'action chez les deux partenaires lors des interactions spontanées. La troisième valide les mesures expérimentales par des simulations biophysiques de paires de cerveaux humains. Elle montre également les effets de la connectivité anatomique sur les dynamiques neurales intra-individuelles et sa facilitation du couplage sensorimoteur inter-individuel.

Mots-clefs

Hyperscanning, Synchronisation, Imitation spontanée, EEG, Agentivité, Connectome, Neurosciences Sociales Computationnelles

Abstract

Since 2002, a new neuroimaging technique called hyperscanning allows to record several participants simultaneously and thus to study social interaction in a reciprocal and spontaneous social context. Meanwhile, neurodynamics and sensorimotor theories suggested to understand social interaction in a more holistic approach by considering the two interacting individuals as a single system, and giving equal importance to behavior and brain activity.

This thesis presents the study of pairs of participants recorded simultaneously during spontaneous imitation of the movement of their hands, by a dual-video combined with a hyperscanning-EEG setup. A fine grained video analysis identified the episodes of interactional synchrony and imitation, thus allowing the neurodynamic characterization of various aspects of the interaction, both at the inter- and intra-individual. The first study showed that episodes of interactional synchrony were accompanied by the emergence of inter-brain phase synchronizations in several frequency bands. The second study showed a neural differentiation between self- and other-attribution of action primacy, and found a signature of the co-ownership of the action in both partners during the spontaneous imitation. The third study validated the experimental measurements with biophysical simulations of pairs of human brains. It also showed the effects of anatomical connectivity on intra-individual neural dynamics and the facilitation of the inter-individual sensorimotor coupling.

Keywords

Hyperscanning, Synchronization, Spontaneous Imitation, EEG, Agency, Connectome, Computational Social Neuroscience

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Foreword

Cognitive science has been since its origin mainly inscribed in a representational and top-down account of cognition. However, studying human cognition relies on the understanding of phenomena spanning from the molecular scales to those of the social world we are deep into. This complex interplay of brain, body and world requires a real integrative and dynamical viewpoint. The 'enactive cognitive science' emerged from this issue and proposed to adopt embodiment and situatedness as a cure for theoretical adverse effects of cognitivism (Thompson and Varela, 2001; Wheeler, 2005). It also promotes non-linear dynamics for capturing cognitive phenomena into dynamical systems that cut across the brain–body–world divisions (Le Van Quyen, 2003).

At the same period, the birth of "social neuroscience" bears witness to this apparent lack of multi-scale view of cognition. Taking into account that humans are intensely social creatures as other primates, it was also a response to this consideration of people as strictly isolated units. Thus, social neuroscience emerged from the development of social psychology to embrace neuroscientific methodologies. Its general agenda has been described in term of seeking "to understand phenomena in terms of interactions between three levels of analysis: the social level, which is concerned with the motivational and social factors that influence behavior and experience; the cognitive level, which is concerned with the information-processing mechanisms that give rise to social-level phenomena; and the neural level, which is concerned with the brain mechanisms that instantiate cognitive level processes" (Ochsner and Lieberman, 2001). This description assesses well the reminiscent influence of cognitivism: despite a clear objective of integrating these three levels of observation, each one is proposed to "giving rise" or "instantiating" the upper ones. Thus, both information processing and hierarchical perspective remained at the core of this nascent field.

Social neuroscience has successfully investigated our basic social abilities by the combination of behavioral assessment, experimental manipulation and physiological measurement, the so-called 'golden triangle' (Decety and Cacioppo, 2010). Thanks to the development of neu-

roimaging, great advance has been made toward the understanding of the potential neurobiological mechanisms underlying human social behavior (Adolphs, 2003). Studies covered different aspects of how humans perform implicit and explicit social judgment through the decoding of social signals such as facial expression (Bruce and Young, 1986; Morris et al., 1996; Phillips et al., 1997), gaze (Hoffman and Haxby, 2000; George et al., 2001), and body movements (Bonda et al., 1996; Allison et al., 2000; Grèzes et al., 2001). But the focus was essentially put on social perception.

An important step was made with the discovery of "mirror neurons" in monkeys (Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996), which respond both to perception, and execution of an action. This aroused great interest in their relevance for imitation (Iacoboni et al., 1999; Rizzolatti et al., 2001; Decety et al., 2002; Chaminade et al., 2002; Iacoboni et al., 2005; ?) and action understanding (Blakemore and Decety, 2001; Grèzes and Decety, 2001).

Later experimental studies demonstrate that action production and understanding dissociate (Pazzaglia et al., 2008; Emmorey et al., 2010). In response, theorists proposed to extend mirror neurons to the combination of a "mirror system" and a "mentalizing network" (Rizzolatti and Sinigaglia, 2010). However, the more areas are integrated, the more the theory loses falsifiability. While the lack of neurophysiological data is invoked another proposal is to make a paradigmatic shift toward a second-person approach in social neuroscience (Schilbach, 2010). Indeed, most of the neuroimaging studies investigate social phenomena from an uni-directional perspective. However, social cognition is grounded in interaction with others (De Jaegher, 2009). This social situation is fundamentally different from a passive observation and implies a bi-directional account (Frith and Wolpert, 2004; Hari and Kujala, 2009). Observational and experimental data of developmental psychology have assessed for years of the importance of social interaction in the construction of our cognitive capacities (Wallon, 1923; Zazzo, 1960; Nadel, 1986; Nadel and Camaioni, 1993), and were the bedrock of a two-body psychology.

Recent social psychology has attempted to go beyond the traditional individualist approach by integrating a dyadic account (Richardson et al., 2005; Issartel et al., 2007; Auvray et al., 2009) however social neuroscience faces number methodological limits. While adopting an embodied and a situated perspective is still an emergent trend (Klin et al., 2003; Schilbach, 2010), the dyadic issue calls for the development of adapted neuroimaging methods allowing to simultaneously record two-people engaged in an interaction. This technique has emerged in functional magnetic resonance imaging (fMRI) under the name of "hyperscanning" (Montague et al., 2002)

and started to bring promising experimental results (Hasson et al., 2004; King-Casas et al., 2005). Then hyperscanning-EEG (Babiloni et al., 2006) brought the sufficient time resolution to capture the dynamical essence of social interaction by giving access to the millisecond timescale. However pioneer EEG hyperscanning studies either averaged neurophysiological data on individual brains (Tognoli et al., 2007) or did not integrate real reciprocal interaction in their protocols (Lindenberger et al., 2009).

This thesis proposes to associate two-body psychology and two-person neuroimaging by combining non linear inter-brain analysis with a real-time interaction protocol. More precisely, it will concentrate on neurodynamics, which study neural oscillations, and developmental psychology, which has a long-lasting experience in the study of social interaction. Although these fields are very distant from a methodological point of view, they nevertheless share conceptual interests.

A common focus of interest is the emergent phenomenon of synchronization, which has been respectively proposed as a mechanism of the neural information integration (Rodriguez et al., 1969; Varela et al., 2001) and the regulation of social interaction (Condon and Sander, 1974; Fogel, 1993b; Isabella et al., 1989). This spontaneous apparition of order is one of the oldest non-linear phenomena studied by humans since it is observable across physical, biological, neural and social levels (Strogatz, 2003). This thesis takes the advantage of the multi-scale property of synchronization for the investigation of the neural dynamics of spontaneous imitative interaction in humans.

The introduction was not written as a synthesis of each paper introduction but rather aims to present the general theoretical framework by providing a multi-scale account of synchronization. It will first delineate how our understanding of this phenomenon has evolved from the early observations of cycles in nature to modern non-linear formalism. The subsequent focus on neurodynamics will then present how this scientific field has investigated neural synchronizations and their potential role in cognition. The social scale will then be discussed in regards to results brought by developmental psychology, developmental and evolutionary robotics, cognitive psychology and social neuroscience. The last part of the introduction will describe the hyperscanning technique as a potential methodological tool for bridging the gap between neural, behavioral and social levels. It will present the existing literature and prepare the floor for the experimental parts of the thesis. The related papers will follow each preceded by introductory comments on how it is connected to the others.

1 Introduction

1.1 Oscillations in nature

Synchronizations are ubiquitous in nature and have fascinated humans from the first astronomers to the recent chaos theoreticians. This first part of this introduction will sketch an illustration of the progress in understanding synchronization and non-linear dynamics. It will describe the contributions of various thinkers to the description and interpretation of observable dynamical phenomena in nature.

1.1.1 Musica Mundana

Although synchronizations are ubiquitous in nature, their emergence is sealed in oscillations and rhythms. Oscillation is inherent to natural mechanisms. From atomic to astronomic scales, they are the signatures of time-invariants. First human cultures have been fascinated by these invariants: the day and night alternation, the cycles of seasons or the precession of equinoxes. Astronomy is thought to be the first human scientific approach. Indeed, the sky offered the most mysterious and obvious patterns to human minds. The abundance of observable cycles gave rise in early cosmologies to the inscription of oscillations at the core of the universe. In Hindu theology for example, the creation and destruction of the universe is considered as the major cyclic process from which other natural cycles emerge. In order to describe them, they developed a very precise metrics of time (Narayan, 2007) ranging from $10^{-7}s$ (trasarenu) to $10^{22}s$ (day of Brahma). Calendars were the first efficient tools to account of these cycles. For instance, the flooding cycle of the Nile was such an important natural cycle and in meantime was so predictive that the Egyptians based their ancient calendar on it. (Parker, 1950)

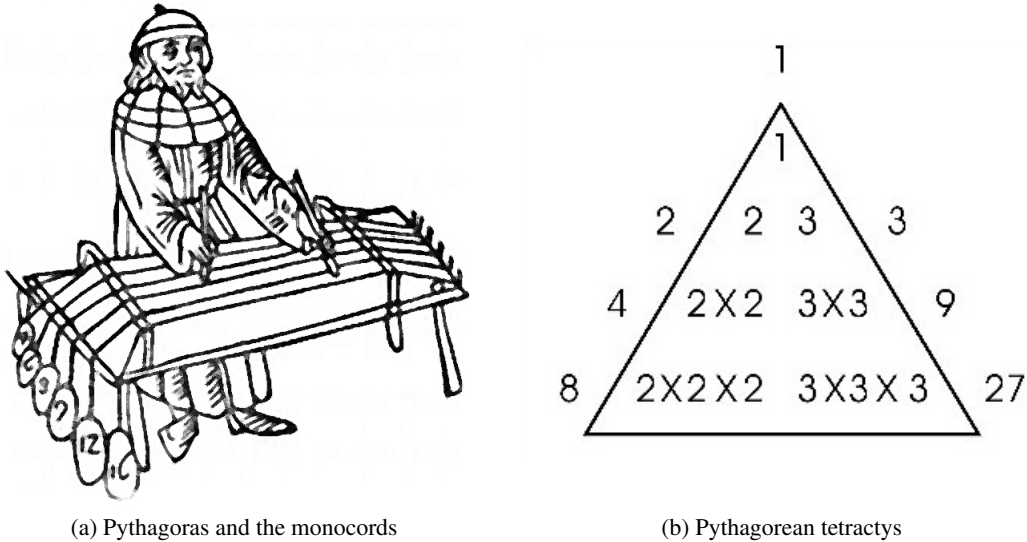


Figure 1.1: a) Illustration depicting Pythagoras performing harmonics experiments with stretched vibrating strings. (from Gaffurius 1487) b) Pythagorean Tetractys of multiplication.

Whereas numerous representations of time were invented to symbolize and study these cycles, Pythagoras (6th century B.C.) was the first to unveil a mathematical formalism for this phenomenon. Interrogated by the variation of sounds made by a blacksmith striking his anvil, he understood that notes were related to the weight of the hammer. Thus, numbers appeared to govern musical tone. Pursuing his investigation with vibrating strings, he discovered that their length changes the pitch of the notes they produce. He embedded the set of proportions governing the interdependent harmonies of tones within the Tetractys, which became the sacred symbol of Pythagorean number mysticism. This set of numbers is at the basis of music but also provided the idea of the "Musica Mundana", the Music of the Spheres. This music was proposed to be present everywhere and to govern all temporal cycles, such as the seasons, biological cycles, and all the rhythms of nature. Plato discussed these underlying mathematical laws of proportion in space and time as the signature of the creation of the universe (Plato, 1888).

1.1.2 Modern physics: the rise of mathematical formalisms

It took a long time to adopt a less mystical description of those natural phenomena. In the 16th century, Galileo Galilei created modern physics by combining systematic methodology and objective descriptions of his observations. Regarding the oscillation phenomenon, he formulated in physical terms the complete laws governing the vibrating string. But he also discovered the

property of isochrony for pendulums (Galilei, 1638). He noticed that the oscillation period of a pendulum remains constant, regardless of the angle of the swing. Christiaan Huygens, a Dutch mathematician, astronomer and physicist, found the first explanation of this isochronous property.

Cycles, clocks and music also fascinated Huygens. He succeeded to make the first formal description of the period T of an ideal mathematical pendulum in function of its length l and the gravitational acceleration g : $T = 2\pi\sqrt{\frac{l}{g}}$ (Huygens, 1673) Because of his use of modern notation in formula, he is considered as one of the first theoretical physicist.

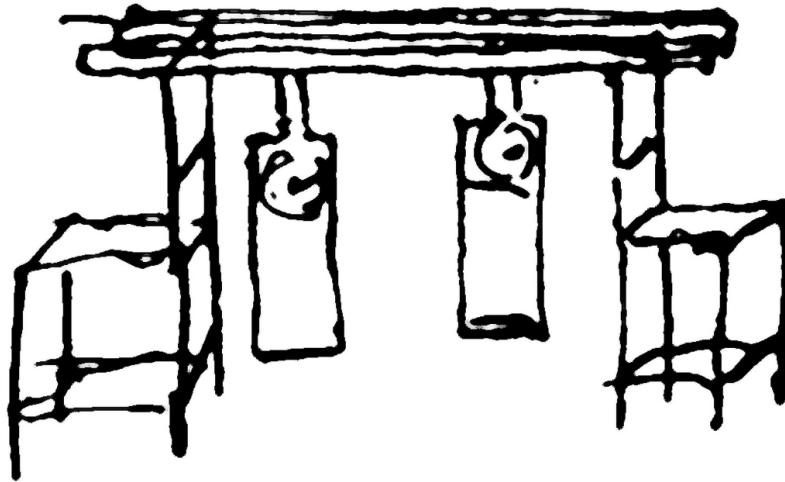


Figure 1.2: Original drawing of Huygens illustrating his experiments with pendulum clocks. (from Huygens 1673)

But Huygens did not restrain his investigation to a single pendulum. In 1665, he wrote to the Royal Society of London to describe the discovery of an "odd kind of sympathy" between the pendulums of two clocks hung on the same support. The pendulums tend to synchronize or swing in opposite directions. This was the first observation of coupled oscillations.

Obsessed by oscillations, he was also the first to describe light as waves. This idea known as the Huygens-Fresnel principle, was part of our understanding of the wave particle complementarity pair more than two centuries later (Huygens, 1678).

But before this modern revolution, an important step was made in the explanation of prevalence of oscillations in the universe. The idea came also from astronomers (Voltaire, 1738). Pursuing the laws describing orbits initiated by Johannes Kepler (1571 – 1630) and pursued by Pierre-Simon Laplace (1749 – 1827), Joseph Louis Lagrange provide in his "Mécanique analytique" (Lagrange, 1811) a powerful framework for describing the laws of conservation in physics, and thus explain-

ing why repetitive motions are so omnipresent in the universe. The Lagrangian formalism captured mathematically the invariants in time, which govern physical entities.

William Rowan Hamilton presented a decade later an even more powerful theory that brings together both mechanics and optics. Its formulation is based on the same physical principles of the Newtonian and Lagrangian mechanics but allow dealing efficiently with the equations of motion.

This was a preparatory step towards the second revolution of physics brought by James Clerk Maxwell in 1865. This Scottish physicist and mathematician made one of the most prominent achievements of the 19th century with his classical electromagnetic theory. For the first time, all previously unrelated phenomena observed in electricity, magnetism and even optics were explained by a consistent theory. The Maxwell's equations demonstrated that electricity, magnetism and light are all manifestations of a unique phenomenon: the electromagnetic field (Maxwell, 1865).

Despite this fundamental breakthrough, particles of matter were still considered to be the fundamental building blocks of everything. Vibrations and waves were just thought as particular phenomena that particles can do together.

At the beginning of the 20th century, a chain of discoveries initiated by Albert Einstein led to the realization that the subatomic "particles" could be seen in fact as waves. Following the work of Max Planck, he postulated that photons transmit light energy not continuously but in "quanta" or bundles of wave. The energy is proportional to the frequency of the wave: $E = h\nu$ (Einstein, 1905).

Interestingly, the orbit concept used by astronomers two centuries before led Louis De Broglie to the extension of this quantified energy to all particles. In his 1924 thesis (De Broglie, 1924), he took the two known expressions of the electron energy: $E = mc^2$ and $E = h\nu$ and expressed them in function of speed and phase. This allowed him to link the momentum of any particle to its associated wavelength: $p = h/\lambda$

In this new world-view, vibrations and waves become the fundamental constitution of the observable universe. Although De Broglie originally thought that particles were associated with a real physical wave, Erwin Schrödinger formalized the wave aspect of matter within his famous equation as a pure probabilistic interpretation: $i\hbar \frac{\partial}{\partial t} \Psi = \hat{H}\Psi$. This mathematical entity does not need any support of physical elements. This opened a fantastic debate in the physicist community

about the limit of formalism towards the interpretation of reality. Quantum mechanics also pointed out the problem of the measurement: any observation perturbs the reality itself.

All these debates were also fueled with the nascent theory of relativity of Einstein. Interestingly, this huge brainstorming catalyzed the emergence of new mathematical tools. John Von Neumann was one of the leading contributors by providing a unified mathematical framework to quantum mechanics (von Neumann, 1955). He adapted the Willard Gibbs concept of phase space within the Hilbert formalism. But this tool gives him a powerful formalism for developing a new field: the ergodic theory.

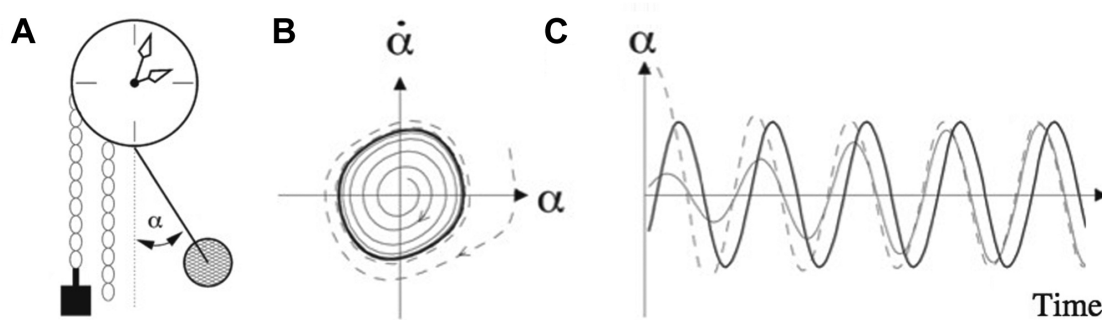


Figure 1.3: A) An example of a self-sustained oscillator, the pendulum clock. The potential energy of the lifted weight is transformed into oscillatory motion of the pendulum and eventually into the rotation of the hands. B) State of the pendulum characterized by its angle α and its time derivative $\dot{\alpha}$. The time evolution of the system can be described in the phase plane $(\alpha; \dot{\alpha})$. The closed curve (bold curve) in the phase plane attracts all the trajectories from its neighborhood, and is therefore called the limit cycle. C) Same trajectories shown as a time plot. (from Rosenblum and Pikovsky 2003)

While quantum mechanics was focused on the constitution of the physical universe, the ergodic theory pursued the dynamical understanding of its evolution through invariant measures. The phase space gave the possibility to interpret the evolution of the system in a geometric manner: each possible state of the considered system is represented by a unique point in this space, thus the evolution of the system can be described as a trajectory, an orbit.

If the classical laws of mechanics can capture simple physical systems, statistical physics revealed that complex systems were far more difficult to describe analytically. Henri Poincaré demonstrated that three bodies submitted to the universal law of gravitation are sufficient to produce a trajectory that cannot be described in form of equation. A small variation in the initial condition could lead to strong difference in the resulting dynamics (Poincaré and Fichot, 1907).

This problem was precursor of the "butterfly effect" described by Edward Lorenz more than sixty years later in these terms: "One meteorologist remarked that if the theory were correct, one flap of a seagull's wings could change the course of weather forever." (Lorenz, 1963).

And Poincaré not only envisioned the chaos theory but also brought the first important result of ergodic theory. If describing analytically the trajectory were impossible, why do not seek other characteristic of the dynamics? His recurrence theorem provides an answer and the starting point of a geometrical account of complex dynamical systems. Any dynamical system could be defined by ordinary differential equations. These equations determine a flow mapping the phase space of the system on itself. Poincaré demonstrated that, if this flow preserves the volume of a set of points in the state space, then there exist orbits that intersect the set infinitely often (Poincaré, 1890). Although the exact trajectory of the whole system cannot be formally described, the recurrence theorem states that some invariants can be expressed.

At the same period a Russian mathematician called Aleksandr Lyapunov was investigating the stability of equilibria and the motion of non-linear systems. He invented the so-called Lyapunov exponent of a dynamical system that characterizes the rate of divergence of two initially separated trajectories in its phase space (Lyapunov, 1892).

The formalism was ready for a more precise study of non-linear phenomena. This is important in the study of synchronization because unlike many classical physical problems, where consideration of nonlinearity gives a correction to a linear theory, here the account of nonlinearity is crucial. Physics of the 20th century were marked by number of advances linked to synchronizations. The most important breakthroughs were made with lasers, in which different atoms give off light waves that all oscillate in unison, and superconductors, in which pairs of electrons oscillate in synchrony, allowing electricity to flow with almost no resistance.

The best conceptual advanced were made with the development of electrical and radio communication. New devices allowed a more efficient study of synchronization within the laboratory. Eccles and Vincent patented in 1920 the triode, the first alternating electric current generator. Appleton and Van der Pol used two of these generators with slightly different frequencies and showed that a coupling between them can force the systems to vibrate at a common frequency. This replicated the famous effect described earlier by Lord Rayleigh in organ pipes: their synchronization when they begin to sound in unison (Rayleigh, 1896). They also replicated the other effect called quenching (oscillation death) when the coupling annihilated the oscillations. But more importantly

Van der Pol and his colleague van der Mark discovered the first instance of deterministic chaos in 1927 (van der Pol and Van der Mark, 1927) The work of Van der Pol has multiple repercussions in physics but also in biology. His oscillator was for instance used for modeling the action potentials of neurons (Fitzhugh, 1961). But many other examples demonstrate how the advances in non-linear dynamics imprinted biology during the 20th century.

1.1.3 Self-organization in biology

Although the non-linear field of biology dates from the seventies, oscillations and synchrony have already been observed in biological system for centuries. For instance, the Dutch physician Kaempfer made in 1680 one of the earliest observation about synchronization in a large population of biological oscillating systems. He described the synchronized flashing of fireflies in Siam in these terms (Rosenblum and Pikovsky, 2003):

‘The glowworms . . . represent another shew, which settle on some Trees, like a fiery cloud, with this surprising circumstance, that a whole swarm of these insects, having taken possession of one Tree, and spread themselves over its branches, sometimes hide their Light all at once, and a moment after make it appear again with the utmost regularity and exactness.’

In 1729, the French astronomer and mathematician Jean-Jacques Dortous de Mairan discovered the circadian rhythm by observing the day and night oscillation of haricot bean leaves (Rosenblum and Pikovsky, 2003). This was the start of chronobiology. Living organisms are framed by the cycles of their environment but they do not passively mirror them: from the circadian generator to heart beat pacemaker cells, biological organisms embed different kind of cycles. More than that, they are themselves embedded in the cycles of birth and death.

In the beginning of the 20th century, while physics was tackling the structures of the universe, the understanding of how living organisms remain coherent while dynamically evolving in their environment was still a mystery. In 1944, Schrödinger published the book "What is life?" (Schrodinger, 1944) where he summarized "how can the events in space and time which take place within the spatial boundary of a living organism be accounted for by physics and chemistry?". Schrödinger proposed that all living organisms are built up from an internal code transmitted through reproduction cycles. He thus envisioned the discovery of DNA made a decade later. But Schrödinger described also a paradox: although the second law of thermodynamics doomed all closed systems to approach a state of maximum disorder, living organisms succeed in maintain-

ing a highly ordered and coherent state. The only solution to this paradox is that life cannot be considered as a closed system. However another paradox emerges: How to conciliate the inner coherence of living organisms with their openness towards the environment?

Despite his visionary point of view, Schrödinger ignored that the structure of the organisms did not rely exclusively on an internal program. Nevertheless, he stated in the 6th chapter of his book that *"...living matter, while not eluding the "laws of physics" as established up to date, is likely to involve "other laws of physics" hitherto unknown, which however, once they have been revealed, will form just as integral a part of science as the former."*

These laws were partly revealed by Alan Turing. Indeed, the father of computer science worked his two last years of life on computational biology. He published a seminal paper called "The Chemical Basis of Morphogenesis" in 1952 where he described a dynamical process by which a biological organism could develop its shape (Turing, 1952). The core mechanism relies on a non-linear chemical phenomenon called "reaction-diffusion". Sadly, non-linear science was cursed at that time and like the Lorenz's chaos paper, last Turing's work was neglected for over a decade and then discovered during the mid-1970s. Despite it is now one of the most cited papers in non-linear science, the developmental biologists seem to still ignore it. This epistemological paradox is well summarized by Richard Lewontin (Scott, 2007):

"The irony is that while Turing's model turns out to be correct in its simple outline form, it did not play a significant part in the production of modern molecular developmental biology. Developmental geneticists now study how the cell's reading of different genes produces spatial patterns of molecules in embryos, but that detailed and messy description, involving large numbers of genes and proteins, owes nothing to Turing's model."

The sad story continued with the biophysicist Boris Belousov who discovered an autocatalytic chemical reaction presenting all the characteristics described by Turing (Belousov, 1959). The Soviet scientific establishment totally rejected Belousov and his work. Although biology is characterized by far-from-equilibrium conditions and non-linear reactions, chemists and biologists remained turned to reductive explanations based on well defined causal chains and rejected totally the concepts of emergence and self-sustain dynamics. Others chemists and bio-chemists were struck by this blinkered conceptions of causality in the 1970s: Colin McClare commit suicide in response to British rejection of his proposals for resonant storage of biological energy and Giorgio Careri's experimental evidences were strongly refused by US physical chemists in the mid-1980s.

Until the 1977 Nobel Prize awarded to Ilya Prigogine, non-linear concepts did not receive a lot of attention of the public and scientific community. Ironically, this has been partly caused by the work of Alan Turing. Indeed, his idea of a universal computing machine was so powerful that it created a whole conceptual revolution towards the adoption of a representationalist vista. The birth of Cognitive Science is perhaps the best illustration. When Warren McCulloch organized the Macy conferences in the late 40s, he invited the most prominent thinkers in all fields concerned by the understanding of human mind. These conferences hosted a fascinating interdisciplinary debate about the best conceptual framework to adopt. Two main approaches were presented: one was taking cognition as an emergent property and the other seeing it as a computational phenomenon. Although the emergentist framework was interesting and pursuing directly ideas from the first cybernetics, no applications were really in sight at that moment.

On the opposite hand, the development of the nascent computer science was synonym of a promising technological development. Thus, the end of the Macy conference imprinted the new-born cognitivism program with the computationalist approach and the main metaphor of the brain as a computer was sealed (Dupuy, 1994).

Of course all scientists were aware of the power of the computer and even people from the emergentist point of view participated actively in its development. Von Neumann for instance designed the first computer architecture that is still used in most modern personal computers. However, he was taking the computer as a tool, not a model. This powerful tool gave the ability to simulate any model and test it. Von Neumann worked with Stanisław Ulam at the Los Alamos National Laboratory on the problem of self-replicating systems. They used cellular automata, simple models integrating basic rules of interaction between multiple simple elements.

Compared to the Artificial Intelligence field, which traditionally adopts a top-down methodology to simulate cognitive agents, Artificial Life tries to simulate the mechanism of life through a bottom-up approach. The conceptual difference is well expressed by the creator of this field, Christopher Langton: it consists in studying not only “life-as-we-know-it”, but also “life-as-it-might-be” (Langton et al., 1992). Thus, the core of this field is the study of emergent patterns through the coordination of basic elements. This process is usually known as self-organization and was first described by Immanuel Kant in his Critique of Judgment (Kant, 1951). He states that a self-organized entity has parts or “organs” that are simultaneously ends and means, and that such a system must be able to behave as if it has a mind of its own, that is, it is capable of governing

itself. He qualified such a system as teleological. Norbert Wiener discussed also the condition of self-organization in his book "Cybernetics: or Control and Communication in the Animal and the Machine" (1973). He mentioned the importance of phase locking or the "attraction of frequencies" and was the first to propose an oscillatory theory of cognition. We will see in the next chapter how these concepts became at the core of the neurodynamics approach.

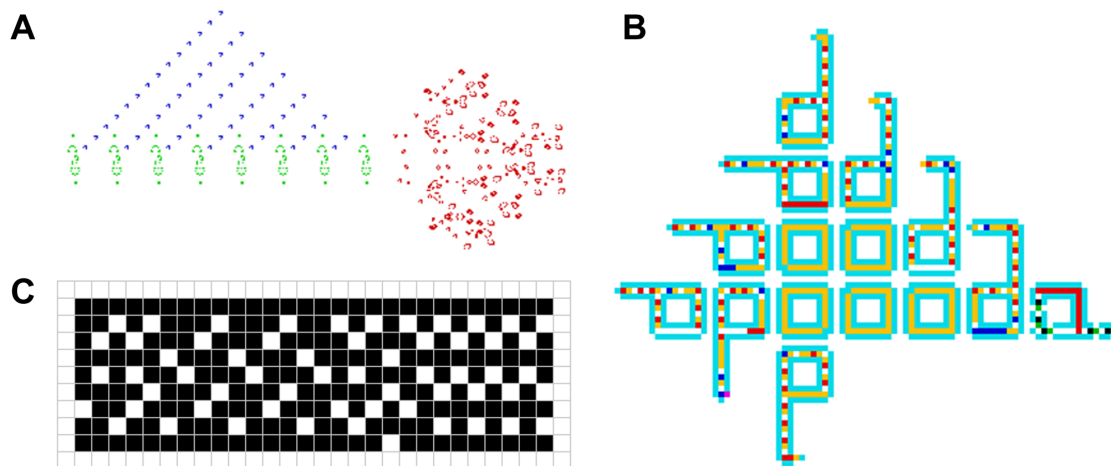


Figure 1.4: A) The Conway Game of Life (1970), the is the first 'zero player' game. Here we can see a 'breeder' structure (red) which create 'guns' (green) while moving. Each of these child structures makes 'gliders' (blue). B) The Langton loop (1984): the first self-replicating cellular automata using 8 states. C) The first 'Eden garden' discovered for The Game of Life (1971). 'Eden Gardens' are structures which have no antecedent according to the rules of the world. (from Wikipedia)

But before leaving biology for neurobiology, a last important conceptual jump has to be mentioned. Beyond self-organized systems is the problem of autonomy. A major breakthrough was made by two Chilean scientists on the formalization of this key issue in living organisms. Umberto Maturana and Francisco Varela developed in the 70s the theory of "autopoiesis" (Varela et al., 1974). Their theory stressed the intimate link between reproduction, evolution and cognition. In viewing the self-production as the key to biological phenomena, the emphasis shifts from a control viewpoint to a focus on the nature of autonomy. The autopoietic organization is characterized by an operational closure, or boundary, which is simultaneously the substrate and the product of the dynamics of the system. The system is not separated from the world, this closure is permeable to the variation of the environment and allows the system to adapt its behavior to it. This principle can be described in details for unicellular and metacellular organisms but also in organisms with a

nervous system. Unlike in the computer metaphor the nervous system is in this framework neither representational nor solipsistic. It is not solipsistic because the closure participates in the interaction of the nervous system with the environment. There is no inside and outside but a maintenance of ever changing correlations. There is no input and output but rather a structural state that conditions which perturbations are possible. The nervous system does not "pick up" information from the environment, it makes the world come up by specifying which patterns of the environment are perturbations and which changes trigger them in the organism.

The next part will focus on the neurodynamic field which is highly compatible with this new way of approaching the nervous system. Through the combination of the described tools in biology and physics, this framework has the power of analyzing the world, the body and the cognitive functions of the brain with the same conceptual tools.

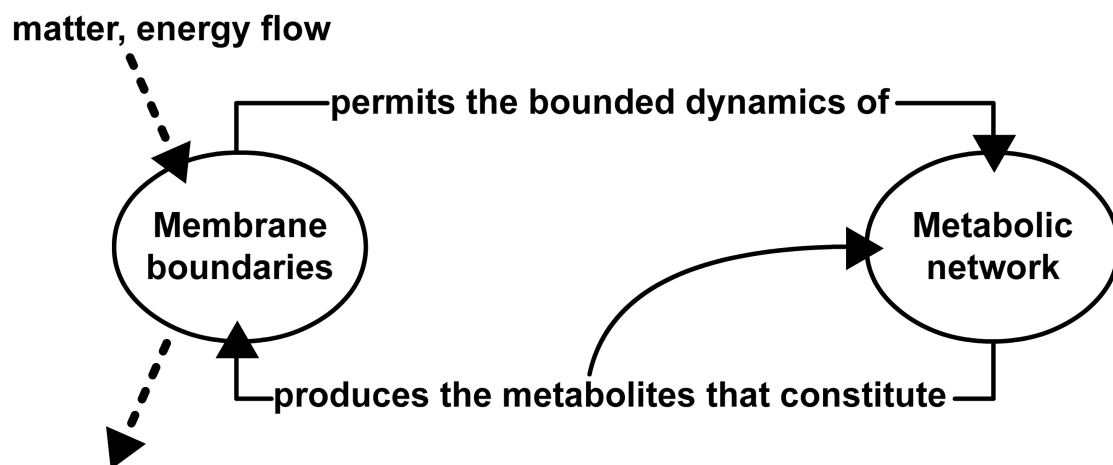


Figure 1.5: The autopoietic organization is defined as a unit by a network of production of components (chemical reactions) which (i) participate recursively in the same network of production of components (chemical reactions) that produced them, and (ii) carry out the network of production as a unit in the space in which the components exist. (from Rudrauf et al. 2003)

1.2 From neurodynamics to enaction

1.2.1 Early works: order and chaos in the brain

Neurodynamics is the field of cognitive neuroscience that focuses on brain oscillations. The term was first introduced by the neuro-cyberneticians of the forties (Burrow, 1943). but its consensual form is usually traced back to the statement of Ashby that the nervous system can be described as a non-linear system (Ashby, 1952). This interest for brainwaves inherited from electrophysiology. Since the discovery by Volta and Galvani of the effect of electricity on the neuromuscular activity of the leg of the frog, physiologists understood that electric potential was an essential vector for the information processed by the nervous system. Hans Berger brought the first assessment of brain electrical oscillations with his invention of the electroencephalogram (EEG) in 1929 (Berger, 1929). Thanks to the progress of radio telecommunication, the electric amplifiers were for the first time able to attain the sufficient signal to noise ratio necessary at the observation of brain rhythms.

The first recording techniques by ink-writer were rather limited. The first graphical Fourier analysis, the 'electrospectrography', was made thanks to electrical planimeters by Drohocki and Drohocka in 1939. This allowed Bertand and Lacape to propose the same year a first classification of the EEG in delta, theta and alpha waves (Etevenon, 1978; Hazemann and Masson, 1980).

The pioneer Grey Walter also succeeded in discovering new EEG methods, specifically in graphical representation and localization. Indeed, Walter developed at the Burden Neurological Institute in Bristol the first localization techniques by triangulation. He was able to demonstrate the occipital sources of alpha-waves but also to locate brain tumors or epileptic lesions thanks to delta waves. He also invented the first EEG topographic device by combining arrays of amplifiers and cathode ray tubes.

After the first 1947 international electroencephalography conference held in London, more international collaborations emerged. Antoine Rémond, a young French scientist visited Walter's lab after the conference and, inspired by the ongoing work, created the next year his own laboratory at the Pitié-Salpêtrière hospital in Paris. The LENA (Laboratoire d'Electroencephalographie et de Neurophysiologie Appliquée) was entirely dedicated to the development of electrophysiology at both methodological and applicative levels. In parallel to a major interest in stereotaxy and

its application for the cure of Parkinsonians, Rémond was also devoted to development of EEG methodology. He extended especially standard averaging methods by taking into account the initial phase of the signal at the stimulus presentation and thus was one of the first to conceive that the amplitude was not the only pertinent information in EEG. His creation of spatiotemporal maps was also a precursor of the representation used in modern softwares (Cherici and Barbara, 2007).

Then, the invention of the first magnetic tape recorder was a revolution because it allowed the first systematic quantitative EEG analysis. Rosenblith and Brazier devised such system in the 50s and used it for studying the autocorrelation of brain potentials (Barlow and Brown, 1955).

They solved the major problem of signal erasure caused by reading the magnetic tape thanks to frequency modulation. Thus, it was possible to play back any recorded signal as many time as needed. The idea of Rosenblith and Brazier was to playback the signal and a time-shifted version of it. By playing with the delay, the autocorrelation of the signal was experimentally at reach and could provide a fine-grained spectral analysis thanks to the Wiener-Khinchine theorem. Walter developed and popularized this technique and quickly these advances were ported to human studies. In the late 60s the EEG community gained its hugest expansion thanks to spectral analysis. Applications ranged from sleep studies, aging, neurophysiology, psychiatry and neuropharmacology.

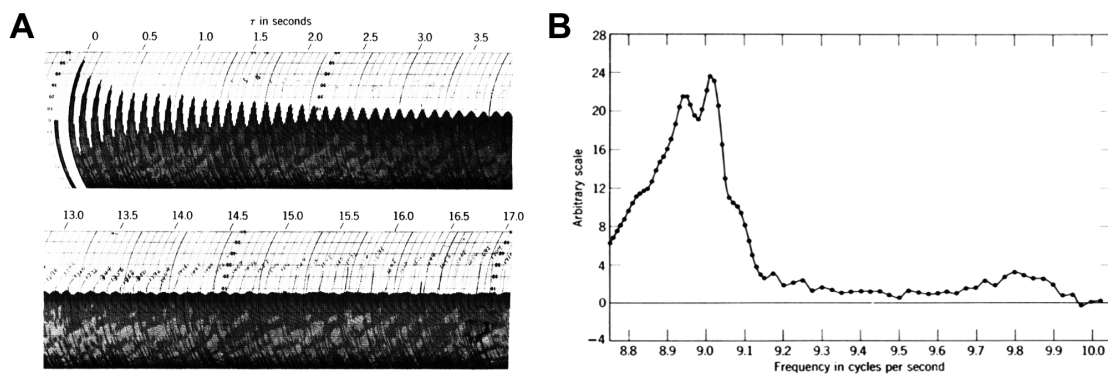


Figure 1.6: A) Analysis of autocorrelation with magnetic tape recordings of alpha waves. B) Frequency spectrum derived from the autocorrelations of the signal. (from Wiener 1973)

In parallel, averaging methods gave rise to the event-related potential (ERP) field. Walter opened also the way with his discovery of the contingent negativity variation (CNV), the first ERP component described so-far. This wave was associated to sensorimotor association expectancy and is considered as the first correlation in brain signal with a psychological feature in human (Walter et al., 1964).

The ERP community grew with studies on auditory and visual stimulation. The techniques of photic and intermittent light stimulation (ILS) were widely used and led to a vast amount of results describing ERP components and their potential functional meaning regarding perception. The most important effort was produced towards the P300 component. Chapman and Bragdon discovered P300 while comparing visual stimuli with meaning or not (Chapman and Bragdon, 1964). They observed a large positivity peak around 300ms after the stimulus presentation when it was meaningful to the subjects. This encouraged the use of ERP methods towards the study of cognition and gave the foundation of the later works on the link between this component and how the brain processes information.

ERP is nowadays a widely used technique in cognitive neuroscience and continues to provide interesting findings. But the seventies marked another milestone in neurodynamics: beyond linear methods, other techniques emerged and focused on the non-linear characteristics of the brain dynamics. Freeman, experimental neurophysiologist and theoretical mathematician, was the pioneer of these new computational approaches. Marked by the work of McCulloch on neural networks, he wanted to go beyond simple descriptions of brain activity and proposed the first model of its potential underlying mechanisms. His book "Mass action in the nervous system" in 1975 sketched his first theory and proposed an explanation of the behavioral significance of the EEG (Freeman, 1975). The key new concept is the "neural masses" defined as a set of neurons. He classified this extension of the "neural assemblies" proposed by Hebb (1949) in hierarchical "Katchalsky sets". Starting with the K0 sets composed of neurons with a common input and the same output sign (+ for excitatory, - for inhibitory), he then described KI sets, similar to K0 but with dense interactions between the neurons within the set, KII sets, composed of two KI sets densely interconnected and finally KIII with feedback loops. He argued that although the interactions within these sets are rather complex, they can be modeled by the spatio-temporal oscillations created by the "neural masses". He proposed a synthetic mathematical approach based on coupled oscillators and differential equations and applied it to neurophysiological experiments on the piriform cortex and olfactory bulb of the cat. This book really proposed innovative hypotheses towards the investigation of brain activity. More than combining state of the art mathematics and electrophysiology, he also envisioned the importance of connectivity and other core concepts such as segregation/integration of the information or phase transition. These major fundamental questions remained however beyond reach of the mathematical tools of this period.

Meanwhile, several other laboratories developed non-linear approaches. Lopez da Silva proposed the first non-linear models of EEG rhythm and pointed out the importance of thalamo-cortical loops (Lopes da Silva et al., 1974). Başar showed potential links between spontaneous EEG and ERP by also using non-linear methodology (Başar et al., 1976). Buzsáki showed the importance of the phase information contained in the hippocampal theta rhythm in rats (Buzsáki et al., 1979).

With the very intense work done by contemporary mathematician like Anosov (1963), Arnol'd (1966), Smale (1967) or Ruelle and Takens (1971), the modern chaos theory was slowly spreading in the scientific community. Some theoretical biologists had the necessary mathematical background to understand the power of such theory and started to explore its applications in biology. Rapp, for instance, concentrated on techniques of chaos quantification and reconstruction of electrophysiological signals. He realized the first quantification of the chaos dimension in EEG signals (Rapp et al., 1985, 1989) thanks to the "embedding" techniques inherited from Whitney (1934).

The Whitney's theorem demonstrated that for any dynamical system trajectory in its phase-space could be partially reconstructed in a new ad-hoc space thanks to embedding. For time-series, this embedding can be done by taking n delayed measurements with a fixed time delay τ between them. Thus, for a time-point t , instead of having only one-dimensional measure $s(t)$, the state of the system is described by a multi-dimensional vector whose coordinates are the delayed measurements: $x(t) = (s(t), s(t - \tau), s(t - 2\tau), \dots, s(t - N\tau))$. These techniques allowed to quantify the complexity of brain signal and applications were quickly found especially in clinics from the prediction of epileptic seizure (Babloyantz and Destexhe, 1986; Martinerie et al., 1998) to the characterization of depression (Nandrino et al., 1994; Pezard et al., 1996).

With these reconstruction techniques, Freeman was finally able to show experimentally the prediction of his earlier hypothesis. Thanks to the use of arrays of closely spaced electrodes placed on the olfactory bulb, he extracted from the usual EEG activity the spatial pattern of amplitude modulation (AM). Unlike the raw time-series, the modulations change significantly under both aversive and appetitive conditioning to odorant. It showed that the AM patterns are determined not by the immediate receptor input but by the cumulative synaptic structure framed by experience. This was strongly linked with the recent hypothesis of a "Neural Darwinism" by Edelman (Edelman, 1989). Freeman added a dynamical system model by studying how the structural constraint the olfactory bulb makes it return to a stable state after a sensory perturbation. These points of

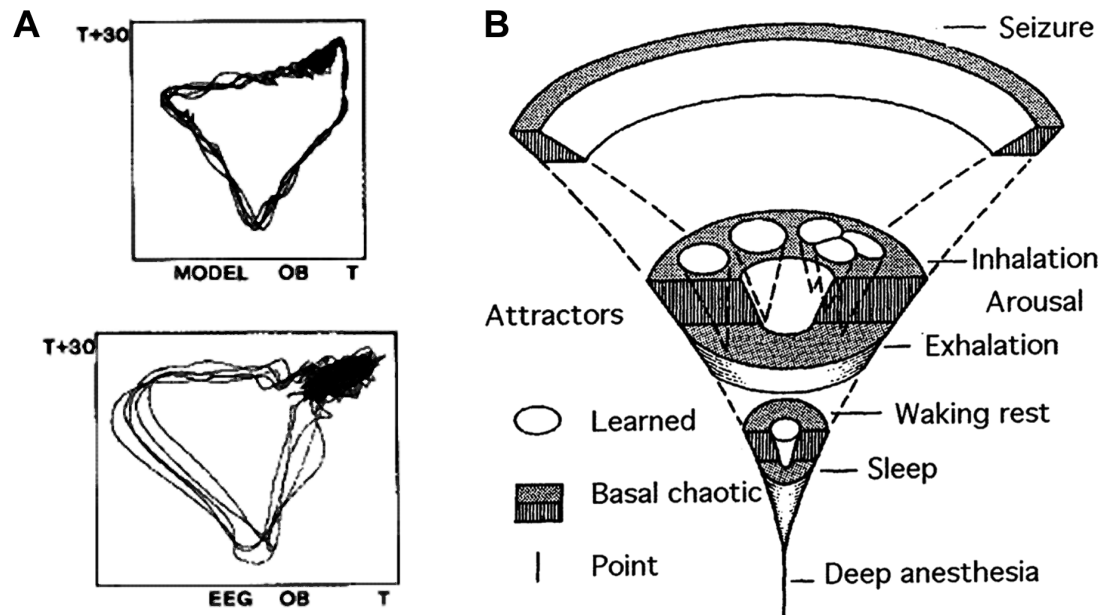


Figure 1.7: A) Comparison of the output of the trace from granule cells in a non-linear model with a real olfactory bulb seizure from a rat. (from Freeman 1987) B) The four states of the olfactory system as revealed by EEGs are linked in a bifurcation diagram, in which the amplitude of olfactory neural activity controlled by brainstem mechanisms serving arousal is used as a bifurcation parameter. (from Skarda and Freeman 1987)

equilibrium called "attractors" govern the dynamics of the system while a perturbation is applied. He stated that the dynamical behaviors of the system are organized along the excitability dimension of the mitral cells. While the excitability increases, the EEG dynamics displays gradually quiescence, low-level chaos, limit cycles and high-level chaos. This hierarchy of chaotic states modeled more accurately the neural dynamics of perceptual processing because this mechanism provides speed, flexibility, adaptiveness, and open-endedness necessary for learning (Freeman and Skarda, 1990). This new hypothesis was clearly challenging the representationalist point of view, and there were growing observation of chaotic dynamics in the brain activity (Soong and Stuart, 1989). However, there was still no demonstration of similar neurophysiological mechanisms operational for other brain functions than odor recognition.

