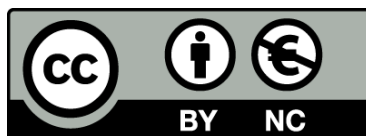




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## Neurophysiological correlates underlying social behavioural adjustment of conformity

Unai Vicente Guirado



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BARCELONA

# **Neurophysiological correlates underlying social behavioural adjustment of conformity**

Unai Vicente Guirado

Supervised by: Dr. Josep Marco-Pallarés & Dr. María Palacín Lois

Department of Cognition, Development and Educational Psychology, University of  
Barcelona

PhD program in  
Brain, Cognition and Behaviour  
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To those who choose to inspire.

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Prometo que seré breve.

Una tesis cambia a una persona, exige esfuerzo y sacrificio como nada que uno haya hecho antes, e invariablemente obliga a sobreponerse a evaluaciones constantes sobre si ese coste sigue mereciendo la pena. Encontrarte cara a cara con tus demonios, tus inseguridades, enfrentarte a tus miedos y a tus fracasos del presente y del pasado hacen que el resultado más relevante de un proceso de este calibre sea precisamente el cambio que este produce en uno mismo. Es un proceso solitario, desafiante, agotador y desesperante por momentos, lo que hace que su consecución este acompañado de una enorme felicidad y un profundo cambio. Llegado este momento, me siento increíblemente afortunado por haber tenido la oportunidad de acabar con este proceso y siento privilegio de poder mirar hacia adelante. He tenido la gran suerte de acompañarme de personas que me han hecho más fácil sobrepasar límites y dificultades. Cuando era pequeño, gracias a un CD-ROM enciclopédico que venía de regalo con mi primer ordenador me obsesioné con Leonardo Da Vinci, y creo que esa admiración por lo que hizo inspiró profundamente y para siempre mi curiosidad por resolver problemas. Más tarde, cuando estudiaba la carrera siempre tuve ganas de dedicarme a investigar, aunque siempre tuve la creencia de que no estaba a mi alcance, de que era algo reservado para gente de clase privilegiada, y las nulas posibilidades que me proporcionaba el estado no hacían más que confirmar mis creencias. He tenido que esperar más de una década para poder pagarme esta oportunidad. ¡Que le den al sistema! Si se trata de perseguir tus sueños a veces es necesario crear tus propias reglas.

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# 1. Abstract

## 1.1. English version

Conformity is the act of changing one's behaviour to adjust to other human beings. It is a crucial social adaptation that happens when people cooperate, where one sacrifices their own perception, expectations, or beliefs to reach convergence with another person. The aim of the present study was to increase the understanding of the neurophysiological underpinnings regarding the social behavioural adjustment of conformity. We start by introducing cooperation and how it is ingrained in human behaviour. Then we explore the different processes that the brain requires for the social behavioural adjustment of conformity. To engage in this social adaptation, a person needs a self-referenced learning mechanism based on a predictive model that helps them track the prediction errors from unexpected events. Also, the brain uses its monitoring and control systems to encode different value functions used in action selection. The use of different learning models in neuroscience, such as reinforcement learning (RL) algorithms, has been a success story identifying learning systems by means of the mapped activity of different regions in the brain. Importantly, experimental paradigms which has been used to study conformity have not been based in a social interaction setting and, hence, the results, cannot be used to explain an inherently social phenomenon.

The main goal of the present thesis is to study the neurophysiological mechanisms underlying the social behavioural adjustment of conformity and its modulation with repeated interaction. To reach this goal, we have first designed a new experimental task where conformity appears spontaneously between two persons and in a reiterative way. This design exposes learning acquisition processes, which require iterative loops, as well as other cognitive control mechanisms such as feedback processing, value-based decision making and attention. The first study shows that people who previously cooperate increase their level of convergence and report a significantly more satisfying overall experience. In addition, participants learning on their counterparts' behaviour can be explained using a RL algorithm as opposed to when they do not have previously cooperated. In the second study, we have studied the event-related potentials (ERP) and oscillatory power underlying conformity. ERP results show different levels of cognitive engagement that are associated to distinct levels of conformity. Also, time-frequency analysis shows evidence in theta, alpha and beta related to different functions such as cognitive control, attention and, also, reward processing, supporting the idea that convergence between dyads acts as a social reward. Finally, in the third study, we explored the intra- and inter-oscillatory connectivity between electrodes related to behavioural convergence. In intra-brain oscillatory connectivity coherence, we have found two different dynamics related to attention and executive functions in alpha. Also, we have found that the learning about peer's behaviour as computed using a RL is mediated by theta oscillatory connectivity. Consequently, combined evidence from Study 2 and Study 3 suggests that both cognitive control and learning computations happening in the social behavioural adaptation of conformity are signalled in theta frequency band.