Vision was the next modality to support Freeman's hypotheses. Electrophysiological recording in the cat visual cortex brought back interest for neural oscillations and renewed an old controversy in the neuroscientific community: the so-called "binding problem". The resulting debate proposed for the first time a functional account of neural synchronizations.

1.2.2 The binding problem and neural synchronizations

Perception of objects implies to put in coherence different features such as color, shape, sound and smell. By the end of the eighties, it was well admitted that these features were processed by different brain regions. However, the mechanism allowing synthesizing in a coherent percept all features was still a mystery. The most influential formulation of this problem was made by Von der Malsburg in 1981 (von der Malsburg, 1994). However, Milner (Milner, 1974) and Freeman (Freeman, 1975) did already similar statement before.

Several hypotheses were made upon the potential mechanism of binding. The first solution was to consider a single representational unit for each possible combination of features. This is the "neural coding hypothesis" proposed by Barlow. He stated that a visual object is encoded by the firing rate of "cardinal neurons" in the visual cortex (Barlow, 1972). This proposal is directly inspired by the work of Hubel and Wiesel and sees the visual cortex as a complex hierarchical structure. Konorsky proposed a similar idea with the concept of "gnostic neuron" (Konorski, 1967), which was later known as "grandmother cell" by Lettvin (Gross, 2002).¹ The idea was imprinted in the scientific community with the discovery of visual neurons in the inferior temporal cortex of the monkey that fired selectively to hands and faces (Gross et al., 1969; Bruce et al., 1981). However, even the most selective face cells observed were also discharging to a variety of other individual faces. Furthermore, in the general binding problem another drawback is the multimodal objects need higher dimensions of the feature space and leads to a "combinatorial explosion" (Singer and Gray, 1995).

In the eighties, the "feature integration theory" (FIT) (Treisman and Gelade, 1980) appeared and was popular thanks to its hypotheses linked with attention. This theory supported that visual features are instantiated across the visual field through separated "feature maps". The binding is then created by the orientation of attention. This top-down effect activates the features at a specific location thanks to their related maps.

Evidence for this theory came from a class of apparent misperceptions called "illusory conjunctions" where perceptual features can become unbound from their original objects and can be recombined to form a new object representation (Treisman, 1999; Wolfe and Cave, 1999). Lesions in the occipito-parietal region lead also to specific functional disabilities in binding features of ob-

1. It is important to make the difference with the "pontifical cell" of James which does not represent but experience the representation provided by the brain (James, 1950).

jects. For instance, the Balint's syndrome is characterized by the inability to perceive one object at a time (Balint, 1909; Roskies, 1999). Friedman-Hill also reported on a patient who could not associate shapes and color (Friedman-Hill et al., 1995). Other data indicated an involvement of cortical areas along the ventral visual pathway (Gilbert et al., 1996) in visual integration process. However, the neurophysiological mechanism underlying the "attentional glue" and "feature maps" were not so clear (Cave and Bichot, 1999; Wolfe and Cave, 1999) and studies demonstrated the presence of binding without attention.

Another theory is the so-called "binding by synchrony" also known as the "ensemble coding hypothesis". It states that simple features are encoded by individual neurons but the object, and cognitive act in general, are linked to the emergence of synchronic cell assemblies (Milner, 1974; Freeman, 1975; von der Malsburg, 1994; Malsburg, 1995). This proposal is strongly linked to early psychological principles of gestalt (Kohler, 1930; Koffka, 1935; Kanizsa and Kanizsa, 1979). This idea that neurons actually synchronize their responses according to Gestalt grouping rules generated debates. The main problem was the absence of mechanism explaining how these assemblies emerge (Ghose and Maunsell, 1999). In the late eighties, new experimental studies brought back a large interest for this approach.

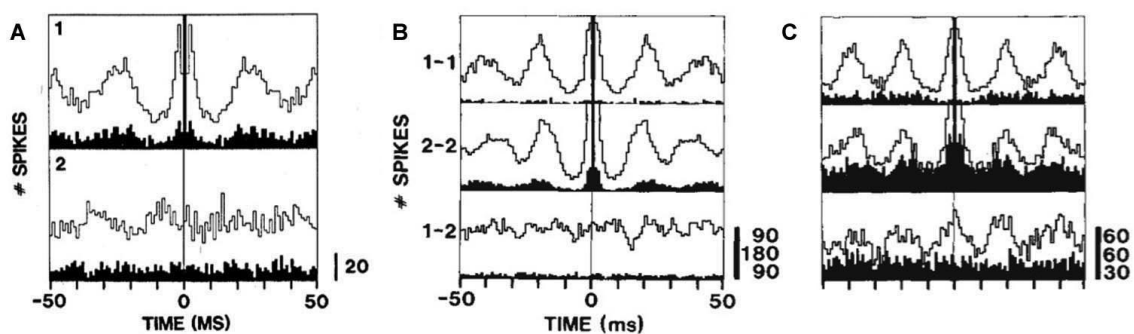


Figure 1.8: A) Temporal properties of the MUA from area 17 in a 5-week-old kitten (1) Autocorrelograms (ACF) for forward (filled bars) and reverse (unfilled bars) direction of stimulus movement. Note the rhythmic firing pattern with a period of 25msec for both directions. (2) Recomputation of the ACF after a shuffling of trial sequence. B) Auto (1-1, 2-2) and cross-correlogram (1-2) computed from neuronal response in two sites of area 17 with different orientation preference. C) Same analysis on two sites of area 17 with similar orientation preference. (A from Gray and Singer 1989, B & C from Gray et al. 1989)

By studying awaken behaving kittens with electrodes array in the visual cortex, the team of Gray and Singer made in 1987 pioneer observations assessing stimulus dependent synchronizations. Quickly a neighbor group published similar results (Eckhorn et al., 1988). The real breakthrough in the community was nevertheless given by two seminal papers by Gray, Singer and their collaborators about the role of oscillations in the coding of visual features (Gray and Singer, 1989) and also about how synchronization could bind them together (Gray et al., 1989). This last observation was the most important since it demonstrated the modulation of the synchronization by the global perceptual characteristics of the stimulus. Thus, synchronization probability appeared to depend on the Gestalt criteria that the visual system applies in order to accomplish scene segmentation and perceptual grouping. The properties of the 'whole' determine the perception of the parts. Similar to FIT, the "ensemble coding hypothesis" was not only providing a potential neurophysiological solution to the binding problem but also hypotheses about "top-down" elements of control as attention (Gray, 1999; Singer, 1999).

While hot controversies arose as to whether these oscillatory patterns did exist and whether the precise synchronization of discharges of spatially segregated neurons was functionally relevant, experimental works showed similar findings in other brain structures (Ahissar et al., 1992; Vaadia et al., 1995; Cobb et al., 1995; Murthy and Fetz, 1996) and with different tasks ranging from perception (Engel et al., 1991; Llinas and Ribary, 1993; Frien et al., 1994; Fries et al., 1997) to sensorimotor integration (Bressler et al., 1993; Roelfsema et al., 1997) or working memory (Tallon-Baudry et al., 1998; Weiss and Rappelsberger, 2000). These new results gave to neural oscillations a great importance since they were likely to play an important role in the generation of a temporal code in the brain (Engel et al., 1992). Indeed, neural oscillations may be an efficient carrier signal representing a population phenomenon. It has been widely observed in local field potential revealed (LFP) but multiunit recording proved also that adjacent neurons in striate and extrastriate areas of the cat visual cortex have strong tendency to burst in synchrony. The resulting coherently active clusters could be seen as a fundamental processing unit in the cortex like the "neural group" proposed by Edelman (Edelman, 1989). Due to the distributed nature of cortical processing, these oscillating neural groups were proposed as efficient not only for the "binding problem" but also for the large scale integration of information across the brain that supports consciousness (Crick and Koch, 1990, 1998; Engel et al., 1999).

1.2.3 Brainweb and beyond...

The late nineties were thus marked by a broad interest in gamma oscillations. The initial Crick and Koch's proposal of the putative mechanism of gamma rhythm in visual consciousness and its link with attention was in good agreement with the feature-integration theory of Treisman (Treisman and Gelade, 1980). Studies also demonstrated this intimate link between gamma activity, attention and consciousness (Munk et al., 1996; Fries et al., 1997; Engel et al., 1999; Tallon-Baudry and Bertrand, 1999). These gamma oscillations reflect local synchronization of neurons either packed within the same cortical macrocolumn (Gray, 1999) or situated in different areas reciprocally linked through mono-synaptic connections and processing similar information (Phillips and Singer, 1997). Large-scale synchronizations however rely on polysynaptic pathways connecting distant brain areas which do not necessarily process the same kind of information (Llinás et al., 1998; Girard et al., 2001). The two brain areas form then a cell assembly. Such long-range synchrony between distant neural populations has been proposed as a plausible candidate to mediate the integration of their respective activities (Bressler, 1995; Varela, 1995).

But while invasive techniques allow precise synchronization recording at the local level, they are not adapted to long-range measurement. On the other side, oscillations brought by mesoscopic recording such as iEEG and EEG were too coarse and needed adapted statistical measurements. This was a key issue for assessing in human the plausible implication of long-range synchronization in the large scale integration problem and its link with consciousness.

The LENA funded by Rémond marked this next step thanks to a conjunction of people and fields. While the new director Renault worked on the installation of the first magnetoencephalography (MEG), the neurodynamics team lead by Martinerie was developing non-linear analysis dedicated to brain signals (Le Van Quyen et al., 1997; Martinerie et al., 1998) and just welcomed Varela as a new researcher. In parallel, Garnero was also developing cortical sources reconstruction methods inspired from tomography imaging (Renault and Garnero, 1996) and she developed with Baillet mathematical tools allowing to go from the scalp to cortical level by injecting anatomical and physiological priors (Baillet and Garnero, 1997). A fruitful environment was thus created for investigating the issue of large scale integration in humans.

Since functional connectivity techniques like coherence were restricted to overall relationship in time, mathematical methods were first developed for detecting transient phase-locking between the oscillations of two local fields (Lachaux et al., 1999; David et al., 2001) and applied in different experiments (Rodriguez et al., 1969; Lutz et al., 2002; Cosmelli et al., 2004). This provided the first experimental evidences of the gamma phase synchrony involvement in human cognition (Varela, 1995). This period marks also the birth of neurophenomenology which aims at combining subjective experience accounts and third person neurophysiological measurements (Varela, 1999b; Lutz and Thompson, 2003).

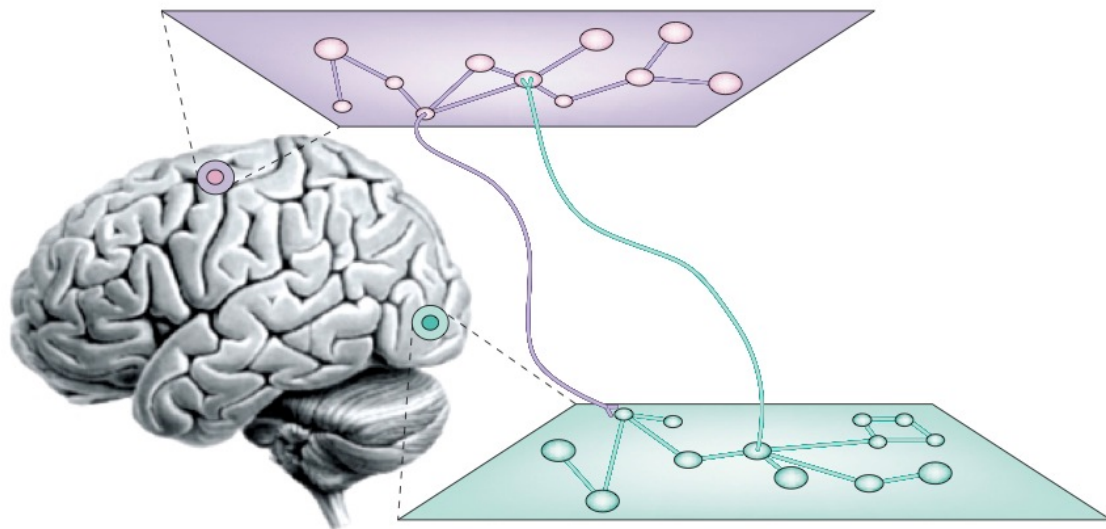


Figure 1.9: Schematic representation of transient distributed neural assemblies with dynamic long-range interactions (from Varela et al. 2001)

A synthesis of all these advances and their link with other works was published in a special issue of *Nature Review Neuroscience*, focusing on neural synchronizations (Varela et al., 2001). In this review entitled "Brainweb", the neural assemblies conceptual framework is wisely presented through an analogy with the Worldwide Web. More than inviting to shift from the "computer" to the "network" metaphor for the brain, the authors showed that the resonant cell assemblies framework gather three fundamental features of cognition: integration, segregation and metastability. It explains why the cells assemblies are so appealing to neuroscience since they could both integrate distributed neural activities and promote particular sets of neural groups above the remaining brain activity. More importantly, this dynamical process features at the global level the necessary dynamical flexibility for evolving and adapting to the environment. Many others neurodynamical frameworks evolved or emerged from this advance (Friston 1997; Edelman and Tononi

2000; Engel and Singer 2001; Dehaene and Naccache 2001; Llinás and Ribary 2001; Ward 2002; Edelman 2003; Crick and Koch 2003; Fries 2005, review in Cosmelli et al. 2007) and were supported by number of studies (Melloni et al., 2007; Cardin et al., 2009; Canolty et al., 2010; Hipp et al., 2011; Fell and Axmacher, 2011), demonstrating in more detail the functional role of neural synchronizations (review in Uhlhaas et al. 2009). The "Brainweb" lead to a more general framework cutting across brain-body-world division and integrating social interactions as a constitutive part of human cognition (Thompson and Varela, 2001). The "radical embodiment" manifesto first focuses on consciousness awareness, defined as "the flow of adapted and unified cognitive moments"¹ experienced by a subject. This consciousness awareness is proposed to rely on the formation and destruction of specific distributed neural assemblies through the establishment of phase synchronization across multiple frequency bands and thus is described as a dynamical operator. This standpoint is really similar to the definition given by Freeman: "Consciousness... is a state variable that constrains the chaotic activities of the parts by quenching local fluctuations. It is an order parameter and an operator that comes into play in the action-perception cycle as an action is being concluded, and as the learning phase of perception begins" (Freeman, 1999). Then, Freeman considers neural synchronization as the ideal objective correlate of consciousness (Freeman, 1999; Freeman and Rogers, 2002). Thompson and Varela's proposal is appealing for the purpose of this thesis since it emphasized that cognition is not brain-bound and rather encompass the body, through the regulation of its organismic cycles, the environment with sensorimotor couplings and the other cognitive agents through intersubjective interactions with them. Interestingly, Bressler and Kelso proposed a complementary integrative framework the same year (Bressler and Kelso, 2001). The so-called "coordination dynamics" is inherently multi-scale since it extend mathematical tools from human motor coordination to the level of cortical dynamics (Kelso, 1995). Taken together, these two theoretical proposals support continuity between the inner and the outer. We will see in the next section how social interaction leads to really similar phenomena as those at works in already mentioned physical and cognitive systems.

1. In reference to the famous chapter "The stream of thought" of *The Principles of Psychology* (James, 1950)

1.3 Behavioral and social synchrony

The phenomenon of synchronization is also present at the social level, although its observation is less obvious at first glance since the complexity and variability of human social behavior overcome physical systems we have already described before. Nevertheless, from the pioneer works of developmental psychologists to a recent trend in social psychology and social neuroscience, behavioral synchrony is progressively understood from its condition of emergence through reciprocal social exchanges and its potential functional role in both the development of our social skills and the later regulatory role in our coordination with the others. More recently, different neuroimaging results have also started to uncover potential neurobiological mechanisms underlying this phenomenon. In this last part of our multi-scale account of synchronization, we will focus on these various works and how they help capturing the phenomenology of synchronization at the social level.

1.3.1 Developmental aspects

Developmental psychologists have studied for years the social abilities of infants. They have understood that the study of these competences is optimally revealed by placing infants in a social meaningful context (Gusella et al., 1988; Muir et al., 1994). Indeed, if child seems biologically preadapted for interaction with other infants and adults, the usual two-dimensional and static stimulations are meaningless for them (Butterworth, 1986). These theoretical, but also pragmatic, considerations helped the developmentalists to escape from the information-processing perspective. Thus, instead of seeing communication as a succession of unidirectional transfer of information from one person to another and consider actions as discrete signals, some of them started to see social interaction in a continuous and dynamical way. New measures were thus needed for moving away from those used in the discrete framework like the transitional probabilities from one action to another (Bakeman and Gottman, 1986). Cognitivist description of the interaction appeared indeed to be misleading when the continuous co-regulation of actions by the partners constitute dynamically the course of the interaction (Fogel, 1990, 1993b). Here there is no more sender or receiver, both partners are continuously influencing each other. Then, dyadic parameters are needed to describe the ongoing interaction in a continuous and holistic manner. While discrete rules are in most cases observer's inference that gives convenient metaphors for describing regularities, they

could hide the emergent process created by the consensual social frame of the co-regulation of the interaction (Fogel, 1993a).

The dynamical posture of developmental psychology has been noticeably applied in the study of mother-infant interactions. Their exchanges are characterized by the emergence of synchronized behaviors at multiple time scales. Although some cultural variations exist, healthy human infants spend most of their time in the proximity of their mothers and thus exchange multi-sensory signals with her. As a consequence, infant and mother influence reciprocally each other's activity patterns. At large timescale the childrearing intervention and care-giving procedures like feeding and changing diapers can cause temporal synchrony during the day. However, this synchronization appears also at smaller timescales during online dyadic interaction. The so-called "interactional synchrony" comes firstly from Condon and Sander 1974 who suggested that infant accord perfectly the speed and direction of their body movements with the phonemic changes of adult speech. Despite this early observation of absolute synchronizations were never replicated (Dowd and Tronick, 1986) apparently because of initial methodological problems (McDowall, 1978), the term was sealed and widely used in subsequent studies. Indeed, even without a total temporal simultaneity in the interaction, the mutual anticipation of the actions leads to quite short lag in the behaviors (about 0.05 seconds, Stern 1974; Kato et al. 1983). But this phenomenon has been extended across different time ranges, from the co-occurrence of movement to the coherence of psychological states. For instance, it has also been associated with the mutual rewarding aspects of influencing each other (Isabella et al., 1989). Indeed, when we adopt a dynamical account of social interaction, the information is not any more in a specific action of one person and its perception by another but rather in the relationship between them experiences as a feeling and motivation (Gibson, 1966; Michaels and Carello, 1981). Then, it escapes from a content based to a participatory-based perspective where information is always "in formation" (Varela, 1979) across the different cognitive levels. From a developmental point of view, the phenomenon of pattern co-creation during communication has been mostly studied with imitation in infant-mother or early peer interactions. If the infants' capacity of matching their behaviors with those of their caretakers has been at first attributed to a learning function (Miller and Dollard, 1941), the later experiments with neonatal imitation proved that the model must perform actions that are already in infant movement repertoire for the imitation to occur more effectively (Kaye and Marcus, 1981; Meltzoff et al., 1991). Thus, the novelty was not specially facilitating imitation but could at con-

trary brake the phenomenon in its earliest stage. This has questioned the unique learning role attributed to imitation. Whereas this idea was strongly imprinted in the psychological community, it has been later challenged by extending the potential functions of imitation and seeing it as a vicarious behavior (Uzgiris, 1981; Nadel et al., 1989).

While the traditional focus on learning did not need to take account of the co-regulation and continuity of the exchanges, these aspects became completely central for the study of imitative communication. Infants need indeed the ability to detect interpersonal contingency in order to understand the relations between their own actions and those of their social partners. The interactional synchrony has been proved as an important role in this detection since it reflects the dynamical inter-dependence of the two partners (Fogel, 1993b). Early works have demonstrated that the ability to detect contingency between self-movement and the environment was present from birth (DeCasper and Carstens, 1981; Walton and Bower, 1993) and represent an important aspect of the early development of self as an autonomous agent able to affect the environment (Gergely and Watson, 1999). During reciprocal exchange, detecting social contingency allows to analyze the responsiveness and attention of the partner and understand social interaction rules (Stern, 1985; Nadel and Tremblay-Leveau, 1999; Rochat et al., 1999). Seminal behavioral studies on mother-infant interaction have demonstrate the presence of such ability at 2-month infants and started to mark a shift by considering them as a real agent with expectations and the sense of sharing the interactional experience (Nadel et al., 1999; Soussignan et al., 2006). Theses studies have used a double video procedure to assess of the difference between online interactions with video replay. More than extending previous still-face design (Tronick, 1978; Fogel et al., 1982), which was strongly criticized for their behavioral discrepancy and under-stimulation, these new paradigms corrected past potential bias induced by video procedures (Murray and Trevarthen, 1985; Rochat et al., 1998). The results demonstrated that very young infants are highly sensitive to social contingency. During interaction with adults, they expect contingent responses more than novelty. This made a clear difference with environmental contingency where at contrary infants are more sensitive to novelty and absence of control (Rochat and Morgan, 1995; Gergely and Watson, 1999).

The later works on spontaneous interaction between mothers and infants confirmed the key role of synchrony. Synchronous imitation represents an important behavior that promotes the ability to find shared topics and start experiencing turn-taking at the preverbal stage. Further, infants

can learn to infer others' intention correctly by recognizing mutual action patterns during these spontaneous mimetic communications. This allows the development of key features of the social abilities before symbolic language (Nadel-Brulfert and Baudonniere, 1982) and differs completely from the usual view of imitation as a teacher-learner unidirectional transmission. Moreover, the ability to perceive whether the social partner is attentive and responsive is also presumed to be involved in the formation of "primary intersubjectivity", the feeling of shared experience. It develops the early self-knowledge of the child, the concept of agency, self-other differentiation and understanding of interaction rules (Bigelow, 1999; Nadel and Tremblay-Leveau, 1999; Rochat et al., 1999). We will see now how it provides insights for designing autonomous artificial agents.

1.3.2 Human-Machine Interface (HMI) perspectives

May it appears at first glance a distant field, robotics has been influenced by developmental psychology in various manner but more specifically with the previous mentioned studies about spontaneous imitation. The so-called "developmental robotics" field has recently taken inspiration from mother-infants studies for giving to artificial agents the ability to interact realistically without pre-programmed patterns. Spontaneous imitation provides certainly one of the ideal framework because communication is completely continuous and could occur without any use of symbolic representation. Furthermore, the vicarious aspect of imitation provides also a potential unsupervised mechanism for learning without any external explicit reinforcement signal. Mostly the extensive work on imitation in robotics deals with the learning function of imitation (Schaal, 1999), Focusing on synchronous imitation, we stress how crucial is the coordination of tempo for the feeling of natural interaction and the affectivity of the ongoing exchange (Jonsdottir et al., 2008). We have seen that spontaneous imitation in humans makes emerge interactional synchrony thanks to its reciprocal and continuous aspects. The same phenomenon has been recreated with robots (Prepin and Revel, 2007). This is inline with the dynamical approach adopted by Gaussier's team which considers interaction as an emergent phenomenon caused by the coupling between two systems, either in robot-robot or human-robot exchanges. An efficient manner of dealing with timing is to control the agents' behavior by oscillators (Andry et al., 2001; Revel and Andry, 2009). When a coupling occurs between two agents such modeling enables to study the emergence of interactional synchrony, turn-taking and the disruptive effect of time delay (Prepin and Pelachaud, 2011). Furthermore, oscillatory models allow combining different perceptual modalities and in-

investigating dynamically how the information they provide is integrated or enters in conflict. Here also results from developmental psychology help for this issue and give potential solutions for the design of future artificial agents (Andry et al., 2001; Nadel et al., 2005). It is clear that oscillators and neural networks are promising techniques in the construction of a dynamical perspective in robotics (Gaussier and Zrehen, 1995; Quoy et al., 2003; Kozma, 2008; Momioli et al., 2010).

While oscillators are intrinsically dynamical units and provide well-framed basic elements within a global dynamical architecture (Barandiaran and Moreno, 2008), neural networks can in parallel support the adaptation of the behavior to the environment in an unsupervised manner. This could be particularly useful for the study of higher-level social phenomena. Ikegami and colleagues have for instance studied the co-creative aspects of interactions and how turn-taking emerge (Ikegami and Iizuka, 2007), illustrating the fact that different styles of motion can be generated through synchronous interaction independently of the neural network structures in each agent. The oscillatory co-regulation of the two agents goes beyond the classical model of information transmission, since the agents can adapt their movements to those originating from the other's repertoire. This leads both partners to perform new patterns without external intervention (Andry et al., 2001; Gaussier et al., 2003). The whole process is constituted through synchronous behaviors and could be seen as a shared intentionality of the dyadic system (Uno and Ikegami, 2003).

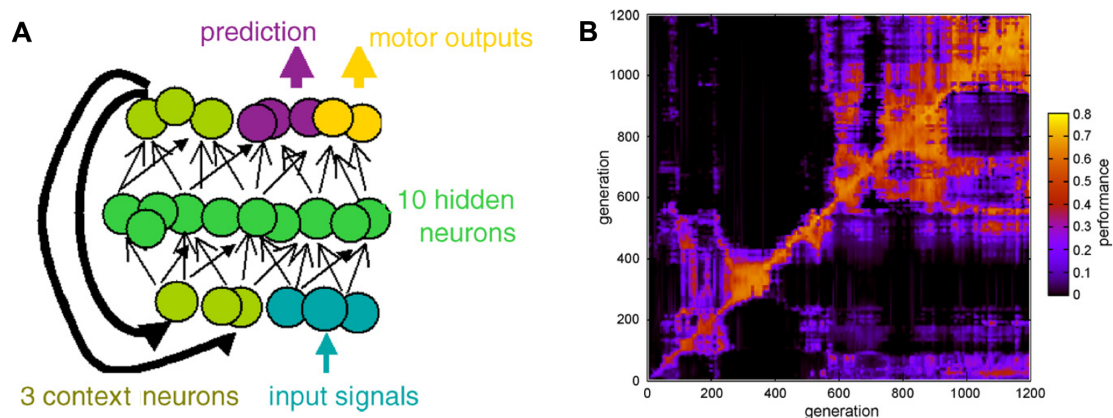


Figure 1.10: A) Schema of the neural architecture of the artificial agents. B) Overall turn-taking performance across the different generations created by the evolutionary algorithm. Notice the joint progression of the turn-taking performance and the adaptation of agents to interact between different generations. (from Ikegami and Iizuka 2007)

Evolutionary robotics has provided other minimalist simulation models of social interaction. Di Paolo and colleagues have extensively developed dynamical analyses of such simulations within an enactive approach (Froese and Ziemke, 2009; Stewart et al., 2011). Their work aims at demonstrating that the behavior of the agents is not an individual achievement alone but rather co-determined by their mutual interaction and organized effectively by this multi-agent interaction process (Froese and Di Paolo, 2009). While they also observed interactional synchrony in their simulations (Di Paolo, 2000), they focused more on the parameters of coordination and co-regulation between agents. Nevertheless, they advocate that within an integrative and enactive account of cognition, synchrony can constitute more than a simple measure (Froese and Di Paolo, 2009).

A recent simulation points out that synchrony is likely to integrate dynamically sensori-motor information and give rise to metastable regimes (Santos et al., 2011). This last study combined the enactive perspective with the dynamical framework of coordination. This is inline with the recent work of Kelso's team, which have also adopted artificial agents as a new tool in the investigation of interpersonal coordination. Their Virtual Partner Interaction (VPI) technique is at the crossroad of robotics and human behavioral psychology (Kelso et al., 2009a). Embedding a dynamical model of motor coordination in a virtual agent allows indeed to analyze in a systematic manner real-time situations like full anti-phase coordination that are difficult to maintain between humans (Schmidt and O'Brien, 1997). It stresses how the amplitude of the oscillations and their center intervene in the underlying laws of interpersonal coordination. It demonstrates also the power of those laws of coordination dynamics. We will see in the next part how they have been investigated in behavioral studies.

1.3.3 Behavioral studies

Interactional synchrony is intimately linked to how two or more people coordinate their actions in space and time (Kendon et al., 1975). In this sense, interpersonal coordination can be defined as "the degree to which the behavior in an interaction are nonrandom, patterned, or synchronized in both timing and form" (Bernieri and Rosenthal, 1991). Such definition however leads to a two-fold account of coordination, one emphasizing on temporal aspects (Grammer et al., 1998), and the other focusing on morphological contingency, often conceived as "behavioral matching" (Chartrand and Bargh, 1999). The perceptual, motor and cognitive processes that enable individuals to

interact with one another have received increasing attention during the last decade across these different aspects of coordination, including an additional distinction between planned and emergent coordination (Knoblich et al., 2011). Here we will focus only on works related to emergent coordination since it is what happens during spontaneous imitative interaction.

Kelso's framework of coordination dynamics is perhaps the most achieved and long-standing framework towards this issue. The VPI technique described in the previous section is grounded in this empirically-based model and continues directly the thirty years of active investigation of the dynamical account of coordination (Kelso, 1979; Kelso et al., 1981; Kelso and Tuller, 1984). Synchronization has been broadly studied since it is the most usual and stable dynamical state encountered in motor coordination (Fraisse, 1966). Anti-phase synchronization is another common pattern but despite its similarity with synchronization, it seems to involve different mechanisms (Fraisse and Ehrlich, 1955; Engstrom et al., 1996). Interestingly, both modes can apparently be described as part of a common formalism, the Haken–Kelso–Bunz (HKB) model (Haken et al., 1985), which is at the core of coordination dynamics formalism. The equations predict that coupling two oscillating systems yield in general either “in-phase” (synchronization) or “anti-phase” (syncopation) patterns. Later studies have demonstrated that this model can be encompassed to most observable coordination cases: either intra-limb (Buchanan and Kelso, 1993) or between limbs (Kelso et al., 1981; Kelso and Tuller, 1984; Mechsner et al., 2001), between different modalities (Lagarde and Kelso, 2006), between two persons (Oullier et al., 2003; Konvalinka et al., 2010) and even between two different species (Lagarde et al., 2005). Some extensions of HKB also integrate the effects of noise, heterogeneous natural frequencies and asymmetry (Fuchs and Jirsa, 2008). Altogether these different results suggest that it exists some general coordination rules encompassing the different scales and types of systems (Kelso, 1995; Kelso and Engstrøm, 2006).

Focusing on the inter-personal level, the nascent Social Coordination Dynamics (SCD) seeks potential underlying mechanisms of human bonding at both individual and collective levels (Oullier and Kelso, 2009). Recent observations have noticeably questioned the view of social coordination as only a simple perceptual-motor coupling, including for instance the so-called “social memory” phenomenon (Issartel et al., 2007; Oullier et al., 2008). Moreover, recent works prove that the “interpersonal entrainment” earlier studied by Condon and Ogston 1967 goes far beyond their initial observations of rhythmic behaviors during social interaction. Schmidt and O'Brien 1997 have shown the difficulty to inhibit unintended coordination with others but this tendency

remains present even if it interferes with the congruency of each individual's movements. Indeed, the partners tend to prefer movements with homologous muscular activation of the other (Oullier et al., 2003). Richardson and colleagues have also shown that two people tend to enter in synchrony while rocking a chair even if their "natural rocking frequencies" were different (Richardson et al., 2007).

To conclude this brief summary about emergent social coordination, it is important to notice that the field goes beyond the dyadic scale. Research has been dedicated to herding behavior and synchronization in groups, as reviewed by Raafat and colleagues 2009. The most famous example is the clapping phenomenon in concert audience when 'the tumultuous applause' converges into a rhythmic and orderly clapping pattern (Néda et al., 2000). These studies are at the edge of sociology and bring similar kinds of results than socio-economic observations of collective trends (Barthélemy et al., 2010). But keeping a perspective centered on individual social phenomena, we will now turn to describe neuroscientific studies linked to behavioral synchronization.

1.3.4 Neuroimaging

Neuroscience has gathered in the two last decades a tremendous number of results thanks to the neuroimaging burst. The burgeoning "social neuroscience" refers to those linked with the study of our socio-cognitive abilities. Despite it constitutes the major part of our daily life practice of social cognition, real-time social interaction forms currently a tiny part of this domain. Indeed, the main interest remains how an isolated human processes socio-emotional stimuli, or what should be called "social perception" (Frith and Wolpert, 2004). These extensive works have provided insights about the brain region underpinning socially relevant functions, and inferred their role in social exchanges. In the case of sensorimotor interaction, one of the key abilities is the understanding of others' intentions through their actions. Early works in positron emission tomography (PET) have suggested the implication of superior temporal sulcus (STS) and inferior parietal lobule (IPL) in motor representation (Decety et al., 1994, 1997; Decety and Grèzes, 1999). The posterior STS seems to be specifically related to biological movement perception (Allison et al., 2000; Grèzes et al., 2001, 2003). Other regions have also been pointed out for subserving this function: the premotor cortex (Saygin et al., 2004), parietal regions (Battelli et al., 2003) and temporal regions (Virji-Babul et al., 2007). A recent study has even extended this list to cortical structures previously linked to mentalizing (Centelles et al., 2011).

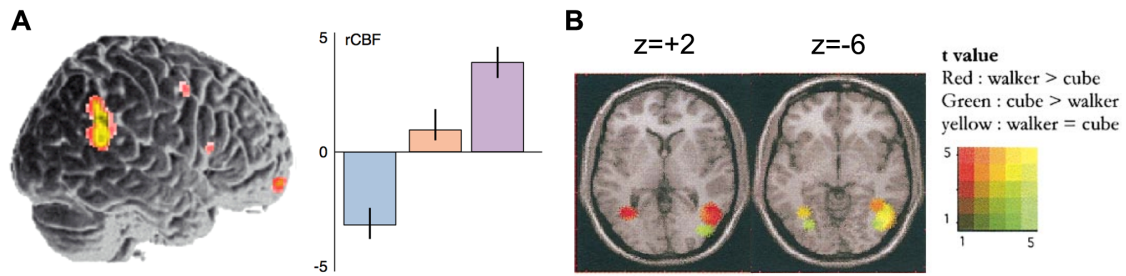


Figure 1.11: A) Right inferior parietal lobule activation and its relative hemodynamic variation during self action (blue), imitation (red) and being imitated (purple). (adapted from Decety and Sommerville 2003) B) Cerebral activations within the occipito-temporal region associated with the perception of point-light walker display or dot cube versus drifting random dots condition (adapted from Grèzes et al. 2001)

The discovery of MNS in monkeys (Pellegrino et al., 1992; Rizzolatti et al., 1996) has a major importance in the generalization of the "social perception" results to the "social interaction" case. The theoretical extension of the concept to humans (Rizzolatti and Arbib, 1998; Gallese and Goldman, 1998) was demonstrated experimentally through Transmagnetic Stimulation (TMS) (Fadiga et al., 1995) or intra-cranial recordings (Mukamel et al., 2010). The above-mentioned structures relative to biological movement perception have been associated to this human mirror neuron system (MNS) (Rizzolatti and Craighero, 2004; Iacoboni et al., 2005). As they are shown to be active during both observation and realization of an action, it consequently legitimates the extension of individual results to the case of interactions. Seminal neuroimaging studies have already supported this hypothesis in the case of imitation although they did not implicate reciprocal and real-time interaction (Iacoboni et al., 1999; Decety et al., 2002; Carr et al., 2003). Molenbergh and colleagues have then pointed out the links between perception and action in the imitative network and its extension to parietal and frontal regions beyond the classical mirror neuron network (Molenberghs et al., 2009, 2010, 2011).

The neural dynamics of interactional synchrony, which emerges through reciprocal interaction, have never been investigated so far. On the other hand several studies have concentrated on the unidirectional synchronization with external stimuli. This so-called "entrainment" phenomenon exists in both social and non-social context. The neural evoked and induced activities have been studied first in the non-social case with photic stimulation (Barlow, 1960) and periodic acoustic stimuli (Neher, 1961). Recent works have proposed entrainment as playing a functional role in attention and expectation (Lakatos et al., 2008; Stefanics et al., 2010), but also memory and learning

(Bhattacharya et al., 2001; Will and Berg, 2007). As interpersonal coordination needs both these mechanisms and perception-action integration, all the above-mentioned works on individuals are a matter of interest.

Importantly, other knowledge has also been provided by neuroimaging studies adopting the perspective of coordination dynamics. They have demonstrated that the metastable states at the neural level follow behavioral synchronization and syncopation (Fuchs et al., 1992; Mayville et al., 2001). fMRI studies with comparable protocols have emphasized the overlapping of cortical structures underpinning these two modes of coordination (Jantzen et al., 2002; Mayville et al., 2002). Despite this common functional network, they however demonstrate that syncopation recruits it more strongly and broadly. Similarity between these brain regions and rhythms were observed with those implicated in motor production and observation. It thus supports the idea that they potentially play a functional role during interactional synchrony (Oullier et al., 2008).

As already mentioned, the absence of real-time and reciprocal paradigms in social neuroscience explains our poor understanding of the potential underlying neurobiological mechanisms of social interaction (Schilbach, 2010). Recently, some studies have nevertheless started to use paradigms where participants could interact in real time with either a virtual (Schilbach et al., 2006) or a real (Guionnet et al., 2011) partner. Another key issue is the creation of experiments embedded in a meaningful context, as such context has been demonstrated to play an active role in the tuning of brain regions linked to social abilities (Umiltà et al., 2001; Jellema and Perrett, 2003). Granting all these progresses, social neuroscience had never yet brought results about our propensity to mutually synchronize during interaction since the classical neuroimaging approach consists in the recording of only one person at a time. The next chapter will present the hyperscanning technique, which basically can extend the recording to two or more people. It will analyze how this new technique has already started to bring interesting results, and how it could help capturing the essence of reciprocal social interaction.

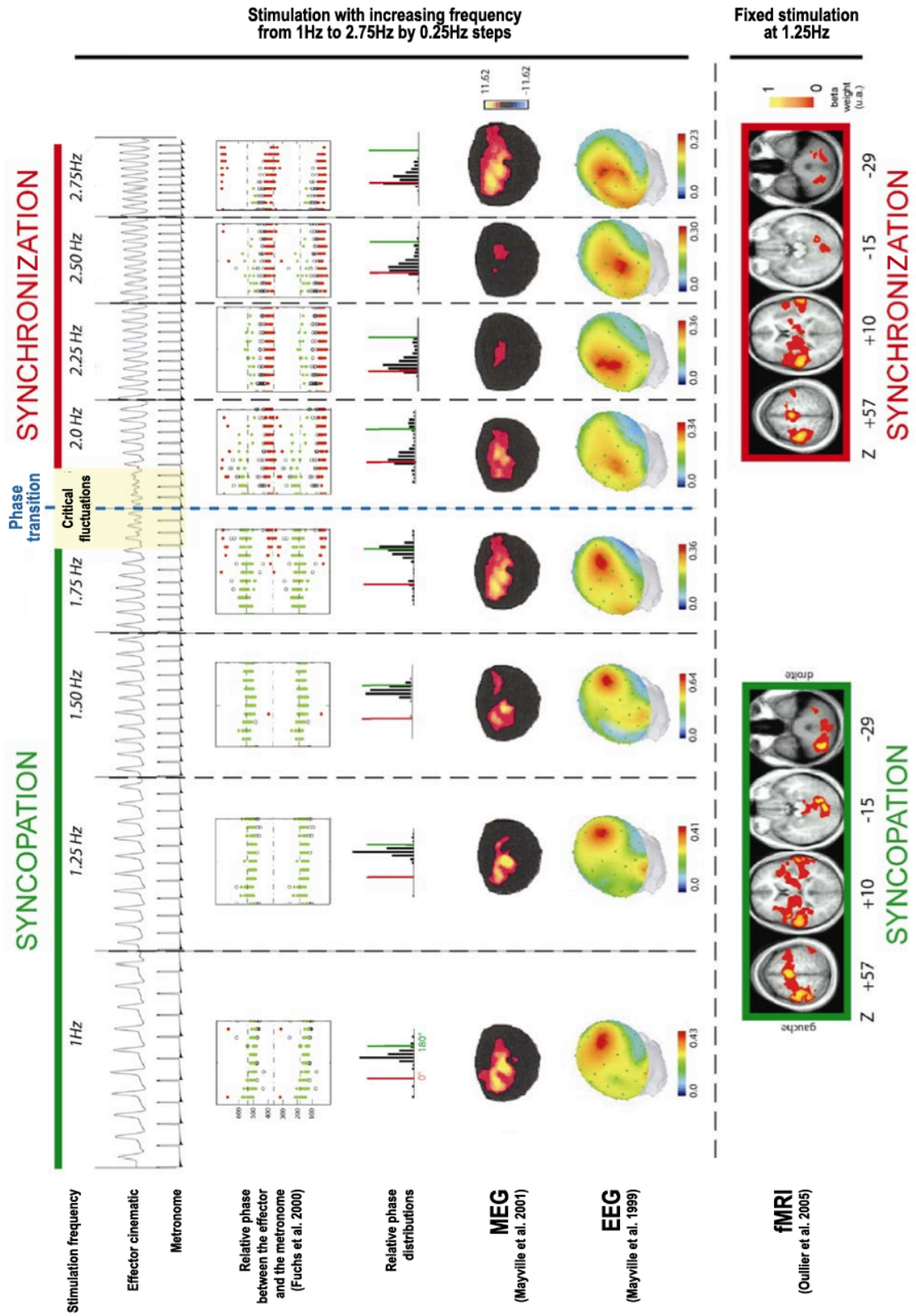


Figure 1.12: Spatiotemporal dynamics at behavioral and neural levels of the phase transition between syncopation and synchronization. (adapted from Oullier et al. 2006)

1.4 Hyperscanning: a bridge between neural and social levels

Until recently, nothing was known about the relationships between brain activities of two or more individuals while they are engaged in a social interaction. This part will describe a neuroimaging method called hyperscanning, which consists in the simultaneous recording of the brain activity in multiple participants. This technique has been applied to both fMRI and EEG, and makes possible to perform within- as well as between-brain analyses. While the idea of jointly study two or more persons was already present in social psychology, the hyperscanning story starts with an uncanny use of the technique. This technique was indeed first applied in the sixties by two ophthalmologists. They published a short communication in *Science* where they told having observed telepathy between twins (Duane and Behrendt, 1965). Although the results were never replicated, many others tried afterwards to investigate a potential transmission of information between the brains of isolated participants. The conclusions raised suspicions because of their ad hoc hypotheses and the lack of control. In a small number of cases, the brain activity of one person was reported to correlate with a partner localized in another room without any communication device linking the two participants (Wackermann et al., 2003; Wackermann, 2004; Standish et al., 2004; Dotta et al., 2009). Many commentaries questioned these studies in their methodology and their idiosyncratic results supported by weak statistics. They mainly pointed out that the positive results obtained were most likely attributable to some dynamical similarity between the two brains engaged in the same perceptual context rather than to an effective transmission of information.

The ‘para-psychological’ use of hyperscanning has perhaps caused the long delay before academic community tried to record two subjects simultaneously. But as seen earlier, it was not before 2002 that Montague and collaborators wrote a seminal paper, where they named the technique "hyperscanning" as they used fMRI.