The present work is one of the first studies describing, with credible evidence, that conformity, when this occurs willingly and spontaneously rather than induced, engages different brain activity underlying reward-guided learning, cognitive control, and attention.

## 1.2. Spanish version

La conformidad es el acto de cambiar el comportamiento de uno a favor de ajustarnos a otros seres humanos. Se trata de una adaptación crucial que ocurre cuando la gente coopera, donde uno sacrifica su propia percepción, expectativas o creencias en aras de conseguir una convergencia con la otra persona. El objetivo del presente estudio ha sido tratar de aportar a la comprensión de las estructuras neurofisiológicas que soportan un ajuste social como el de la conformidad. En la primera parte de esta tesis comenzamos hablando de la cooperación y lo profundamente arraigada que está en nuestro comportamiento. Más tarde exploramos diferentes procesos que el cerebro requiere en el ajuste social de la conformidad. Así pues, para involucrarse en esta adaptación social, una persona requiere de un mecanismo de aprendizaje auto-referenciado basado en un modelo predictivo que le ayude a seguir el rastro de los errores de predicción que acompañan a los eventos inesperados. Además, el cerebro usa sus sistemas de control y predicción para codificar diferentes funciones de valor usadas en la selección de acción. El uso de diferentes modelos de aprendizaje en neurociencia, como los algoritmos de aprendizaje por refuerzo (RL), han sido una historia de éxito a la hora de identificar los sistemas de aprendizaje a través del mapeo de la actividad de diferentes regiones del cerebro. Es importante destacar que los paradigmas experimentales que se han usado para estudiar la conformidad no se han basado en entornos de interacción social y que, por lo tanto, sus resultados no pueden usarse para explicar un fenómeno inherentemente social.

El objetivo principal de la presente tesis es el estudio de los mecanismos neurofisiológicos que fundamentan el comportamiento de ajuste social de la conformidad y su modulación con la interacción repetida. Para alcanzar este objetivo, primero hemos diseñado una nueva tarea experimental en la que la conformidad aparece de forma espontánea entre dos personas y, además, de forma reiterativa. Este diseño permite exponer tanto los procesos de adquisición del aprendizaje, que requieren de ciclos iterativos, así como otros mecanismos de control cognitivo tales como el procesamiento de la retroalimentación, las tomas de decisiones basadas en procesos valorativos y la atención. El primer estudio nos muestra que la gente que coopera previamente incrementa sus niveles de convergencia y reportan significativamente una experiencia generalmente más satisfactoria en el experimento. Adicionalmente, un modelo de RL nos explica que los participantes tratan de aprender del comportamiento de sus parejas en mayor medida si estos han cooperado previamente. En el segundo estudio, hemos estudiado los potenciales relacionados con eventos (ERP) y el poder de las oscilaciones que sustentan la conformidad. Los estudios de ERP muestran diferentes niveles de implicación cognitiva asociados con diferentes niveles de conformidad. Además, los análisis de tiempo-frecuencia muestran evidencia en theta, alfa y beta relacionados con diferentes funciones como el control cognitivo, la atención, y, también, el procesamiento de la recompensa, apoyando la idea de que la convergencia entre díadas actúa como una recompensa social. Finalmente, en el tercer estudio, exploramos la conectividad oscilatoria intra e inter entre electrodos que se pudieran relacionar con la conducta de convergencia. A propósito de la conectividad oscilatoria coherente intra, hemos hallado dos dinámicas relacionadas con la atención y las funciones ejecutivas en alfa. Asimismo, hemos encontrado que el aprendizaje de la conducta de la pareja computada a través de RL está mediada a través de la conectividad oscilatoria de theta. Consecuentemente, la evidencia combinada entre el estudio 2 y el estudio 3 sugiere que conjuntamente el control cognitivo y las computaciones de aprendizaje que ocurren en la conducta de adaptación social de la conformidad están relacionadas con la actividad de la banda de frecuencia theta.

Este trabajo constituye uno de los primeros estudios que describen, con evidencia creíble, que la conformidad, cuando ocurre voluntaria y espontáneamente a diferencia cuando esta es inducida, involucra actividad del cerebro que se fundamenta en el aprendizaje guiado por reforzamiento, el control cognitivo y la atención.





## 2. Introduction

## 2.1. What is Cooperation?

Evolutionary biology and palaeontology claim modern humans, as well as its ancestor species, have been a gregarious species since the earliest genus of this and the other great ape lineages. In 1859, Charles Darwin introduced a revolutionary idea (Darwin, 1859) which proposed that individual organisms fitting the best to an environment and its characteristics, are the ones suited to survive and have offspring. Consequently, because these individuals will have a higher probability of surviving and mating, this genetic advantage will gradually become the commonality in a species under a certain environmental context. This proposal is known as natural selection.

The scientific discussion around this Darwinist concept led to question on how the best average fitness in a population manages to achieve an optimal success rate probability. At the end, the biological goal of a species is no other than to adapt to keep the race of survival in a presumably volatile, limitedly resourced, and hostile environment, so they can precisely increase the rate of success of their descendant generation and avoid extinction. One of such adaptations is precisely becoming social to seek strength in numbers. But, if biology builds the foundation of cooperation under the reason of offspring, how is that humans organize themselves towards this goal?

Here, as philosopher David Hume (1738) suggested, we confront research under a problem of induction, as we ourselves are the agents as well as the objects of observation. Because of that, this is a question that will open multiple perspectives of study as well as different conceptualizations that will take to a diverse and unessential understanding of cooperation. According to this philosopher, humans are greedy but, at the same time, they possess a disposition to kindness, specially directed towards friends, kin and, to lesser extent, to strangers. Even when this dichotomy exists and all these are behaviours present in our portfolio, which one is more definitory? Hume thinks human natural drives and dispositions are to some extent also the genesis of moral requirements. In other words, our virtues are as natural as products of our own convention, making us complex beings who can act loving and selfishly with the same extent of normality. Therefore, a governing entity would be, in Hume's view, particularly useful and legitimate, as it represents, through a duty to submit, a reason to preserve order and society.

Years before Hume, Thomas Hobbes (1651) stated men should have a guided executor that would lead the way to an organisational structure because, as he wrote, the condition of men is "*a condition of war of everyone against everyone*". However, this conceptualization of "*someone external favouring our will and freedom*", as Rousseau (1762) wrote, could only work favouring cooperation in a condition of *deus ex machina* (Taylor, 1976; 1987) as the organizing entity of the state might acquire, in the execution of the role, all the human flaws. As Hume defined, humans are kind but also mean, and this, as inherent as definitory as it is, stays when humans govern other humans.

Therefore, the essence of cooperation inspires the mechanistic of politics as a collateral to social architecture, a need that this *two-faced* nature imposes to humans to lean the balance towards preserving common interest. Similarly, as it has also been suggested (Olson, 1965), the larger the group the less likely it will further its common interest. Thus, classically, humans are considered to fundamentally fail to contain their selfish nature in

society and, hence, they need of other superior instances to maintain duty above selfish behaviours.

However, this conceptualization assumes every human decision leans towards a side of the balance by a cost-benefits relationship, but this is a rather simplistic and unrealistic (Taylor, 1987). The choice of cooperation is based on diversely weighted incentives, preferences, or indifferences together with costs and benefits. All these different factors make cooperation a preferred and highly favoured choice regardless of its rational justification.

At the end, it is safe to say cooperation is inherent to the human's behaviour as we are defined social by choice the same as by design. In the next section we will make an introductory and multidisciplinary approximation on the different perspectives on the concept of cooperation.

### 2.1.1. The evolutionary anomaly of Cooperation

Cooperation is a crucial and interesting phenomenon, as it is not always the optimal choice regarding one's interests or instincts. However, from a purely rational point of view, it might be difficult to explain why humans willingly decide to go against their beliefs or their surviving logic and why they sacrifice interests or at times their most fundamental drives, to favour cooperation. Importantly, cooperation in humans is so decisive and constitutes a basis to our organization, but it is not an exclusive human attribute. Indeed, from cellular bonding to social organization in other non-human species, cooperation is an extensively common mechanism in nature.

Diverse fields of research have tried to conceptualize cooperation from different perspectives to understand why organisms engage in behaviours that might apparently go contrary to what natural selection would suggest. One of the first attempts to tackling this question happened in the field of evolutionary biology and genetics, with the proposal of the *inclusive fitness theory* (Hamilton, 1964). This theory states that an altruistic act from an individual which pushes the survival of the other, enhances their genetic fitness. This idea has been used to explain behaviour of eusocial organisms (such as social insects) as well as other cooperative breeding in some vertebrate species (Bourke, 2011). Essentially, cooperation is considered an inclusive fitness effect of a social trait influenced by direct (reproductive) and indirect (aided by a neighbour, a relative or a member of a colony or community) components (note that, under this perspective, fitness is a property that defines the probability to have offspring). However, this theory is not without controversy. Some authors (Nowak, Tarnita and Wilson, 2010) have proposed a mathematical model which claims to demonstrate that the evolution of behaviours of altruistically helping others at some cost is not correlated with relatedness. Anyhow, this critique has also been questioned by other authors (Bourke, 2011; Liao, Rong, Queller, 2015) suggesting that, even with this concern, the theory still has an important predictability power.