1.4.1 fMRI studies

The imprinting of neuroeconomics

This first exploratory experiment of Montague’s team (Montague et al., 2002) paved the way for the use of hyperscanning. It has clearly caused a (re-)gain of interest toward recording the brain activity of two subjects or more simultaneously. In their protocol, the authors recorded with fMRI

the brain activities of two participants engaging through a video link in a guessing game where the participants have to presume the location of an object hidden in one of the two hands of the other participant. Later, the same group made a similar experiment with a multi-round trust game of economic exchange (King-Casas et al., 2005). They found a correlation between the “intention of trust” and the BOLD response magnitude in the caudate nucleus. Interestingly, they also were able to quantify the transfer of the intention of trust in cross- and within-brain correlations. While the response met usual reward predictions, the delay was translating the sequence of the social exchange and thus proved for the first time a causal relationship between one brain activity and the other. They published the following year another hyperscanning experiment about economic exchange (Tomlin et al., 2006) where they investigated agent-specific responses in the social domain (“me” and “not me”). They found a systematic spatial pattern of activation in the cingulate cortex that did not depend on metrical aspects of the exchange and disappeared in the absence of a responding partner.

A third Science paper mixing hyperscanning and neuroeconomy was published soon after by Fliessbach and collaborator (Fliessbach et al., 2007). Their protocol used a classical reward estimation task with subjects scanned in two adjacent MRI scanners. Their task also integrated a social comparison after each trial. The pairs of subjects were thus engaged in a competitive monetary rewarded task. Their reward expectations showed an immediate impact of contextual social information on ventral striatal responses. The use of hyperscanning well suited to study the consequences of the different income for an identical performance under the same conditions. It assured that the effect was not caused by variation in the experimental environment.

Natural scene perception and inter-individual similarities

At the same period, other studies published under the label of hyperscanning did not use hyperscanning per se, but searched for correlations between the brain activities of different individuals recorded separately. In an fMRI study, Hasson and collaborators (Hasson et al., 2004) recorded the brain activities of participants watching the same part of a movie. Even though they recorded isolated participants, the key innovative result is that they found strong functional and anatomical similarities across individuals. In the following years, they replicated similar experiments (Hasson et al. 2008a,b, review in Hasson et al. 2010). Their second finding was a specific increase of correlation across the brain activities of different subjects for the movie parts successfully en-

coded in their episodic memory. The method was an update intersubject correlation (ICS) based on subjects' subsequent memory (ISC-SM) performance. Their third finding was the presence of temporal receptive fields, namely a hierarchy of brain regions which respond to specific temporal windows. Altogether, they showed the potential of scanning several subjects immersed in the same context for the understanding of natural vision, temporal scales of processing, memory and neural basis of inter-group differences. Indeed, the combination of intra-subject, inter-subject and inter-group correlations allow to dissociate between neural processes that are either shared by all people, uniquely expressed in a given sub-group or idiosyncratically present in individuals. Other studies replicated the intersubject correlation of hemodynamic activity during natural vision (Jääskeläinen et al., 2008; Kauppi et al., 2010). Additionally, they found new inter-subject correlations in frontal areas, which were related to social interaction events. Such events occurred over longer time periods than those previously mentioned by Hasson and colleagues in the visual areas. It thus questions the initial description of a hierarchical organization of temporal receptive field.

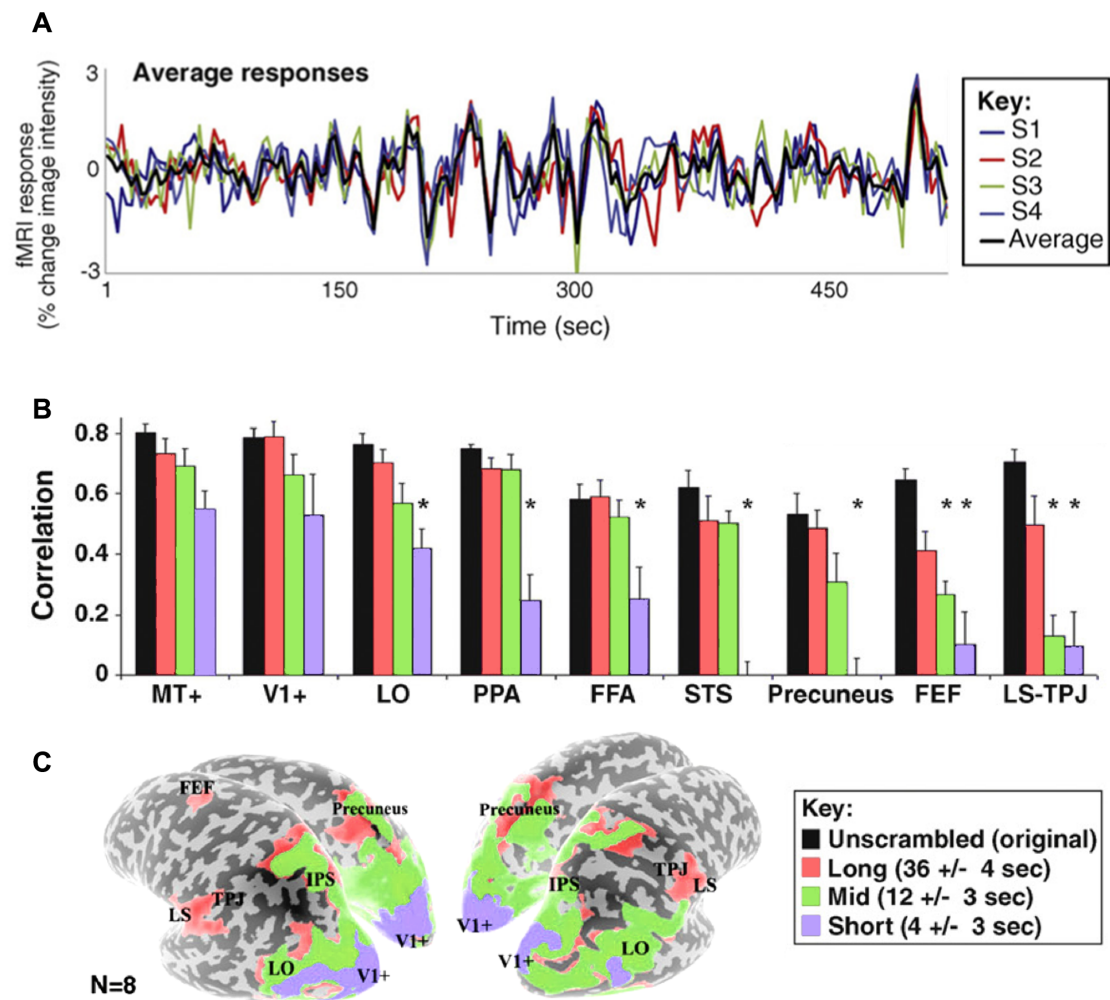


Figure 1.13: A) Times series of BOLD responses evoked by the Sergio Leone movie "The good, the bad and the ugly" for each subject, averaged across the two repetitions, and grand mean averaged across the four subjects. B) Response correlation across repeated presentations, as a function of temporal disruption of the same movie, in each of several brain regions. C) Map of brain regions with different temporal receptive windows. (adapted from Hasson et al. 2010)

Verbal and non-verbal social communications

The first hyperscanning investigation of social exchanges was focused on narrative speech comprehension (Wilson et al., 2008). Similarly to Hasson's, the study consisted in the separated presentation of auditory and audiovisual narratives to multiple subjects. Though again it was not really hyperscanning, the study had the interest to underline the intimate relationship between the need of ecological paradigms integrating meaningful stimuli and the potential of recording multiple subjects in order to achieve a sufficient robustness of the analysis. The study of Wilson and collaborators confirmed the role of the superior temporal cortex in speech comprehension but also completed the networks of regions involved in understanding language in ecologically valid context. Their inter-subject correlation analyses revealed that the activity of areas belonging to the "default mode" network is modulated by the time-varying properties of the stimuli. Furthermore, the premotor regions and the inferior frontal areas were also bilaterally implicated in language comprehension. The authors proposed that this uncovered network, more than reflecting merely higher-level linguistic processes, also participates in the interface with extra-linguistic systems of emotional and interpersonal cognitive functions. The intimate relationship between speech production and perception was also assessed by another hyperscanning study by Stephens and collaborators (Stephens et al., 2010). They scanned the brain of a speaker reciting a monologue and then those of participants listening to it. The authors found an extended temporal and spatial coupling between the speaker's and the listener's brains. Interestingly, this coupling vanished when the communication failed. They also looked at the coupling delays and observed a correlation between the story comprehension and the anticipatory speaker-listener coupling. This suggests the important aspect of prediction in successful communication.

Later studies in hyperscanning fMRI shifted to non-verbal communication. Anders and collaborators (Anders et al., 2011) were interested in the facial communication of affects between love partners. They found that the communication of emotion leads to similar brain activations in the sender's and the receiver's brain. Moreover, the receiver's neural activations could be predicted from those of the sender. Similarly to the first Montague et al.'s hyperscanning study, the authors found a temporal succession of the "flow of affective information" from the sender's brain to the receiver's brain. They also showed a progressive tuning of this flow while the experiment was in progress. It was the first neurophysiological illustration of the phenomenon of social resonance

reported in behavioral studies (Issartel et al., 2007; Richardson et al., 2007). In addition it raised new questions on how this neurobehavioral resonance emerges and leads to the construction of a "shared space" of affect.

In another fMRI study, Schippers and collaborators (Schippers et al., 2010) recorded separately the brain responses of pairs of subject playing the game of charade. Each subject had to guess the meaning of the other's gestures. Authors used between-brain Granger-causality mapping (bbGCM) to observe the between-brain statistical influence. They found that the guesser's brain regions involved in mentalizing and mirroring were temporally synchronized with the gesturer's brain. These results provide new evidence for the resonance theories but also assess a fine-grained temporal interplay of brain activities in areas implicated in motor planning and mentalizing during social perception.

Finally, at the time where our first hyperscanning paper was in press, an fMRI study used also real simultaneous recording and real-time interaction (Saito et al., 2010). Saito and collaborators investigated the neural correlates of mutual gaze and joint attention in pairs of adults. The eye contact served as baseline for both averted and joint gaze periods. Dissociations appeared between the conditions of gaze aversion and joint attention at the individual level but inter-individual correlations between paired and non-paired subjects revealed a "face-to-face" effect in the right inferior frontal gyrus: the authors thus suggested a specific involvement of this area in joint attention.

Recently, a patent has been deposited regarding a dual-fMRI head coil (Lee et al., 2010) that allows scanning two subjects simultaneously in the same MRI scanner while they socially interact. This bears witness to the growing investment in methodological improvement of hyperscanning setting and apparatus opening promising avenues to social neurosciences.

1.4.2 EEG studies

Hypermethods and decision making

Although fMRI studies have been most welcomed by academic journals, EEG has also adopted successfully the hyperscanning techniques. To our knowledge, Babiloni and colleagues (Babiloni et al., 2006) were the first to engage hyperscanning-EEG studies. They recorded the brain activities of four participants playing a card game and tested so-called "hypermethods" taking into account the particular characteristics of simultaneous multiple brain recordings. Their key mea-

surement aimed at quantifying concurrent activities across participants, and more precisely the "hyperconnectivity" depicting causal connections between regions of different brains. They used partial direct coherence (PDC) which presents the advantage of taking into account simultaneously all the signals thanks to a multivariate autoregressive modeling (MVAR). PDC allows studying the directional influences between any given pair of signals and correcting the indirect influence between them, unlike with Granger causality. By applying graph theoretical tools to the resultant network, in-degree and out-degree of the causal links between participants were compared across the different phases of the game. The analysis revealed Granger-sense causal relations between the EEG activities in high-level brain structures of the two cooperating humans, the team-leader influencing the subsequent brain activities of his partner (Babiloni et al., 2007b; Astolfi et al., 2010b).

Babiloni's group investigated two other economic games where subjects had either to cooperate or to defect each other (Babiloni et al., 2007a; Astolfi et al., 2010a). Results show a strong involvement of the frontal regions during the exchanges and dissociations of the causal flow while comparing cooperation with defection strategies. Furthermore, a later study demonstrate the possibility to predict the defecting strategy from the changes of connectivity pattern in the hyper-brain network (Fallani et al., 2010). Using decision making tasks, a Korean team replicated these results with dual EEG. They observed a similar relationship between decision and increase of activity in fronto-central regions in high frequency band (Chung et al., 2008; Yun et al., 2008) and showed the information flow between the proposer and the responder (Yun et al., 2008, 2010). Interestingly, they used a different measure of connectivity, the nonlinear interdependence prediction error. This is coherent with the methodological comparison of effective and functional connectivity conducted by Babiloni's group (Astolfi et al., 2009). They investigated in individual brain both linear and non-linear methods for neuroelectric and hemodynamic signals. Their conclusions assessed a similar global picture given by all these measurements (Structural Equation Modeling (SEM), Directed Transfer Function (DTF), Partial Directed Coherence (PDC), (Phase Synchronization Index (PSI) and direct Directed Transfer Function (dDTF).

Coordination dynamics

One of the major advantage of EEG in neuroimaging is its good temporal resolution. It indeed provides information at the millisecond scale about the dynamics of brain activity. The already mentioned "coordination dynamics" framework developed by Kelso and Bressler (Kelso, 1995; Bressler and Kelso, 2001) pointed out the potential links between neural, behavioral and social coordination phenomena. Combined with hyperscanning, this framework is well designed for the study of the complex and temporally structured aspects of inter-individual sensorimotor interaction. Kelso's team made a pioneer work in this sense. Tognoli and collaborators (Tognoli et al., 2007), inspired by the earlier works of Kelso on inter-personal finger tapping studies, conducted an hyperscanning experiment where participants were instructed to perform a rhythmic finger movement with or without the vision of the other participant's movement. The authors observed the usual behavioral coordination but more interestingly discovered in the alpha-mu frequency range a pair of oscillatory components located above right centroparietal cortex that they called the "phi complex", with one sub-component favoring independent behavior (ϕ_1) and the other (ϕ_2) favoring behavioral coordination. Consistent with neuroanatomical sources within the MNS, they are suggested to reflect the influence of the other on each partner via the inhibition or the enhancement of the MNS.

This experiment was the first to integrate real reciprocal interaction between persons, although the results were related to individual activity and not inter-individual functional connectivity. The group also observed several other spatio-temporal patterns in the continuous brain dynamics specifically associated with the loss of coordination (Benites et al., 2009). Moreover, they reported idiosyncratic synchronizations between the brain oscillations of the two subjects during the phases of sensorimotor coordination (Kelso et al., 2009b). The same year, Lindenberger and collaborators (Lindenberger et al., 2009) were able to show statistical evidence of inter-brain synchronization between pairs of guitar players. The authors demonstrated that coordinated action and perception, induced by playing the same guitar melody with a common metronome, were preceded and accompanied by phase coupling between-brain oscillations in the two guitarists. However the coordination shown emerged from convergent responses to an external signal (metronome) and thus was not based upon reciprocal interaction.

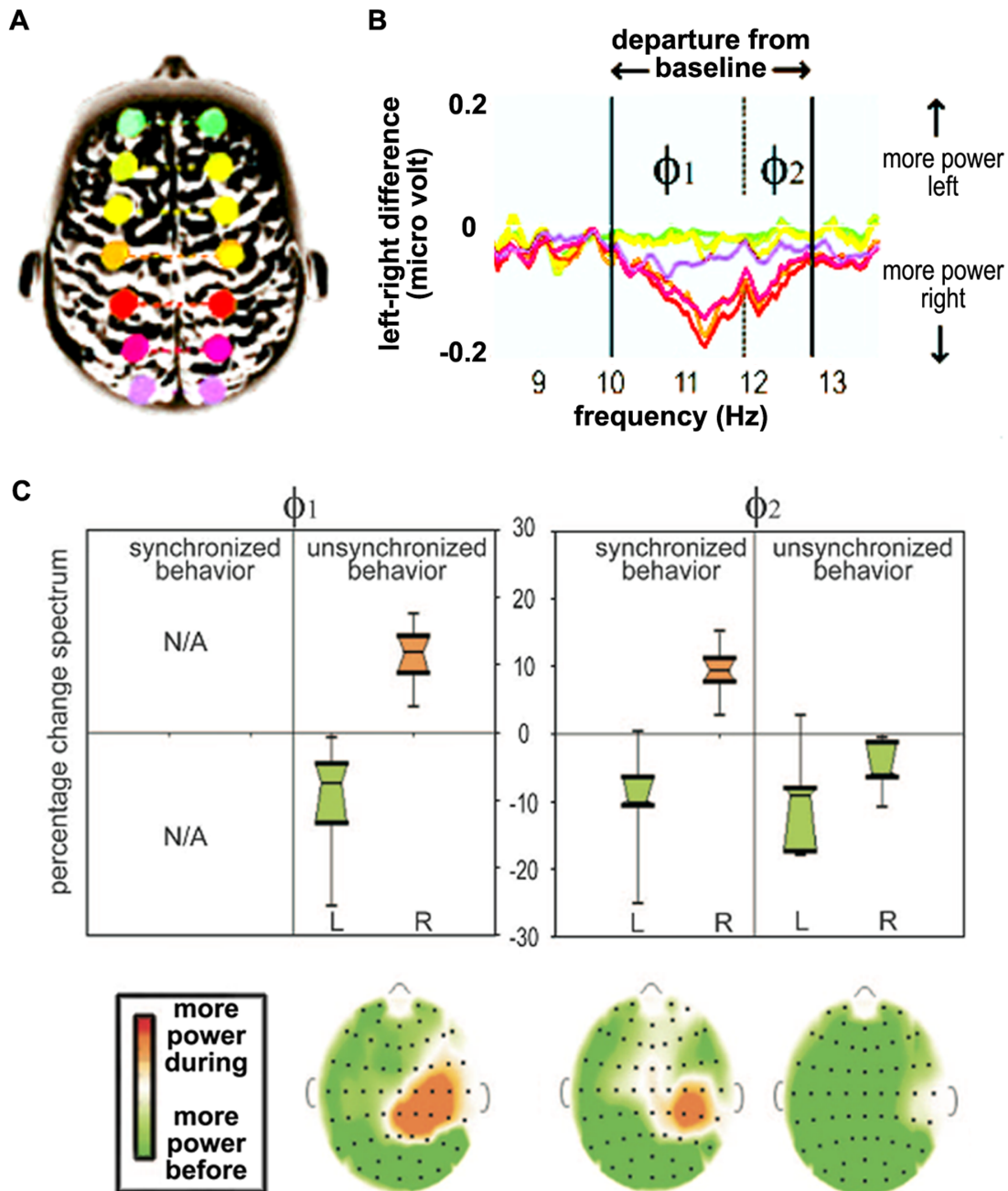


Figure 1.14: Phi1 (unsynchronized behavior) and Phi2 (synchronized behaviors) rhythms distinguish synchronized and unsynchronized (intrinsic) behavior. A) Electrodes pairs used to identify the Phi complex. B) Power differences between left and right electrodes. C) Box-and-whiskers plot of power changes in Phi1 and Phi2 and representative examples of corresponding maps of power change. (adapted from Tognoli et al. 2007)

Table 1.1: Summary of the hyperscanning studies until 2010

Date	Authors	Source	Topic	S	B	Mod.
1965	Duane and Behrendt	Science	Telepathy	2	X	EEG
2002	Montague et al.	Neuroimage	Neuroeconomics	2		fMRI
2003	Wackermann et al.	Neurosci. Lett.	Telepathy	2	X	EEG
2004	Hasson et al.	Science	Perception	1	X	fMRI
2005	King-Casas et al.	Science	Neuroeconomics	2	X	fMRI
2006	Babiloni et al.	IEEE En. Med. Biol.	Neuroeconomics	4	X	EEG
	Tomlin et al.	Science	Neuroeconomics	2	X	fMRI
2007	Babiloni et al.	29th IEEE EMBS	Neuroeconomics	4	X	EEG
	Babiloni et al.	29th IEEE EMBS	Neuroeconomics	2	X	EEG
	Fliessbach et al.	Science	Social judgement	2		fMRI
	Tognoli et al.	PNAS	Sensorimotor coord.	2		EEG
2008	Chung et al.	6th ICCS	Neuroeconomics	2		EEG
	Hasson et al.	Neuron	Perception	1	X	fMRI
	Hasson et al.	J. of Neuroscience	Perception	1		fMRI
	Jääskeläinen et al.	The Open Neuroimaging J.	Perception	1	X	fMRI
	Wilson et al.	Cerebral Cortex	Perception	1	X	fMRI
	Yun et al.	6th ICCS	Neuroeconomics	2	X	EEG
	Benites et al.	JAM 2009	Sensorimotor coord.	2		EEG
2009	Hasson et al.	TICS	Perception (Review)	1	X	fMRI
	Kelso et al.	Neuroscience 2009	Sensorimotor coord.	2		EEG
	Lindenberger et al.	BMC Neurosci.	Perception / Action	2	X	EEG
	Anders et al.	Neuroimage	Delayed non-verbal com.	2	X	fMRI
2010	Astolfi et al.	Brain Topography	Neuroeconomics	4	X	EEG
	Astolfi et al.	IEEE En. Med. Biol.	Neuroeconomics	2	X	EEG
	Dumas et al.	PLoS ONE	Non-verb. com.	2	X	EEG
	Fallani et al.	PLoS ONE	Neuroeconomics	2	X	EEG
	Kauppi et al.	Front. in Neuroinf.	Perception	1	X	fMRI
	Lee et al.	IEEE En. Med. Biol.	Methods	2		fMRI
	Saito et al.	Front. in Integ. Neurosci.	Gaze / Joint attention	2	X	fMRI
	Schippers et al.	PNAS	Delayed non-verbal com.	1	X	fMRI
	Stephens et al.	PNAS	Delayed verbal com.	1	X	fMRI
	Yun et al.	HBM 2010	Neuroeconomics	2	X	EEG

S : number of subjects scanned simultaneously

B : brain to brain result

Mod. : modality

2 General methodology

The current study was born from the encountering of two research groups from the Pitié-Salpêtrière Hospital: the Cognitive Neuroscience and Brain Imaging Laboratory, which host specialists of non-linear analysis of brain activity that played a key role in the development of the study of neural synchronizations, and Jacqueline Nadel's team at the CNRS Centre Emotion, specialized in psychological approaches of spontaneous imitation and behavioral synchrony. The goal of this collaboration was to build up a multidisciplinary approach of social interactions at the crossroad between socially-situated psychology, nonlinear dynamics and the emerging hyperscanning techniques.

While synchronization at neural and social levels have been separately observed and studied for more than a decade, there was no evidence of their relationship, at the start of the project. The observations of Kelso's group concerning idiosyncratic brain-to-brain synchronization during sensorimotor coordination, and the publication of Lindeberger's group, came later. They confirmed that bridging the gap between neural and interactional synchrony was possible. However, a situated interactive protocol remained to be found as none of the above-mentioned studies caught up the emergent properties of a mutual and live social interaction. Hari and Kujala (2009). were claiming for more ecological procedures where participants could interact freely in real-time and reciprocally. Though adopting this perspective, Kelso's group failed to measure inter-brain relationships.

The starting point of this thesis was to combine the dual-video system earlier developed by the psychology team with a new hyperscanning-EEG setup in order to simultaneously record both behavior and brain activities of two people engaged in free reciprocal imitation. This part presents the global methodological approach of the project. It describes the principal obstacles encountered and how technical choices were done. The detailed description of the methodology is to be found in the related section of each paper.

2.1 Setting apparatus

Although the core idea of the hyperscanning technique is rather simple, we had to overcome several technical challenges for the making up of the setting. The first version of the setup was an extension of the original dual-video setup designed by Nadel's team for the studies of mother-infant interaction (Nadel et al., 1999; Soussignan et al., 2006) and the imitative procedure was also derived from Nadel's work (Nadel, 1986; Nadel and Butterworth, 1999). Here we also wanted to keep the interaction at the non-verbal level. This was made for several reasons: language interactions imply the use of semantic and we wanted to keep the interaction as intransitive and non-symbolic as possible. Furthermore, electrophysiological recordings of language tasks show a weak neural activity and usually need averaging methods across large number of trials. In our cases, the real-time constraints forbid any stimulus locked paradigm. Hand movements however create strong cortical activity that can be detect in real time with EEG. This has been widely used for Brain Computer Interfaces (Kalcher et al., 1994; Babiloni et al., 2000).

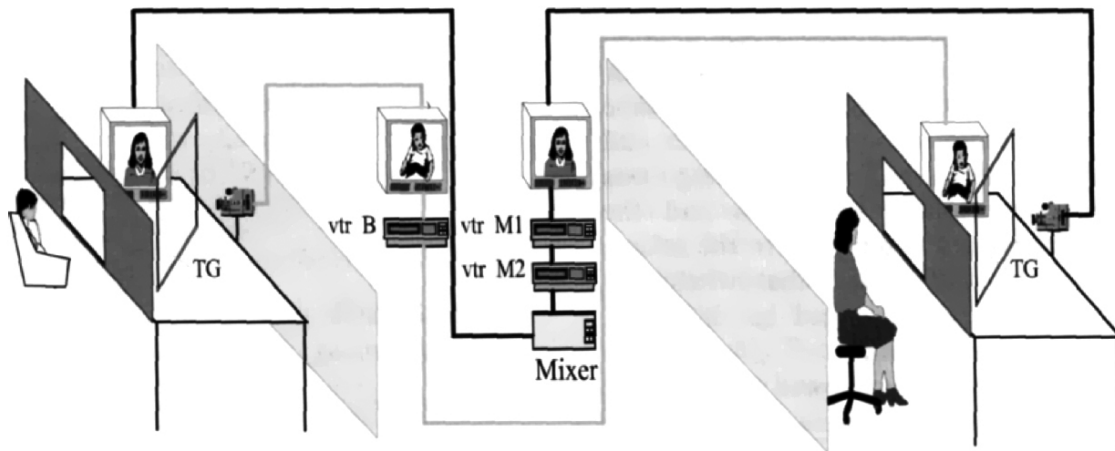


Figure 2.1: Original dual-video setup by Nadel et al. 1999. The equipment involves three video recorders, one for the baby and two for the mother, since two simultaneous records of the mother are needed (one for live and one for replay).

The original setup was constituted by two separated rooms each containing a video camera and a television. Both were respectively linked to a control device situated in a third control room. This system allowed to show either the real-time images of each participant to the other while recording both videos, or to play recorded video. Thus, within the same perceptual context, real reciprocal interaction can be compared with fake one.



Figure 2.2: Photo from one of the two experimental rooms

For our study, the dual-video setup was combined with a dual-EEG system. Both participants' brain activities were thus continuously recorded during the experiment. The two EEG helmets were plugged on the same amplifier so that the signals were kept synchronized at the millisecond scale. The two cameras recording the hand movements of each participant were synchronized. Two light-emitting diodes (LED) were put in the cameras' field to synchronize videos with the EEG signals. These LEDs indicated the different steps of the experimental conditions and their signals were sent to the amplifier for the subsequent segmentation of the recordings.

2.2 Paradigm

Pilot experiments allowed achieving key choices concerning the protocol, the blocks timing, the baselines and the instructions to the participants. They were also useful to verify the synchronization of the recordings and the approximative time needed for entering in active interaction. Finally they provided data offering the opportunity to adjust the coding criteria.

Based on earlier works by Nadel, two basic parameters, imitation, synchrony were selected. Computerized annotations were added in order to indicate moment by moment who was the initiator of the movement imitated by the other. We then calibrated the common window size for behavioral and neural measures, taking into account coherent behavioral segmentation and neural stability.

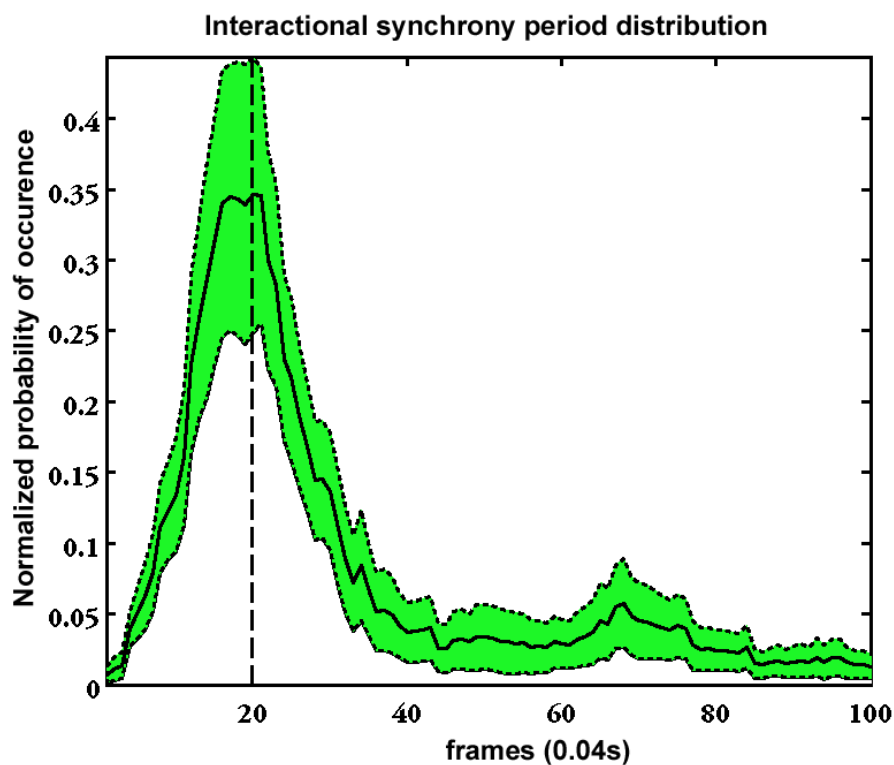


Figure 2.3: Normalized distribution of behavioral periods of interactional synchrony. The areas stand for standard error across the 9 dyads.

The sampling rate of the behavioral analysis was 40 ms (DV Video at 25 frames/s) and thus the window length for the neurodynamics analysis had to be a multiple of that period. As we wanted to explore theta rhythm (3-7Hz), the windows had to be at least 800 ms in order to get two cycles at least. Since it was coherent with the modal peak of the synchronous periods of interaction (See figure 2.3), we adopted this size.

2.3 Data analysis

2.3.1 Artifacts correction

The real time constraints of our paradigm that lead to deal with continuous EEG recordings generate twice more chance than usual to get artifacts because of the hyperscanning methodology. Furthermore, the experimental condition of long visuo-motor behavior is likely to add also artifacts despite explicit instructions to blink as less as possible and to keep both elbows on the arm rests of the armchair while moving the forearms and hands. In usual neuroimaging studies multiple event related stimulations allow to discard trials corrupted by artifacts. Here, since we have fewer but longer trials, the pre-processing started with an indexing of physiological artifacts such as blinks, eye movements and both muscles and cardiac activity. Spatial filters based on artifact and brain signal topographies allow then to remove the majority of the artifacts without distortion of relevant brain activity.

Although independent component analysis (ICA) are usually used, their potential impact on non-linear measurement such as brain synchronizations leads us to rather adopt a principal component analysis (PCA) decomposition. We thus adapted a classical PCA algorithm which discard the PCA components strongly correlated with the electro-oculogram. The corrected signal is then reconstructed by an inverse recombination of remaining components. Signals from the two helmets were preprocessed separately, and visually controlled afterwards.

2.3.2 Measures

Following filtering corrections, EEG data were re-referenced to a common average reference (CAR). Before looking at non-linear measurements, we first focused on basic linear measures such as power spectrum and raw correlation of the signals. Amplitude covariation has also been investigated since it could mark similarities between the dynamical states of the subjects at larger timescales. For instance, alternate states of attention and relaxation were thought to possibly correlate with the behavioral rhythm of turn-taking.

Univariate

The first power analyses were done with classical fast Fourier and wavelet transforms. Both of them gave preliminary results in the alpha and beta band. The analyses allowed also us to check the impact of artifact corrections on the characteristics of the signals.

We found the classical alpha and beta desynchronizations (ERD) and compared their frequency peaks. Their ratio was two and thus the beta ERD appeared rather as an harmonic of the alpha ERD than the usual beta activity. This questioned the general EEG classification since the beta oscillations observed in cortical slices has a "golden-mean" ratio with the alpha (Roopun et al., 2008; Pletzer et al., 2010).

Bivariate

After this control of the preprocessing part, we moved to bi-variate measurements as our main interest was the investigation of the inter-brain relationships. We thus tested different types of measurements for the functional connectivity between the two brain activities of the participants.

Raw correlations of EEG signals were computed but did not show any effects at the inter-brain level, even after a band-pass filtering in the classical frequency bands. The real time constraints of our paradigm did not allow us to use the usual linear bivariate measurements such as coherence. Indeed, this methods usually need long periods of recording and a stationarity of the signals. Furthermore, considering past neurodynamics and cortico-muscular coherence results (Jerbi et al., 2007), we had strong assumptions on the sharing of phase information between the brain rhythms of the two participants while they were interacting. Then, we focused on non-linear analyses which allows phase analyses in a continuous manner. We used Hilbert transform since it has been proven to give similar results as wavelet based analysis with faster computation (Le Van Quyen et al., 2001). The extracted analytics signal giving also access to instantaneous amplitude, we analyzed the covariance of their envelopes. However, only sparse relationships in the alpha-band were observed so far.

For the analysis of the phase, we faced two different approaches: the phase locking value (PLV) developed and already applied in our team for individuals analysis (Lachaux et al., 1999, 2000) and the magnitude phase difference (MPD) designed later by Alba and collaborators (Alba et al., 2007, 2010).

For a given electrode pair (k, l) at a time t , and a window analysis of N timepoint, these two measures are calculated as follow:

$$PLV_{(k,l)}(t) = \frac{1}{N} \left| \sum_{s=0}^{N-1} (e^{j(\phi_k(t+s) - \phi_l(t+s))}) \right|$$

$$MPD_{(k,l)}(t) = 1 - \frac{1}{\pi N} \sum_{s=0}^{N-1} |\text{wrap}(\phi_k(t+s) - \phi_l(t+s))|$$

where $\phi_k(t)$ represent the phase of the signal k at time t and $\text{wrap}()$ wraps its angular parameter in the range $[-\pi, +\pi[$.

The MPD measure equals 1 if the signals are perfectly in-phase through all the trials, and zero if their phases are completely opposite. It hence presents the advantage to quantify if two signals are in-phase or anti-phase locked. According to the literature, behavioral coordination has only in-phase and out-of-phase synchronization as stable cases (Kelso et al., 1987). However, at the brain level, various delays could be measured because of synaptic propagation (McKenna et al., 1994). Thus, while in-phase and anti-phase synchronization can characterize the coordination between two complex dynamical systems, the coordination between neural populations could occur but are indeed mixed with delayed synchronizations caused by the finite velocity of axonal transfers.

We compared with AR models the robustness of these two measures regarding both noise and the strength of coupling between the signals. The model dynamics was defined by the equation:

$$\begin{cases} x(n+2) = a_1 x(n+1) + b_1 x(n) + v_1 \\ y(n+2) = a_2 y(n+1) + b_2 y(n) + v_2 + K(y(n+1) - x(n+1)) \end{cases}$$

where $a_1 = 1.95$, $a_2 = 1.96$, $b_1 = b_2 = -0.99$, $v_{(1,2)}$ stands for two independent dynamic noises of 0.05 amplitude and K was the coupling strength. Initialization was done with random values taken from the interval $[0, 0.05]$. Simulations were run over 10000 samples and then an independent static noise ϵ was added to the final time series.

Oscillators can be fully phase locked but the difference between their phase can vary. The PLV do not make a difference between the different types of phase-lock and only quantify between 0 and 1 the intensity of the locking. The MPD gives 0 if the oscillators are in opposite phase and 1 when they are perfectly in-phase. However, the main problem is that MPD gives 0.5 in the case of a $\pm \frac{\pi}{2}$ phase difference and also when the oscillators are fully unsynchronized. This leads to an ambiguity of the MPD measurement and we thus finally keep only the PLV for our analysis.

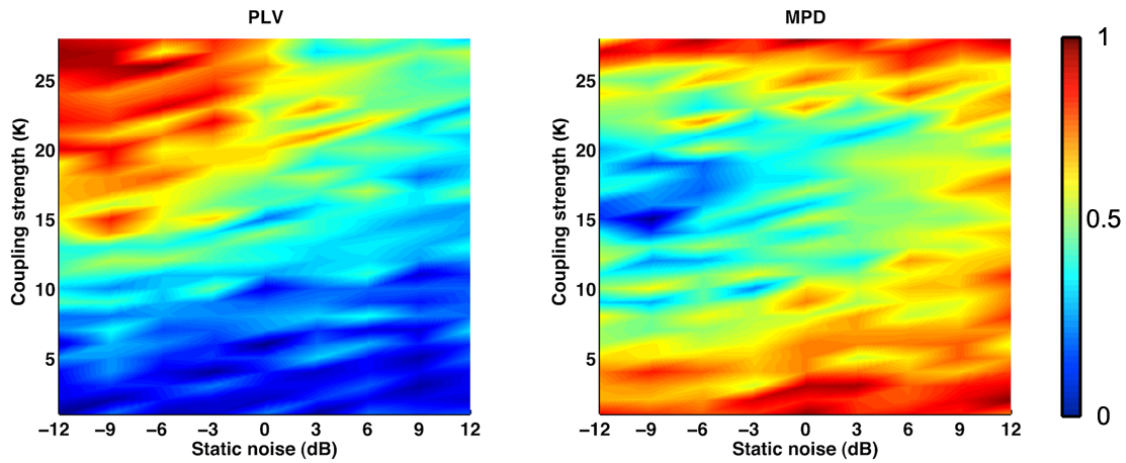


Figure 2.4: Analysis of the noise and coupling strength of AR models on PLV and MPD measurements.

It is important to notice that virtual synchronizations could occur at the scalp level (Tognoli and Kelso, 2009). They are caused by two main phenomena spurious synchronization due to single sources and electrical diffusion at the scalp level. While the first issue is still difficult to correct, some techniques have been proposed to diminish the diffusion phenomenon (Nunez and Westdorp, 1994; Nolte et al., 2004). The Laplacian technique transform the signals in current densities and decrease the diffusion effect. However, if it could creates artificial correlation between neighbor electrodes and furthermore need to get rid of all electrodes at the limits of the helmet.

2.3.3 Statistics

The analysis of high-dimensional data-set lead to the multiple comparison problem (MCP). This problem is caused by the fact that a large number of sensors, time points or other measures need to be evaluated. In the case of bivariate measurement, the combinatory explosion of the data conducts to a large number of statistical tests and thus increases the chance to make a false positive detection. In this case, the so-called family-wise error rate (FWER) is the probability under the null hypothesis to conclude falsely at difference between two conditions. In order to reduce the effect of MCP, some mathematical techniques are available to control the FWER at some critical alpha-level (usually, $p_c = 0.05$ or $p_c = 0.01$). The most naive is the Bonferoni correction which consist in dividing the initial statistical threshold by the number of comparisons made. But this method is very conservative and do not use the potential priors on the considered data. Various techniques has been developed to overcome this ubiquitous statistical problem.

In our study, we used a non-parametric statistical testing since it is easier to solve the MCP in this framework (Nichols and Holmes, 2002). Furthermore, this statistical framework is extremely general because its neither depends on the probability distribution of the data (i.e., whether it shows a normal or some other distribution) nor on the test statistic on which the statistical inference is based (Maris and Oostenveld, 2007). Indeed, the statistical threshold is built up in a data-driven. The usual methods is as follow:

1. Combine the data from the two conditions in a single set.
2. Do a random partitions in two subsets.
3. Calculate the test statistics between the sets.
4. Repeat steps 2 and 3 to obtain the null hypothesis distribution.
5. Calculate the test statistics between the real sets
6. Calculate the proportion of random partition that have given a larger test statistics than the real one¹
7. If this proportion is under the critical alpha-level, then the two real sets are significantly different.

The non-parametric approach has been widely used in MEEG at the sensor level (Blair and Karniski, 1993), time-point level (Karniski et al., 1994; Galán et al., 1997), spatio-temporal matrices (Maris, 2004), time-frequency transforms (Lutzenberger et al., 2002) and distributed inverse solutions (Singh et al., 2003; Pantazis et al., 2005). It has been also recently extended to coherence with a combination of a clustering technique (Maris and Oostenveld, 2007). The clustering techniques could be added to incorporated priors in the analysis and thus enhance both the robustness and sensibility of the statistics. In the case of bivariate measurements, the number of signal pairs can become very large even with few sensors. The technique then consists in operating the statistics test at a second order. Instead of analyzing each elements separately, it evaluates the distribution of a Cluster Statistics (CS) which integrates a first order measure across neighbor selected elements. Most of the time, the elements are selected by a thresholding adapted to the first-order measure used. Here, since we computed for each element a t-value, we selected only those with an absolute t-value above a critical value T_c relative to a probability risk of taking into

1. This proportion is called the Monte Carlo p-value.

account a false positive element p_c . We normalized this thresholding critical value by keeping constant the ratio of the critical p-value and the average number of neighbors in the considered space (amplitudes/power or phase synchronization). We fixed the $p_c = 0.05$ for the amplitudes. Both univariate and bivariate space average numbers of neighbors were computed numerically according to the EEG montage.

The usual algorithm used for the detection of clusters could be summarized as follows:

While it exists an unassigned upper threshold element:

1. Create a new cluster list by adding one unassigned upper threshold element.
2. While it exists an element in the cluster list unmarked.
 - (a) Take one unmarked element.
 - (b) Mark it as analyzed.
 - (c) Add to the cluster list its unmarked and upper threshold neighbors.
3. Store the Cluster Statistics by taking either the size or the sum of the statistical values of the elements in the cluster.

Depending of the data, the notion of neighborhood varies. In the above figure, three cases are illustrated. The univariate case corresponds to the usual power or amplitude analyses. In this case, the cluster is built by taking adjacent electrodes on the scalp. In the bivariate case like in coherence or PLV, each electrode of the considered pair have to be adjacent (or identical at one extremity). Finally, in the bipartite bivariate case like in the h-PLV measures, this is similar to bivariate measure except that the two electrodes can also be identical on both heads.

Then, the distribution of CS under the null hypothesis is constructed as in the classical non-parametric approach by taking the maximum of the Cluster Statistics for each permutation. By taking the 5 percents maximum of this distribution, we obtain a statistical threshold for the real Clusters Statistics.

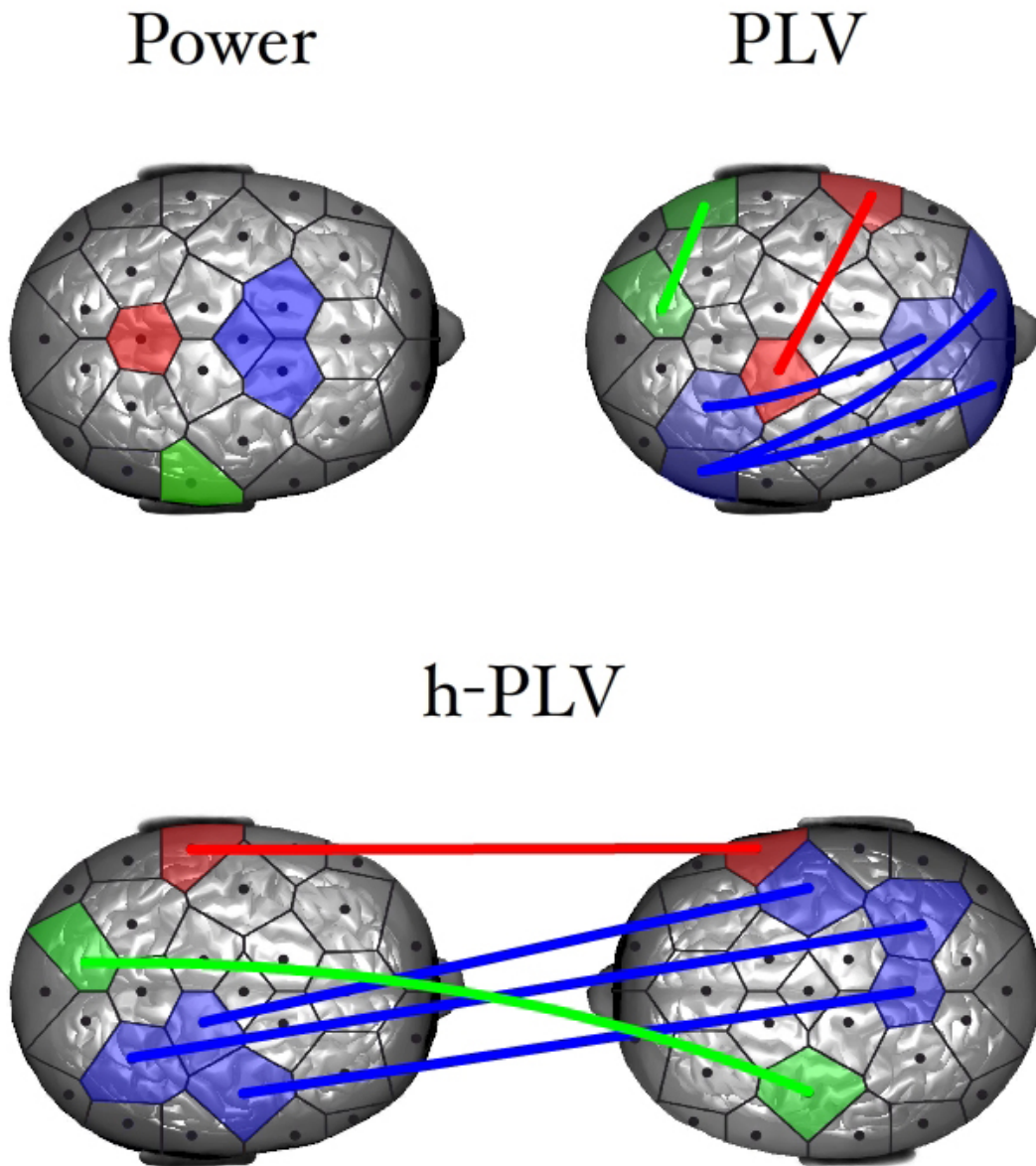


Figure 2.5: Schema of the clustering algorithm used for: Power (univariate), PLV (bi-variate) and h-PLV (bivariate, bipartite graph). The current cluster is in blue. Red and green represent element over threshold but not satisfying the neighborhood condition.