In terms of cost-benefit trade-off (focussing on the cost of the individual for the benefit of another), the idea of cooperation goes straight against the natural selection. In the words of Martin Nowak (Nowak, 2006) "*Cooperation means that selfish replicators forgo some of their reproductive potential to help one another*", which attending to the competitive justification of evolution would constitute an anomaly. In fact, according to this consideration, we can identify two roles by the types of action choices an individual takes towards a collective. First, the co-operators, who lose for the gain of others, and then, the defectors, who gain for the loss of others. In this rationale, it might seem reasonable to suggest that, when natural selection operates and all the evolutionary efforts focus on getting the maximum gain or survival options, co-operators might theoretically rapidly vanish from population. However, evidence (Nowak, 2006) suggests a population of only co-operators has the maximum average fitness, understanding fitness as the equilibrium between cost and benefit for the members of the system. In other words, individualistic tendencies decrease the fitness of a population's optimal resource allocation. In contrast, in systems in which participants have mixed priorities, the drive to cooperate might end up being vanished before having the chance to flourish.

However, the reason why this argument might sound overly pessimistic might be in part because it relies on a rather simplistic approach to the concept of cooperation. The amount



of cooperation and the type of cooperation is dependent on multiple variables which have been widely described such as reciprocity, reward, punishment, limited dispersal, kin discrimination, status... (West, Griffin and Gardner, 2007). There is even evidence that the distribution of shared values and beliefs by a collective and the number of strategic behaviours of the members of a particular group in a certain environment affects the preferences for cooperation. In this sense, even the relative exposition to the behaviour of a selfish minority might alter the tendencies of most fair-minded people to behave selfishly (Fehr and Schmidt, 1999).

Based on a more predominantly biologic approach and understanding of the concept, direct reciprocity (Axelrod and Hamilton, 1981), as well as other indirect types of reciprocity related to more complex social rewards (such as context preserving reasons or benevolence that leads to an increased chance of receiving help from others, Riolo, Cohen and Axelrod, 2001), constitute a powerful force for change in the evolution of the Darwinist approach based on individual advantage. However, as stated before, reciprocity only considers the cost-benefits relationship, which might not apply as straightforwardly to human cooperation compared to other species. In addition, it has been described how human decision-making influenced by a social interaction is highly focused on finding reciprocity through the valuation of fair or unfair cues (Sanfey et al., 2003).

Game theory is based in the study of mathematical models that intent to predict the strategic interactions executed by rational agents. This paradigm has been used in many different areas, from biology to cognitive and social sciences, computer sciences, logic, or economics. In the field of biology, one of the most interesting applications to this paradigm belong to the application of game theory to evolution (Smith, 1972; Axelrod and Hamilton, 1981) which arise with concepts such as the *evolutionarily stable strategy* that explains how a population reaches to a certain *Nash equilibrium*, through different processes of population refining, so *ceteris paribus* (all other things equal), natural selection alone is sufficient to prevent apparently “mutant” strategies to take over. At the end, among the benefits sought by living organisms, game theory shows that cooperative groups have these benefits disproportionately available. In other words, game theory allows to understand that among the different strategic possibilities, cooperation can lead to a win-win equilibrium in the long-term but is a losing strategy when players are destined to never meet again (Axelrod and Hamilton, 1981). However, in real life, the likelihood that two living organisms meet again is high, and it is even higher in the case of humans. In conclusion, game theory applied to evolution shows that human cooperation, rationally speaking, is an evolutionarily advanced behaviour to follow. Importantly, the game theory framework has not only been important in evolutionary biology but has also been the foundation of the study of cooperation in human decision making.

		Player B	
		C	D
Player A	C	R=3 Reward for mutual cooperation	S=0 Sucker's payoff
	D	T=5 Temptation to deceive	P=1 Punishment for mutual deception

Figure 2.1: The Prisoner's Dilemma game. The payoff to player A is shown with illustrative numerical values. The game is defined by  $T > R > O > S$  and  $R(S+T)/2$  (adapted from Axelrod and Hamilton, 1981)

World War II bloomed the use of science to explain and understand human choices. The study of how individuals decide within choices and how they strategize to optimum performance was aligned to the needs of the time in a period of military prioritization. The use of game theory started to give a solution to the modelling of human choices in an environment where transactional or rational cost-benefit interchanges were the norm (Von Neumann and Morgenstern, 1944). Prisoner's Dilemma (PD) is a widely used scenario that defies game theory, which assumes individuals will always rationally decide based on their best interest, making two individuals go against cooperation even when it yields to the best possible outcome for both (Flood et al., 1950). Briefly explained, participants in PD need to decide their course of action between two different strategies: cooperate or defect to their counter partners. Figure 2.1 depicts examples of different payoffs in two players according to their choices and their counter partners'.

The plot is proposed as follows: Two suspects are potential candidates to be blamed for a crime, and they are now being interrogated in two separate rooms that impede their communication. The prosecutor raises the following questions to the suspects:

- If A confesses and testifies against B, and B decides not to confess, the charges to A will be dropped and A will be released.
- If A does not confess and B does, prosecution will seek maximum sentence for A of 5 years.
- If both A and B confess, both will be sentenced to 3 years in prison.
- If neither of them confesses, they will be charged with minor misdemeanours and will be sentenced to 1 year in prison.