3 Inter-brain synchronization during social interaction

We have seen in the introduction how pervasive is the synchronization phenomenon, and in contrast how late were the first attempts to study inter-brain synchronization. One explanation why the investigation of interactional synchrony remains so scarcely studied in neuroscience is related to the double requirement to record two people simultaneously and to immerse the pair of participants in a meaningful social context where they are able to interact freely. When imitation is at will, it is likely to provide such a context via the simultaneous perception-action coupling arising from the two partners. In this case, the two roles of imitator and model are spontaneously alternated. As seen in the last part of the introduction, studies of interpersonal coordination have shown that this alternation of roles is intimately linked with a synchronized behavior of the interactants. Interestingly, there are no neuroimaging results concerning this phenomenon, although imitation has generated a rich literature.

In the first study, we aimed at demonstrating how an enactive approach of social interaction could provide new insights towards the understanding of reciprocal interaction. While the new hyperscanning techniques allow recording simultaneously the brain activity of multiple subjects, first hyperscanning studies either averaged their results on one brain or used tasks that did not implicate reciprocal interaction. By the combination of an embodied social protocol based on spontaneous imitation of hand movements, a dual-video and hyperscanning-EEG setup and inter-brain neurodynamical analysis, we aimed at testing dynamical neural correlates of emerging interactional synchrony. One of the harder obstacle to overcome concerned the multi-scale aspects of a comparison between behavioral and brain activity units. Not only did we have to synchronize the behavioral recordings of the pairs of partners, the dual EEG recordings, and behavioral and brain recordings, but we had also to find a relevant common time-window. The following paper describes our solutions to the multiple problems raised by recording two persons in a meaningful social context where they are free to behave at will.

Inter-Brain Synchronization during Social Interaction

Guillaume Dumas^{1,2,3*}, Jacqueline Nadel⁴, Robert Soussignan⁵, Jacques Martinerie^{1,2,3},
Line Garnero^{1,2,3†}

1 Université Pierre et Marie Curie-Paris 6, Centre de Recherche de l'Institut du Cerveau et de la Moelle épinière, UMR-S975, Paris, France, **2** Inserm, U975, Paris, France, **3** CNRS, UMR 7225, Paris, France, **4** CNRS, USR 3246, Centre émotion, Pavillon Clérambault, Hôpital de La Salpêtrière, Paris, France, **5** Centre des Sciences du Goût et de l'Alimentation, UMR-6265 CNRS, 1324 INRA, U-B, Dijon, France

Abstract

During social interaction, both participants are continuously active, each modifying their own actions in response to the continuously changing actions of the partner. This continuous mutual adaptation results in interactional synchrony to which both members contribute. Freely exchanging the role of imitator and model is a well-framed example of interactional synchrony resulting from a mutual behavioral negotiation. How the participants' brain activity underlies this process is currently a question that hyperscanning recordings allow us to explore. In particular, it remains largely unknown to what extent oscillatory synchronization could emerge between two brains during social interaction. To explore this issue, 18 participants paired as 9 dyads were recorded with dual-video and dual-EEG setups while they were engaged in spontaneous imitation of hand movements. We measured interactional synchrony and the turn-taking between model and imitator. We discovered by the use of nonlinear techniques that states of interactional synchrony correlate with the emergence of an interbrain synchronizing network in the alpha-mu band between the right centroparietal regions. These regions have been suggested to play a pivotal role in social interaction. Here, they acted symmetrically as key functional hubs in the interindividual brainweb. Additionally, neural synchronization became asymmetrical in the higher frequency bands possibly reflecting a top-down modulation of the roles of model and imitator in the ongoing interaction.

Citation: Dumas G, Nadel J, Soussignan R, Martinerie J, Garnero L (2010) Inter-Brain Synchronization during Social Interaction. *PLoS ONE* 5(8): e12166. doi:10.1371/journal.pone.0012166

Editor: Jan Lauwereyns, Kyushu University, Japan

Received: June 3, 2010; **Accepted:** July 19, 2010; **Published:** August 17, 2010

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Funding: This work was supported in part by funds from the French National Center for Scientific Research (<http://www.cnrs.fr/>). This work was also supported by a PhD fellowship of the Direction générale de l'armement (DGA) (<http://www.defense.gouv.fr/dga/>) and the Computer Neuroscience Program n°070005IPAM. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: guillaume.dumas@upmc.fr

† Deceased

Introduction

From a traditional information-processing perspective, communication is said to occur when messages flow from one location to another and cause a change in the receiver [1]. In this emit/receive/answer telegraphist model of communication, the actions of the partners are taken to be discrete signals. A more appropriate model of human communication, however, consists in considering both synchronic and diachronic aspects of communication to be entwined [2]. Indeed, during communication, both participants are continuously active, each modifying their own actions in response to the continuously changing actions of their partner. This continuous mutual adaptation generates synchrony [3] and turn-taking [4–6] between partners, resulting in interactional synchrony.

Taking seriously the neural exploration of communication is challenging in two ways. The first challenge is to design a suitable procedure for the study of interactional synchrony. So-called interactive paradigms mainly consist in non contingent social stimuli that do not allow true social interaction [7]. Our choice was to delineate an imitative procedure allowing synchrony and turn-taking to spontaneously take place. In effect, during an imitative interaction, each partner alternately initiates or imitates actions and both coregulate the synchronous matching [8,9]. As a

paradigm, imitative interaction offers the double advantage of delineating brain areas of interest already informed by previous research on imitation, and of recording new data concerning spontaneous interactional synchrony.

Recording interactional synchrony in an attempt to elucidate the interindividual neural mechanisms of human interaction remains an open challenge, as is the objective of moving toward two-person neuroscience [10]. Until now indeed, most fMRI explorations of interpersonal processes have scanned one individual only [11,12] or several individuals separately in front of the same visual scene [13].

Simultaneous fMRI or EEG recordings of several brains (i.e. hyperscanning) have recently opened a new field [14–17]. This new field, however, has revealed rapidly how difficult it is to 'let humans interact socially while probing their brain activity', as said by Montague and colleagues [18]. Using dual-EEG recordings, Tognoli, Lagarde, DeGuzman and Kelso [19] asked pairs of participants to execute self-paced rhythmic finger movements with and without vision of each other. Episodes with vision generated in-phase and anti-phase motor coordination. A neuromarker of social coordination (called the phi complex) was detected over the right centroparietal area in the 9.2–11.5 Hz range for each subject of the pair separately, but interbrain synchronization of social coordination was not directly tested. Lindenberger and colleagues

[20] actually explored interbrain dynamics as they found phase synchronization in the theta frequency range between frontal areas of pairs of guitarists coordinated via a metronome. However they did not reach social interaction since the coordination was obtained via an external medium. More recently, Astolfi and colleagues [15] achieved the challenge to estimate functional interbrain connectivity related to decision making in a card game task during EEG hyperscanning recording. Only the players belonging to the same team across the different tables showed significant functional connectivity between the estimated cortical signals in the α , β and γ frequency bands, with a causal relation appearing between the prefrontal area 8 and 9/46 of the first player and the anterior cingulate cortex and parietal areas of the second player. It was suggested that this causal relation may reflect cooperation between individuals, at least when decision making is related to an anticipation of the other's intention.

In the present study, we scanned pairs of subjects imitating each other at will. Though imitation is commonly considered as a foundation for learning, socialization and communication [21,22], its use as a paradigm has been limited so far to test the direct matching hypothesis in an intraindividual perspective [23–27]. Here imitation was used in an interpersonal context with the aim to contribute identifying neurodynamic signatures of human interactions.

Adapted to the new challenge of understanding how neural networks exchange information [28,29], neurodynamic tools provided by nonlinear methods [28,30] allow measuring neural synchronizations between distant brain regions of interacting individuals. We hypothesized interbrain synchronization in parietal and frontal regions, based on intraindividual fMRI results in imitation of hand movements [27]. We expected phase synchronization of the right parietal cortices of the two partners given the pivotal role attributed to the right temporoparietal junction in social interaction [31], self-other discrimination and perspective taking [31–33]. Following the suggestion that multi frequency synchrony is a signature of integrative brain processes [28,34], we expected a distributed pattern of interbrain oscillatory couplings when the interacting dyads are engaged in synchronous hand movements with turn-taking between model and imitator.

Methods

Ethics statement

Experiments were approved by the Ethical Committee for Biomedical Research of Pitié-Salpêtrière Hospital in Paris (agreement #07024). Participants had given their written informed consent according to the declaration of Helsinki and were paid for their participation to the study.

Participants

Twenty two healthy young adults (5 female-female and 6 male-male pairs) of mean age 24.5 years ($SD=2.8$) participated in the study. They were all right-handed and had normal or corrected-to-normal vision. None of them reported a history of psychiatric or neurological disease.

Dual behavioral data acquisition

The experiment was conducted in three connected laboratory rooms, one for each participant and the third one for the computerized monitoring of the experiment. The participants were comfortably seated, their forearms resting on a small table in order to prevent arms and neck movements. They were told that they will have to move their hands with meaningless gestures and will watch a library of meaningless movements that will give them

some examples. They could see their partner's hands through a 21-in. TV screen. Two synchronized digital video cameras filmed the hand movements. The set-up was similar to the double-video system designed by Nadel and colleagues for their developmental studies of sensitivity to social contingency in infants [9,35,36], except that a dual-EEG recording system was added (see Figure 1A). The session start was signaled by a LED light controlled manually, via a switch, by an experimenter located in the recording room. The output of the video records was transmitted to two TV monitors installed in the recording room allowing the experimenter to control that participants followed the requested instructions.

Dual-EEG data acquisition

Neuroelectric activity in both participants of each dyad was simultaneously and continuously recorded at a time scale enabling to compare the EEG activity among four frequency bands: theta (4Hz–7Hz), alpha-mu (8–12 Hz), beta (13–30 Hz) and gamma (31–48 Hz). The system was composed of two Acticap helmets with 32 active electrodes arranged according to the international 10/20 system. We modified the helmets in order to cover at best the occipito-parietal regions. Four electrodes T7, T8, CP9 and CP10 were rejected due to artifacts. Ground electrode was placed on the right shoulder of the participants and the reference was fixed on the nasion. The impedances were maintained below 10k Ω . Data acquisition was performed using a 64-channels Brainamp MR amplifier from the Brain Products Company (Germany). Signals were analog filtered between 0.16Hz and 250Hz, amplified and digitalized at 500Hz with a 16-bit vertical resolution in the range of ± 3.2 mV. Note that both subjects were connected to the same amplifier that guaranteed millisecond-range synchrony between the two EEG recordings.

Protocol

The experimental protocol (See Table 1) was divided into two blocks separated by a 10 min rest. Each block comprised four runs of 1 min 30 sec. A run was composed of three conditions: a joint observation of a prerecorded Library of 20 Intransitive (meaningless) Hand Movements (LIHM), a Spontaneous Imitation episode where the partners were told to imitate whenever they would like it (SI), and an episode where one of the partner was told to imitate the other (Induced Imitation: II) while the other was asked to move hands, with a counterbalanced order in block 2. Each run started by a 15 sec 'No View (blank screen) No Motion (NVNM) baseline. For SI and II conditions, a 15 sec 'No View Motion' (NVM) baseline followed where the participants were asked to move their hands with meaningless gestures.

Behavioral data analysis

The video records of hand movements during the free episodes of imitation of each other's hand movements were digitized. Then, the LED signals recorded on the two video at the beginning of each session was used to synchronize the frames of the two partners. They were coded using a revised version of the ELAN program [37,38] that offers a simultaneous presentation of two frames from different sources on the ELAN window. This software allows an analysis of the behavioral frames on separate channels of the window and a recording of time (latency, duration) and occurrence of behavioral events. This way, two main events were analyzed in each run of SI for the two partners: imitation and synchrony of hand movements.

Synchrony was assessed when the hands of the two participants started and ended a movement simultaneously, thus showing a

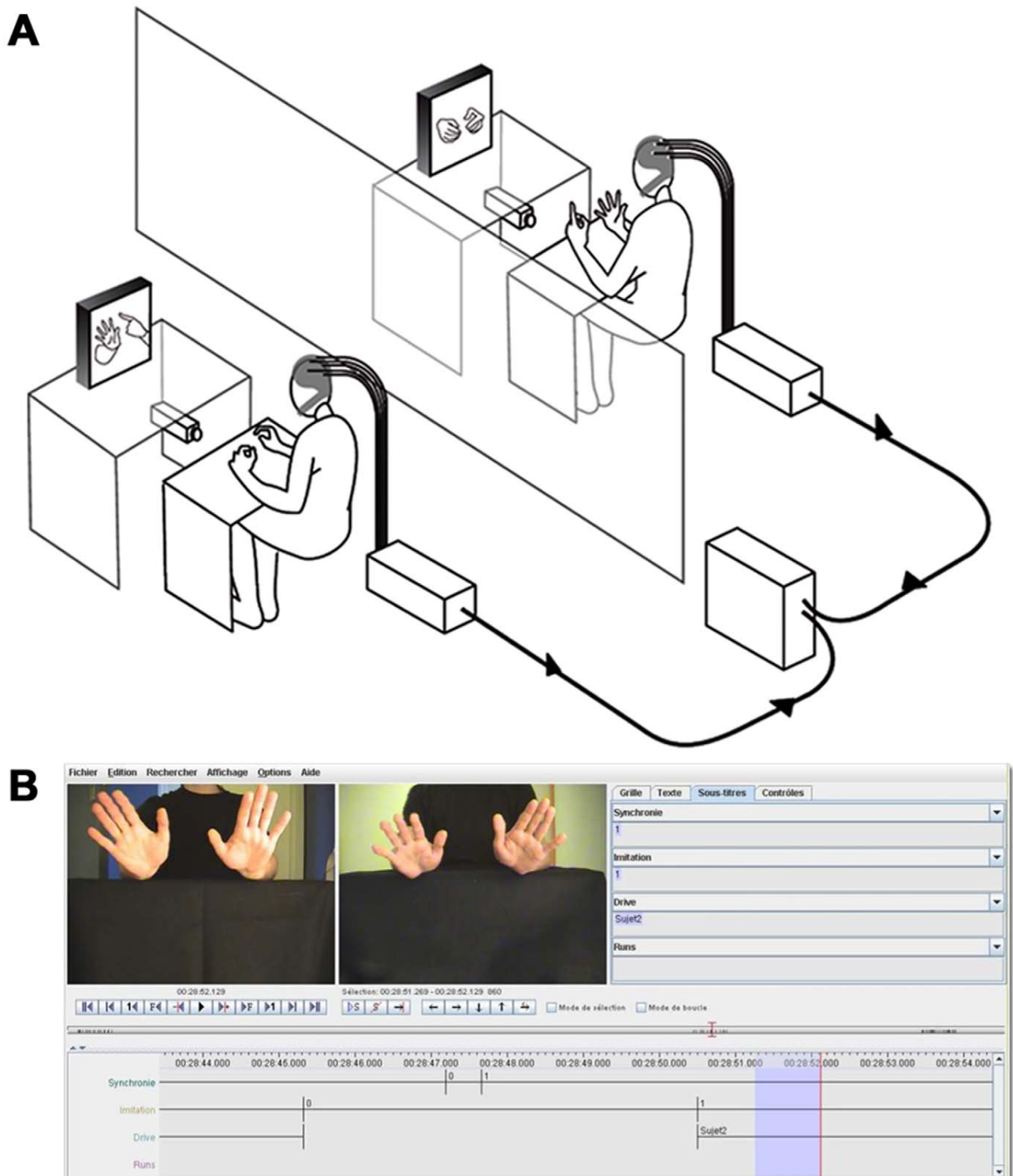


Figure 1. Experimental design and coding software. A. Apparatus and experimental setting of the double video system and dual-EEG recording. B. ELAN software window during an indexing session.
doi:10.1371/journal.pone.0012166.g001

coordinated rhythm. The criterion of simultaneity used was the co-occurrence of two gestural movements within the same video frame. This rhythm could include similar or different movements. We labeled respectively *Sync* and *NSync* the periods with and

without synchrony. Imitation was assessed when the hand movements of the two partners showed a similar morphology (describing a circle, waving, swinging ...) and a similar direction (up, down, right, left...). We labeled respectively *Im* and *NIm* the

Table 1. Experimental schedule.

Condition(Block 1)	NVNM+Library of Intransitive Movements (LIHM)	NVNM+NVM+Spontaneous Imitation (SI)	NVNM+NVM+Induced Imitation (II) Subject A: imitator Subject B: model	NVNM+NVM+Induced Imitation (II) Subject B: imitator Subject A: model
Pause: 10 min				
Condition (Block 2)	NVNM+Library of Intransitive Movements (LIHM)	NVNM+NVM+Spontaneous Imitation (SI)	NVNM+NVM+Induced Imitation (II) Subject B: imitator Subject A: model	NVNM+NVM+Induced Imitation (II) Subject A: imitator Subject B: model
Duration	15s+1min 30s	15s+15s+1min 30s	15s+15s+1min 30s	15s+15s+1min 30s

doi:10.1371/journal.pone.0012166.t001

periods with imitation and without imitation. For each imitative episode, the individual who started a hand movement followed by the partner was labeled *the model*, and the follower was labeled *the imitator*.

The reliability of our fine grained analysis was assessed using Cohen’s kappa. Inter-observer agreement between two independent coders was performed on 25% of the recordings. The values of kappa coefficients were 0.83 for imitation, 0.91 for synchrony, and 0.82 for the roles of model and imitator.

The number of switches between the model and the imitator was also computed for the SI condition, thus providing information concerning turn-taking. Finally we computed the degree of symmetry of roles within each pair of dyads, using the formula:

$$b = \frac{S1dr - S2dr}{S1dr + S2dr} \tag{1}$$

where S1dr and S2dr represent the time spent as model by subject 1 and subject 2 respectively in the SI condition, $b = 0$ indicating a perfect symmetry of the two roles.

EEG artifacts

The correction of eye blink artifacts in the EEG data was performed using a classical PCA filtering algorithm [39]. All the computations mentioned here and afterwards were performed within the Matlab environment. We used 800ms windows with 400ms of overlap. For each window, a principal component analysis (PCA) was performed on the raw signal and all the components were compared to an estimation of the electrooculogram (EOG) from the difference between the mean of the raw channels FP1 and FP2 and the nasion reference. If the correlation between the reconstructed EOG signal and each component of the PCA exceeded an adaptive threshold, the eigen value related to the component was fixed to zero. Then the converted EEG signal was reconstructed by using the inverse solution of the PCA. The adaptive threshold was proportional to the standard deviation of the considered i^{th} component divided by those of the current window signal:

$$Threshold_i = 0.7 \times \frac{\sigma(c_i)}{\sigma(\sum_i c_i)} \tag{2}$$

where $\sigma(c_i)$ stands for the standard deviation of the i^{th} component of the PCA and $\sigma(\sum_i c_i)$ is the standard deviation of the signal.

EEG signals were then visually checked to exclude muscular artifacts from the analysis. A Hamming window was used to control for artifacts resulting from data splicing.

EEG neurodynamic analysis

EEG data during SI and II conditions were analyzed using the phase locking value (PLV) in order to detect adjustment of rhythmicity between two distant brain recordings. Following filtering corrections, EEG data were re-referenced to a common average reference (CAR) and transformed by discrete Hilbert methods for specific narrow frequency bands: theta (4–7Hz), alpha-mu (8–12Hz), beta (13–30Hz) and gamma (31–48Hz). Phases and amplitudes extracted using the Hilbert transform on all band passed signals met the reliability criteria defined in past studies [40]. For the SI condition, the EEG data were segmented into 800ms windows and mapped with the corresponding behavioral samples of synchrony (*Sync*), no synchrony (*NSync*), imitation (*Im*), and no imitation (*NIm*).

The interbrain analysis was done with the PLV for each pair (i,k) of electrodes between the two helmets (electrode i and k respectively for the helmets 1 and 2). This was done for each frequency band according to the relation:

$$PLV_{i,k} = \frac{1}{N} \left| \sum_{t=1}^N \exp^{j(\phi_i(t) - \phi_k(t))} \right| \tag{3}$$

where N is the number of samples considered in each 800ms window, ϕ is the phase and $| \cdot |$ the complex modulus. Thus, PLV measure equates 1 if the two signals are perfectly phase locked across the whole time window observed, and equates 0 if they are totally unsynchronized. Thus, PLV is equal to one minus the circular variance of phases’ differences.

Statistical analysis

For the SI condition, nonparametric methods were used to compare phase synchronization of oscillatory activity during 800ms epochs for synchronous versus non-synchronous acts (*Sync vs. NSync*), and for imitative versus non imitative acts (*Im vs. NIm*). The II condition and the No View Motion baseline condition were compared (*II vs. NVM*) similarly. The high dimension of the PLV spaces leads to create an extension of the classic clustering algorithm adapted to the hyperscanning. Notably, t-values were first computed for the PLVs related to all electrodes of helmet 1 paired one by one with all electrodes of helmet 2. Following previous studies [41,42], the resulting t-value matrices were then thresholded for absolute values larger than 2. Selected pairs of electrodes were then clustered according to a neighborhood criterion adapted to PLVs between two helmets. Pairs of electrodes between two EEG helmets are couple of electrodes formed by one electrode on one helmet with one electrode on the other helmet. Two pairs of electrodes on two helmets were considered neighbors if the two electrodes on the same helmet were neighbors. Two pairs of electrodes can also share a common electrode on the same

helmet. In this case, the other extremities of the pairs have to be neighbors. Thus, three cases of neighborhood can be found:

- two side-by-side electrodes on the helmet of subject 1 connected respectively to two side-by-side electrodes on the helmet of subject 2.
- one electrode on the helmet of subject 1 connected with two side-by-side electrodes on the helmet of subject 2.
- one electrode on the helmet of subject 2 connected with two side-by-side electrodes on the helmet of subject 1.

We took as the cluster statistics the sum of all t-values of the pairs members of the cluster. We performed multiple comparisons procedures by doing bootstraps on the cluster statistics [43]. The thresholds that control the family wise error rate (FWER), representing the probability of making false discoveries, were determined by non parametrical permutation methods. Statistics were corrected through both spatial (pairs of electrodes) and spectral dimensions (frequency bands) by taking the maximal t-value for each permutation. All randomizations were done for a rejection of the null hypothesis and a control of false alarm rate at $p = 0.05$.

Results

Behavioral data

Symmetry of roles of imitator and model. Symmetry of roles of model and imitator within each pair of subjects was computed, a value of 0 indicating an ideal balance between the two roles within a dyad. Two dyads of subjects were excluded from further analyses as they exceeded 3 standard deviations from mean index of symmetry. The mean value across the remaining 9 dyads was close to 0 ($M = 0.02$ $SD = 0.14$), thus revealing a good turn-taking of roles.

Dyadic episodes of imitation and synchrony for SI. The proportion of time spent imitating the partner's hand movements, exhibiting interactional synchrony and imitating synchronically the partner's hand movements, was measured in all runs for SI condition (See Table 2). The participants were preferentially involved in imitation ($M = 64.69\%$ of the interaction time) rather than in moving their hands independently, and were most often synchronized ($M = 78\%$ of the time).

Neurodynamic results

Using fine grained video coding of behavioral parameters in the SI condition, we compared EEG contrasts between synchronized versus non-synchronized episodes and between imitative versus non imitative episodes.

Synchronized versus non-synchronized episodes of SI condition. Significant EEG contrasts were found between Sync and NSync episodes (which mostly included imitation). Figure 2 depicts the interbrain dynamical networks of phase synchronization among alpha-mu, beta and gamma frequency bands. The cluster statistics (CS) provide inter-frequency comparisons with the following absolute thresholds: 6.3, 7.8, 8.9 and 11.5 for respectively $p < 0.05$, $p < 0.01$, $p < 0.005$ and $p < 0.001$.

Symmetrical increase in PLV was found between the right parietal regions of the model (CP6, P8) and of the imitator (CP6, P4, P8) in the alpha-mu frequency band (see Figure 2A with $CS = +6.7$, $p < 0.05$). The central region (FC1, Cz) of the model's brain and the parieto-occipital brain region (P8, PO2, PO10) of the imitator were synchronized in the beta frequency band (see Figure 2B; with $CS = +6.4$, $p < 0.05$). Finally, a wide frontal central area (F4, FC2, Czar, C4, CP6) of the model's brain was synchronized with the parietal area (CP2, PZ, P4, P8, PO2, PO10) of the imitator's brain for the gamma frequency band (see Figure 2C, with $CS = +17.4$, $p < 0.001$). As an example, Figure 3 illustrates phase synchronizations between brains in a dyad during episodes of spontaneous imitative exchanges.

Figure 4 shows the mean PLV of all pairs within each significant cluster (cPLV) during Sync and NSync periods of SI. The global trends across all dyads confirmed that interbrain synchronization within our clusters corresponds to interactional synchrony.

To test the validity of our experimental data, the PLV measure during episodes of behavioral Sync vs. Nsync was submitted to the technique of surrogate data. With this procedure, the timing between EEG data and behavioral data was broken by a shuffling of behavioral Sync and Nsync episodes. Accordingly, a surrogate PLV was obtained and compared to our experimental PLV data. Differences between the mean PLV over each cluster for *Sync vs. NSync* episodes were then computed using a Wilcoxon test. The analysis revealed that the PLV contrast was larger in the experimental than in the surrogate condition for the alpha-mu rhythm frequency (See Figure 5; $T = 5$, $p < 0.05$).

Imitative versus Non Imitative episodes of SI condition. EEG contrasts performed between Im versus NIm episodes of the SI condition did not reveal significant differences for the distinct frequency bands whatever the scalp regions ($CS < 5.0$, $p > 0.05$).

Induced Imitation versus No View Motion. Significant EEG contrasts between II and NVM were found in the theta frequency bands only. The cluster statistics (CS) provided inter-frequency comparisons with the following absolute thresholds: 5.8, 10.5, 13.6 and 20.4 for respectively $p < 0.05$, $p < 0.01$, $p < 0.005$ and $p < 0.001$. Symmetrical increase in PLV was revealed between the right parieto-occipital regions of the model (CP2, P4, P8, PO10) and of the imitator (CP2, P3, PZ, PO2, POZ, PO10) in the theta frequency band ($CS = +19.0$, $p < 0.005$).

Discussion

To the best of our knowledge, this is the first study that recorded dual-EEG activity in dyads of subjects during spontaneous non verbal interaction. A few dual-EEG studies [14,15,20] have recently reported synchronous oscillations between brains in a social context. During true live interaction, our study provided evidence that behavioral synchrony and turn taking are accompanied by brain oscillatory couplings. Within one brain, synchronous neural oscillations have been previously observed in a range of processes such as conscious perception [44–46], working and long term memory [47,48], states of anticipation or attention [48,49] and empathy [50]. Such phase synchronizations

Table 2. Mean (and SD) percent time spent synchronizing and/or imitating hand movement during spontaneous imitation condition.

	Imitation		Non-Imitation		Total	
	M	SD	M	SD	M	SD
Synchrony	51.27%	16.59%	26.66%	12.77%	77.93%	17.63%
Non-Synchrony	13.42%	13.62%	08.65%	05.56%	22.07%	17.63%
Total	64.69%	13.74%	35.31%	13.74%		

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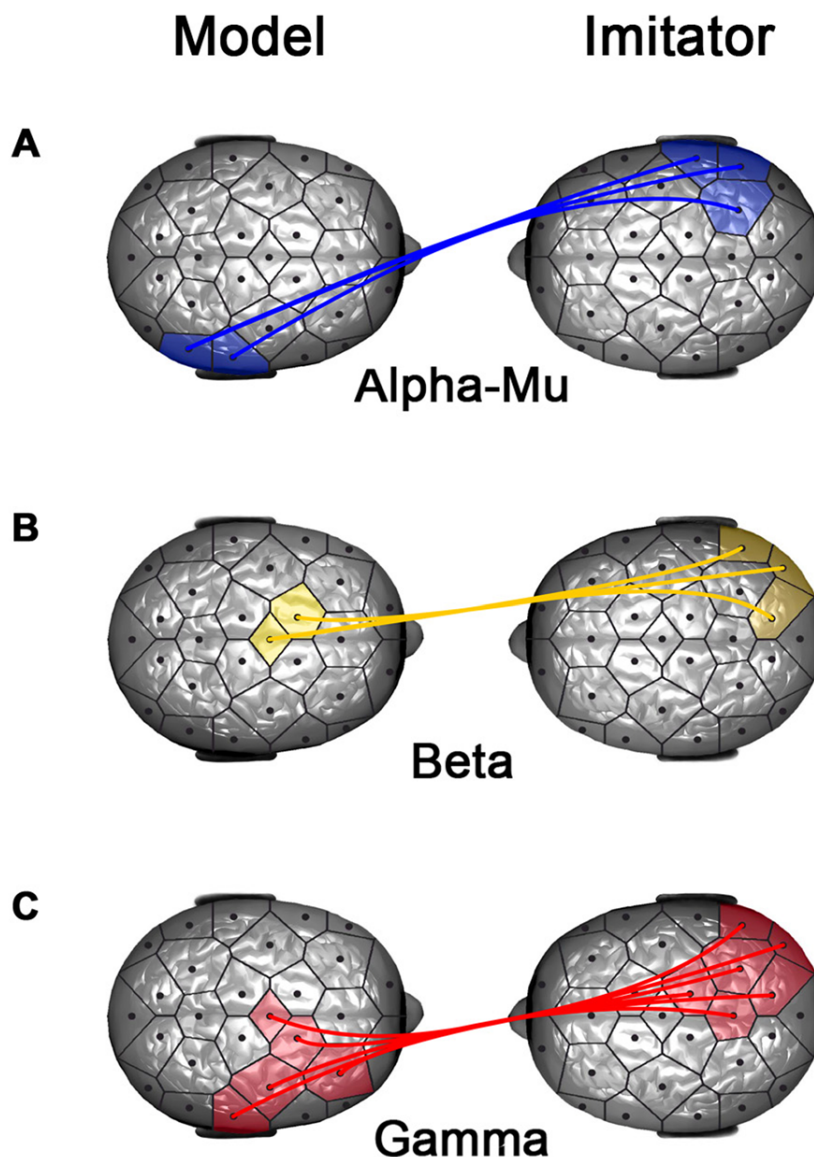


Figure 2. Intersubject neural synchronizations during interactional synchrony. Representation of statistically significant ($P < 0.05$, nonparametric permutation test, corrected for multiple comparisons) coupling (PLV) for all subjects between electrodes of the model and the imitator: comparison for spontaneous imitation trials between behavioral synchrony episodes and those with no behavioral synchrony (Sync vs. NSync). On the left of the figures the participants are models, on the right the participants are imitators. A. Alpha-Mu band cluster between right centro-parietal regions. B. Beta band cluster between central and right parieto-occipital regions. C. Gamma band cluster between centroparietal and parieto-occipital regions.

doi:10.1371/journal.pone.0012166.g002

have been proposed as a key mechanism for information integration [28], temporal binding [51], flexible neuronal communication [34,52] and unified cognitive processes [45,53]. Examining phase synchronizations between two brains, we discovered that they were related to several oscillatory frequency bands in the right centroparietal scalp regions of the two partners. The right temporoparietal region has been suggested to play a pivotal role in social interaction [31]. Previous fMRI studies indicated that the right temporoparietal region is consistently activated in both sociocognitive processes involving attention orientation, the sense of agency, self-other discrimination, perspective-taking [31,32], and in the temporal analysis of visuomotor processing [54,55]. Imitative interaction requires that

participants share attention and compare cues arising from temporally distributed self and other's actions. Within a neurodynamic framework, the right parietal lobes of the two interactants could be seen as two functional hubs expected to synchronize during interaction.

During synchronous episodes, the emergence of a distributed functional network of interbrain neural synchronizations was found among several oscillatory bands. This is in line with current neurodynamic frameworks proposing that multiband synchronous oscillatory activity supports unified complex cognitive processes [45,53], or serves as a mechanism for flexible and efficient communication among distinct or widely distributed cortical areas [56].

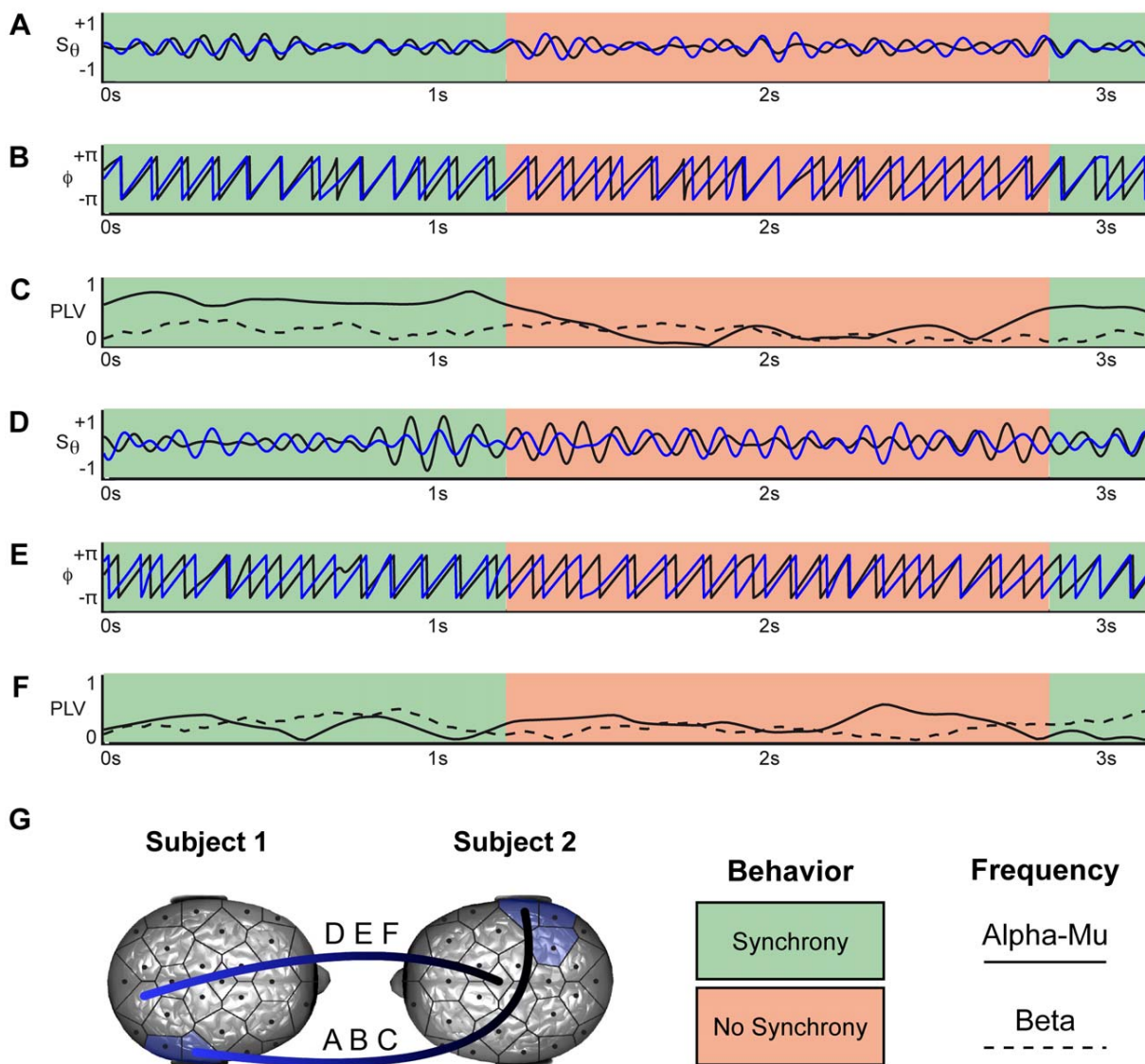


Figure 3. Brain synchronization: online example. Samples of spontaneous imitation episodes in the dyad $n=3$ showing the correspondence between inter-brain synchrony and brain activities. The green areas indicate periods where subjects were behaviorally synchronized and the red ones periods without behavioral synchrony. A. Time course of normalized EEG signal filtered in the alpha-mu frequency band for the channels P8 of both subjects. These channels are members of the cluster shown in figure 2A. B. Phase extracted from the signals. C. PLV calculated with sliding centred time windows of 800ms length in the alpha-mu band (related to A and B) quantifying the neural synchronization between the two subjects. Beta band PLV for the same electrodes is also shown in dashed line. D. Time course of normalized EEG signal filtered in alpha-mu frequency band for the channels PO2 in Subject 1 and Cz in Subject 2. Those channels are not members of any clusters. E. Phase extracted from the signals. F. PLV calculated with sliding centred time windows of 800ms length in the alpha-mu band (related to D and E) quantifying the neural synchronization between the two subjects. Beta band PLV for the same electrodes is also shown in dashed line. G Representation of the pairs of electrodes P8-P8 (A,B,C) and PO2-Cz (D,E,F).
doi:10.1371/journal.pone.0012166.g003

The comparison between synchronized and non synchronized acts showed statistical differences in inter-brain phase synchronies for all frequency bands analyzed (alpha-mu, beta, and gamma) except for the theta band. Designing specific inter-brain statistical analyses, we were able to show that the alpha-mu rhythm was the most robust inter-brain oscillatory activity discriminating behavioral synchrony vs. non synchrony in the centroparietal regions of the two interacting partners. The alpha-mu band is considered as a neural correlate of the mirror neuron system functioning [57]. Specific frequencies of this band (9.2–11.5 Hz) over the right centroparietal region have been proposed as a neuromarker of

social coordination [19]. The symmetrical pattern found for the model and the imitator possibly reflects a coordinated dynamics of hand movements. The pattern however became asymmetrical in the higher frequency bands and should be seen as a brain-to-brain top-down modulation reflecting the differential roles of model and imitator. This is consistent with motor transient activities involved in the beta band [57] and the implication of gamma in attentional processes, perceptual awareness and cognitive control [34,58].

The other contrasts performed complement these findings. The absence of a significant difference between imitative and non-imitative episodes during spontaneous imitation assesses that

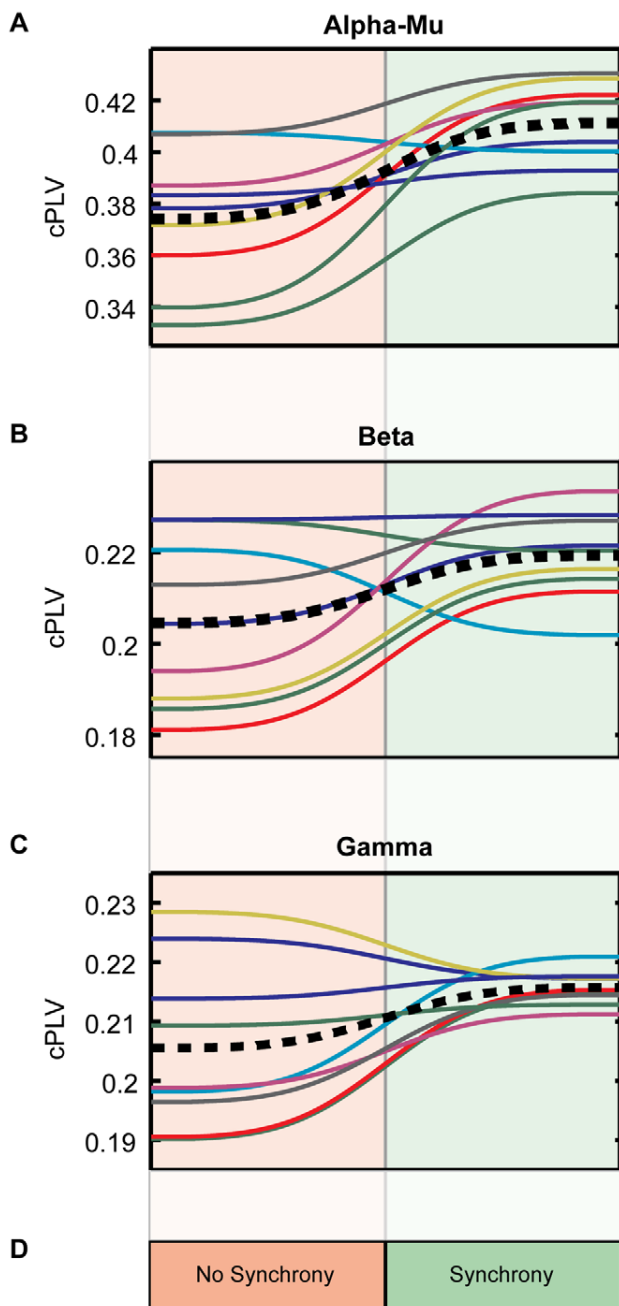


Figure 4. Summary of relevant intersubject synchronizations for all dyads according to interactional synchrony. cPLV values indicate the averaged PLVs on all pairs of electrodes members of clusters shown in Figure 2. Averages cPLV across dyads are shown in black dashed lines.
doi:10.1371/journal.pone.0012166.g004

interbrain synchronizations do not exclusively reflect the execution and perception of similar movements. By contrasting induced imitation with the NVM baseline no interbrain synchronization appeared, except in the theta band. The theta synchronization was found between the two right parietal regions but not in motor regions, although theta band is involved in the encoding of low level parameters of hand movements such as position [59–61] and speed [62]. Our finding could be explained by the fact that subjects move hands continuously in the two conditions, thus

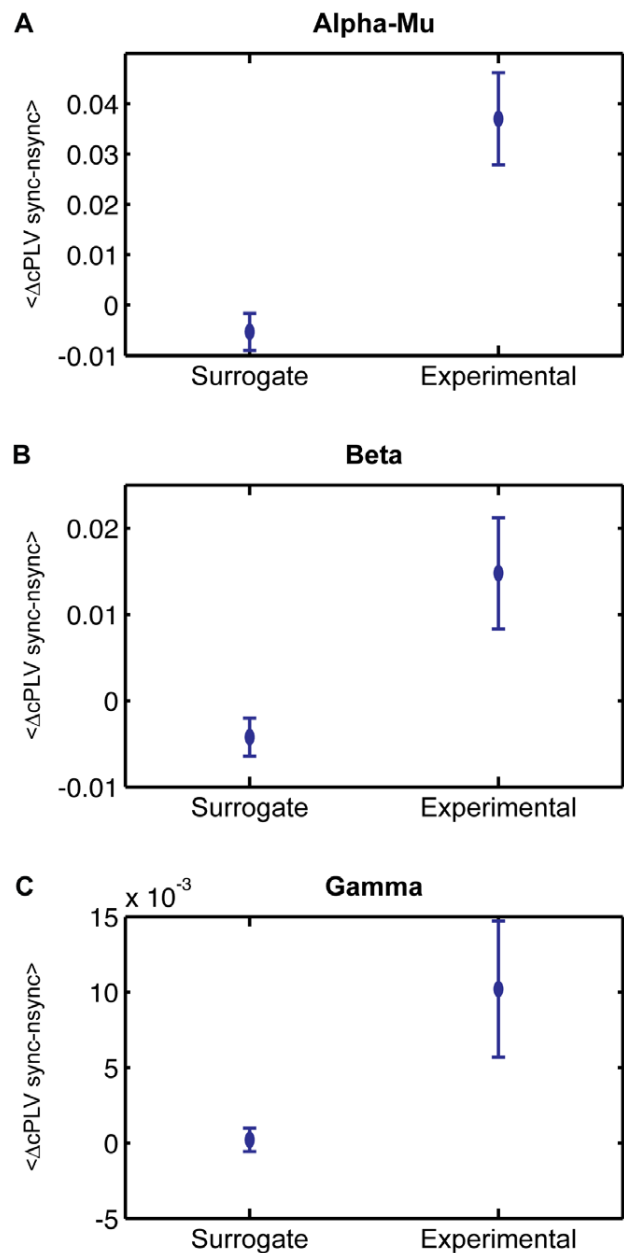


Figure 5. Averaged intersubject clustered PLV (cPLV) difference between synchronous and non-synchronous interactions (Sync - NSync) compared for experimental and surrogate behavioral analysis. Bars represent standard errors.
doi:10.1371/journal.pone.0012166.g005

eliminating motor regions from the contrast. Right parietal locus could reflect a shift toward the processing of self-other similarities in the matched hand movements.

Overall, this study highlights the crucial and multiple roles of the right parietal regions in social interaction. Considering that subjects performed bimanual movements, the functional asymmetry between the two parietal areas is pointed out. What are the specificities of the right parietal regions? They have been considered as the “when pathway” [63,64] because of its implication in the perception of time [65]. Beyond synchrony, alternation of roles involves temporal estimation and anticipation. Wilson & Wilson [6] have proposed that turn-taking, as a

regulation of social interaction, should be supported by endogenous oscillators. The turn-taking phenomenon has been modeled in computer science and robotics studies [4,5,66] but never investigated so far in neuroscience. Here we show that interbrain neural synchronizations can be seen as reflecting in different bands several aspects of the ongoing social interaction, such as interactional synchrony, anticipation of other's actions and co-regulation of turn-taking. Although far more work is needed, the novel methodology used here offers a promising way to capture the brain to brain bases of the continuous flow of reciprocal influence that defines the core of social interaction.