Interestingly, several results from 37 paper meta-analysis (Oosterbeek, Sloof and Van de Kuilen, 2004) have shown a systematic bias towards cooperative tendencies despite what would be predicted by rationality is playing in favour of self-interest. However, the PD is based in its foundation in a bias towards non-cooperation, as defection (betrayal) provides a higher reward (free jail pass) than cooperation (minimum of 1 year of jail).

The emergence of cooperation in PD arises from the iteration of such dilemma, where individuals are repeatedly exposed to the decision so they could refine and update their strategies with prior knowledge of the other participant. Under these circumstances, and

as stated above, Axelrod (1984) tested in humans his previously defined theorems (Axelrod 1981) which proposed that strategies that started on greedy intentions performed worse in the long run, while the ones that started from a more altruistic starting point showed a better performance. According to the author, iteration allows the possibility to profile the other person and change the behaviour. On the bases of the results, Axelrod stated that the top-scoring strategies were based in four different principles:

1. Don't be envious (when losing)
2. Don't be the first to defect
3. Reciprocate both cooperation and defection
4. Don't be too clever

The first principle assumes one should careful not focus too much on scoring more than the opponent in order to reach the highest possible score. The second principle alludes to the fact that one should start being nice as one will rarely defect first before the opponent does. The third one states there should be a certain level of forgiveness of the defective decisions. Last stance, one should be ready to retaliate and update their strategies because if they are trying to provoke an adjustment only in the opponent, not to them, and this ends up being too explicit, they will most likely end up failing. The experiment concluded the optimal strategy, the one that fitted well with the four previous assumptions and seemed to have the best possible outcome in a non-zero-sum situation, was tit-for-tat or equivalent retaliation. Therefore, Axelrod proposes that cooperation appears when there is a payoff, that is, when cooperation is reciprocated. Later in the decade, another contemporary author (Alexander, 1987) included the kin relationship concept, stating individuals are more willing to cooperate with genetically related individuals. Kin relationship is more complex in humans than in other organisms and is subject to a wide subtlety (Palmer and Steadman, 1997) such as traditions and other type of categories or symbolic power that affect the psychological construct of kinship.

Van den Berg and Weissing (2015), who centred their study only in mathematical modelling considerations, used a computational approach to the iterated PD and demonstrated how underlying mechanisms, and not simply fitness considerations, are important drives to the average level of cooperation. Putting it another way, what would happen in situations where individuals encounter multiple levels of equilibria? What if different choices have apparently equal levels of optimality? For instance, imagine there are two different local maxima that represent two equally attractive drives. This multiple sources (and weights) of reward are very common when multiple living organisms interact, and they can lead to different preferences or aims. In this situation, the choice leading to a maximum fitness would not be that straightforward. Far from being an exception, this is a common situation in social contexts and there, the evolutionary choice would be more influenced by social mechanics than on choices solely affecting natural selection or, in words we used earlier in the text, fitness considerations. Therefore, as the authors demonstrate (Van den Berg and Weissing, 2015), because these mechanical dynamics affect probabilities, they consequently affect arising phenotypes or, in other words, they also affect the likelihood of alternative evolutionary trajectories. This drifts in what seems a more competitive or logic path according to the principle of survival of the fittest, solely from a Darwinian perspective, might, according to the authors, explain the fundamental bias of cooperation present in all social beings.

Nevertheless, even though so much can be appreciated from these experiments, perhaps one of the most significant learnings stands at its core: the possibility of cooperation (e.g., the likelihood to adjust the behaviour to the other and the willingness to cooperate correspondingly) increases with the opportunities of interaction. Additionally, in another simulation study, Delton et al. (2011), in one-shot decision-making under uncertain situations, proposed that generosity is a high return cooperative strategy. The authors concluded that when participants decided to engage in reciprocity, they balanced the cost of mistaking a one-shot interaction with a repeated interaction as a high-stake risk. What if I deceive this person thinking it is a one-time interaction and for some reason I must interact again? Moreover, the same study proposes the consequence of using motivational as well as representational systems in the decision-making process as a species might have been a way of forcing generosity even in situations that do not apparently result in a potential benefit to the individual. Thus, the fact that one-shot generosity should coevolve with reciprocity is a powerful ingrained belief that serves as an evolutionary adaptation. This idea converges with the statement stated in the previous paragraph (Van den Berg and Weissing, 2015) which highlights the importance of structural mechanics weighing in favour of different optimized outcomes in a context of multiple equilibria.

This whole idea provides an interesting hint: a cooperative setting, from its fundamentally social nature, is a situation of multiple equilibria, where usually there is not a straightforward optimal solution to a problem, increasing the complexity of optimization. In other words, in cooperative situations individuals follow a decision approximation of multiple optimal representations of choice which leads to a computation about what will be considered as the right course of action.

Therefore, from the first experimental pursues of studying social behaviour, researchers have observed these different behavioural influences (mechanics) in an attempt to measure different weighs governing our decision-making framework under cooperative contexts. In the next section, we will further explore these seminal works and findings, to determine how they have impacted our understanding of human cooperation.

### 2.1.2. Mechanisms of Cooperation: From conformity to interdependence

Cooperation is a phenomenon which involves different types of individual compromises in favour of a social decision. As we introduced in the previous section, there are different drives and influences that lean a balance towards it even if it is not the option that favours the individual interests of a person the most.

In the history of experimental psychology, different authors have explored how humans bias and compromise their own views in favour of social rewards, such as consensus or convergence. The first author that experimentally studied this phenomenon was Arthur Jenness (1932) who used an estimation task, with a bottle full of beans. Here, participants were required to guess the number of beans inside the bottle under different conditions, first individually and then within a group. At the end, participants were asked again individually if they wanted to alter their initial estimates or approximate to the group's estimate. More than 90% (between 93 to 98% depending on whether discussion was or wasn't allowed) changed their initial guesses to match the group's estimate. Therefore, social estimate weighted significantly more than one's estimation alone.

Not long after, Muzafer Sherif (1935) conducted another study, the famous "Autokinetic Effect Experiment", which intended to demonstrate how people conform to group norms when they are put under an ambiguous situation. Participants were presented a small spot of light projected to a wall in a dark room. Due to a visual illusion, the spot of light resembled to be moving even if it was still. Then, participants, first individually and later accompanied by two more participants, were asked to tell their estimates on how far the light moved. The author manipulated the groups with two persons having a close initial estimation with another one whose estimate was considerably different. At the end, Sherif found over different trials that the person whose estimate was more distinct to the other two conformed to the view of the majority. In other words, groups ended up converging into a common estimate under ambiguous situations. Results concluded that people, by lack of precise information, tend to observe others to make or complete their judgements.

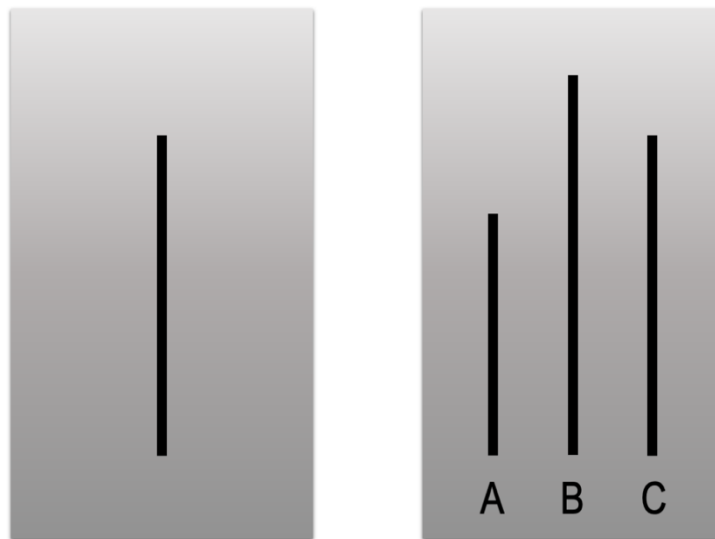


Figure 2.2: Example of the Asch's line judgment task with a reference (left) and the multiple choices (right) (adapted from Asch, 1951).

Years later, Solomon Asch (1951) argued that Sherif's experiment was conducted under ambiguous situations and, therefore, lacked a correct answer. Therefore, he wanted to test the distortion (more than the convergence tendencies), of socially biased judgements. Asch designed a line judgment task (Figure 2.2), putting a participant in a room with seven other confederates who had previously agreed on their responses. Results described by the author showed that 32% of participants conformed with the clearly incorrect majority. Also, over the course of 12 trials, about 75% of participants conformed at least once. In the control group, where confederates were not required to conform in their results, less than 1% of participants chose the incorrect option. Deutsch and Gerrard (1955), on the basis of these two experiments, proposed two types of the explanations behind conformity: first, the one extracted from Sherif's experiment, informative conformity, which assumes the majority is better informed than the actor; and second, normative conformity, where the actors decide to conform driven by the reward of fitting within the group.

Herbert Kelman (1958) defined three different types of conformity. First, *compliance*, in line with Asch's experiment, that occurs when the influence is accepted in expectance of receiving back a favourable reaction from another person or group, which stops when the pressures to conform disappear. Second, *internalization*, which happens when the subject accepts group norms because it is congruent to their value system. This is the deepest level of conformity as the group and individual's belief system merge. Third, *identification*, which describes the individual's acceptance of influence to maintain or establish a self-defining relationship to another person or group. Years later, Leon Mann (1969), in his famous handbook *Social Psychology*, defined a fourth type of conformity, the *ingratiational*, which describes the conformity happening to impress or gain favour or acceptance from other people. The difference with compliance is that the ingratiational

is motivated by social rewards rather than the threat of rejection. In other words, if the group pressure stops, the motivation to conform continues.