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Acknowledgments

We are grateful to Line Garnero (1955–2009) for her insightful contribution and for having until the end found the strength to follow this project of which she was one of the initiators. We thank Florence Bouchet for her generous assistance in the EEG preparation, Pierre Canet and Laurent Hugueville for their technical assistance. Finally, we thank Mario Chavez for helpful comments in neurodynamics analysis.

Author Contributions

Conceived and designed the experiments: GD JN RS JM LG. Performed the experiments: GD JN JM LG. Analyzed the data: GD RS JM. Wrote the paper: GD JN RS JM LG.

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4 Distinct brain dynamics underlie self- and other-ascription of action primacy during reciprocal imitation

The mirror neural theory has successfully demonstrated the ‘double duty’ of the mirror neurons involved altogether in the production and observation of the same action. It thus strongly supports a symmetrical relationship between the brain activities of two persons engaged in reciprocal imitation. However, besides the inter-brain synchronization found during interactional synchrony, our first study accounts clearly for a symmetry-breaking and a spontaneous emergence of an alternation of roles taken by the interactants. This turn-taking phenomenon illustrates one of the limits of the neuromimetic theory (Petit, 2003). It points out the co-occurrence of differentiation and similarity between persons engaged in a spontaneous social exchange (Wilson and Wilson, 2005). In the same way as segregation and integration form a complementary pair in brain activity, a successful communication needs altogether a clear repartition of the roles and a co-regulation of the exchange (Fogel, 1993b). This co-regulation and the sharing of purpose between the interactants ensure the autonomy of the two partners as well as their ability to make the distinction about what originates from the self and what originates from the other (De Jaegher, 2009).

Despite the vast amount of studies about agency, protocols mainly compare self- versus non-self produced actions (Sperduti et al., 2011). While they clearly demonstrate that different neural correlates can be observed depending of the self- or external agency ascription, it is rather mysterious how to disentangle the role of multi-sensory interactions from the cognitive attribution of the causal origin of action to self or to other. Free imitative interaction provide an ideal test-bed for this multifactorial aspects of agency since both agents produce the similar actions and are able to simultaneously associate its origin to self or to other. To explore the neural correlates of self and other’s ascription of agency during interactional synchrony, we thus conducted another

neurodynamical analysis on the previous hyperscanning data. As imitative paradigms in social neuroscience rely on unidirectional or induced imitation, we also investigated the influence of the social context upon individual neural dynamics. The issue was explored in the wider objective of dissociating the specific structures and dynamical parameters recruited for the regulation of social interactions from those involved in the core realization of these interactions. In this perspective, we took advantage of the non-parametrical statistics and clustering strategy developed in the first study to investigate the whole regions and spectrum simultaneously.

Distinct brain dynamics underlie self- and other-ascription of action primacy during reciprocal imitation

Guillaume Dumas^{a,b,c}, Jacques Martinerie^{a,b,c}, Robert Soussignan^e & Jacqueline Nadel^d

Abstract

While growing evidence demonstrate a strong overlap in brain activity related to perceiving and producing an action, the issue of agency remains largely restricted to self-versus non-self attribution of action perception. The recent definition of agency as a multifactorial phenomenon combining bottom-up and top-down processes suggests the exploration of more complex situations, such as social situations where two agents imitate each other: Who then is at the origin of what, and who controls what? To investigate these questions we recorded with dual EEG and video set-ups twenty-two subjects interacting via spontaneous or induced imitation of hand movements. Results demonstrated dissociations between self- and other-ascription of action primacy in delta, alpha and beta frequency bands. Theta and gamma activities were found to differentiate spontaneous versus induced context. Taken together, the results highlight the different levels of agency ascription during live reciprocal interactions.

Keywords: agency, hyperscanning, EEG, imitation, social interaction

^a Université Pierre et Marie Curie-Paris 6, Centre de Recherche de l'Institut du Cerveau et de la Moelle épinière, UMR-S975, 47, bd. de l'Hôpital, 75651 Paris Cedex 13, France.

^b Inserm, U975, 47, bd. de l'Hôpital, 75651 Paris Cedex 13, France.

^c CNRS, UMR 7225, 47, bd. de l'Hôpital, 75651 Paris Cedex 13, France.

^d Centre émotion, CNRS, USR 3246, Pavillon Clérambault Hôpital de la Salpêtrière, 47, bd. de l'Hôpital, 75013, Paris, France.

^e Centre des Sciences du Goût et de l'Alimentation, CNRS UMR 6265, Université de Bourgogne, Inra, 15 Rue Hugues Picardet, 21000 Dijon, France.

1. Introduction

A growing body of neuroimaging studies explore agency as the capacity to locate the origin of an action in self. Meanwhile philosophers show us how complex it is to define an experience or a sense of agency (Gallagher, 2007). To solve the question, the proposal has been to distinguish the sense of agency from the sense of ownership of own movements (Gallagher, 2000; Marcel, 2003). A distinction between a feeling and judgment of agency and a feeling and judgment of ownership was then added to stress the multifactorial aspect of agency, seen as a combination of bottom-up and top-down processes (Synofzik et al., 2008) and to clarify the contribution of basic sensory experiences to the sense of agency (Fournieret et al., 2002). A main distinction between the sense of agency and the sense of ownership relies in the fact that the sense of agency is restricted to voluntary actions, but the sense of body ownership is not. The rubber hand illusion, for example, shows that watching a rubber hand being stroked together with the subject's own unseen hand causes the rubber hand to be ascribed as part of the subject's body (Botvinick and Cohen, 1998; Ehrsson et al., 2005; Tsakiris and Haggard, 2005). In the stroking synchronous condition, the participants felt the illusion more strongly than in asynchronous conditions, and the strength of the illusion was related to higher level of premotor activity (Ehrsson et al., 2004). A multi-sensory integration is suggested to be the underlying mechanism of self-attribution of body ownership. Tsakiris, Schütz-Bosbach and Gallagher (Tsakiris et al., 2007) underlined the methodological confounds related to the respective roles attributed in many studies to efferent and afferent information for body awareness. A social situation of synchronic imitation generating simultaneous afferent and efferent messages in each partner may be useful to disentangle the role of multisensory interactions from the role of cognitive attribution of the causal origin of action to self or to other. It may lead to better delineate the role of structures such as the

temporo-parietal junction (TPJ) in other's ascription of agency.

Neuroimaging studies have recently confirmed the idea that parietal and temporal regions surrounding the TPJ are involved in the sense of agency (Brass et al., 2009; David et al., 2007; Nahab et al., 2011; Schnell et al., 2007; Spengler et al., 2009; Yomogida et al., 2010). A major emphasis has been posed on TPJ as the neural basis of the sense of agency, even if different brain regions beyond the TPJ, such as insula (Farrer et al., 2003; Farrer and Frith, 2002), dorsolateral prefrontal cortex (DLPFC) (Fink et al., 1999), precuneus (Farrer and Frith, 2002; Ruby and Decety, 2001) and supplementary and pre-supplementary motor area (SMA/pre-SMA) (Farrer et al., 2003; Nahab et al., 2011; Yomogida et al., 2010), have been reported in agency studies. There are several reasons to attribute a great importance to TPJ, from "the alien hand" syndrome (Bundick and Spinella, 2000) or limbs misattributions (Daprati et al., 2000) caused by lesions of these regions, to the involvement in action awareness (Frith et al., 2000) and perspective taking (Ruby and Decety, 2003; Thirioux et al., 2010).

Representative of this trend is the fact that the only two meta-analyses concerning the sense of agency have designed an a priori region of interest in the TPJ (Decety and Lamm, 2007; Spengler et al., 2009). Moore and coworkers (Moore et al., 2010) in a recent work argued that the TPJ seems more involved in the feeling of non-agency than in a sense of self-agency. This consideration leaves the possibility that the sense of self- versus other-agency could be supported by partially different neural correlates. A recent meta-analysis led by our team started from a definition of sense of agency instead of starting from a definition of regions of interest (Sperduti et al., 2011). Using activation likelihood estimation (ALE) method, the meta-analysis revealed dissociation between brain regions involved in self- and external agency ascription. More specifically, TPJ activity appeared to be more present in external-

than in self- agency ascription. This may be due to the tasks chosen, all derived from the comparator model (Jeannerod, 2003b). In these tasks, brain effects of a congruent visual feedback of self-movements are compared to brain effects of a non-congruent visual feedback. The task is a solitary task comparing the visual and kinesthetic feedbacks of an individual in two experimental conditions. A challenger to this indirect test of other's agency is the immersion of subjects in a social experience of turn-taking. As De Jaegher and Froese propose (De Jaegher and Froese, 2009), individual agency is rooted in the dynamics of interaction between agents.

Interacting freely via imitation provides a test case of the multifactorial aspects of agency in everyday social life. In Jeannerod's words, 'an observer monitoring an action performed by someone else is never far from also being the agent of that action' (Jeannerod, 2003a). We argue that simultaneously performing the same action generates in both partners a similar sense of body ownership and a similar sense of agency, but will lead to a contrasted ascription of action primacy between the initiator and the responder. Many other cases in the domain of social interaction, such as joint attention/activity and social coordination are well described by a shared sense of agency of action to which is added an opposite ascription of authorship of interaction. This may explain turn-taking as a way to socially regulate this sense of leadership in social interaction.

The hyperscanning methodology constitutes a relevant tool to explore social phenomena (Babiloni et al., 2006; Hasson et al., 2004; Montague et al., 2002). Hyperscanning methods have been recently used to explore interpersonal coordination (Lindenberger et al., 2009; Tognoli et al., 2007), interbrain connectivity related to decision making (Astolfi et al., 2010), or interbrain synchronization during imitative interaction (Dumas et al., 2010). So far, to our own knowledge, they have not been devoted to study self- versus other-agency.

Our choice to explore the multifactorial account of agency via hyperscanning method derived

from our first findings that beyond right centroparietal synchronizations between the two brains, there remained asymmetry related to the role of model or imitator. Given its high temporal resolution, instantaneous EEG recording is well adapted to measure brain dynamics correlated with emergent dyadic processes such as turn-taking and shared sense of ownership of gestures. This led us to a holistic intra-individual analysis without restricting to specific regions of interest or frequency bands.

The design of our experiment offers the possibility to approach a multifactorial account of agency by comparing brain activity for two roles (initiator and imitator of a gesture) and two imitative conditions. The two conditions, Induced Imitation (II) and Spontaneous Imitation (SI) allow differentiate further the roles: II was designed to privilege a clear-cut ascription of primacy of action to self (as a model, I am the source of what I see the other doing) as opposed to primacy of action to other (the other is the source of what I am doing as an imitator). Thus the “model vs. NVM” contrast should be indicative of an ascription of primacy of action to self and the “imitator vs. NVM” contrast should be indicative of an ascription of primacy of action to other. The contrast “imitator vs. model” will test a possible overlap in brain dynamics between ascription of action primacy to self and ascription of action primacy to other. Whereas in II the roles are externally defined, in SI the roles are freely negotiated between partners who thus alternate action primacy. However the exchange is negotiated at will which should provide a shared feeling of being in control of the turn-taking (co-regulation). Neural correlates of self-ascription of action primacy, other-ascription of action primacy, co-ownership of action and shared sense of agency will be extracted from the different contrasts available in SI.

2. Methods

2.1. Participants

Twenty-two healthy adults (5 female-female and 6 male-male pairs) of mean age 24.5 years ($SD = 2.8$) participated in the study. All of them were right-handed. They had normal or corrected-to-normal vision and none of them reported a history of psychiatric or neurological diseases. The participants had given their written informed consent according to the declaration of Helsinki and the chart of the local ethics committee. The subjects were paid for their participation.

2.2. Apparatus and setting

The experiment was conducted in two separate laboratory rooms. Figure 1 describes the design and equipment that was similar to the double-video system designed by Nadel and colleagues for their developmental studies of sensitivity to social contingency in infants (Nadel et al., 1999; Soussignan et al., 2006), except that a dual EEG recording system was added to the setup. Two synchronized DV video cameras filmed the hand movements of each partner. Each participant could see the partner's hands through 21-in. TV monitors, the forearms lying on a small table to prevent arm and neck movements. The monitoring of the experiment was performed in a third room where two computers managed both the dual EEG and video recordings.

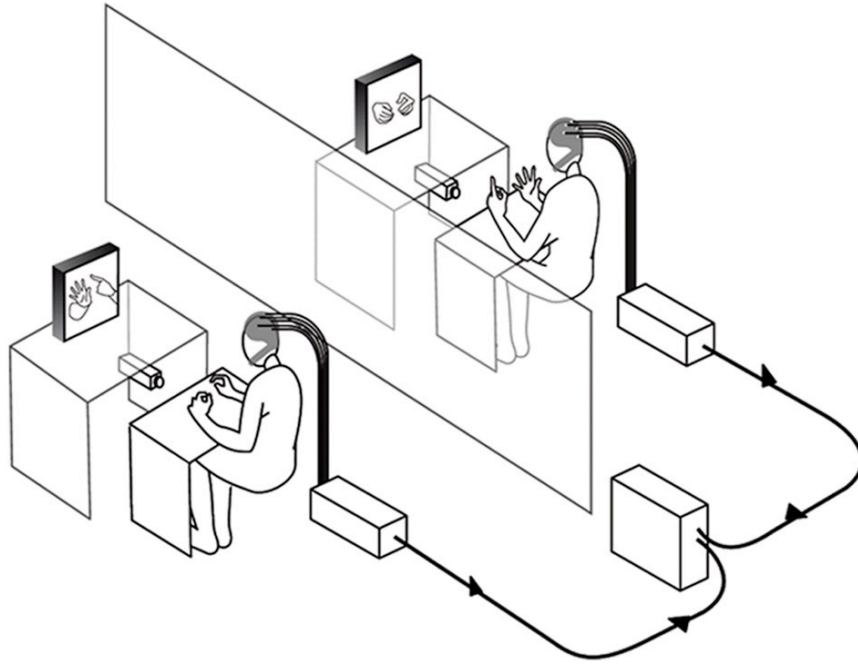


Figure 1: Apparatus and experimental setting of the double video system and dual-EEG recording.

Condition (Block 1)	NVNM + Library of Intransitive Movements (LIHM)	NVNM + NVM + Spontaneous Imitation (SI)	NVNM + NVM + Induced Imitation (II) Subject A: imitator Subject B: model	NVNM + NVM + Induced Imitation (II) Subject B: imitator Subject A: model
Pause : 10 min				
Condition (Block 2)	NVNM + Library of Intransitive Movements (LIHM)	NVNM + NVM + Spontaneous Imitation (SI)	NVNM + NVM + Induced Imitation (II) Subject B: imitator Subject A: model	NVNM + NVM + Induced Imitation (II) Subject A: imitator Subject B: model
Duration	15s + 1min 30s	15s + 15s + 1min 30s	15s + 15s + 1min 30s	15s + 15s + 1min 30s

Table 1: Timetable of the experiment

2.3. Procedure

Table 1 describes the protocol schedule. It was divided into two blocks, each composed of four runs of 1.30 minutes. Each run started by a *No View* (blank screen) *No Motion* (NVNM) baseline lasting 15 s, followed by three conditions: “Library of Intransitive Hand Movements” (LIHM), “Spontaneous Imitation” (SI) and “Induced Imitation” (II). A 15 s *No View Motion* (NVM) baseline followed the NVNM baseline before SI and II conditions. Following a 10 min. pause, the second block was performed. In the NVM baseline, each participant moved his/her hands without receiving visual input of his/her partner. In the LIHM condition the two participants of each pair observed simultaneously 20 intransitive hand/finger movements. The “Spontaneous Imitation” condition (SI) proposed to the two participants to move their hands and to imitate their partner whenever they would like it. This leads to spontaneously coordinate two roles: imitate and be imitated. In the “Induced Instructed Imitation” condition (II), subject 1 (S1) was asked to imitate continuously the hand movements of subject 2 (S2) who was told to move hands freely, and vice-versa, with a counterbalanced order in block 2 (see Table 1).

2.4. Dual EEG data-acquisition

The neural activities of the two participants were simultaneously recorded with a dual-EEG recording system. It was composed of two Acticap helmets with 32 active electrodes arranged according to the 10% system. We modified the helmets in order to cover at best the occipito-parietal regions. Four electrodes T7, T8, CP9 and CP10 were rejected due to artifacts. Ground electrode was placed on the right shoulder of the subjects and the reference was fixed on the nasion. The impedances were maintained below 10k Ω . Data acquisition was performed using a 64-channels Brainamp MR amplifier from the Brain Products Company (Germany). Signals were analog filtered between 0.16Hz and 250Hz, amplified and digitalized at 500Hz with a 16-bit vertical resolution in the range of +/- 3.2 mV.

2.5. Behavioral analysis of the video

The double video recordings were coded according to three parameters during spontaneous imitative interaction:

- Imitative acts referring to the similarity of morphology and direction of hands/digits movement.
- Behavioral synchrony, referring to the temporal dynamics between the movements of the partners, namely the overlap of the start and the end of a movement, even if the movements were different.
- Role, defining who was imitating and who was imitated.

The coding was done using a revised version of the ELAN software developed by the Max Planck Institute for Psycholinguistics (Sloetjes and Wittenburg, 2008). The software allowed a simultaneous presentation of the frames from the two partners on the ELAN window and a recording of time (latency, duration) and occurrence of behavioral events. Digitalized videotapes of each participant were synchronized and the behavioral components (imitation and synchrony) as well as the role (imitator/model) in the interaction were coded frame-by-frame. In a previous study, the analysis of temporal co-occurrence and spatial similarity of gesture movements within 200-ms time windows indicated an acceptable inter-observer reliability (kappa coefficients > 0.80) between the main coder (GD) and a second coder (RS) who independently scored 25% of the files depicting imitative social interactions (Dumas et al., 2010).

2.6. EEG artifacts

The correction of eye blink artifacts in the EEG data was performed using a classical PCA filtering algorithm (Wallstrom et al., 2004a, b). We used 800 ms windows with 400ms of overlap. For each window, a principal component analysis (PCA) was performed on the raw signal and all the PCA-components were compared to an estimation of the electro-oculogram

(EOG) computed from the difference between the mean of the raw channels FP1 and FP2 and the nasion reference. If the correlation between the reconstructed EOG signal and each PCA-component exceeded an adaptive threshold, the eigenvalue related to the component was fixed to zero. Then the converted EEG signal can be reconstructed by using the inverse solution of the PCA. The adaptive threshold was proportional to the standard deviation of the considered i^{th} component divided by those of the current window signal:

$$Threshold_i = 0.7 \times \frac{\sigma(c_i)}{\sigma(\sum_i c_i)} \quad [2]$$

where $\sigma(c_i)$ stands for the standard deviation of the i^{th} component of the PCA and $\sigma(\sum_i c_i)$ is the standard deviation of the signal.

EEG signals were then controlled visually another time in order to eliminate muscular artifacts. These EEG segments were excluded of the analysis and, in order to avoid border artifacts induced by their suppression, we smoothed the joints by a convolution with a half-Hanning window of 400ms.

2.7. EEG neurodynamic analysis

This study uses the data recorded in a previous research (Dumas et al., 2010). However, whereas our previous paper focused exclusively on inter-individual brain synchronization during spontaneous imitative interactions, we performed here an intra-individual analysis of EEG amplitude signals within a theoretical framework of agency and ownership. Furthermore, instead of using selected large frequency bands, we covered the whole spectrum (0-48Hz) with 1Hz frequency bins. It provides a total data-driven approach of the spectral dimension.

Following corrections, EEG data were re-referenced to a common average reference (CAR). Then the data were segmented by the behavioral analysis for each experimental condition and

a Fast Fourier Transform (FFT) was applied on 800ms half-overlapping windows.

2.8. Statistical analysis

Significance of the differences in all contrasts was established using a nonparametric cluster randomization test across spatial and spectral domains (Maris and Oostenveld, 2007; Maris et al., 2007; Nichols and Holmes, 2002). This test effectively controls the false discovery rate in situations involving multiple comparisons by clustering neighboring quantities that exhibit the same effect. For the amplitude analysis, the neighborhood was univariate across space (adjacent electrode over the scalp) and frequencies (side-by-side frequency bins). The permutation method exhibits values whose t statistics exceeded a given critical value when comparing two conditions value by value. In order to correct for multiple comparisons, neighbor values exceeding the critical value were considered as a member of the same cluster. The cluster-statistic (CS) was taken as the sum of t values in a given cluster. Evaluating the cluster-statistic distribution through 1000 permutations controlled the false discovery rate (Pantazis et al., 2005). Each permutation represents a randomization of the data between the two conditions and across multiple subjects. For each permutation the cluster-statistics were computed by taking the cluster with the maximum sum of t statistics. The threshold that controls the family wise error rate (FWER) was determined according to the proportion of the randomization null distribution exceeding the observed maximum cluster-statistic (Monte Carlo test). Clusters, which contained less than three different electrodes or three different frequency bins, were excluded. We used a threshold critical value of $|2\alpha|$.

3. Results

We first report upon control conditions of passive observation of movement (LIHM) or simple execution of movement (NVM) contrasted with rest (NVNM), so as to pinpoint further

the original role played by observing and executing the same movements (see Table 2).

3.1. Passive observation of movement: LIHM vs. NVNM

Passive observation of hand movements (LIHM) induced an increase in theta and delta amplitudes in the parietal (6-8Hz; CP6, P7, P3, Pz, P4, PO1; CS = 223.7, $p < 0.001$) and fronto-central (1-5Hz; FC1, FC2, C4, CP6; CS = 184.4, $p < 0.001$) regions (See Fig. 3), respectively and a decrease of high alpha-mu rhythm in the centro-parietal region (11-13Hz; CP1, CP2, P3, PO1; CS = -123.0, $p < 0.001$).

3.2. Execution of movement: NVM vs. NVNM

Moving hands increased the delta band amplitude in the frontal (2-4Hz; Fz, FC1, C3; CS = 28.3, $p < 0.05$) region, whereas decrease in the alpha-mu and beta bands was respectively observed in the parieto-central (10-12Hz; CP2, CP6, P3, PZ, P4, P8, PO1; CS = -68.4, $p < 0.05$) and fronto-central (19-25Hz; Fz, F4, FC2, Cz, C4; CS = -66.2, $p < 0.05$) regions (See Fig. 2).

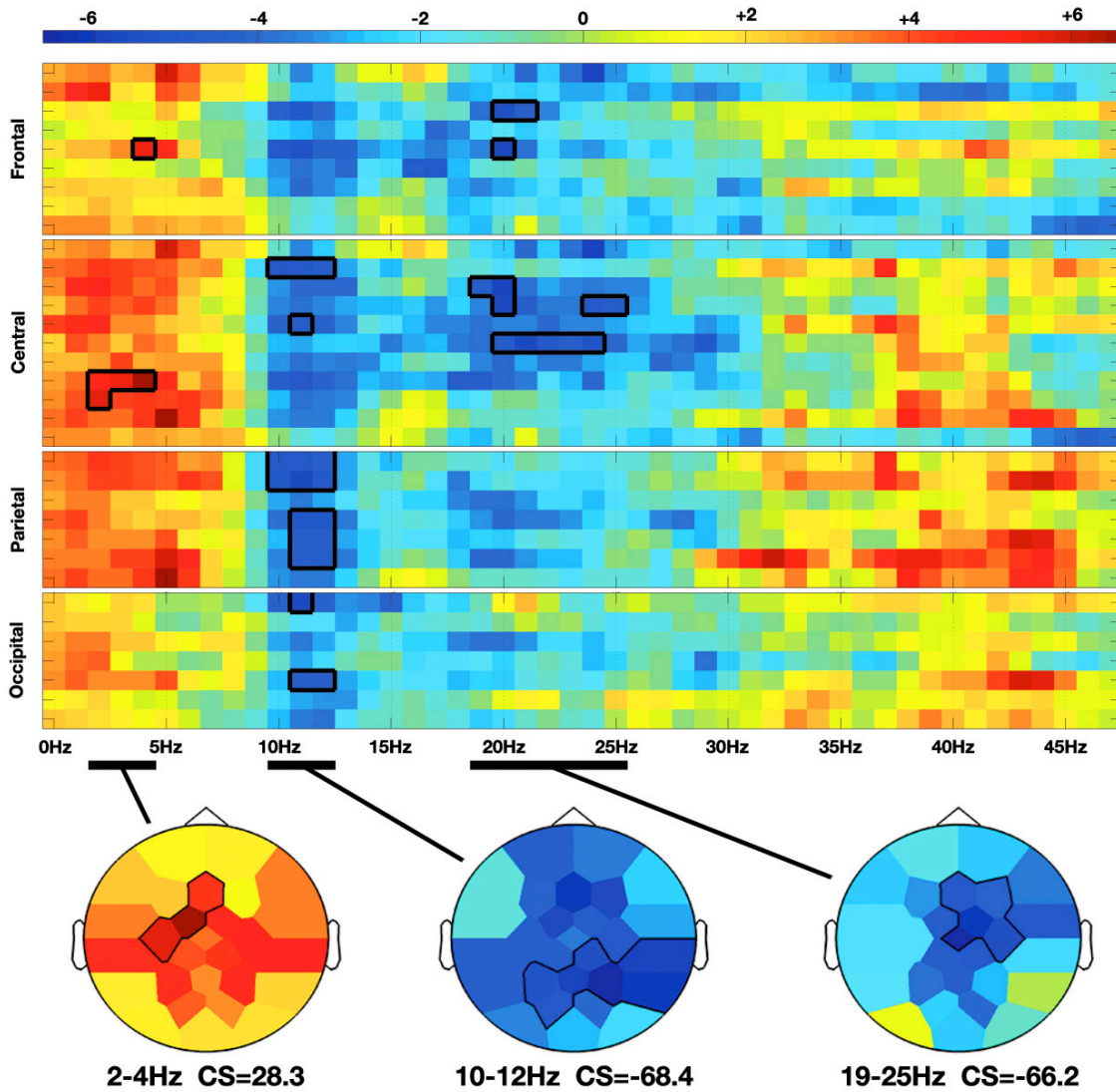


Figure 2: Non-parametric clustering analysis applied to the NVM-NVNM contrast. Rows and columns represent respectively electrodes and frequency bins. Electrodes are grouped by anatomical region. The color stands for the t-values calculated between the two conditions with the subject average fast Fourier transform (FFT) components. Topographies at the bottom represent the mean t-values across the frequency range of the considered clusters. Statistical clusters are outlined in thick black lines for both representations. NVM, No View Motion; NVNM, No View No Motion.

3.3. EEG correlates of self- and other-primacy of action

3.3.1. Other-primacy of action: Imitator vs. NVM (II)

Amplitude increased in the delta band over the right fronto-central region (2-4Hz; FC1, FC2, C4, CP2; CS = 136.8, $p < 0.001$; See Fig 3). There was also a decrease of alpha-mu activity in the parietal region (12-14Hz; CP1, CP2, P3; CS = -106.6, $p < 0.001$).

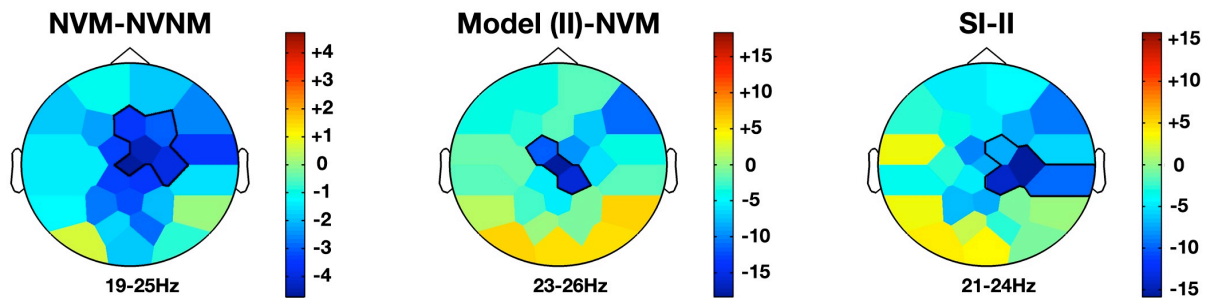


Figure 3: Self agency and beta frequency band effects. NVM-NVNM, Model in II-NVM and SI-II show a similar decrease of the beta activity (19-26Hz) across the right fronto-central regions. The color stands for the mean t-values across the frequency range of the considered clusters. Statistical clusters are outlined in thick black lines for both representations. II, induced imitation; SI, spontaneous imitation. For other abbreviations, see Fig. 2.

3.3.2. Self-primacy of action: Model vs NVM (II)

An increase of amplitude was observed in the theta band over centro-parietal region (4-8Hz; CP1, P3, Pz, PO1; CS = 131.4, $p < 0.001$; See Fig 5) whereas a decrease in alpha-mu rhythm was found over parietal region (11-14Hz; CP1, CP2, P3, Pz, P4, P8, PO1; CS = -244.6, $p < 0.001$). There was also a decrease of activity in the beta band over the fronto-central region (23-26Hz; FC1, Cz, CP2; CS = -135.6, $p < 0.001$; See Fig 4).

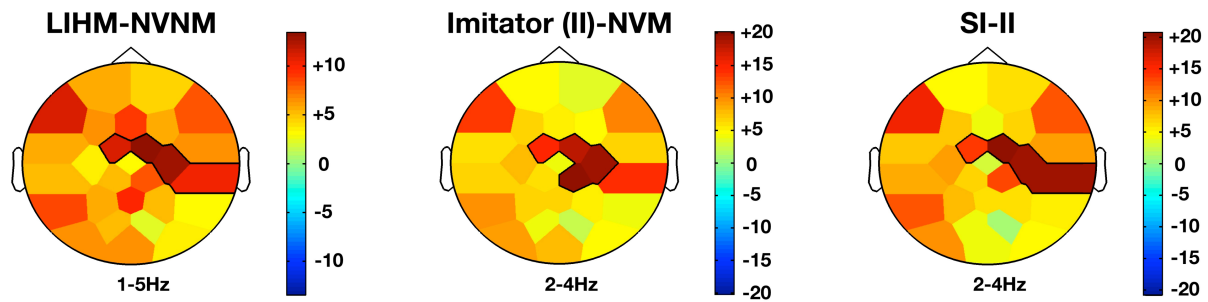


Figure 4: Other agency and delta frequency band effects. LIHM-NVNM, Imitator in II-NVM and SI-II show a similar increase of delta activity (>0-5Hz) mostly over the right central region. The color stands for the mean t-values across the frequency range of the considered clusters. Statistical clusters are outlined in thick black lines for both representations. For abbreviations, see previous figures. LIHM, library of intransitive hand movements.

3.3.3. Other- vs. Self-ascription of primacy of action: Imitator vs. Model (II)

Amplitude increased for several frequency bands from 2Hz to 9 Hz in the centro-parietal region (CP6, P4, P8, PO9, Oz, PO2, PO10; CS = 154.2, $p < 0.05$).

3.4. EEG correlates of co-ownership of action

3.4.1. Other-agency & co-ownership: Imitator vs NVM (SI)

An increase of amplitude in the gamma band was found in the centro-parietal region (38-47Hz; CP6, P4, P8, PO1, Oz, PO2; CS = 130.2, $p < 0.001$; See Fig 5). There was also a decrease in the alpha-mu band over the parietal region (10-14Hz; Pz, P4, P8, Oz, PO2; CS = -63.4, $p < 0.05$).

3.4.2. Self-agency and co-ownership: Model vs NVM (SI)

Gamma amplitude increased over centro-parietal region (42-47Hz; C4, CP6, P4, P8, PO1, PO2; CS = 117.0, $p < 0.001$; See Fig 5) whereas a decrease was observed in the alpha-mu band over the parietal region (10-14Hz; Pz, P4, P8, PO1, Oz, PO2; CS = -73.4, $p < 0.05$).

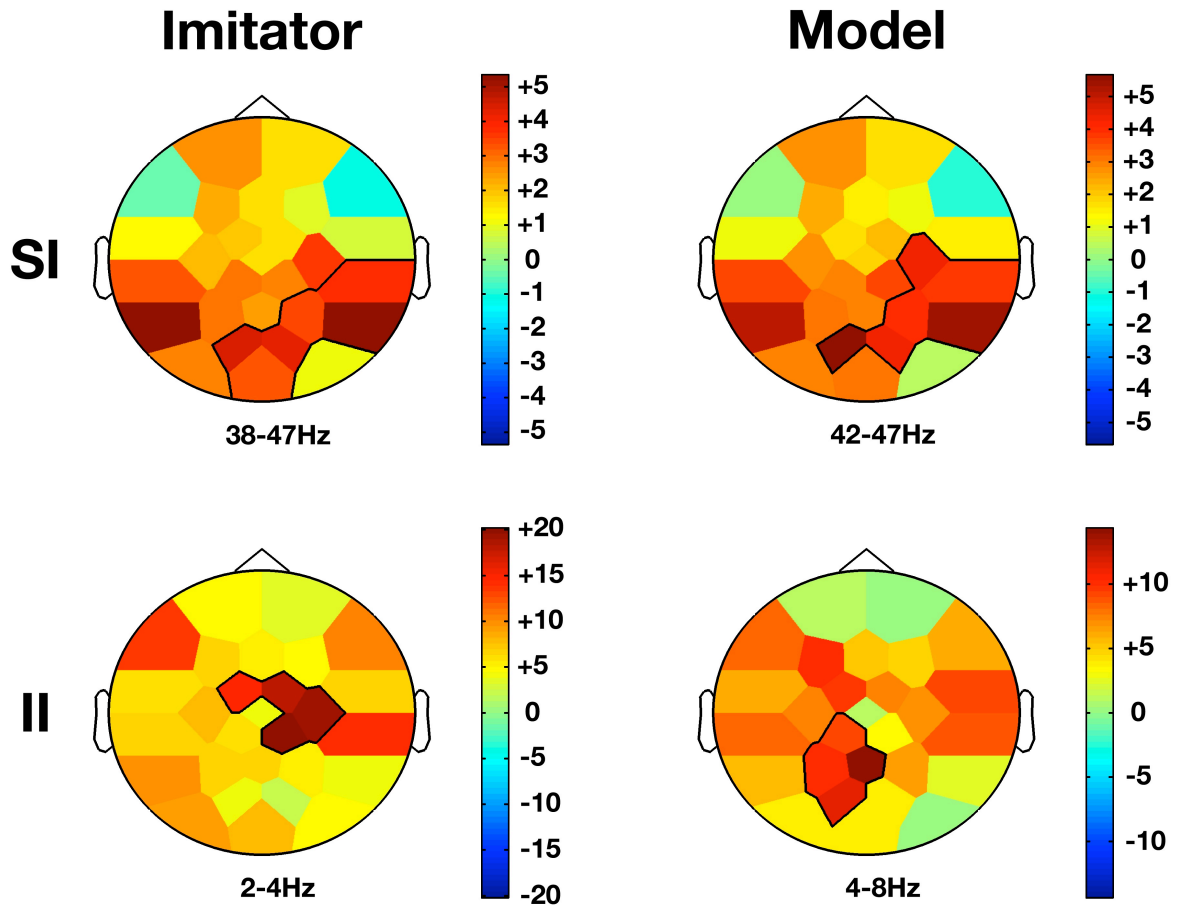


Figure 5: Co-ownership and low/high frequency bands effects. Compared to baseline (NVM), Imitator and Model show a similar increase in gamma activity (38-47Hz) in parietal regions during SI while this effect was not present in II. However there is an increase for both delta/theta activity (2-8Hz) in II but topographies are different. While this change occurs in the right central region for the Imitator, it is more localized over the precuneus region for the Model. The color stands for the mean t-values across the frequency range of the considered clusters. Statistical clusters are outlined in thick black lines for both representations. For abbreviations, see previous figures.

3.4.3. Asymmetry in co-ownership: Imitator vs. Model during SI

An increase in the amplitude of low-beta band across the parietal region (13-18Hz; CP2, P3, Pz, P4, P8, PO1, PO2; CS=167.8 p<0.001) was found.

3.4.4. Co-ownership: Synchronous imitation during SI vs II

This contrast revealed no significant differences.

3.4.5. Co-ownership and turn-taking: SI vs II

Concerning the amplitude, an increase in the delta band (2-5Hz) and a decrease in the beta band (21-24Hz) were detected in the fronto-central region (Fz, FC1, FC2, C4, CP6; CS = 165.4, p<0.001; See Fig 3) and in the right central region (FC2, C4, CP2, CP6; CS = -147.1, p<0.001; See Fig 4), respectively.

3.4.6. Co-ownership from the imitator perspective: Imitator in SI vs. Imitator in II

A decrease in the theta/alpha band amplitude was found in occipito-parietal region (4-9Hz; CP6, P4, P8, PO9, Oz, PO2; CS = -68.0 p<0.05).

3.4.7. Co-ownership from the model viewpoint: Model in SI vs Model in II

No difference was found between these two conditions

	Delta	Theta	Alpha-Mu	Beta	Gamma
Frontal	LIHM-NVNM (+) NVM-NVNM (+) Imitator-NVM (II) (+) SI-II (+)			NVM-NVNM (-) Model-NVM (II) (-) SI-II (-)	
Central	LIHM-NVNM (+) NVM-NVNM (+) Imitator-NVM (II) (+) Imitator-Model (II) (+) SI-II (+)	LIHM-NVNM (+) Model-NVM (II) (+) Imitator-Model (II) (+) Imitator II-SI (+)	LIHM-NVNM (-) NVM-NVNM (-) Imitator-NVM (II) (-) Model-NVM (II) (-)	Imitator-Model (SI) (+) NVM-NVNM (-) Model-NVM (II) (-) SI-II (-) Model II-SI (-)	Imitator-NVM (SI) (+) Model-NVM (SI) (+)
Parietal	LIHM-NVNM (+) Imitator-Model (II) (+)	LIHM-NVNM (+) Model-NVM (II) (+) Imitator-Model (II) (+) Imitator II-SI (+)	Imitator II-SI (+) LIHM-NVNM (-) NVM-NVNM (-) Imitator-NVM (II) (-) Imitator-NVM (SI) (-) Model-NVM (II) (-) Model-NVM (SI) (-)	Imitator-Model (SI) (+) SI-II (-)	Imitator-NVM (SI) (+) Model-NVM (SI) (+)
Occipital	Imitator-Model (II) (+)	Imitator-Model (II) (+) Imitator II-SI (+)	Imitator II-SI (+) Imitator-NVM (SI) (-) Model-NVM (SI) (-)	Imitator-Model (SI) (+)	Imitator-NVM (SI) (+)

Table 2: Summary of amplitude findings for delta, theta, alpha-mu, beta and gamma frequency bands. (+) and (-) indicate an increase and a decrease of EEG amplitudes, respectively. NVNM, no view no motion; NVM, no view motion; LIHM, library of intransitive hand movements; SI, spontaneous imitation; II, induced imitation.

4. Discussion

Using reciprocal imitation as a test-case for the multifactorial account of agency, we aimed at delineating the brain dynamics specificities related to different components of agency as they emerge from a live interaction between two persons. In such a situation indeed, one has to differentiate who is at the origin of the action imitated (the model), who is in control of the imitation (the imitator) and who feels the action as one's own (both partners). A simultaneous EEG recording of pairs of dyads engaged in different imitative conditions allowed us to show dissociation between self- and other-ascription of action primacy, and to find correlates of shared feeling of agency.

4.1. Beta rhythm and ascription of action primacy to self

Beta desynchronization over the central and frontal regions was found when action primacy was attributed to self (NVM/NVNM and Model in II/NVM). This finding converges with the description of a decrease of the beta frequency band over central and medio-frontal regions during movement production (Gross et al., 2005; Pfurtscheller et al., 2003), planning of movement (Ridderinkhof et al., 2004), (Tzagarakis et al., 2010) and motor imagery (Pfurtscheller et al., 2005). The stronger decrease in Model during II compared with the baseline NVM can be attributed to a motor resonance created by the similarity between afferent and efferent messages during imitation. Meanwhile, the absence of significant decrease in beta amplitude when Imitator in II was contrasted to NVM points on the sensitivity of beta rhythm to the intentional reproduction of the movement observed. This is consistent with the proposal that the beta rhythm is involved in the maintenance of neurodynamical patterns (Engel and Fries, 2010). For the production of real or imagined action, this maintenance appears to be a crucial neural mechanism. In the cases of motor

perception (LIHM) or imitation (Imitator in II), the flow of incoming sensory information drives continuously the motor cortices and thus should recruit less endogenous pattern maintenance mechanism.

4.2. Delta rhythm and ascription of action primacy to other

Specific correlates of attribution of action primacy to other were found in the delta band with increase over fronto-central and parietal regions for the contrasts between passive observation of movement (LIHM) and rest as for the contrasts between Imitation in II and NVM. The contrast Imitator-Model in II showed an increase over centro-parietal regions. The delta frequency band is poorly documented concerning motor-related tasks but this increase could reflect a potential top-down control (Anastassiou et al., 2011; Lakatos et al., 2008). The focal increase in delta activity suggests an attentional control over the primary motor cortex.

To sum up, the observed variations related to ascription of action primacy to self or to other in beta and delta frequency band were opposed. The contrasts SI-II showed an increase in the delta rhythms and a decrease in beta rhythms over the same regions. Accounting for the contrast Imitator (II)–NVM, the increase in the delta activity should relate to the intentional reproduction of the movement observed, whereas the decreased beta activity should relate to the intentional initiation of movement, as accounted by the contrast between Model (II) and NVM.

4.3. Shared feeling of agency and influence imitative context

Another major issue in this study was related to the potential neural correlates of the shared feeling of ownership of gestures. During spontaneous imitation, rhythms were more similar for model and imitator when contrasted with simple movement baseline than during induced imitation (See Fig. 5). Gamma frequency activity, which was specifically sensitive to this symmetric involvement of the two participants, could be related to more complex processing

than that involved in motor perception and production. Gamma-frequency activity has been associated with various cognitive functions (e.g., attention and memory) (Jensen et al., 2007) and is reported to reflect local processing at the cortical level (Fries, 2009). Here, SI condition only generated a significant difference in this frequency band and it appeared over the right parietal regions for the imitator as well as for the model. This region has been suggested to play critical functions in attention, agency and social interaction (Decety and Lamm, 2007) and an increase in gamma activity has been reported over this region during the perception of biological movement (Pavlova et al., 2006). Thus, the symmetric increase of gamma activity over the parietal regions could reflect an increase in the allocation of attention in the two participants engaged in dyadic exchanges and reflect their role as key functional hubs in the interindividual brainweb (Dumas et al., 2010) when sense of agency is shared whatever the role: imitation is at will thus involving the feeling of being associated to the control of the ongoing interaction.

A theta decrease was also observed for the imitator in spontaneous imitation compared to induced imitation. Theta-frequency activity has been reported to be involved in working memory (Brookes et al., 2010; Scheeringa et al., 2009) and thus its recruitment can point out a cognitive load during instructed imitation.

4.4. Alpha mu rhythm and motor processing

The classical desynchronization of alpha-mu rhythm over centro-parietal regions was present in all motor-related contrasts. A similar decrease in the alpha-mu frequency band was found for the passive observation of movement (LIHM-NVNM) and during the imitation of movement (Imitator-NVM in II), thus reflecting mainly ascription of action primacy to other. A decrease was also found in the same regions during the solitary production of movement (NVM-NVNM) and during the production of imitated movement (Model-NVM in II), thus

reflecting mainly ascription of action primacy to self. It is noteworthy that both desynchronization phenomena were found in the same frequency range (10-14Hz). Taken together, these results confirm the regulatory function of alpha-mu rhythm on cortical motor processing (Neuper et al., 2005; Pfurtscheller and Aranibar, 1978) but additionally suggest that the topography of this frequency band could allow dissociating self- and other-ascription of action primacy. Pfurtscheller and colleagues (Pfurtscheller et al., 2000) also found dissociative functions of alpha-mu but for different frequency ranges and at the somatotopic level. In the same direction, the discovery of phi markers over the right parietal (Tognoli et al., 2007) suggests that mu rhythms could have more specific social meaning in other regions than the sensori-motor cortices, albeit mu rhythm is currently the main EEG signature proposed for the Mirror Neuron System (MNS) (Oberman et al., 2008; Pineda, 2005).

4.5. Methodological issues

Convergent evidence in neuroscience leads to underline that cortical mechanisms are not fully described by a simple functional specificity of spatial regions or electrophysiological rhythms. However temptation remains high, in the realm of social neuroscience, to search for a specific signature of social interaction, even in the case of a connectivity approach. If we take as an example the fronto-parietal network, it has been proposed by Rizzolatti and Sinigaglia (Rizzolatti and Sinigaglia, 2010) to be at the core of social cognition, but it could as well be considered having a more general function. Indeed, strong functional links between parietal and frontal regions have been found to play a key role in perceptual awareness (Gaillard et al., 2009) without the presence of any social context. On another hand, neural oscillations in distinct frequency bands of a central and fronto-parietal network have been closely associated with socio-cognitive processes involving sensorimotor integration (Basar et al., 2001; Palva and Palva, 2007), perception-action coupling (Calmels et al., 2008; Hari et al., 1998; Pineda, 2005) or control of spatial attention (Capotosto et al., 2009). Social cognition taken within a

systemic and dynamical approach may lead more easily to interweave multiple correlates into a coherent whole.

In order to capture the subtlety underlying the dynamics of human brain, novel methods are needed that will avoid collapsing brain dynamics. The discovery of the phi markers (Tognoli et al., 2007) illustrates how successful can be the exploration of high-density spectrum through the whole scalp. Similarly exploring the whole scalp, we used a combination of FFT and cluster-based statistics so that there will be no constraint upon the multiple contrasts.

4.6. Beyond symmetry

Symmetry of observation and action has been strongly demonstrated by the discovery of the MNS (Caetano et al., 2007; Rizzolatti and Craighero, 2004). Symmetry is served by biological similarities and constraints among conspecifics (Hasson et al., 2004). However the neuromimetic hypothesis needs to be completed when social interaction is concerned (Petit, 2003). Beyond symmetry indeed, another component of any social interaction is to take into account: alternation in complementary social roles, yielding asymmetry of action processing in the interacting partners. This is especially important to assess agency. While the symmetry of action generates shared feeling of agency, the asymmetry of roles leads to alternate who is the agent of what.

Acknowledgements

We thank Florence Bouchet for her generous assistance in the EEG preparation, Pierre Canet and Laurent Hugueville for their technical assistance. Finally, we thank Mario Chavez for helpful comments in neurodynamics analysis. The work of GD was supported by a Ph.D. grant of the DGA.

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5 Modeling the impact of the human brain connectivity on individual and inter-individual neural dynamics

Following the two experimental studies, this modeling work focused on methodological and theoretical issues. The initial goal was to provide a numerical testbed for statistical analysis and functional connectivity measures both intra- and inter-brain. This aimed firstly at evaluating the robustness of h-PLV as a measure of cortical coupling, at the scalp level and secondly to test systematically hypotheses relative to the intertwining of structure and dynamics at individual and inter-individual levels.

Entering the nascent connectomic field was a clear motivation for designing a realistic biophysical model. With the rise of diffusion tensor imaging (Le Bihan et al., 2001), the structural core of the human brain was brought to reach (Hagmann et al., 2007, 2010). The topology of this anatomical backbone has been uncovered recently and intensively studied with graph theoretical approaches (Sporns et al., 2005; Bressler and Menon, 2010), which lead for instance to demonstrate that it possesses the physicist's « small-world » topology. This particular topology exhibits with a parsimonious number of links the interesting property of simultaneously facilitating the transmission of information and giving robustness to disconnections or deletions of nodes (Watts and Strogatz, 1998; Boccaletti et al., 2006). Moreover, it seems to facilitate metastable dynamical states, which has been pointed out as a key feature of human brain activity (Sporns et al., 2004).

Computational neuroscience has recently integrated these real connectivity dataset in whole brain simulations. By the combination of the "human connectome" with well-designed dynamical models, some numerical simulations have already given insightful results regarding the resting state functional networks and mechanisms underlying the coordination of neural information across distributed brain regions. Following this nascent virtual brain trend, we adapted neuro-computational techniques to our two-body perspective. Despite the growing interests in social neuroscience, only some seminal works in robotics have approached social interaction in such manner. Their designs have shown the efficiency of oscillator networks for handling sensorimotor tasks. In physics, one of the most studied oscillatory model in the graph dynamics field is the Kuramoto model (Kuramoto, 1975). Kuramoto model has been widely used for investigating the synchronization phenomenon (Strogatz, 2000) and appears to be a plausible approximation of neurobiological oscillating processes (Breakspear et al., 2010). It creates a rich dynamical repertoire when combined with complex networks topology. As our neurodynamical perspective is centered on phase synchronization between distant brain regions, we designed our biophysical model by adapting Kuramoto's equations to integrate the anatomical connectivity data. Two virtual brains were created simultaneously by duplication with different random oscillation frequencies for each. We simulated an artificial perception-action coupling by linking the motor regions of one virtual brain to the visual regions of the other and vice-versa. Simulated data could then be confronted to the real hyperscanning-EEG data thanks to forward modeling.

More than allowing to test processing and statistical methods, the complete model was also an ideal tool for exploring two important issues raised by the experimental results: the functional meaning of inter-brain synchronization and how two different brains could at the same time enter in coupling while keeping their coherent endogenous dynamics. The following paper will present the impact of the anatomical structure of the human brain on the neural dynamics at intra- and inter-individual levels, and its potential role in our ability to enter in synchrony with others.

Modeling the impact of the human brain connectivity on individual and inter-individual neural dynamics

Guillaume Dumas^{a,b,c}, Mario Chavez^{a,b,c}, Jacqueline Nadel^d, Jacques Martinerie^{a,b,c}

Abstract

With the recent development of diffusion MRI, a new approach called connectomics has introduced a growing number of anatomical datasets in order to enrich our understanding of brain structure. In parallel, functional simulation in the neurodynamics field has also enlightened our understanding of the variety of dynamics emerging in the brain. With the combination of these two fields the intertwined problem of structures and dynamics can be tackled a little further. Nascent social neuroscience has also started to provide a new vista of the coupling of social systems. The new hyperscanning techniques give access to a measurement of this coupling through simultaneous cerebral recordings of humans while they interact. Here, we propose a biophysical model of pairs of human brains at rest as well as coupled by sensorimotor interaction. It has used a modified version of the Kuramoto model integrating real anatomical connectivity. The resulting numerical simulations were compared to real hyperscanning-EEG data using forward modeling. Results provide new insights on how anatomical connectivity influence individual neural dynamics and facilitate inter-individual coupling.

Keywords: human connectome, neural synchronization, coupled oscillators, hyperscanning, EEG

^a Université Pierre et Marie Curie-Paris 6, Centre de Recherche de l'Institut du Cerveau et de la Moelle épinière, 47, bd. de l'Hôpital, 75651 Paris Cedex 13, France.

^b Inserm, U975, 47, bd. de l'Hôpital, 75651 Paris Cedex 13, France.

^c CNRS, UMR 7225, 47, bd. de l'Hôpital, 75651 Paris Cedex 13, France.

^d Centre émotion, CNRS, USR 3246, Pavillon Clérambault Hôpital de la Salpêtrière, 47, bd. de l'Hôpital, 75013, Paris, France.

Introduction

The complementarity between structure and dynamics is a long lasting topic in complex systems research. While structure shapes the dynamics by providing constraints, dynamics reciprocally modify the structure itself. In neuroscience, this complementary pair has been increasingly studied for years [1]. Indeed, both structure and dynamics contribute to the evolution of the nervous system via their mutual coordination [2, 3]. Non-linear dynamics have unveiled some characterizations of the intertwined causalities behind auto-organization. Furthermore, a lot of experimental data have been grabbed thanks to the recent advances in anatomical and functional neuroimaging [4]. By giving access both to structural and functional views concerning the nervous system, neuroimaging techniques give access to their complementarities [1].

Numerical simulations also represent a promising tool to investigate this problem and test theoretical models inherited from experimental observation [5]. They could now integrate experimental data such as the anatomical structure. For instance, a new field called connectomics [6] specifically tries to reconstruct the whole nervous system network with histological and neuroimaging techniques. Various studies in this nascent domain have revealed complex network topology in the human brain [7]. This kind of networks seems astonishingly efficient for both the exchange of information and the creation of metastable dynamics in chaotic systems [8, 9]. Modern cognitive science has recently started to adopt a graph vista of the brain [10-13]. This movement is linked to a rise in interest in functional connectivity. With the nascent "Virtual Brain" approach[5] it is now possible to study normal and pathological brain processes within a computational environnement. In the fMRI community, these new models concentrate on the fonctionnal connectivity specific to mamalian brain during its resting state [14]. Indeed, a recent study demonstrates the predictive power of such methodology [15] for simulating observed anti-correlated BOLD functional network.

On the other hand, EEG/MEG community is more interested in neural synchronizations [16-19]. Indeed, one of the major problems in the study of perception is the binding where different perceptual characteristics have to be integrated in a coherent manner to perceive a unified object. Synchronization has been proposed as a neural mechanism to solve this binding problem [20]. Although a growing number of studies are interested in neural

synchronisations and propose the hypothesis that they support the coordination of cognitive information in the brain [21], the fundamental functional meaning of neural synchronization remains quite uncertain and debated [22].

Recently, our team has demonstrated that neural synchronizations could also be observed between the brains of two different persons engaged in a reciprocal social interaction [23]. This has been done thanks to a new technique called hyperscanning, which allows the simultaneous recording of two people's brain [24, 25], from which we investigated the phase locking of scalp EEG signals from the interacting participants. Our objective in the present paper is to propose a model of this phenomenon thanks to numerical simulation based on a connectomic dataset. We investigate to what extent inter-individual synchronizations are related to the anatomical and functional similarity of the two brains in interaction. By a statistical comparison with real data, we aim at calibrating our model parameters. The results provide insight about the impact of the real anatomical structure of the human brain on the functional dynamics observable at both intra- and inter-individual levels.

Methods

Experimental data

The experimental data used in this paper are taken from our former study about inter-brain synchronizations [23] where 18 participants paired as 9 dyads were recorded simultaneously with dual-video and dual-EEG setups while they were engaged in spontaneous imitation of hand movements.

Apparatus and setting

The experiment was conducted in two separate laboratory rooms. The design and equipment were similar to the double-video system designed by Nadel and colleagues for their developmental studies of sensitivity to social contingency in infants [26], except that a dual EEG recording system was added to the setup (Fig. 1A).

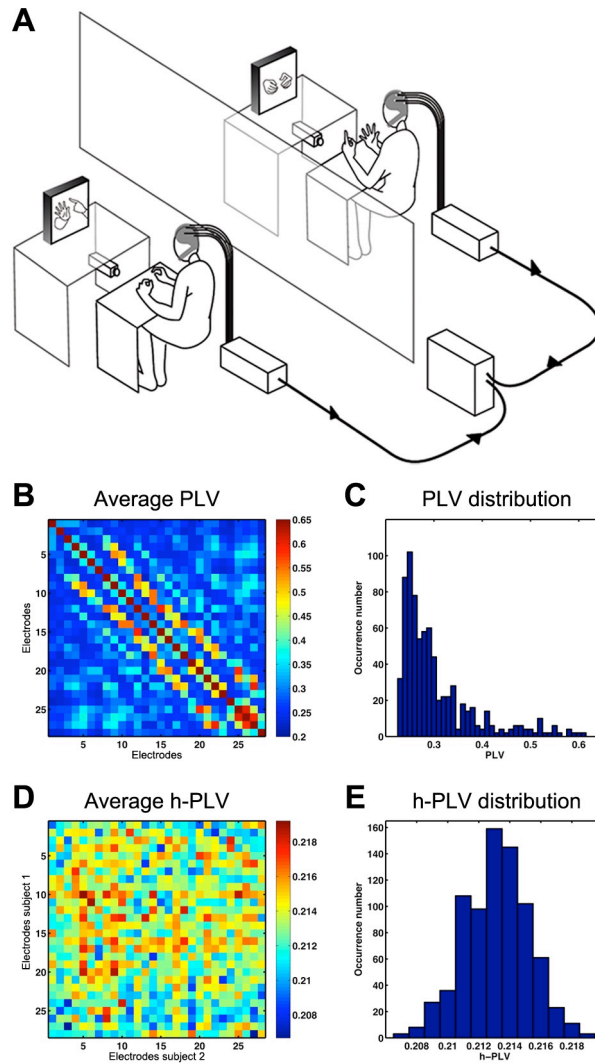


Fig. 1: Real functional data. (A) Apparatus and experimental setting of the double video system and dual-EEG recording [23]. (B) PLV matrix and related histogram (C) for the 18 real subjects during resting state condition. (D) h-PLV matrix and related histogram (E) for the 9 dyads during the resting state condition.

Protocol

The protocol was composed of two different conditions. Here, we used a control condition where subjects were asked to move their hands without seeing each others, and a spontaneous imitation condition where subjects were able to see each-others hands, moved their hands freely and imitated the other at will. All the movements were bi-manual and intransitive (meaningless gestures). Each session would begin with a 15 seconds long resting state recording and would be followed by a spontaneous imitative interaction of 90 seconds.

Recordings

The simultaneous neural activities of the two subjects were recorded with a dual-EEG recording system. This system was composed of two Acticap helmets with 32 active electrodes each. The ground electrode was placed on the right shoulder of the subjects and the reference was fixed on the nasion. The impedances were maintained below 10k Ω . Data acquisition was performed using a 64-channels Brainamp MR amplifier from the Brain Products Company (Germany). Signals were analog filtered between 0.16Hz and 250Hz, amplified and digitalized at 500Hz with a 16-bit vertical resolution in the range of +/- 3.2 mV. Spatial positions of the electrodes were recorded with a Polhemus system for all subjects.

Four electrodes were excluded from the analysis (T7, T8, CP9, CP10) because of too low signal to noise ratio. The correction of eye blink artifacts in the remaining EEG data was performed using a classical PCA filtering algorithm [27]. We used 800 ms windows with 400ms of overlap. EEG signals were then controlled visually another time in order to eliminate remaining artifacts. These were excluded from the analysis and, in order to avoid border artifacts induced by their suppression, we smoothed the joints by a convolution with a half-Hanning window.

Structural modeling

In order to represent the two structures of our virtual subjects we used two connectomes, which describe the probabilities of connections by nervous fibers between all the 90 regions of the Tzourio-Mazoyer brain atlas [28]. The anatomical connectivity matrix (Fig. 2D) was generated over 20 participants thanks to a new methodology based on Diffusion Magnetic Resonance Imaging (DW-MRI) and Graph Theory described in refs [29, 30].

Each matrix (See Fig. 2D) was embedded as a spatial weighted and non-oriented graph where the positions in the MNI coordinates of each region were taken as the barycentre of all the voxels of the region in the Automated Anatomical Labeling (AAL) atlas [28] (See Fig. 2 A, B & C).

Shuffled intra-individual versions of the connectome were created by permuting the connectivity matrix while keeping it symmetric and with zeros over the diagonal.

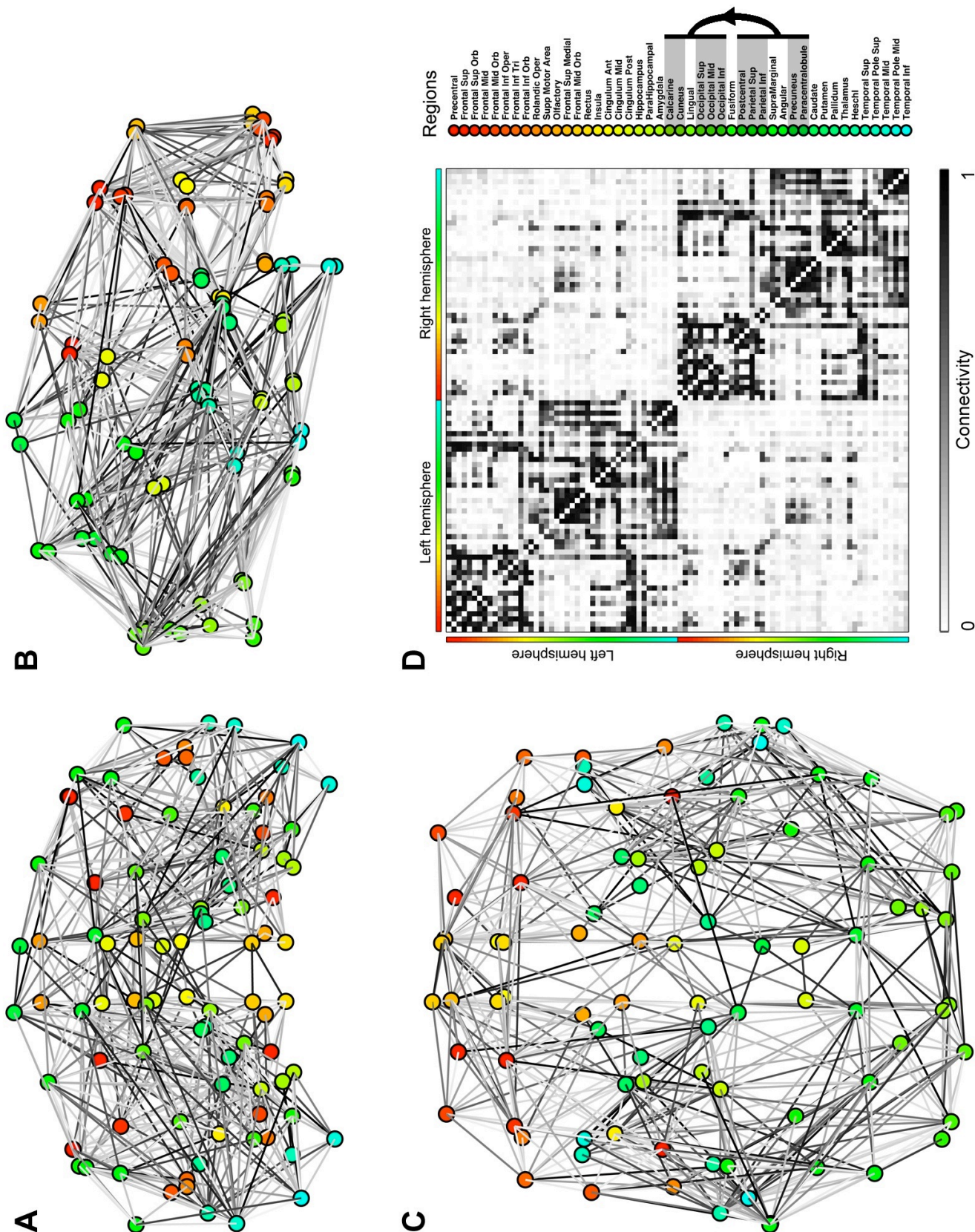


Fig. 2: The connectivity backbone. (A) Rear view. (B) Right view. (C) Top view. (D) Adgency matrix and legend.

Dynamical modeling

The dynamical model derives from the multiple oscillators model of Kuramoto [31, 32] which is thought to be a plausible approximation of neurobiological oscillating processes [33]. Each region was represented as an oscillator.

The model equations read as :

$$\frac{\partial \phi_i(t)}{\partial t} = \omega_i + C_{\text{intra}} \sum_{j \neq i} W_{i,j} \sin(\phi_i(t) - \phi_j(t - \tau_{ij})) + \nu(t) \quad [1]$$

where $\phi_i(t)$ stands for the phase of the i^{th} oscillator at the time t , ω_i is the natural frequency of the i^{th} oscillator taken randomly from a normal distribution centred on 40Hz and with a standard deviation of 8Hz, according to the values of the average gamma band activity observed in real data; $\tau_{i,j}$ is the propagation delay between the i^{th} region and the j^{th} region based on Euclidian distance between the two nodes multiplied by a standard axonal velocity of 1.65m.s^{-1} [34]; $\nu(t)$ is a dynamical random perturbation such that $\langle \nu(t) \rangle = 0$ and $\langle \nu(t)\nu(t') \rangle = 2D\delta(t - t')$ with $D=0.1$ and $W_{i,j}$ is the coupling parameter between the i^{th} and j^{th} regions based on the connectivity dataset. The simulations were run over 5000 samples using the Euler technique at a sampling frequency of 500Hz, i.e. $dt=0.02$. They were initialized with random phases. The 1000 first transitory samples were discarded from the analysis.

In order to model the two virtual partners, we create a 180-squared matrix W with two blocks of 90 regions for each subject (See Fig 2D). Thus, the 91th region corresponds to the region 1 of subject 2. W also integrates inter-individual coupling elements equal to C_{inter} between the motor regions of each partner with the visual regions of the other and vice-versa, thus simulating the perception-action loops between them [35]. Motor regions were left and right paracentral lobules (TZ n°: 69, 70), left and right post-central areas (TZ n°: 57, 58), left and right parietal areas (TZ n°: 59, 60, 61, 62) and left and right precuneus (TZ n°: 67, 68). Visual regions were left and right calcarine areas (TZ n°: 43, 44), left and right cuneus (TZ n°: 45, 46) and left and right occipital areas (TZ n°: 49, 50, 51, 52, 53, 54). The delay for this intersubject coupling was taken as null considering that it takes into account that causal influence of the behavioral interaction is mediated by photons through the dual-video system.

For assessing the role of anatomical individual connectivity on intersubject interactions, we added two additional types of simulations using shuffled versions of the connectomes: one where paired subjects shared the same shuffled connectomes, and the other where each

subject had a different shuffled version. This aimed to quantify the effect of the anatomical structure at both intra- and inter-individual levels.

Different simulations were generated for different values (C_{intra} , C_{inter}) of the parameter space. All simulations used different sets of pulsations for the two connectomes and the initial state of phases was taken from a uniform random distribution between $-\pi$ and $+\pi$. Programming was done with Matlab (RC2009b, The MathWorks). GPU implementation used the GPUmat toolbox (<http://gp-you.org/>) for the implementation on GPU.

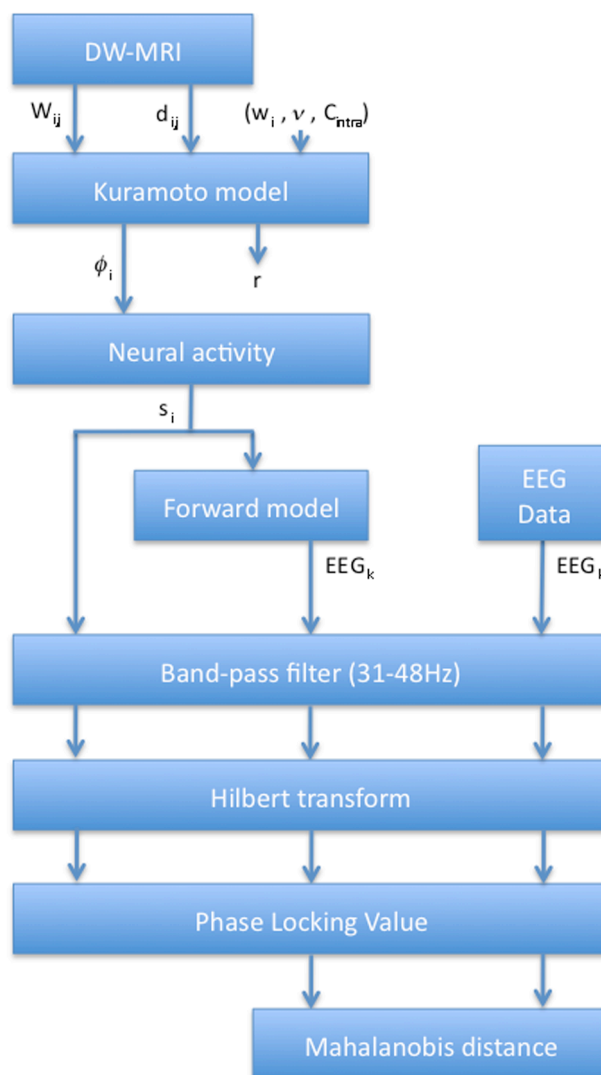


Fig. 3: Procedure Flowchart illustrating the different steps of the simulations and their comparisons with the real EEG data.

Forward model

In order to compare real EEG and EEG-like simulated data (obtained by applying a cosinus function to the phases of Eq. 1), we computed a forward model with the Brainstorm matlab toolbox [36] on the anatomical MNI template Colin27 [37] after repositioning of the electrodes according to the average spatial positions across real subjects which were recorded with a Polhemus system. It gave us a gain matrix G referring to the virtual EEG signal that could be observed at the scalp level for each Kuramoto's system.

Thus we obtained $EEG=G*S$, where G stands for the gain matrix of the forward model and S for cortical sources signals: $\cos(\phi(\text{areas,time}))$.

Data analysis

We used the phase locking value (PLV) [38] to quantify the brain dynamics. After a band pass filtering of the scalp signal in the gamma range between 31 and 48Hz, we apply a Hilbert transform to extract the instantaneous phase ϕ of each signal. The PLV formula for two channel p and q is given by:

$$PLV_{p,q} = \frac{1}{T} \left| \sum_{t=1}^T \exp(i(\phi_p(t) - \phi_q(t))) \right|$$

where T is the number of samples considered in each 800 ms time window and || the absolute value.

In the following, we will use PLV when both electrodes are taken from the same subject and h-PLV (or hyper-PLV) when each electrode belongs to each two subjects.

In order to study the global interaction of oscillators, we also computed the average order parameter of each connectome following the formula:

$$\langle r \rangle = \frac{1}{T} \sum_{t=1}^T \frac{1}{N} \left| \sum_{k=1}^N \exp(i\phi_k(t)) \right|$$

where k is the region of the considered connectomes, N=90 regions and T=4000 samples=8s

Statistics

The similarity distances between simulated and real PLV data were calculated by the Mahalanobis distance [39] for PLV and h-PLV matrices respectively (See Fig. 1B, C, D& E for average matrices and distributions of the real data).

Results

1. Anatomical influence on the intra-individual functional connectivity

For no anatomical coupling ($C_{\text{intra}}=0$), all oscillators were independent and the same distribution of frequency was observed at both ROIs and scalp levels. Then, while the strength of the anatomical connectivity increased, clustering was observed between ROIs.

As expected, a phase transition was then assessed at the ROIs level by a change on the order parameter while the anatomical strength increased (Fig. 4A). This transition first occurred for the real connectome and then for the shuffled versions. The transition was sharper for simulations with shuffled connectomes. The two shuffling strategies did not make any differences at the intra-individual level.

Interestingly, an alpha rhythm appeared after this transition and shranked the gamma rhythms (Fig. 4C and 4D). Furthermore, intermediate beta rhythms peaks (between 21Hz and 34Hz) appeared during the transition around $C_{\text{intra}}=0.45$ (Fig. 4D).

At the scalp level, we band-pass filtered the simulated EEG signals in the gamma band to compare their PLV with those of real resting state data ($C_{\text{inter}}=0$). We observed the same transition phenomenon (Fig. 5). PLV in the gamma band rhythm collapsed (Fig. 5A) after the transition and the power spectrum was shifted to theta (Fig. 5C).

The minimum statistical distance between simulated and real resting data was reached with real connectivity during the described phase transition. This distance was smaller than those obtained from shuffled conditions (Fig. 6A).

2. Anatomical influence on the inter-individual functional connectivity

In the simulated resting state ($C_{\text{inter}}=0$), the h-PLV between the two virtual partners were not null and proportionally increased with the strength of anatomical connectivity before the phase transition (Fig. 6B) and then collapsed for $C_{\text{intra}}=0.45$ as for the PLV. After the phase transition - i.e. the best fitting area with the real data (Fig. 6C) - the average h-PLV increase as the strength of the artificial sensorimotor coupling C_{inter} was incremented between the two connectomes. It is interesting to observe that simulations with shuffled versions of the connectome did not show this effect. Nevertheless, the average h-PLV was higher for connectome sharing the same shuffled version than for those with different shuffled versions.

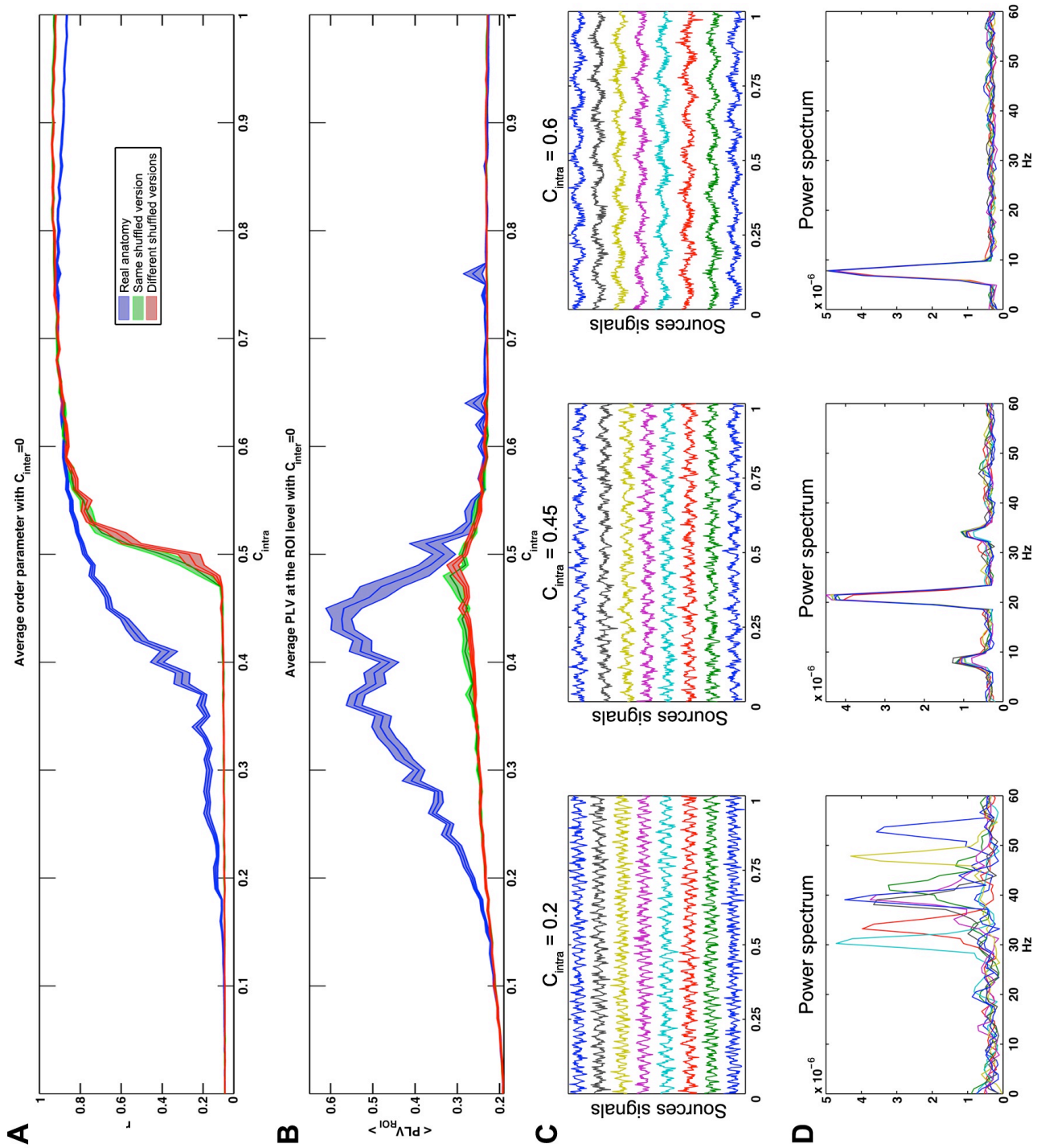


Fig. 4: Influence of the global anatomical connectivity strength at the ROIs level. Results are averaged across 18 simulations with $C_{inter}=0$. Areas stand for the standard error. Blue: real connectivity. Green: identic shuffled connectivity for the two virtual subjects in same dyads. Red: different shuffled connectivity for all virtual subjects. (A) Average order parameter across the 90 ROIs. (B) Average PLV in the gamma band between all the ROIs inside each connectome. (C) Example of simulated data at the ROIs level for $C_{intra}=0.2$; 0.45 and 0.6 (D) Power spectrum for signals shown in B.

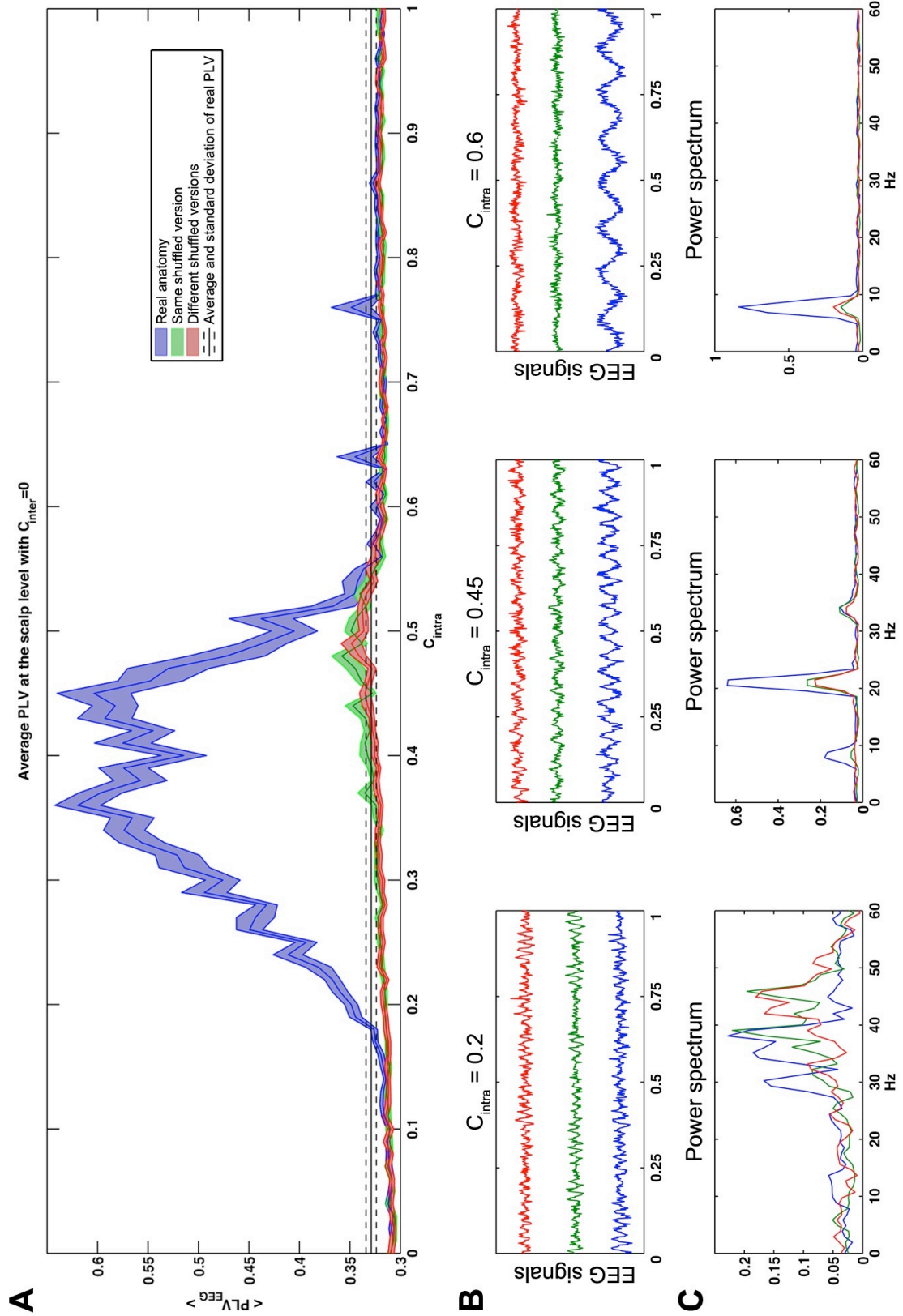


Fig. 5: Influence of the global anatomical connectivity strength at the scalp level. (A) Average PLV across all pairs of electrodes inside each virtual subject helmet. (B) Example of simulated EEG signals relative to simulation shown in Fig. 4C. (C) Power spectrum for each EEG signals of B.

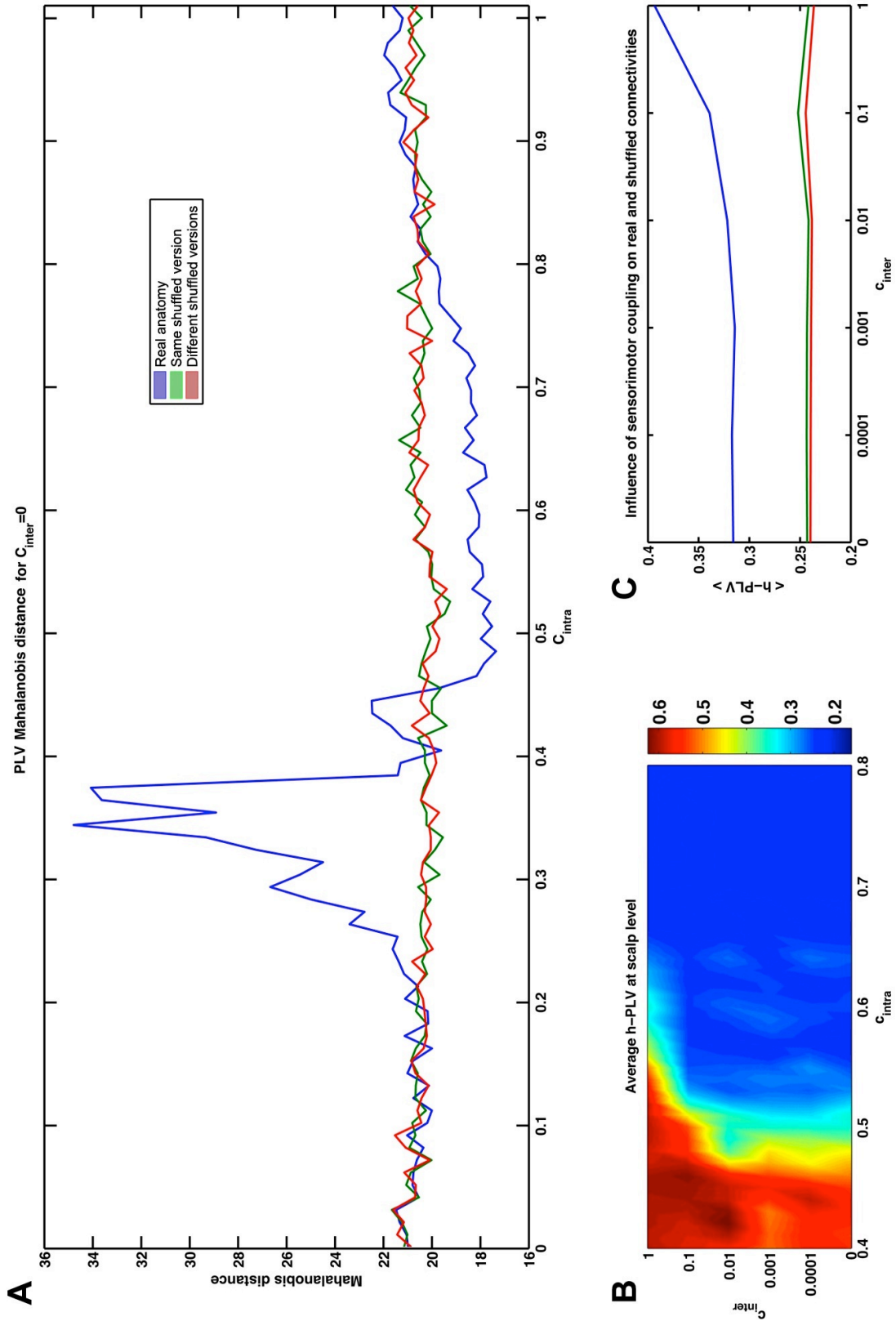


Fig. 6: Statistical distances and inter-brain synchronization (A) Mahalanobis distances between simulated and real resting state data based on PLV matrices. (B) Average h-PLV values. (C) Influence of the artificial sensorimotor coupling strength on h-PLV around the best fitting area (C_{intra} between 0.5 and 0.6).

Discussion

The aim of this paper was to investigate the influence of the anatomical connectivity on neural dynamics at both individual and inter-individual levels.

We created a biophysics model integrating a real anatomical connectivity dataset based on the 90 ROIs atlas of Tsourio-Mazoyer. These ROIs represent the structural level of the dynamical modeling based on the Kuramoto's weakly coupled oscillators. This current version integrates realistic coupling based on the anatomical connectivity and delay proportional to the average spatial distances between the ROIs. The simulated data were compared to real hyperscanning-EEG data. As these recordings were at the scalp level, we applied a forward model to our brain simulation to create virtual EEG recordings.

The frequencies of the oscillators were fixed in the gamma band (between 30 and 50Hz) since this brain rhythm is related to neural processing at the local level [40, 41]. Furthermore, long range gamma phase synchronization has been related to the integration of information at the individual level [17] and were also observed in our former hyperscanning study between two brains [23].

In order to quantify the real effect of the anatomical structure, we used two different shuffled strategies of the anatomical backbone. The first strategy was to keep a constant shuffled version across all simulations and thus quantifies the impact on dynamics of sharing the same anatomical structure. The second strategy was to change the shuffling for each simulation thus allows measuring the residual synchronization related to the similarity of the oscillators frequency and the forward model.

Intra-individual dynamics

The first part of our analysis concentrated on the individual brain where we tuned the gain of the anatomical connectivity (C_{intra}) in order to fit the model with the real resting state data. At the level of the sources (ROIs), the order parameter gives access to a coarse synthesis of the dynamics by quantifying the spatial coherence of all oscillators. Two main states were observed by varying the anatomical coupling strength: the first one where the oscillators kept

their high frequency and tend to clusterize most the anatomical connectivity increase, the other one was characterized by a coherent oscillatory state in the low frequency band.

The order parameter increased proportionally to C_{intra} until the clustering phenomenon appeared around $C_{\text{intra}}=0.4$. As expected, oscillators within anatomical clusters or sharing similar pulsations tend to easily synchronize. Functional clusters adopt a coherent pulsation and thus have a high order parameter locally. However, it does not necessary give a high global order parameter since these clusters could stay independent from each other's. The sigmoidal transition reflects the aggregation of coherent clusters in a finite network that create progressively a single global synchronized group.

The transition was interestingly different in the real and in the shuffled cases: with the same structural connectivity strength, the real anatomical backbone was more efficient to synchronize the oscillators. This is consistent with past results pointing out the structural efficiency of small-world network to synchronize large number of oscillators [8, 42, 43]. However, the transition between the two dynamical states was also larger in the real anatomical case (See related C_{intra} intervals in Fig. 4A). It confirmed that the real structure of the brain thanks to its “small-worldness” allows a smoother transition [3, 44]. Phase transitions in non-linear systems always give rise to large numbers of dynamical states and attractors. By smoothing the transition, the topology of the human brain allows a more controllable way to explore these attractors. Neurocomputational models show a similar effect of the delay in enhancing synchronization [45]. A delay could also increase stability of the dynamics within perturbative environment [46]. A recent study by Perez and collaborators [47] proved that the combination of a real network topology and time delayed conduction create coherent dynamics. Here, we observed this phenomenon after the phase transition interval where the dynamics converge to a very stable 8hz limit cycle. This 8 Hz rhythm observed after the transition correspond exactly to the average back and forth propagation across the whole connectome. This frequency is similar with the Alpha rhythm typically observed in electrophysiology studies and thus questions of the origins of the EEG frequencies since their constraints are simultaneously the local loops within macrocolumns and the global structure of the brain.

In order to tune our model, we then compute a statistical distance between the PLV observed in real data and those reconstructed after forward modeling in our simulated time courses. A

striking result was that the best fitting point (where the Mahalanobis distance reaches its minimum) was at the transition discussed above. A mix of remaining gamma oscillations but also the emergence of theta characterized this interval. As there is a growing interest toward cross-frequency, these results could question the functional role of alpha as a regulatory rhythm. Indeed, the more alpha appeared, the more gamma oscillations were reduced with an intermittent and not stable synchronization between them.

Inter-individual dynamics

In the second part of the study we focused on the inter-individual synchronizations. We aimed at quantifying the synchronization that could be observed even without any inter-individual interaction. These inter-brain "residual synchronizations" are the consequences of the similarities between the two individuals - either real or simulated - at both structural and dynamical levels. By comparing with the two scramble conditions, we were able to observe the facilitating role of the real anatomical connectivity in these "residual synchronizations". Indeed, while the strength of the connectivity (C_{intra}) increased, real versions of the connectomes tended to synchronize more than the shuffled versions. That suggests a potential dynamical property of the topological structure of the human brain: facilitating "residual synchronizations" between each-others and thus also facilitating our dynamical coupling. Interestingly, if the connectomes were scrambled, the fact that the two networks share or not the same structure had no apparent influence. There was in both cases weak residual synchronizations caused by the dynamical similarity of all the oscillators.

We finally look at the effect of sensorimotor coupling on the inter-brain synchronization. We focused on the best fitting region of the model and increased progressively the coupling between visual regions of one connectome with motor regions of the other, and vice-versa. The effect of this coupling on the inter-brain synchronization was maximal in the best fitting interval of the model (Fig. 6C). Before the transition, the internal coupling is probably not sufficient to spread the information from the visual area to the rest of the connectome. After the transition, the disappearing of gamma oscillations vanishes the h-PLV despite a strong coupling. Statistically, the simulations remain realistic at the intra-individual level for weak coupling while inter-brain synchronizations increase. This assess of the stability of the endogenous dynamics even with an external perturbation characterized here by the effect of the second connectome.

Conclusion

All these results support the view of the complementary nature of structure and dynamics of the human brain. This topic is intensively studied and has already demonstrated that the biological structure of the human brain allows a rich panel of dynamical states with a global efficiency [48] and information processing enhancement [49]. Here, we focused on how our anatomical structure facilitate the internal processing of cognitive information and meanwhile the ability to enter in coupling with the environment and the other persons [50].

At the intra-individual level, the real anatomical connectivity of the human brain enhances synchronization in high frequency band and in meanwhile makes emerge endogenous rhythms in the low frequency band. This allows a metastable state where the high synchronizability in the gamma band coexisted with the emergence of large-scale alpha oscillations that disrupt global synchronized patterns. This metastable state gives a possible mechanism of the active desynchronization observed more than ten years ago by Rodriguez et al [51] and interpreted as an "active uncoupling of the neural assemblies, necessary to proceed from one cognitive state to another".