However, conformity is only one of the social psychological mechanisms that facilitate a prosocial behaviour such as cooperation. If we base the decision to cooperate on the actor's choices, there is vast research focusing on incentives (Balliet, Mulder and Van Lange, 2011), norm deviation (Klucharev et al., 2009), learning (King-Casas et al., 2005), social context cues (Delgado, Frank and Phelps, 2005) or ties (Van Winden, Stallen and Ridderinkhof, 2008; De Dreu, 2012).

This topic has also been tackled in different personality research studies. In fact, evidence shows an influence of certain traits in cooperative behaviours in mixed-motive games (Ashton, Lee and De Vries, 2014), such as the PD. For instance, given a task with interdependence among participants, there are individual differences in certain social constructs which affect the decision to cooperate or defect (Griesinger and Livingston, 1973; Haesevoets, Folmer and Van Hiel, 2015). Hence, researchers have tried to define the dispositional factors that lead a person to cooperate, rather than to act as a "free rider".

One of the first attempts to explain the dispositional patterns that lead to cooperative behaviour is an individual differences factor defined as the "Social Value Orientation" (SVO) (Messick and McClintock, 1968). Briefly, SVO weights a person's preference to allocate resources according to their interests and welfare in relation to another person's. In their studies, researchers removed the strategic component of the dilemmas assuring participants they would not receive feedback regarding the choice of the other person. Consequently, they could decompose motives and preferences, so they could identify why a person decided to allocate resources in a particular way. Thus, SVO reflected how consciously a person acts regarding the influence of the other. This systematic approach led to a geometric model of preference (Griesinger and Livingston, 1973) that characterized a motivational orientation representing the weights assigned to oneself and other player's outcomes. In *Figure 2.3* the two axes represent two different persons, A and B whereas the vector  $\vec{M}$  represents the motivational orientation of A. Authors relate each orientation of the vector to a different preference profile: (a) individualistic or preferring own gain; (b) cooperative or preferring joint gain; (c) competitive or preferring relative gain; (d) altruistic or preferring other's gain; (e) sadistic or preferring other's loss; (f) masochistic or preferring own loss.

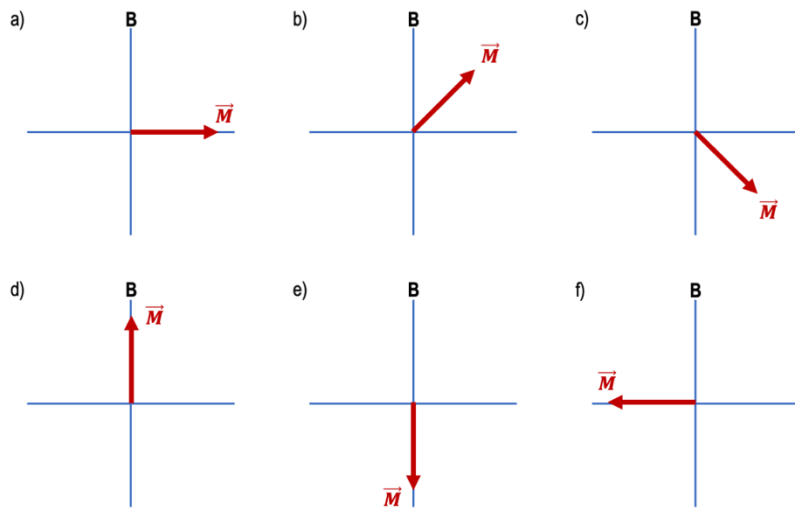


Figure 2.3: Social Value Orientation approach. Being  $A$  one player,  $B$  the other and  $\vec{M}$  is the motivational orientation of  $A$ : (a) individualistic or preferring own gain; (b) cooperative or preferring joint gain; (c) competitive or preferring relative gain; (d) altruistic or preferring other's gain; (e) sadistic or preferring other's loss; (f) masochistic or preferring own loss. (adapted from Griesinger and Livingston, 1973)

Following this idea, in a recent study, Epstein, Peysakovich and Rand, (2016), using machine learning techniques to predict the responses from outcome-based features, found that cooperative willingness correlates with stable individual preferences over outcomes rather than ephemeral sentiments, such as momentary mood or emotional state. This is consistent with the proposition that there might be a “*cooperative phenotype*” (Peysakovich, Nowak and Rand, 2014), an inclination to cooperate, that is domain-general and temporally stable.

Nevertheless, under cooperative settings when two actors decide individually whether to cooperate or defect, research has traditionally focused more in the study of the actor's choice and rationale rather than the influence dynamics happening in the co-action. In other words, if we want to understand the mechanics of a cooperation, we cannot separate the behaviour to the specifics of the context where this cooperation is happening and assume that is just a consequence of the choice of two free agents. As the reader might have realized, this view is convergent to the one raised by the evolutionists presented in the previous section (Delton et al., 2011; Van den Berg and Weissing, 2015).