As already proposed, the anatomo-functional similarity across humans could explain a tendency to enter in synchronization while immersed in the same perceptual context [52] or doing the same perceptuo-motor task [53]. Our results suggest that similar endogenous dynamics but also the sharing of the same anatomical structure support this effect. They also demonstrate that the structural connectivity of the human brain enhanced dynamical similarities and thus facilitate coupling with the others.

To conclude, the nascent social neuroscience could be taken as a new theoretical and experimental workspace in the study of complex systems coupling [54]. Previous studies have already demonstrated the theoretical possibility of dynamically modelling complex social behavior [55] and sensori-motor coupling in individual agents [56]. In parallel, neurobiological models have also been proposed to adopt a dynamical and developmental account of socio-cognitive functions at the neural level [57,58]. The hyperscanning technique starts to provide evidence of the complementarity between neural and social coordination dynamics [59]. Our findings encourage the development of a computational social neuroscience through the extension of existent models to an inter-individual level. It could provide new insights about the neurobiological mechanisms underlying social cognition and related pathologies. Indeed,

while individual brain simulations are starting to provide new path for the understanding of brain lesions [60], inter-individual computational models combined with hyperscanning data may represent a powerful tool to tackle pathologies with self-other dysfunctions. Indeed, a growing number of studies demonstrate the distributed nature of the structural and functional differences in autism [61-63] and schizophrenia [64, 65]. Inter-individual neurocomputational model could help in the future to match these differences with social behavior and help in the integrative understanding of this impairment.

Acknowledgement

GD was supported by a PhD fellowship of the French Délégation Générale pour l'Armement (DGA). We thank Yasser Iturria-Medina for sharing the DTI connectivity matrix used In the study. Many thanks also to Lionel Thivard for all the insightful discussions about connectomics and Yohan Attal for his advises on forward modeling.

Author Contributions

Experimental acquisition: GD JN JM. Conceived and designed the simulations: GD MC JM. Analyzed the data: GD. Wrote the paper: GD MC JN JM.

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6 General discussion

6.1 Synthesis of the findings

This thesis can be seen as a neurodynamic attempt to investigate social interaction within an embodied and situated approach. All the data provided, be they inter-brain or intra-brain, live or simulated, originate from a social context of reciprocal interaction. Such embeddedness was aimed at exploring the possibilities offered by moving away from the traditional focus on recording brains in isolation with designs that explore offline social cognition. Connectionist approaches and the Gibsonian theory in psychology have stressed the need of a more dynamic and holistic perspective. Sensory-motor theories of cognition have shown that the dynamical coupling of cognitive agents with their environment is an inherent part of cognition (Varela, 1979; Clark, 1999; Varela et al., 1999). The importance of embodiment and situatedness has been strongly emphasized by the dynamical systems framework (Kelso, 1995; Freeman, 1999; Le Van Quyen, 2003). It provides a perspective where the same conceptual tools can be applied to phenomena of different scales (Thompson and Varela, 2001). We have used synchronization to cut across different levels from behavioral synchrony to synchronized brain oscillations in given ranges. By adopting such methodology, both the body and the brain can be seen in an integrative manner within their continuous biological adaptation to the environment. The term "structural coupling" (Maturana and Varela, 1987) refers to how the structure of the organism and its coupling with the surrounding environment create statistical regularities that shape the structure of information in the nervous system (Sporns et al., 2005). Cognition is thus seen here as an exploratory process that cannot be reduced to merely an internal computation on representations of the external world (Noë, 2004): the organism is taken as a dynamical systems evolving continuously and co-dependently with the environment.

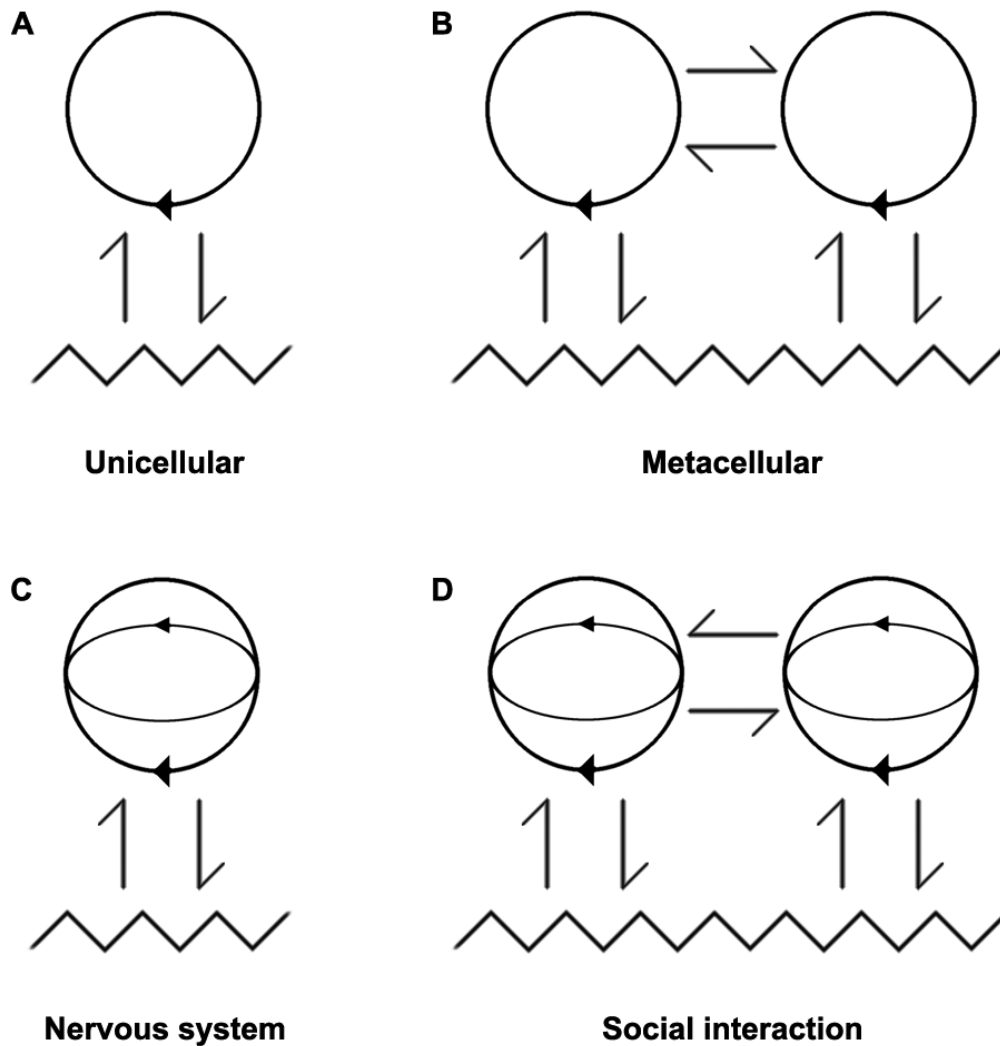


Figure 6.1: A) The unicellular autopoietic unit. B) Meta-cellular organism emerging from a second-order structural coupling. C) Organism with nervous system: the second-order coupling leads to an inner loop within the organism which enhance its ability to integrate its own state in its behaviors. D) Social interaction: a third order structural coupling. (inspired by ideograms from Maturana and Varela 1987)

Similarly, in spite of our propensity to interact with others, our ability to socialize is neither given nor fixed once for ever. Development provides numerous examples of transitory adaptations to both the physical and social environment. For instance, several studies have shown that imitation is crucial for infants to communicate before verbal language (Nadel-Brulfert and Baudonniere, 1982). Later, our interactions start before any words have been pronounced via eye contact, facial expressions, and postures that allow to guess the other's mood (Frith and Wolpert, 2004; Hari and Kujala, 2009). Although verbal communication can appear as a succession of unidirec-

tional transfers of contingent information, non-verbal interaction is more easily understandable as a sensory-motor coupling, or "third-order structural coupling". Paradoxically, this advantage of non-verbal interaction to study social synchrony has been largely ignored by social psychology and social neurosciences, focused on offline social cognition or social perception. This paradox has also been caused by the technical constraints of neuroimaging which, until recently, has only allowed the recording of one brain at a time.

Our program aimed at combining both the developmental account of social interaction and the neurodynamical perspective towards cognition. Taking the synchronization phenomenon as a multi-scale invariant pattern (Strogatz, 2003), it combined a socially situated paradigm with neurodynamic analyses of brain activity and searched for potential links between interactional synchrony at the behavioral level and phase synchronization at the neural level. To bridge these two levels, the design combined a dual-video system and an EEG-hyperscanning setup. Thus, we were able to record simultaneously both behavior and brain activity of dyads engaged in spontaneous and reciprocal imitation of their hands movements. We also tested the classical form of imitation, namely induced imitation, and passive observation of movements in order to compare our results with existing results in the literature. Numerical simulations have finally led to model the experimental brain data and investigate the link between neural dynamics and the anatomical structure of the human brain.

6.1.1 Social neurodynamics and inter-brain synchronization

We have first analyzed the link between interactional synchrony and brain synchronization between pairs of participants. The hypothesis of such a link was drawn from growing evidence that long-range neural synchronization is a potential mechanism for the integration of cognitive information distributed across different brain areas (Varela et al., 2001). To test this hypothesis, we used the Phase Locking Value (PLV) developed by our team (Lachaux et al., 1999) and adapted here as a hyper-Phase Locking Value (h-PLV), to measure synchrony between two separated brains. As the h-PLV is an innovation, searching converging results in the literature is not straightforward. Indirect convergence can be found however from different perspectives. For example, the fMRI hyperscanning studies conducted by Hasson and collaborators have shown temporal correlation of BOLD signals between the brains of different subjects immersed in the perceptual context of a same movie (Hasson et al., 2004). Despite these correlations were done at the timescale of

a second, they traduce strong anatomical and functional similarities across different individuals responding to the same perception (Hasson et al., 2010). In the case of reciprocal imitation (as in our experiment) both perceptual and motor contexts are shared by the two participants at the milliseconds timescale. We adopted a frame-by-frame behavioral analysis of the videos in order to keep this timescale for the subsequent neurodynamical analyses.

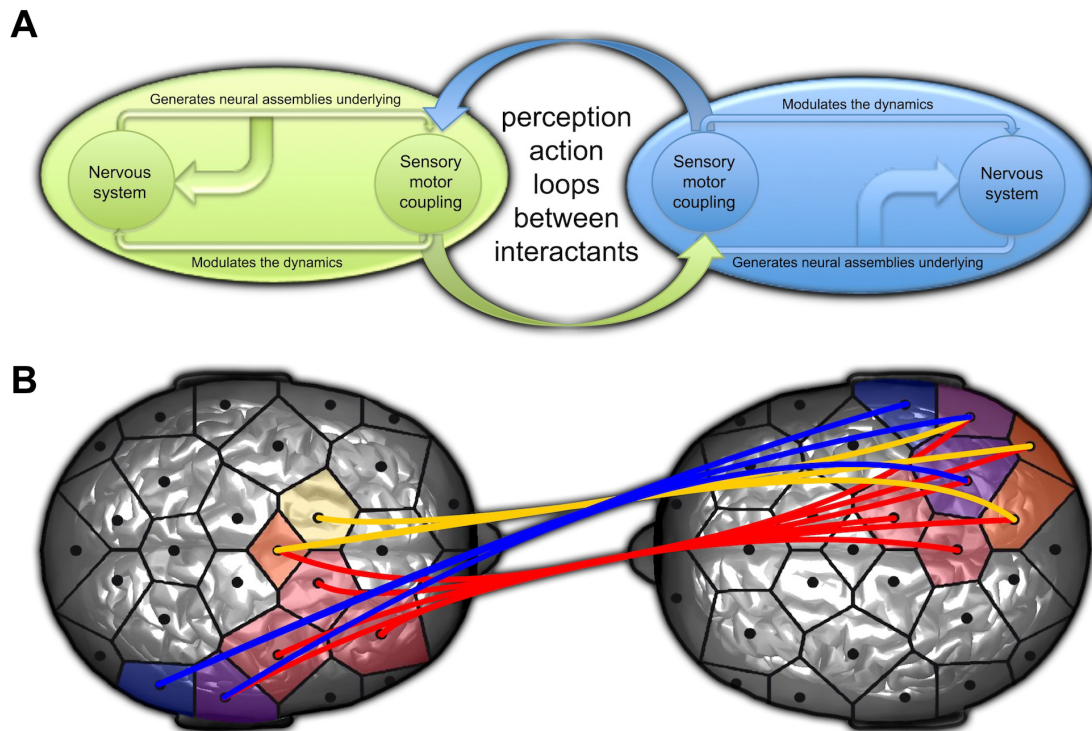


Figure 6.2: A) Schematic view of dyadic social interaction taken as a dynamical sensory-motor coupling. B) Inter-brain synchronization in alpha (blue), beta (orange) and gamma (red) frequency bands related to interactional synchrony during spontaneous imitation of hand movements.

Taking into account that the phases of oscillatory activity in both sensory and motor areas have been linked to low-level information such as visual motion (Rager and Singer, 1998; Singer, 1999; Gangitano et al., 2001; Aissani et al., 2011) or movement velocity (Jerbi et al., 2007; Muthukumaraswamy, 2011), in the case of reciprocal imitation, these low-level sensory-motor informations have to flow inside and between the two brains (see Figure 6.2 A). Thus, the h-PLV could reflect information being dynamically shared through an inter-individual sensory-motor loop. These loops emerge from a bi-directional coupling between the participants, with the behavior of each influencing the other's behavior, and inter-brain synchronizations reflecting their perception-action entanglement. Our results not only demonstrate the existence of inter-brain synchronization but also inform about their topological properties in different frequency bands (see Figure 6.2 B).

Inter-brain synchronizations were symmetrical in the alpha-mu frequency band, during episodes of interactional synchrony. The right parieto-occipital regions of the two subjects was pointed out as the main functional hub of this inter-individual brainweb. This is in coherence with the early works of Decety in Petscan. These works have given extensive evidence of the implication of the parietal regions in imitation (Decety et al., 1994, 1997; Decety and Grèzes, 1999). The authors however claimed a differentiation between right versus left parietal lobes when the act of imitating was contrasted with the state of being imitated (Decety et al., 2002). There is nowadays extensive evidence of stronger recruitment of the right parietal (Grosbras et al., 2011; Guionnet et al., 2011). Our use of bi-manual movement aimed also at correcting the eventual bias induced by the systematic use of the right hand in the experiment quoted. The right lateralization has furthermore been reported to be present in the perception of biological movements, notably at the level of the posterior STS (Grèzes et al., 2001, 2003; Grosbras et al., 2011) and of perspective taking (Ruby and Decety 2001).

The discovery of mirror neurons has noticeably marked an interest for parietal areas and their link with frontal structures. EEG results have shows a corresponding alpha-mu deactivation (ERD) in these regions during production and perception of the same action (Pineda et al., 2000; Babiloni et al., 2002; Pineda, 2005; Oberman et al., 2007). Interestingly, the Phi complex discovered by Tognoli and colleagues is within this alpha-mu range and linked the right parietal (Tognoli et al., 2007). Its implication in the synchronization with others is supported by a recent psychophysic theory proposing the right parietal, more precisely the right IPL, as underpinning the computation of the order of events. This so-called "When pathway" of the right parietal lobe is thought to subserve the attentional temporal processing of intermediate time-scale (Battelli et al., 2007) and to be linked with alpha activity (VanRullen et al., 2006). The phase of cortical alpha as been already proved to underly the attentional framing in vision (Varela et al., 1981; Vanrullen et al., 2011; Busch et al., 2009).

Our results confirmed the right parietal lobe as the ideal structure for the integration of sensorimotor information by linking visual and kinesthetic afferences with outgoing motor commands. Moreover, the control analysis, done by shuffling the behavioral analysis, has revealed that the inter-brain synchronizations were more robust for alpha-mu oscillations. They could thus play an active role in the temporal framing of sensorimotor information convey in the right parietal lobe, although this rhythm is usually associated with inhibition.

We also observed inter-brain synchronization in the higher frequency bands. These synchronizations presented a spatial asymmetry between the two participants with an involvement of posterior areas for the imitator and centro-frontal areas for the model. In both case they were situated in the right hemisphere as in low frequency bands. Inter-brain synchronization for higher rhythms thus do not seems to reflect the low-level similarity of the movements executed by the two participants. Taking into account multiple studies related to the functional role of beta and gamma (Jensen et al., 2007; Wyart and Tallon-Baudry, 2008) these synchronizations could bear testimony of attentional effects in both participants. The imitator has indeed to put more attentional resources on visual perception. At contrary, the model has to create continuously new motor pattern and thus focus on the planning of his movements. The analyses of brain activity at the individual level supported this hypothesis since they revealed an increase in beta activity for the same regions. Considering that beta activity has been linked to motor command uncertainty (Tzagarakis et al., 2010) and decision making (Haegens et al., 2011), we could propose the inter-brain synchronization as reflecting a joint strategy of motor control of the two subjects in order to stay in interactional synchrony: the imitator using visual and kinesthetic information to correct his own movements, the model using higher level cortical areas for his motor planning.

Further analysis should be made about the stability of the phase synchronizations in the different frequency bands. Perhaps higher rhythms phase synchronization is more transient and thus reflect specific period of the interaction such as those at the end of interactional synchrony. Analysis has been conducted specifically at this transition between synchronous and non-synchronous episodes but no robust results were found. However, they pointed out a collapsing of inter-brain synchronization. Interestingly, at the behavioral level this transition was also intimately linked with the change in the roles of the interactants. This “Turn-taking” is another emergent phenomena that can be observed during these real-time reciprocal interactions. Indeed, the alternation roles cannot be integrally tackled through classically-induced contexts and one-brain recordings. Although we observed “turn-taking” during the experiment, the real-time constraints prevented us from investigating neural dynamics potentially linked to this phenomenon (Wilson and Wilson, 2005). It shows the extreme complexity of creating balanced paradigms that permit both real reciprocal interactions while providing sufficient control over specific emergent behaviors (Hari and Kujala, 2009). Further hyperscanning studies should design experiments that can provide innovative ways to tackle such transient dynamics, which are strongly linked to inter-individual

coordination.

6.1.2 The three dimensions of agency

As we have just seen, the inter-brain analyses showed symmetrical synchronizations in low-frequency bands but revealed also asymmetries in higher frequency bands (see Figure 6.2 B). This double-faceted phenomenon reflects the similarities in the two participants due to the shared perception-action context, and also depicts the different role hold by each participant in the interaction (here model and imitator). Such complex dynamics clearly demonstrate that social interaction cannot be restricted to the activities of each brain taken separately and is not solely caused by the similarity of action and perception in the two partners. Although previous studies have cued the subjects to make movements synchronously (Lindenberger et al., 2009), in our study the hand movements of the two participants converge spontaneously to the state of interactional synchrony through a mutual coordination. This coherent state however does not impede each participant to hold a different social role in the ongoing interaction. Most approaches of the neural bases of social cognition adopt a symmetrical standpoint from which the brain activities of one person are either mirroring, or simulating the other's actions or thoughts. Using the hyperscanning methodology allows to capture the inherent asymmetries between people interacting, a phenomenon that remained unexplored until now.

In our intra-brain analysis, we focused on the asymmetrical patterns between model and imitator at individual level. Given that the partners synchronize similar movements, they can both attribute the action to themselves, thus sharing a feeling of 'co-ownership of action'. The asymmetry or roles arises from the fact that one is the initiator of the action imitated by the other: the primacy of action is ascribed to the initiator. The main goal here was to disentangle the different levels of agency ascription related to self and other to the sharing of the ongoing action. Studying the different neural correlates relative to these different feelings of agency could indeed favor a deeper understanding of the complexity of agency ascription. In our study, we primarily observed the usual decrease in alpha-mu and beta bands as it has been widely reported in the literature (Pfurtscheller et al., 1996; Pfurtscheller, 1981). These desynchronizations indeed follow gradually the motor engagement of the participants and thus reflect their position towards the generation of motor patterns (model) or the reproduction of perceived gestures (imitator). Whereas previous studies have extensively investigate the modulation of the alpha-mu power during perception-

action coupling (Pineda, 2005), in our study the alpha-mu band was the less dissociative rhythm across the different contrasts and mainly reflected the processing of motor information. By contrast, the beta band decrease over central and medio-frontal regions was specific to self-ascription of primacy of action. Indeed, the initiation of movement by the model correlated with this pattern, contrarily to the reproduction of movement by the imitator. This was consistent with the report of beta activity as related to intentional production of real or imagined movements (Kilner et al., 2009; McFarland et al., 2000; Tzagarakis et al., 2010).

While the above results validated our method by their coherence with previous study, the subsequent observations appeared rather new as regards the motor literature. We indeed observed an opposite variation of the delta rhythm activity over the centro-parietal regions compared to the rhythm of beta band. It correlated specifically with imitation and observation of action and not with the intentional initiation of movement. Past studies proposed the delta rhythm as subserving top-down control (Lakatos et al., 2008; Anastassiou et al., 2011). Here, it could reflect such attentional control over the primary motor cortex by facilitating the detection of elementary movement patterns. This topography of this increase was remarkably overlapped with those of previous decreases in alpha and beta bands. This was not the only case observed in our results and this points out how different rhythms can functionally correlate within a specific area for different behaviors. While it could complicate the interpretation of these correlates and thus explain the tendency in studies to focus on a particular rhythm in a specific region of interest, it nevertheless demonstrates the pluri-potentiality of both brain oscillatory activities and anatomical structures. These vicarious aspects represent a real challenge for the future. While the "neuronal recycling hypothesis" (Dehaene and Cohen, 2007) begins to uncover some theoretical basis on the structural side, a similar attempt in neurodynamics would be fruitful. Cross-frequency is a promising field (Canolty et al., 2006; Roopun et al., 2008) and such relationships may exist in our case although preliminary analysis revealed no statistical results.

The major innovative observation depends directly on our paradigm and the use of hyperscanning. Spontaneous imitation is specifically characterized by a shared neuromarker in both model and imitator. This correlate was not present in the induced context and the region implicated was similar to those implicated in the inter-brain synchronizations emerging during interactional synchrony, namely the right parietal areas. In the same way as Hasson and colleagues showed a strong anatomo-functional similarity across humans immersed in the same perceptual context

(Hasson et al., 2004), these two results reflect an anatomo-functional similarity during reciprocal perception-action coupling, but here at the millisecond scale. This also strongly assesses the key role of right parietal area as a functional hub for our interaction with the others and supports theories which claim that it could subserve the function of agency (Decety and Sommerville, 2003).

Furthermore, on the behavioral level, these shared brain dynamics demonstrate the possibility to objectively measure the “co-ownership of action” that emerges between interactants through interactional synchrony. This co-ownership possibly underlies the active construction of a common ground between the interactants. This shared space has been reported by several participants. Indeed, the interviews with participants following the experiments have revealed that despite using only intransitive movements without any meaning, they tended to associate sense to certain gestures. This active creation of meaning as been reported in psychology as the phenomenon of participatory sense-making (De Jaegher and Di Paolo, 2007). The participants create endogenously through their interaction symbolic gestures which for instance indicate the turn-taking, like infants who use microcodes to propose role switching (Eckerman and Peterman, 2001). Further analysis at the behavioral level could uncover this correlation between occurrences of specific gestural patterns and turn-taking. Automatic video indexing could provide the technical tools towards such analysis and facilitate the objective characterization of behavioral parameters.

6.1.3 Neurocomputational modeling of social interaction

Numerical simulations were done in order to model our experimental observations. They were designed for uncovering the different factors of inter-brain synchronizations and their relationships with endogenous oscillatory dynamics of the individual brain. Cognitive science has demonstrated the human brain ability not only to integrate but also to coordinate information at multiple scales in space and time (Le Van Quyen, 2011). Brain complexity guarantees a balance between local specificity and connectivity, between functional segregation and integration (Tononi and Edelman, 1998). However, how information generated by multiple brain areas is integrated and coordinated across the brain is still a matter of debate. Several mechanisms have been proposed, including neural phase synchronization, which is based on the fact that brain information processing relies strongly on oscillatory activity (Varela et al., 2001; Uhlhaas et al., 2009). The observation of neural phase synchronizations between two separate brains support this hypothesis by demonstrating a link between the phase of brain oscillations and the shared information between people at multiple

level during social interaction.

Following the recent growing interests in whole brain modeling (Izhikevich and Edelman, 2008; Jirsa et al., 2010) and fine grained structural connectivity analysis (Sporns et al., 2005; Hagmann et al., 2007), we combined a real connectivity dataset of the human brain, the so-called "human connectome", with the Kuramoto model of weakly coupled oscillators. The oscillators represented the local gamma oscillatory dynamics of each brain regions. The coupling between each pair of oscillators was proportional to the number of neural fiber tracts linking their related regions. This model has already proposed underlying mechanisms of the Default Mode Network through simulations of the dynamics of resting states (Honey et al., 2009). Here the design allowed to test anatomical and neurodynamical hypotheses not only at individual brain level but also at the inter-individual level by creating artificially a perception-action coupling between two copies of the "virtual brain" (Jirsa et al., 2010).

Results assess specific properties of the human brain anatomical structure. At the individual level, it confirms its faculty to enhance the "synchronizability" between distant brain regions and thus facilitates the integration of information (Bullmore and Sporns, 2009). Meanwhile, the global structure makes emerge low-frequency rhythms that interfere with the high-frequency ones because of the conduction delays in the couplings between distant brain regions (Jirsa et al., 2010). The competition between the two dynamics creates a transition where metastable properties emerge (Rubinov et al., 2011; Kitzbichler et al., 2009). This is coherent with observations in physics regarding similar topologies of networks (Boccaletti et al., 2006) but also with neurophysiological studies that bear witness to the presence of metastability in the brain (Werner, 2007).

At the inter-individual level, the simulations demonstrated another property of the anatomical structure of the human brain: while favoring the complexity of endogenous dynamics, simultaneously it allows an easier coupling with other systems sharing this structure (ie. other human beings). Open questions remain however regarding the strong anatomical-functional similarities observed between humans and their potential links with our social abilities. For instance, to what extent could alterations of the distributed neural networks that underlie sensory-motor couplings between self and others lead to dynamic perturbations and cause social disturbances?

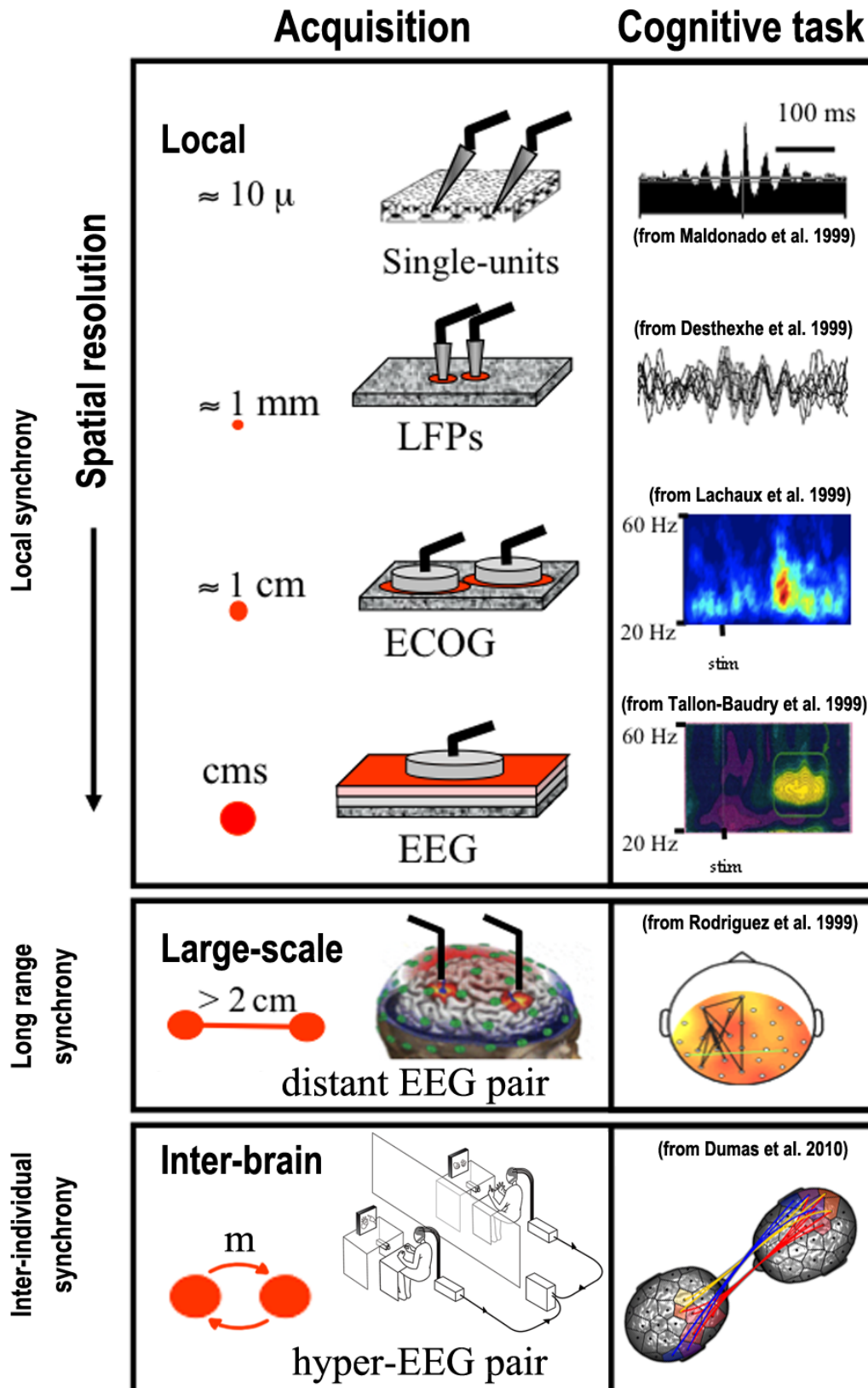


Figure 6.3: The multiple scales of synchrony. Local scale has three levels of analysis: single units, local field potential (LFP) and ECoG/EEG. At larger scale, long range synchrony could be observed between distant brain regions. At the inter-individual scale, neural synchronization could emerge between different brains through reciprocal social interaction. (adapted from Varela et al. 2001)

6.2 Perspectives

Beyond this work, a fundamental question remains: to what extent do neural synchronizations play an active functional role in social interaction? Inter-brain synchronizations may facilitate the transmission of information between two interacting brains in a similar fashion than synchronization within a single brain mediate communication between various brain regions (Fries, 2005). Experimental results were purely correlative and thus no causal conclusion could be stated. Furthermore, the content of the information conveyed by the inter-brain synchronization remains unclear for the moment. Here I will present two perspectives likely to allow going a step further than the present results do. A first perspective is a neurodynamical approach of autism which could provide a test-bed for both tackling the role of structure and dynamics in inter-brain synchronization and their link with social interaction. A second perspective will concern the problem of multi-scale synchronizations and attempt to tackle the question of how are neural, behavioral and social factors coordinated in real time so as to make possible the emergence of social cognition.

6.2.1 Dynamical approach of autism

Among social developmental dysfunctions, autism is certainly the most studied. Developmental psychopathology has already uncovered a wide range of behavioral peculiarities of persons with autism. Although numerous accounts of the autistic brain have attempted to demonstrate links between behavioral specificities and anatomical (Brambilla et al., 2003; Barnea-Goraly et al., 2004; McAlonan et al., 2005) or functional (Just et al., 2004, 2007; Wilson et al., 2007) differences, a precise unified theory of autism is missing, partly due to the heterogeneity of the syndrome, but also related to the complexity of the links between brain, mind and behavior. Hyperscanning techniques could provide a powerful tool for the investigation of those multiple levels. Neurocomputational models similar to the one presented in this thesis could support the experimental studies in a more systematic manner. For instance, it is possible to quantify how the differences in anatomical connectivity in autistic brains could impact their ability to enter in dynamical resonance with others. We thus planned to use connectivity datasets from brains of people with autism with the simulated brains and apply our previous analysis. Such simple test could give fruitful information on how distributed brain modifications could affect sociocognitive functions.

According to some previous studies, the dynamics observed via EEG show dissociations compared to healthy subjects. This is especially true for rolandic rhythms, also called Mu that are in the motor cortex and in the frequency band between 8 and 12 Hertz. These rhythms classically decrease during execution, imagination or observation of a movement. In the case of people with autism, this reduction is not observed or at least diminished (Oberman et al., 2005, 2008). It was suggested that this difference reflects a dysfunction of the mirror system, however, no theoretical demonstration is available today and the "broken mirror" hypothesis is debated (Southgate et al., 2008; Dinstein et al., 2010). Our main hypothesis is that there are brain markers of social interaction in these oscillatory phenomena at the interpersonal as well as at the intrapersonal level. For the study of communicative synchrony, this study seeks to go beyond the now classic paradigm of mirror neurons by incorporating a dimension of coupling between the subjects. For this we will use the EEG-hyperscanning setup for recording coupled two subjects during an interactive task of imitation. In this new paradigm, it is expected that the different behavioral parameters of imitation can highlight different aspects of autistic brain and behavior. Given the results on the involvement of electrophysiological frequency bands and mu alpha-beta in motor activities and social coordination, it is expected that changing the context of imitation will be accompanied by changes in these frequency bands. But knowing the characteristics of autism spectrum is a deficit on lowering mu, it is expected that a differentiation with the "neurotypical" control subjects will be found on these oscillatory activities at both individual and inter-individual levels.

The experiment has just started recently. Compared to the first one, the main difference is the use of two 64 electrodes helmets and a new protocol. This greater spatial resolution will allow to apply source reconstruction methods and better confront our results to those of structural and functional MRI. Furthermore, some amelioration has been made on the setting and apparatus. Now the two experimental rooms have been covered with black fabrics in order to have exactly the same neutral background. More than assessing an enhanced symmetry between the subjects, it will allow to test automatic algorithms for the analysis of the video since the only not-black elements are now the hands of the participants. All the instructions are now prerecorded and given through the TV monitor during the experiment. The whole setup is fully controlled by a unique computer. We also take the advantage of conducting this new study for doing a control condition which lacked in the first experiment. In this new condition the subjects are doing the same movements

without interacting. These could be easily done by the joint imitation of a third person. While doing it in real-time is an option, we opted for a prerecorded video. Indeed, it provides exactly the same imitation across the whole participants and thus guarantee a better control. Meanwhile, this gives access to a great averaging across the group in a similar fashion to the Hasson study on natural visual perception. However here, this averaging is extended to a full perception-action context. Having the same stereotyped sensorimotor entrainment in all subject should also provide the needed stability at the behavioral level to investigate causality and even cross-frequency relationships between signals. Furthermore, as we use prerecording, it will allow to shift the videos in time for one subject compared to the other and analyze the effect of delay on the inter-brain synchronization level.

By the use of neurofeedback it is now possible to modify specific brain rhythms with the appropriate training. Such approaches applied to the Mu rhythms have already shown results in people with autism (Pineda et al., 2008; Coben et al., 2010; Kouijzer et al., 2010). Whereas it is not part of our new experiment, future investigations will potentially integrate the joint use of neurofeedback and virtual reality. Indeed, persons with autism have been reported to appreciate virtual characters and Kelso's team have developed a Virtual Partner Interaction (VPI) technology allowing a dynamical interaction with a simulated agent. The combination of neurofeedback and VPI could provide a simultaneous effect on both behavioral and neural dynamics. Although autism could not be considered as a "dynamical disease" (Mackey and Milton, 1987) per se, adopting such integrative strategy can extend or complement existing therapeutic approaches.

6.2.2 Multi-scale coordination dynamics

How are neural, behavioral and social factors coordinated in real time so as to make possible the emergence of social cognition? Cognitive neuroscience and psychology have been facing this question for years. Social neuroscience has pointed out the limits of strictly cognitive approaches and started to study the dynamics of coordination in real human interactions. However, even at the simplest dyadic scale, methodological and theoretical challenges remain (Tognoli et al., 2010). Several theories have been proposed to infer the link between neurobiology and social psychology (Gallese et al., 2004), however the dynamical components of human interaction are still poorly explored. Adopting a full integrative approach remains a major challenge (Adolphs, 2003).

Mirror Neuron System (MNS) theory has failed until now to explain how to disentangle the self from the other, and how coordination dynamics emerges between both (Schilbach, 2010). If the Hebbian perspective of social cognition proposed by Keysers and Perrett (Keysers and Perrett, 2004) suggests a more dynamical alternative to the ontogeny of mirror features, further conceptual jumps remain to be performed. We have seen in this thesis how through the combined use of hyperscanning and embodied social paradigms, the multi-scale study of social interaction can be addressed in an operational manner. However, additional tools are necessary. Indeed we need a conceptual framework and a formalism that encompasses neural, behavioral and social levels.

Growing evidence suggests that complex systems form an ideal framework to build up a unifying theory of cognition. One striking phenomenon is that coordination dynamics at neurobiological, behavioral and social levels present similarities. Although these observations have been reported, they still need to be integrated in an effective model allows grasping their potential universal laws. The work of Kelso and his team has concentrated for years on the elaboration of "coordination dynamics" in that perspective (Fuchs and Jirsa, 2008). They have already included the hyperscanning techniques in their neuroimaging panoply (Tognoli et al., 2007), but they have yet to exploit at the inter-brain level the full benefit of simultaneously recording two brains. It would be interesting to analyze the relationships between neuromarkers at the individual brain level and inter-brain measurement. Such investigation of the links between intra- and inter-brain synchronizations could help in the understanding of integration~segregation, one of the key complementarity pairs of coordination dynamics (Kelso and Engstrøm, 2006).

Capturing the multi-scale levels of coordination dynamics should thus not only shed new light on social interaction, but also provide useful insights into how and why our nervous system has the ability to massively integrate information, thereby giving rise to human cognition. The human brain itself disposes of multiple levels of organization. Neuroscience disposes of large datasets describing these levels in both space and time. It has demonstrated that its activity relies on entangled anatomical and functional networks interacting at multiple frequencies and on different spatial scales (Le Van Quyen, 2011). Synchronizations are one of the most pervasive dynamical phenomena occurring in this brainweb. They show how small-scale interactions can make emerge large-scale patterns in an upward causation. On the other hand, these large-scale patterns can re-influence the small-scale interactions that generated them. This "downward causation" is at play at multiple scales in the brain (see Figure 6.4 A). Cross-frequency analyses (Jensen and Colgin, 2007) are promising toward a better investigation of its link with cognitive functions.

Similar modulations of neurocognitive networks exist at greater timescale than the millisecond (Bressler and Tognoli 2006, see Figure 6.4 B). Social interaction could play an active role in these modulations noticeably during development where a radical cortical neuroplasticity occurs (Allen and Williams, 2011). Cultural influence illustrates also this phenomenon with the neural recycling of cortical structures (Dehaene and Cohen, 2007; Vogeley and Roepstorff, 2009). Both social interaction and cultural influence should be seen as downward causality since they influence cognitive agents from outer.

This thesis stressed the interplay between individuals engaged in social interaction. While there is yet no direct results related to causal relationships, it has demonstrated the existence of functional correlations between behavioral and neural dynamical states at the inter-individual level. Furthermore, the neurocomputational model has demonstrated the influence of structural constraints on human brain dynamics but also on its facilitating role towards the sensorimotor coupling with other conspecifics. Future studies will focus on non-linear methods for quantifying the potential downward causation from dyadic to individual parameters.

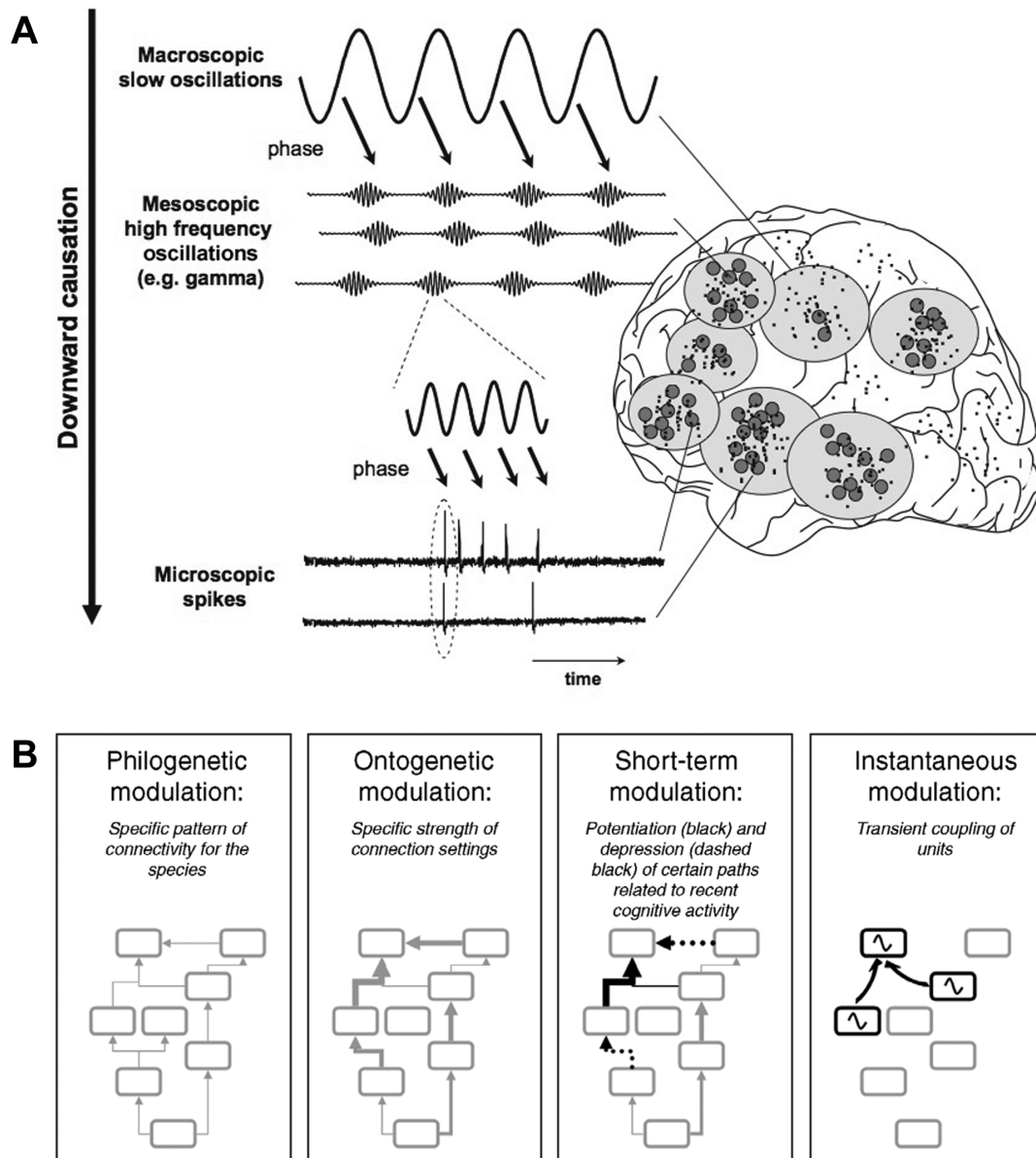


Figure 6.4: The brain across space and time. A) The macro-, meso- and micro-scopic processes are braided together by co-occurring oscillations at successively faster frequencies that modulate each other by variations of the underlying neuronal excitability. In particular, through their phases, global brain oscillations in the low-frequency range (< 4 Hz) may constrain local oscillations in the high-frequency range (40–200 Hz, e.g. gamma oscillations). In turn, these high-frequency oscillations determine, in the millisecond range, the probability of occurrence of spikes and of their temporal coincidences between different brain regions. (adapted from Le Van Quyen 2011). B) Modulation of the neurocognitive network. The basic pattern of anatomical connectivity is determined by evolution of the species (phylogenetic modulation). This anatomical pattern undergoes maturational and experience-dependent modulation over the life span (ontogenetic modulation). The anatomical patterning may undergo synaptic modulation on a short time scale of seconds to minutes with respect to cognitive factors such as emotion, attention, and working memory (short-term modulation). Sub-second modulation occurs by the transient coordination of neuronal assembly activity (instantaneous modulation). (adapted from Bressler and Tognoli 2006).

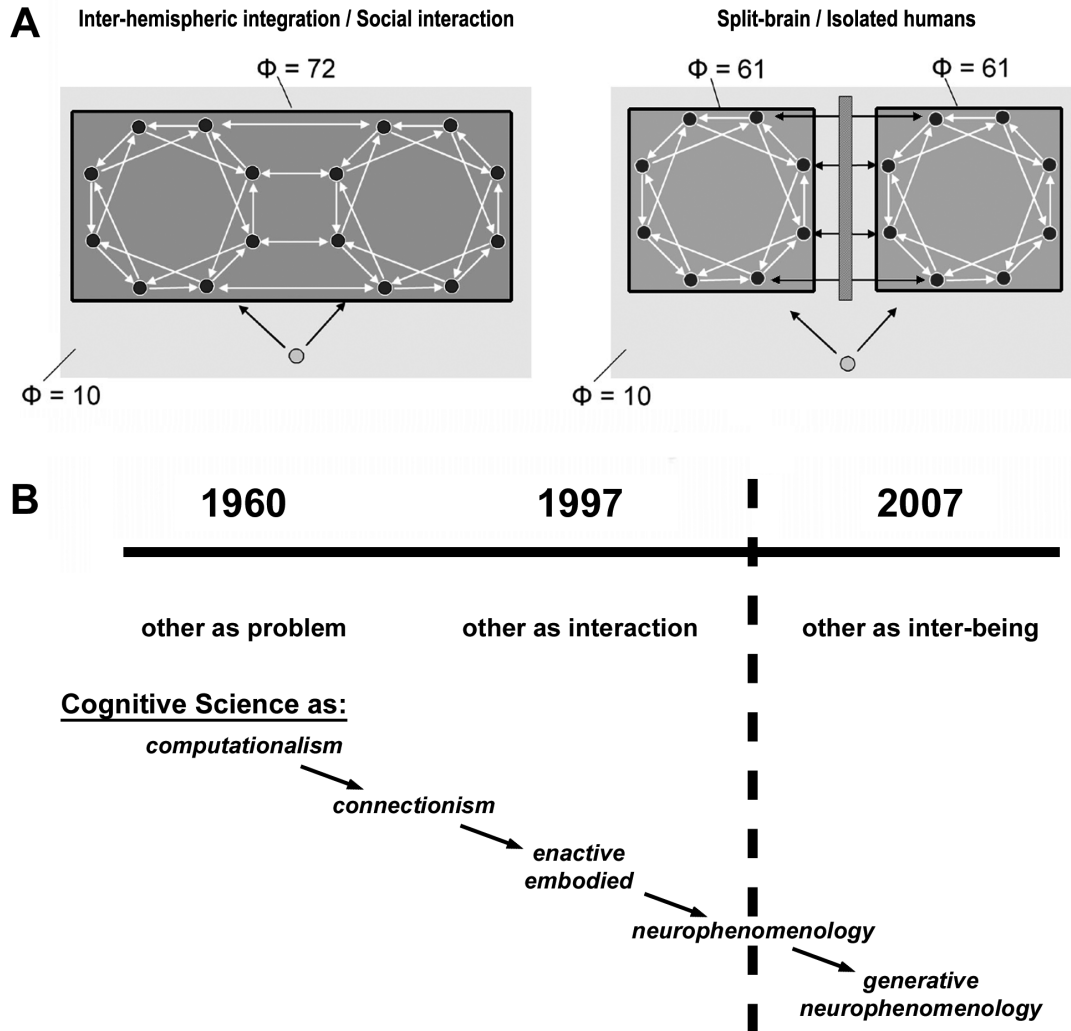


Figure 6.5: Beyond individual cognition. A) Information integration and complexes: schematic of a split-brain-like anatomical disconnection and analogy with social interaction. The figure on the left shows the large main complex obtained by connecting two thalamocortical-like subsets (or individual brains) through "callosum-like" reciprocal connections (or social interaction). The figure on the right shows the same system if "callosum-like" connections are cut, one obtains two 8-element complexes, corresponding to the two "hemispheres" (or isolated brains). (adapted from Tononi 2004). B) Toward a science of interbeing. Francisco Varela's sketch of the story of cognitive sciences and their further development in relation to the issue of others and the integration of phenomenology. (adapted from Varela 2000)

6.3 Beyond individual consciousness

From a theoretical standpoint, the investigation of inter-brain relationships questions also the link between objective measures and behaviors. The vast problem behind neuroimaging is often expressed in the study of consciousness where the neural correlates of consciousness cannot be disentangled from consciousness itself (Chalmers, 2007). This strongly questions the whole field and new alternatives may emerge for escaping the brain/mind dualism (Schilbach, 2010). Extending the definition of consciousness (Thompson, 2007; Allen and Williams, 2011) is one possible way to escape the semantic boundaries (Korzybski, 1933) constraining our understanding of this complex phenomenon.

Recent studies have demonstrated that a form of collective intelligence can be measured (Ernst, 2010; Woolley et al., 2010; Bahrami et al., 2010). Theoretical approaches such as the Integrated Information Theory proposed by Tononi (Tononi, 2008; Balduzzi and Tononi, 2008) give rise to a novel kind of formalism of consciousness that could go beyond a classical individual consciousness and could be extended to a social group (see Figure 6.5 A). This announces for the coming years a renewed interest in cognitive science for the concept of “collective consciousness” designed by Durkheim more than a century ago (Durkheim, 1997). Hence, in addition to offering another take at the “hard problem”, nascent two-body neuroscience also has the potential to reshape our existing definitions of consciousness itself.

I wish upcoming experimental results will better emphasize the intersubjective and empathic openness of human mind (Thompson, 2001). This is a long-standing issue in cognitive science (Varela 2000, see Figure 6.5 B) and as the progress of this field is intimately linked to the understanding of our own humanity (Varela, 1999a; Naccache, 2010), developing an “ego-less” perspective of cognition should potentially participate in the development of a more humane society.

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Appendix



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IRBM xxx (2011) xxx–xxx

Original article

From social behaviour to brain synchronization: Review and perspectives in hyperscanning

De la synchronisation comportementale à la synchronisation cérébrale : état de l'art et perspectives en hyperscanning

G. Dumas^{a,b,c,1}, F. Lachat^{a,*,b,c,1}, J. Martinerie^{a,b,c}, J. Nadel^d, N. George^{a,b,c}

^a UMR-S975, centre de recherche de l'institut du cerveau et de la moelle épinière, université Pierre-et-Marie-Curie-Paris 6, Paris, France

^b CNRS, UMR 7225, CRICM, hôpital de la Salpêtrière, 47, boulevard de l'Hôpital, 75651 Paris cedex 13, France

^c Inserm U 975, CRICM, Paris, France

^d CNRS, USR 3246, centre émotion, pavillon Clérambault, hôpital de La Salpêtrière, Paris, France

Received 8 November 2010; received in revised form 4 January 2011; accepted 9 January 2011

Abstract

Recently, the neuroscience field took a particular interest in the use of a neuroimaging technique called 'hyperscanning'. This new technique consists in the simultaneous recording of the hemodynamic or neuroelectric activities of multiple subjects. Behind this small technical step lays a giant methodological leap. Groundbreaking insight in the understanding of social cognition shall be achieved if the right paradigms are implemented. A growing number of studies demonstrate the potential of this recent technique. In this paper, we will focus on current issues and future perspectives of brain studies using hyperscanning. We will also add to this review two studies initiated by Line Garnero. These studies will illustrate the promising possibilities offered by hyperscanning through two different key phenomena pertaining to social interaction: gesture imitation and joint attention.

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Keywords: Hyperscanning; Synchronization; Spontaneous imitation; Joint attention; Gaze; EEG

Résumé

Récemment, un intérêt particulier a été porté à l'utilisation d'une technique de neuro-imagerie appelée *hyperscanning*. Cette nouvelle technique consiste en l'enregistrement simultané de l'activité hémodynamique ou neuroélectrique de plusieurs sujets. Derrière ce petit pas technique se cache un grand pas méthodologique. Il peut nous conduire à une meilleure compréhension de la cognition sociale si toutefois les bons paradigmes expérimentaux sont développés. Le nombre croissant d'études utilisant l'*hyperscanning* démontre le potentiel de cette technique. Dans cet article, nous traiterons à la fois de son récent historique mais surtout des futurs potentiels qu'elle ouvre. Nous illustrerons cela par deux réalisations en *hyperscanning* dont Line Garnero a été l'instigatrice. Ces réalisations serviront d'exemple pour montrer les possibilités prometteuses par l'*hyperscanning* au travers de deux phénomènes clés dans les interactions sociales: l'imitation gestuelle et les comportements de regard en attention conjointe.

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Mots clés : *Hyperscanning* ; Synchronisation ; Imitation spontanée ; Attention conjointe ; Regard ; EEG

1. From behaviour synchronization. . .

"The most important things in human life come down to relationships with other people," says Michael Huerta (associate director of Neuroscience and Basic behavioural science at the National Institute of Mental Health). Our actions, feelings,

* Corresponding author.

E-mail address: fanny.lachat@upmc.fr (F. Lachat).

¹ Contributed equally to this work.

and thoughts take place in a social world where communicating with others is an everyday challenge. Wilson and Wilson [1] theorised on a particular type of interindividual interaction: conversation. According to the authors, during conversation, several oscillators in the brain of the listener are led by some oscillators of the speaker's brain. In this oscillatory interplay, the two brains become synchronized. Even though the authors based their model on conversation properties, the idea of inter-brain synchronization can be generalized to any social situation, which generates coordination between partners. This paper especially takes interest in two phenomena that entail behaviour synchronization: gesture imitation and gaze following.

Gesture imitation has been pointed out as a keystone of human social interaction because of the ability it gives us to know others as persons like ourselves [2,3]. Pragmatically, the matching of our own behaviour with that of others allows us to detect contingencies in our social world. This enables us to synchronize with others, copy them, and learn in which context particular behaviours have to be used [4,5]. Growing evidence at the developmental [6], psychological, and neuroscientific levels indicates that perception and action are in fact intertwined processes. The recent discovery of mirror neurons provides a direct demonstration of this overlap between perception and action networks. Furthermore this discovery also puts in light the major role of this overlap in motor imitation. However, imitation is only related to morphological similarities of gestures. Thus it is not the only component of motor social interaction. Behavioural synchrony complements imitation during interindividual interaction by providing a temporal coherence between the interacting partners. Developmental studies have demonstrated a very early ability to detect interactive synchrony in humans: the introduction of a delay in the loop of interaction between a baby and his/her mother leads to a breakdown of the ongoing communication [7,8].

These results suggest an intrinsic human capacity for perceiving and producing events in synchrony with other individuals. Immediate imitation is an almost perfect example of interactive synchrony [6]. It was suggested that the dynamics of neuronal coupling plays a role in the emergence of such synchrony, providing a neural substrate for interpersonal exchanges and synchronizations among individuals at the behavioural level [1]. The modelling approach further suggests that the phenomenon of turn-taking may emerge from the synchrony itself [9,10].

Thus, spontaneous gestural imitation is an ideal case for the study of behavioural synchrony and its neuronal correlates. It possesses all the features of social interaction and leads to phases of behavioural synchronies. Furthermore, it is mainly a motor interaction. In comparison with a verbal interaction, the hypothesized underlying interindividual neural synchronization should be easier to detect.

Other types of interindividual interactions may generate such neural synchronizations. For instance, gaze following is a key example of behavioural synchronization in everyday life. Interestingly, it is easier for humans than other species to follow the eye direction of their conspecifics. Indeed, the human eyes have evolved to allow perceiving clearly the contrast between the (white) sclera and the (darker) iris. This facilitates the detec-

tion of someone's eyes and more importantly it makes it easier and faster to identify the direction of the gaze of seen fellows [11,12]. Gaze direction subtends referential communication and synchronization during interindividual exchanges. For example, during conversation, gaze contributes to speech understanding as well as to the organization of turn-taking with eye contact enabling the converses to be coordinated and synchronized [13].

Furthermore, eye direction perception is a core process of joint attention, which is a fulcrum of social cognition. Joint attention results from the alignment of an observer's attention with that of a seen fellow, enabling both persons to attend to the same external object [14–16]. This behavioural synchronization is crucial to social interaction as it subtends the understanding of others' attentional focus and intention. Joint attention is proposed to be one of the precursors of Theory Of Mind (TOM) [17]. TOM is the skill to attribute mental states to others and to understand that their beliefs, emotions, intentions, desires might differ from our own. This ability is essential for understanding others and for adaptive communication and interaction with others. We believe that engaging in joint attention processes prompt coordinated actions between the participants, which might lead to interindividual neural synchronizations.

In sum, both gestural imitation and joint attention involve another partner with whom a non-verbal, interpersonal communication is established. They provide good ecological paradigms for the study of human social interaction. Combined with the use of a new neuroimaging technique called hyperscanning, they also open the way for the investigation of interindividual neural synchronizations that might accompany behavioural synchronies. This brain-to-brain synchronization emerges from the sensorimotor couplings created through the social interactions.

2. . . .to brain synchronization

Almost nothing is known about the brain activities of two individuals while those individuals are engaged in a social interaction. Recently, a new technique made possible for researchers to record at the same time two persons engaging in an interpersonal exchange. This technique is called hyperscanning and has been applied with fMRI and EEG. Hyperscanning is a very powerful method as it makes possible to perform within- as well as between-brain analyses.

The hyperscanning story starts with an uncanny use of the technique. Indeed, this technique was first applied to parapsychology issues [18,19]. The main purpose of these studies was to investigate telepathy, namely the brain information transmission between isolated participants. The conclusions were highly suspicious. In a small number of cases, the brain activity of one person was reported to correlate with that of a partner localised in another room without any communication device linking the two participants. Many commentaries questioned these idiosyncratic results. They pointed out that the positive results obtained were most likely attributable to some dynamical similarity between the two brains engaged in the same perceptual context rather than to an effective transmission of information.

A small number of studies used hyperscanning in the interest of investigating the brain activities of participants committed into social interaction. The first exploratory experiment of Montague et al. [20] paved the way for the use of hyperscanning. These authors recorded with fMRI the brain activities of two participants engaging through a video link in the game of “handy dandy”, a guessing game in which a participant has to presume the location of an object hidden by the other participant. King-Casas et al. [21] used hyperscanning in participants playing a multiround trust game of economic exchange. The authors found that response magnitude correlated with the “intention of trust” in the caudate nucleus. They also found a temporal transfer of the intention of trust in cross- and within-brain correlations. This response timing was similar to a reward prediction but, for the first time, it was observed in the context of a social exchange. Babiloni et al. [22] were the first to use hyperscanning with EEG. They recorded the brain activities of participants playing prisoner’s dilemma. They found that the most consistently activated region during this type of interaction was the medial prefrontal cortex. In 2009, the same group of authors [23] reported a similar study but this time, they found that the orbital frontal cortex was the region that was most involved in such competitive interaction. In another study, Babiloni et al. [24] made a quartet of participants play a card game and recorded the players’ brain activities with EEG hyperscanning. They found that, before playing the card in response, the companion of the first player develops a brain activity in the right prefrontal and parietal areas, which is correlated with that of the first player. Babiloni et al. also reported a larger activity in prefrontal and anterior cingulate cortices for the player who starts the game as compared to the other players. Yun et al. [25] used the ultimatum game to probe decision making in two participants whose neural activities were recorded with EEG hyperscanning. The results demonstrated that “high frequency oscillations of frontocentral regions of the brain are closely related to the social interaction”. They also proved that the information flow of these regions correlated with decision making in both participants. Lindenberg et al. [26] used EEG hyperscanning on pairs of guitar players. The authors demonstrated that coordinated actions, such as playing guitar or even just listening to a metronome, are preceded and come with between-brains oscillatory couplings. Tognoli et al. [27] used EEG hyperscanning in participants who were instructed to perform a rhythmic finger movement with or without the vision of the other participant’s movement. The authors observed that when participant could see each other they coordinate their behaviour. More interestingly, they discovered a particular oscillatory component (ϕ complex) that either favored independent movement (ϕ_1) or to the contrary favored behavioural synchronization (ϕ_2). Anders et al. [28] were interested in the facial communication of affects between love partners. They found that the sender’s and the receiver’s brains activate the same neural regions during the communication of emotion. The receiver’s neural activations can be predicted from those of the sender. The authors also found a temporal succession of the flow of affective information from the sender’s brain to the receiver’s brain. Moreover, they showed a progressive tuning of this flow while the exper-

iment was in progress. This is a neurophysiological illustration of the social resonance found in behavioural studies [29,30] and raises new questions on how such neurobehavioural resonance emerges.

These studies have used hyperscanning to solve different questions, but their common denominator is the investigation of neuronal activities in participants involved in social interaction.

It is important to note that other studies did not use hyperscanning *per se* as they did not record simultaneously two participants. Nevertheless, these studies used neuroimaging across multiple participants and look at relationships between their brain activities. In an fMRI study, Hasson et al. [31] recorded the brain activities of participants watching the same part of a movie. Even though they recorded isolated participants, they found a strong functional and anatomical similarity across the individuals who were immersed in the same natural settings. In another fMRI study, Schippers et al. [32] recorded separately the brain responses of the guesser and the gesturer during a social game, namely a game of charade. They found that the guesser’s the brain regions involved in mentalizing and mirroring are temporally synchronized with the gesturers’ brain. Stephens et al. [33] scanned the brain of a speaker reciting a monologue. Then, they scanned the brain of a participant listening to the speaker’s monologue. The authors found temporal and spatial coupling between the speaker’s and the listener’s brains during the monologue. The three above-mentioned studies could not catch up the emergent properties of a mutual and live interaction between subjects since they did not record the subjects simultaneously. Moreover, there was no real social presence involved. By contrast, rather than giving access to the activities of each actor individually, hyperscanning – which involves recording the activities of multiple individual’s brains simultaneously – makes possible the investigation of the effects of actions on several actors at the same time. This opens an avenue to the study of interbrain relationships. Moreover, hyperscanning paradigms lead to more ecological procedures: participants are immersed in a common environmental setting and real-time reciprocal interactions can be achieved in a laboratory context [34].

With these concerns in mind, we built up hyperscanning paradigms where the electrical brain activities of two participants were recorded at the same time while these participants were involved in a reciprocal social interaction.

3. Ongoing programs

Our research group has always been participating in pioneering methodological trends in the neuroimaging community. In this line, Line Garnerio initiated a collaborative reflection on how to set up a hyperscanning facility on the site of the Hôpital Pitié-Salpêtrière.

The idea of a hyperscanning facility emerged initially during meetings involving our neuroimaging group and psychologists from the “Centre émotion” (CNRS USR 3246). The evocation of the neural synchronization elicited a conceptual analogy with behavioural synchrony. This gave a starting point for collaborations between the two research groups. The initial objective was

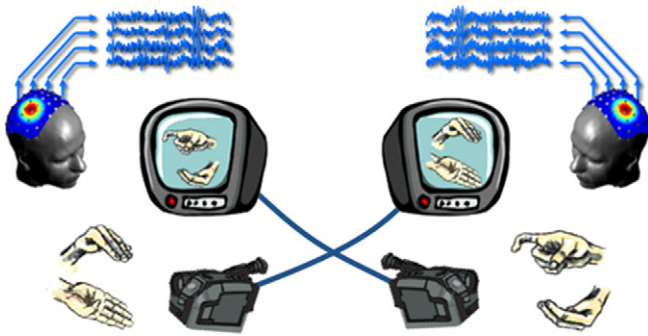


Fig. 1. Brain-to-brain communication experimental setup. Each participant sees the other through a dual-video system. The two EEG helmets are synchronized together and with the video cameras.

to combine knowledge of the two fields toward the creation of an experimental paradigm in order to test the hypothetical link between behavioural and neural synchronization. Spontaneous gesture imitation was chosen as the basic task. Interestingly, the developmental psychologists' group had already developed a "behavioural hyperscanning setup" by simultaneously video recording two participants engaged in social interaction [7]. Two EEG helmets were added and synchronized to this setup in order to also record neuroelectric activity in both participants. This formed the initial hyperscanning facility. Later on, based on other previous reflections in our group regarding social attention driven by gaze [35], the idea grew up to use this hyperscanning facility for the study of joint attention. Thus, two studies have been conducted under the leadership of Line Garnero. Both of them aim at bridging the gap between neural and behavioural synchronization. They will also allow the comparison of the interindividual neural synchronizations in two different social contexts.

In the first study [36], the purpose of the experiment was mainly to test the existence of a neurodynamical phenomenon associated with the behavioural synchrony. In order to test this hypothesis, we recorded 22 participants paired by sex and age in 11 dyads, during spontaneous exchanges of intransitive bi-manual movements (Fig. 1).

We used a fine grain behavioural analysis thanks to a revised version of the ELAN software [37,38]. By a frame-by-frame analysis we were able to extract separately periods of imitation and behavioural synchrony: imitation was assessed when the two partners showed similar morphology and similar direction in their hand movements, behavioural synchrony was assessed when both participants started and ended their movements simultaneously (within the same video frame). This behavioural analysis showed first that participants prefer to imitate each other than to act separately. Moreover, even if they were not engaged in imitation – thus not executing the same movements – they were most of the time in behavioural synchrony.

By the use of a non-linear measure called Phase Locking Value (PLV) [39], we were able to exhibit the emergence of an interindividual brain-web across several frequency bands when the participants were engaged in these synchronous exchanges (Fig. 2). These interbrain synchronizations were directly related to the sensorimotor information flowing through the two interac-

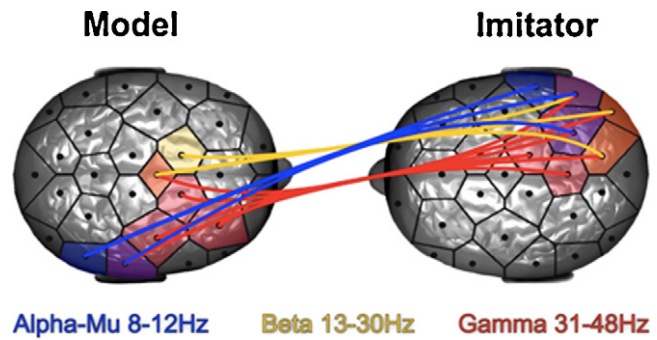


Fig. 2. Interbrain neural synchronizations during interactional synchrony. Adapted from Dumas et al. [32]. The links represent statistical increases of neural synchronization across the subjects when they are engaged in interactional synchrony. Notice the symmetric pattern in the low frequency band that become asymmetric in the highest ones.

tants. Interestingly, this interbrain network was symmetric in the lowest frequency bands and became asymmetric for the highest frequency bands. This could reflect the different levels of information processing from the low-level coding of movements to the higher-level coding of the social roles (model/imitator).

The positive results of this experiment validated technically the hyperscanning facility and demonstrated the feasibility of detecting between-brains synchronization during social interaction. Furthermore, this is the first neuroimaging program to study real spontaneous and reciprocal interactions. This reveals the strong potential offered by scanning two brains at the same time because such real-time spontaneous interactions could not be reproduced artificially first for one subject and later on for the other participant, as it would have to be done in classical neuroimaging paradigms. It demonstrates the possibility to move paradigmatically from a one-body to a two-body neuroscience.

The second study used the same EEG hyperscanning setup adapted to a paradigm of joint attention. In this study, the two participants of each pair were in the same experimental room and faced each other. A pierced wooden board with four light-emitting diodes (LEDs) was placed in between them so that they could see each other through the board hole as well as gaze at the LEDs. This setup enables us to record the brain activities of the two participants in three different stages of gaze communication: eye contact, joint attention (when both participants look at the same LED) or "anti-joint attention" (when each participant looks at a different LED) (Fig. 3).

We expect that joint attention and mutual gaze induce synchronization between parts of the brain both intra- and interindividually. We also assume that the brain synchronization between the partners will be more important during joint than anti-joint attention periods. To date, 16 couples of participants (32 participants for individual analyses) took part in the experiment. We are currently beginning the first stages of the analyses. First, we are going to evaluate the temporal dynamics of joint attention in the brain. Second, we aim at analysing the variations in brain synchronizations between the participants according to the different tasks. We expect that interbrain synchronization during joint relative to anti-joint attention conditions might occur in the gamma band, which is known to play a crucial

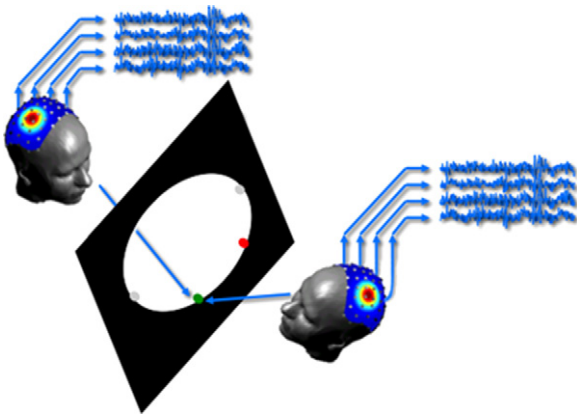


Fig. 3. Dual gaze experimental setup. Each participant seats face-to-face with the other; the wooden device is placed in between them. Both participants can see the LEDs attached to the border of the hole, and they can see each other through the hole. The participants move their eyes either to the same lighted up LEDs (joint attention, presented here) or to different LEDs (anti-joint attention).

role in gaze perception [40]. This innovative research program should help understanding the mechanism of joint attention in a real face-to-face situation while retaining the advantages of a laboratory-based task. We thus offer a new paradigm to shed light on the intra- and interbrain synchronization mechanisms occurring during joint attention.

4. Conclusion

More and more studies try to take a real look into ecological experimental settings. Some authors plead for cognitive ethology, meaning an observation of what happens in real life or at least creating situations that simulate the real world [41]. Scientific researches desperately need to get more and more real. Bringing the daily life into the lab is clearly a challenge for the next years [34] and more especially in the field of social neuroscience. In continuity with what was started under the direction of Line Garnero, our studies pursue this goal. These studies are compromises between the rigorous constraints of the scientific methods and the ecological needs of realistic tasks. We believe that they make a step further in the investigation of behaviour and brain synchronization during social interaction.

Conflict of interest statement

Nothing to declared.

Acknowledgment

The authors want to thank particularly Robert Soussignan and Laurence Conty who are actively implicated respectively in the first and the second programs. Both programs are technically possible thanks to the work and patience of Laurent Hugueville. We are grateful to Florence Bouchet for her help and expertise during the EEG recordings. They all have spent a lot of time with Line Garnero and are part of this tribute.

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Towards a two-body neuroscience

Guillaume Dumas

Cognitive Neuroscience and Brain Imaging Laboratory; Center for Research of the Institute of the Brain and of the Spinal Cord (CRICM);
Hôpital de la Salpêtrière; Paris, France

Recent work from our interdisciplinary research group has revealed the emergence of inter-brain synchronization across multiple frequency bands during social interaction.¹ Our findings result from the close collaboration between experts who study neural dynamics and developmental psychology. The initial aim of the collaboration was to combine knowledge from these two fields in order to move from a classical one-brain neuroscience towards a novel two-body approach. A new technique called hyperscanning has made it possible to study the neural activity of two individuals simultaneously. However, this advanced methodology was not sufficient in itself. What remained to be found was a way to promote real-time reciprocal social interaction between two individuals during brain recording and analyze the neural and behavioral phenomenon from an inter-individual perspective. Approaches used in infancy research to study nonverbal communication and coordination, between a mother and her child for example, have so far been poorly applied to neuroimaging experiments. We thus adapted an ecological two-body experiment inspired by the use of spontaneous imitation in preverbal infants. Numerous methodological and theoretical problems had to be overcome, ranging from the choice of a common time-unit for behavioral and brain recordings to the creation of algorithms for data processing between distant brain regions in different brains. This article will discuss the underlying issues and perspectives involved in elucidating the pathway from individual to social theories of cognition.

Is Neuroscience One-Brain Bound?

The major focus in neuroscience remains the isolated brain whereby hypotheses are drawn about the neurophysiologic mechanisms underlying our socio-cognitive abilities. Such “stand-alone” or “self-sufficient” approach to brain dynamics is in-line with early computational cognitive sciences inherited from information theory. The later connectionist approach, however, introduced a more dynamic and holistic perspective.

While Gibsonian theories pointed out the importance of the environment in cognition, only a small community of neuroscientists moved away from the “one brain-bound” perspective inscribed in the computer metaphor. For instance, sensorimotor theories of cognition such as enaction² and dynamical system approaches³⁻⁵ have started to show that the dynamical coupling of cognitive agents with their environment is an inherent part of the cognitive mechanisms.⁶ Indeed, the structure of the organism and the perception-action loops with the surrounding environment create statistical regularities that shape the information structure of the nervous system.⁷ Thus, perception of the world is seen as an exploratory process that cannot be reduced to merely an internal representation or reconstruction of the world.⁸ For instance, perception of space relies on intertwined neural spatial maps and motor functional networks.⁹ As Husserl proposed: “Our way to perceive space seems not to be given but rather built up by the experience of exploring the space itself.”¹⁰ Moreover, this perception

Key words: social neuroscience, developmental psychology, hyperscanning, non-linear dynamics, synchrony, top-down control, interpersonal coordination, consciousness

Submitted: 02/09/11

Accepted: 02/09/11

DOI: 10.4161/cib.4.3.15110

Correspondence to: Guillaume Dumas;
Email: guillaume.dumas@upmc.fr

Addendum to: Dumas G, Nadel J, Soussignan R, Martinerie J, Garnero L. Inter-brain synchronization during social interaction. *PLoS One* 2010; 5:278-88. PMID: 20808907; DOI: 10.1371/journal.pone.0012166.

varies between organisms according to the intrinsic properties of their body, including their sensory organs.¹¹

Similarly, in spite of our cultural propensity to interact with others, our ability to socialize is neither a given nor fixed once and for all. Development provides numerous examples of transitory adaptations to both the physical and social environment. For instance, several studies have shown that imitation is crucial for infants to communicate before verbal language.¹² Later, our daily life interactions even start before any words have been pronounced: before they even speak to each other, people look at each other and try to guess what each other's moods are from their facial expressions, posture and movements. Now imagine two adults who can not speak to each other, who can see only each other's hands via a double video system, and who are told to move their hands and imitate whenever they feel like it: will they come back to this nonverbal imitative method as used by young children? Will they imitate each other and take turns as imitator and model? In addition to successfully demonstrating that they do this, our experimental design provided simultaneous dual recordings of their brain activity.¹ However, the question still remains, how should we relate the brain recordings of the two partners and what can such data tell us?

A Neurodynamic Approach to Social Interactions

The human brain not only integrates but coordinates information at multiple scales in space and time.⁵ The brain's complexity guarantees a balance between local specificity and connectivity, between functional segregation and integration.¹³ However, how information generated by multiple brain areas is integrated and coordinated across the brain is still a matter of debate. Several mechanisms have been proposed, including neural phase synchronization, which is based on the fact that brain information processing relies strongly on oscillatory activity.¹⁴⁻¹⁶ The Phase Locking Value (PLV) is a practical method for the quantification of neural synchronization between two neuroelectric signals in a specific frequency band.¹⁷

The fact that the perception-action loops of the two participants were intertwined in our experiment leads us to hypothesize that neural synchronizations, as measured by PLV, may exist between their two brains during periods in which the two subjects imitated one another reciprocally. Rather than using the classical PLV used to measure synchrony in the individual brain, we measured synchrony between two separated brains using a hyper-phase locking value (h-PLV). What can this h-PLV measure?

First, it is important to notice that despite inter-individual variability, the first hyperscanning studies done in fMRI have demonstrated strong anatomical and functional similarities between different human brains embedded in the same natural perceptual context.¹⁸ However, these similarities were observed at the timescale of seconds. In the case of reciprocal imitation, in which we used in our experiment, both perceptual and motor contexts are shared between the two participants on a milliseconds timescale. Taking into account that the phases of oscillatory activity in both sensory and motor areas have been linked to low-level information such as visual motion¹⁹ or hand velocity,²⁰ in the case of reciprocal imitation, this low-level sensory-motor information has to flow inside and between the two brains (see Fig. 1A). Thus, the h-PLV could reflect information being dynamically shared through an interindividual sensory-motor loop. These loops emerge from a bi-directional coupling between the participants, with the behavior of each one influencing the other's behavior, and inter-brain synchronizations reflecting their perception-action entanglement. This synchronization may facilitate the transmission of information between two interacting brains in a similar fashion to synchronization within a single brain mediating communication between various brain regions.^{14,15}

Interestingly, this dynamical phenomenon is purely emergent and asymmetric (see Fig. 1B). It cannot be reduced to the activities of each brain taken separately and is not only caused by the similarity of action and perception of the two players. Although previous studies have cued the subjects to make movements

synchronously,²¹ in our study both participants movements converge through a mutual coordination to the state of interactional synchrony. "Turn-taking" is another emergent phenomena that can be observed during these real-time reciprocal interactions. Interestingly, the alternation roles between model and imitator cannot be integrally tackled through classically-induced contexts and one-brain recordings. Although we observed "turn-taking" during the experiment, the real-time constraints prevented us from investigating neural dynamics potentially linked to this phenomenon. It shows the extreme complexity of creating balanced paradigms that permit both real reciprocal interactions while providing sufficient control over specific emergent behaviors. Further hyperscanning studies should find well-designed experiments that can provide innovative ways to tackle such transient dynamics, which are strongly linked to inter-individual coordination.

Open questions also remain regarding the strong anatomical-functional similarities observed between humans¹⁸ and their potential links with our social abilities. For instance, to what extent could alterations of the distributed neural networks that underlie sensorimotor couplings between self and others lead to dynamic perturbations and cause social disturbances? If the Hebbian perspective of social cognition proposed by Keyzers and Perrett²² suggests a more dynamical alternative to the classical mirror hypothesis, further conceptual jumps remain to be performed. For example, most approaches of the neural basis of social cognition adopt a symmetrical standpoint from which the brain activities of one person are either mirroring, or simulating, others actions and thoughts. The hyperscanning methodology could help develop paradigms that also capture the inherent asymmetries between people interacting, a phenomenon that remains unexplored.

Beyond Individual Consciousness?

We have seen that moving from a one-brain to a two-body perspective provides both new methodological and theoretical

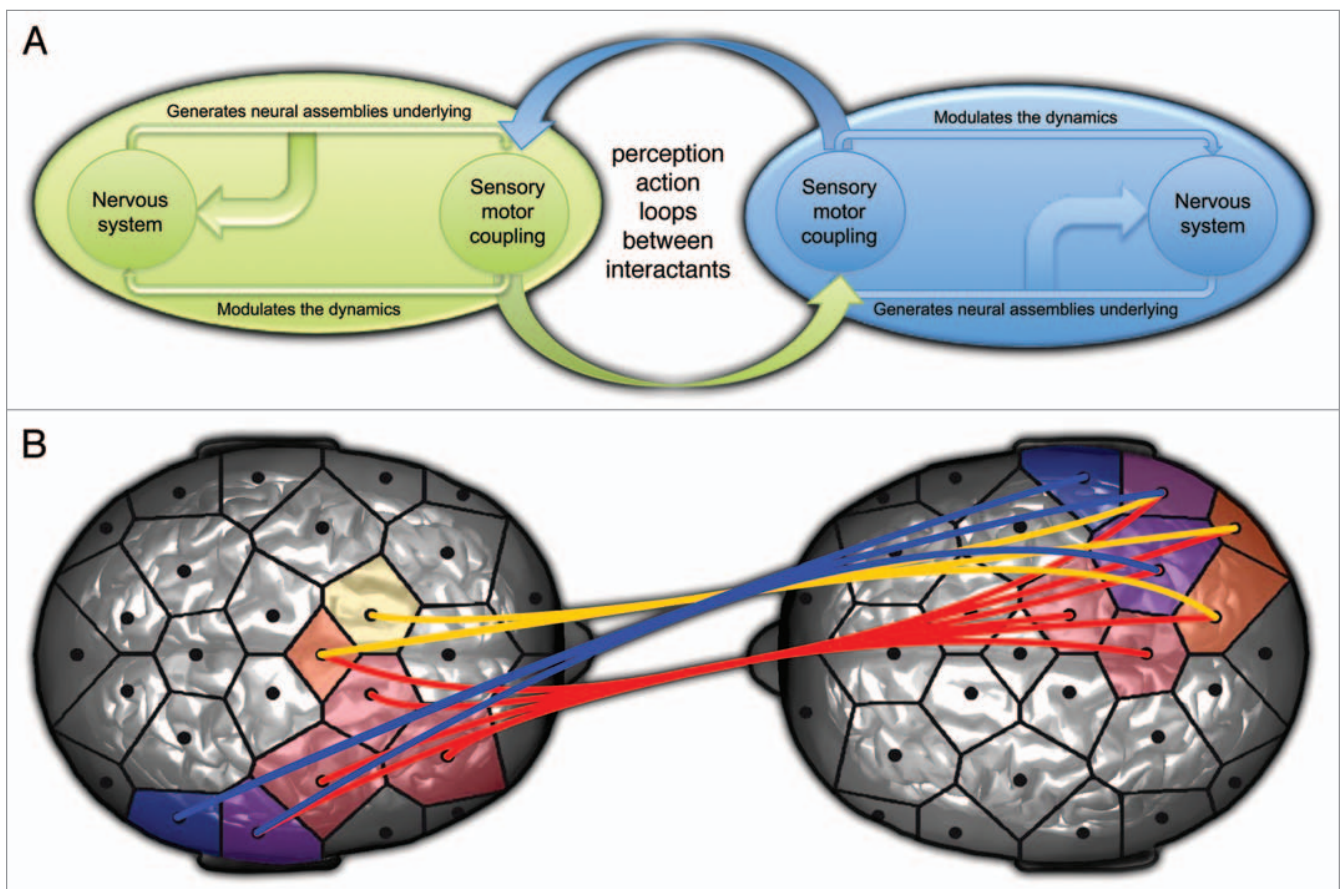


Figure 1. (A) Schematic view of dyadic social interaction taken as a dynamical sensorimotor coupling. Inspired by Le Van Quyen, 2001. (B) Inter-brain synchronization in alpha (blue), beta (orange) and gamma (red) frequency bands related to interactional synchrony during spontaneous imitation of hand movements. Inspired by Dumas et al. 2010.

spaces where neuroscience can tackle everyday reciprocal social interactions.^{23,24} But this shift can do more than answering this issue and providing new tools, it may also allow us to address entirely new questions. For instance, key issues such as the influence of structural constraints on dynamics can, for instance, be tackled at both the behavioral and the neural level throughout development so as to better understand how they are intertwined. The opportunity to record two individuals interacting could also give new observations towards the study of multiscale dynamics and discover general laws governing complex systems and their interactions.

From a theoretical standpoint, the investigation of inter-brain relationships questions also the link between objective measures and behaviors. The vast problem behind neuroimaging is often

expressed in the study of consciousness where the neural correlates of consciousness can not be disentangled from consciousness itself.²⁵ This strongly questions the whole field and new alternatives may emerge for escaping this dualism²⁶ and extending the definition of consciousness.²⁷ For instance, recent studies have demonstrated that a form of collective intelligence can be measured.²⁸⁻³⁰ Theoretical approaches such as the Integrated Information Theory proposed by Tononi³¹ give also rise to a novel kind of formalism of consciousness and be extended to a social group. This announces for the coming years a renewed interest in cognitive science for the concept of “collective consciousness” designed by Durkheim more than a century ago.³² Hence, in addition to offering another take at the “hard problem”, nascent two-body neuroscience also has

the potential to reshape our existing definitions of consciousness itself.

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A.3 Written communications

A.3.1 Peer reviewed publications

Brain to brain communication via synchronous imitative interaction

PLoS ONE 2010

Dumas G, Nadel J, Soussignan R, Martinerie J and Garnero L

Imitation et synchronie, les bases du développement social chez l'enfant

Metiers de la Petite Enfance 2010

Dumas G

From social behaviour to brain synchronization: review and perspectives in Hyperscanning

IRBM 2011

Dumas G, F. Lachat, Martinerie J, Nadel J, George N

Towards a two-body neuroscience

Communication, Integrative Biology 2011

Dumas G

Magnetoencephalographic signatures of visual form, motion binding

Brain research 2011

Aissani C, Cottureau B, **Dumas G**, Paradis A-L, Lorenceau J

A.3.2 Submitted publications

Distinct brain dynamics underlie self- and other-ascription of action primacy during reciprocal imitation

Dumas G, Martinerie J, Soussignan R, Nadel J

Modeling the impact of the human brain connectivity on individual and inter-individual neural dynamics

Dumas G, Chavez M, Nadel J, Martinerie J

A.4 Oral communications

A.4.1 Posters

Entangled brains: toward an enactive approach of social cognition through hyperscanning

16th Annual Meeting of the Organization for Human Brain Mapping 2010, Barcelona, Spain

Dumas G, Martinerie J, Nadel J, Soussignan R, Chavez M, Garnero L

Bringing real life in the laboratory: EEG hyperscanning of joint attention

Cognitive Neuroscience Society Meeting 2010, Montreal, Canada

Lachat F, Conty L, Hugelville L, **Dumas G**, Martinerie J, George N

Entangled brains: toward an enactive approach of social cognition through hyperscanning

Riken BSI Summer School, Tokyo, Japan

Dumas G, Martinerie J, Nadel J, Soussignan R, Chavez M, Garnero L

A.4.2 Oral presentation

Entangled brains: toward an enactive approach of social cognition through hyperscanning
Riken BSI Summer School, Tokyo, Japan

Coupled human connectomes exhibit variety of dynamical properties
Les Houches Physics School : Data driven dynamical networks

Going from one-brain to two-body neuroscience
Hyperscanning seminar, Paris

Quand les cerveaux battent en rythme: synchronisation dual-EEG et dual-vidéo
French Cognitive Engineering Symposium, Marseilles

Vers une neuroscience à deux corps
Phiteco seminar on Technological otherness, Compiègne
Séminaire du Laboratoire de Psychology Cognitive, Marseilles

Toward a two-body neuroscience: Inter-brain synchronization during social interaction
Pr Vogeley's team, Zentrum für Neurology und Psychiatry, Uniklinik Köln, Germany
Laboratoire de Génétique humaine et Fonctions cognitives, Institut Pasteur, Paris

A.5 Technical contributions

Hyperscanning acquisition platform

This part was done in collaboration with Laurent Hugueville, research engineer at Cogimage.

- adaptation of the initial dual-video system of Pierre Canet, technician at the Centre Emotion
- synchronization between the dual-video and dual-EEG acquisition
- automatic audio instructions, video presentation and DV acquisition (Linux shell)

Hyperscanning software toolkit

This part was used in the studies presented in the thesis and for Fanny Lachat hyperscanning experiment.

- interface to the behavioral analysis files generated with ELAN (Matlab)
- interface to the manual artifacts annotations files made with EEG Vue (Matlab)
- adaptive thresholded artifact correction with PCA (Matlab)
- advanced preprocessing and signal analysis pipelines (Matlab, Linux shell)
- optic flow analysis of the behavioral videos (Matlab)

Neurocomputational simulation framework (Matlab)

This part was used in the third paper presented in this thesis.

- Kuramoto model integration
- support of graph topology (non-euclidean)
- GPU integration

Universal non-parametric clustering algorithm (Matlab)

This part was used in all the studies presented in the thesis and in Aissani et al. (2011).

- adaptive to the data dimensions
- multiple thresholding mode: fixed, parametric, non-parametric
- support of univariate and bivariate measurements
- support bipartite graph topology
- interface to non-parametric statistics scripts

Contribution to the Brainstorm Matlab toolbox

- update of group anatomy registration algorithm with a non-linear algorithm
- automatic anatomical labeling of sources (CPU & GPU)

Information about the toolbox in Tadel et al. (2011) or at neuroimage.usc.edu/brainstorm/

Dynamiques neuronales de l'interaction imitative synchrone

Depuis 2002, une nouvelle technique de neuroimagerie appelée hyperscanning permet l'enregistrement de plusieurs participants simultanément. Que cela soit en imagerie à résonance magnétique fonctionnelle (IRMf) ou en électroencéphalographie (EEG), cette nouvelle méthode ouvre la voie à des paradigmes plus adaptés à l'étude de l'interaction sociale. Parallèlement, les approches neurodynamique et sensorimotrice ont suggéré d'appréhender l'interaction sociale de manière plus holistique en considérant les deux individus en interaction comme un seul système, et en donnant autant d'importance au comportement qu'à l'activité neurale des deux cerveaux séparés. Toutefois enregistrer deux individus simultanément n'est pas suffisant : il est également nécessaire que leur interaction réciproque soit dans un cadre social spontané. De plus, l'analyse comportementale doit être suffisamment fine pour pouvoir être combinée à une analyse neurodynamique.

Cette thèse présente une étude dynamique de l'interaction sociale utilisant l'hyperscanning. Dix-huit participants répartis en 9 dyades ont été enregistrés simultanément, lors d'imitations spontanées du mouvement de leurs mains, par un système de double-vidéo combiné à un dispositif d'hyperscanning-EEG. Une analyse comportementale fine de leurs interactions a permis de procéder à une caractérisation neurodynamique des différents aspects de l'interaction, à la fois à l'échelle inter- et intra-individuelle. La première étude s'est concentrée sur les mesures inter-cerveaux relative à l'interaction synchrone. Un réseau fonctionnel inter-cerveaux a été mis en évidence dans la bande alpha-mu entre les régions centro-pariétales des deux partenaires. Dans les rythmes de plus haute fréquence, ce réseau inter-cérébral se déplace entre les régions plus antérieures du modèle et plus postérieures de l'imitateur. La seconde étude s'est concentrée sur l'analyse intra-individuelle chez le modèle et l'imitateur de l'attribution de l'origine de l'action. Une différenciation entre l'agentivité attribuée à soi ou à l'autre fut observée dans les bandes delta, alpha-mu et bêta. Un marqueur dans la bande gamma a également été découvert dans le cas de l'imitation spontanée. Il est présent chez les deux partenaires simultanément et traduit leur co-appropriation de l'action pendant l'interaction. La troisième étude propose enfin des simulations biophysiques de paires de cerveaux humains au repos ou lors d'un couplage perception-action. Ces simulations numériques utilisent une version modifiée du modèle de Kuramoto et intègrent des données réelles de connectivité anatomique issues de l'imagerie à tenseur de diffusion. Les signaux générés furent comparés aux enregistrements hyperscanning à l'aide de la technique du problème direct. Les résultats valident les mesures expérimentales et montrent également certains effets de la connectivité anatomique sur les dynamiques neuronales intra-individuelles, ainsi que sa facilitation du couplage inter-cerveaux.