The first researchers exploring this idea were the fathers of Group Psychology such as Kurt Lewin, who refined Koffka's explanation in his seminal handbook *Principles of Gestalt Psychology* (Koffka, 1935). Lewin suggested groups were dynamic systems with varying interdependences, which led him to propose the “Field Theory” (Lewin, 1951). This theory claimed that common goals is what makes group members act in interdependence. In other words, members of a group act as a dynamic whole where any change in the system (for instance, a personal conflict by a member) affects and changes



the state of all the other members of the group. Following this work and based on these ideas, Lewin's student Morton Deutsch (Deutsch, 1949; 1962, expanded later by Johnson and Johnson 1989), proposed a theory of social interdependence. This theory states individuals who share common goals and outcomes are affected by the actions of others and seek to help to obtain outcomes beneficial to those they are cooperatively linked with. Because the motives of interdependence are diverse, the authors proposed a way of categorizing them inside three groups of outcomes: (1) effort to achieve, (2) positive relationships, and (3) psychological health (*Figure 2.4*). However, even when this proposal was based on the interdependence among individuals, and somehow identified the justifications to act in favour of a common goal, it also focused on the drives and motives of person's action rather than the characteristics of the interaction separated from individual motives.

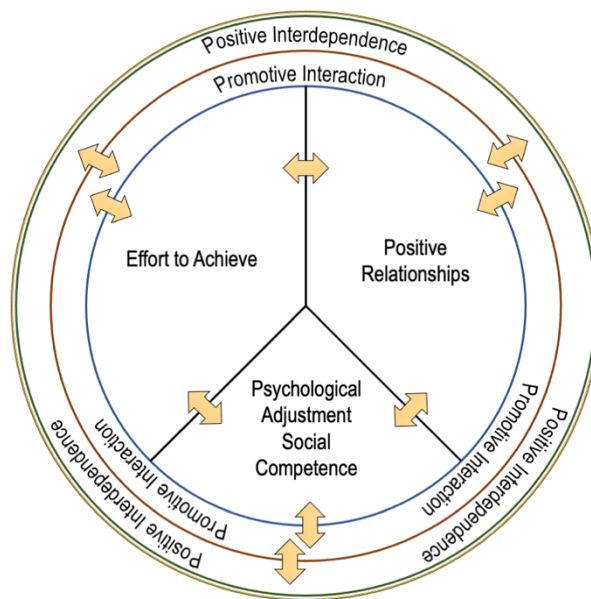


Figure 2.4: Outcomes of Cooperative Learning (adapted from Johnson and Johnson, 1989).

The first authors that focused on the study of the inter-personal relationship and not on the individuals who participate on it were Harold Kelley and John Thibaut (1978) proposing their Interdependence theory. In this proposal, between-person relations are as meaningful as the individuals by themselves. The theory proposes four different interacting situation structures, from which they extracted four dimensions. Later, two more were added (Kelley et al., 2003) to a final total of six, which provide a comprehensive analysis to describe the relevance to the motives of the people in these situations: (1) *level of dependence*: which confronts the comfort or discomfort with dependence or independence; (2) *mutuality of dependence*: confronts the comfort/discomfort with vulnerability (as dependent) or responsibility (as dominant or power holder); (3) *basis of dependence*: dominance (leading) versus submissiveness (following) and/or assertiveness versus passivity; (4) *covariation of interests*: prosocial confronts self-interest motives (rules for self) and/or trust confronts distrust of partner

motives (expectations about others); (5) *temporal structure*: confronts dependability to unreliability and/or loyalty to disloyalty; (6) *information availability*: openness interacting against need for certainty and/or optimism against pessimism. Later, these authors (Kelley et al., 2003) identified 21 interaction patterns coming out from the combination of these dimensions, which they called basic interaction situations, that can be analysed by their interdependent features, psychological processes, and the interaction processes that they evoke.

As a mere comment, the study of interaction dynamics in social settings have other interesting derivations into the study of socially influenced psychological dynamics. For instance, different authors have researched what it is in human groups that enables conflict and adaptive behaviours which not necessarily favour cooperation. Here, socially induced self-categorizations (also known as Social Categorization) have been widely described in classical Social Psychology. It was Allport (1954) the first to describe this as the main source of human prejudice although, later, the “Social Identity” theory (SIT) (Turner, Brown and Tajfel, 1979) provided a more expanded and elegant view on intergroup relationships and its influence in perception, self-identification, and categorization (Tajfel et al., 1979). The core proposition of SIT states people endeavours to reach a positive social identity through the identification to social groups, that provides them with self-esteem and group validation (Abrams and Hogg, 1988). Moreover, the foundations of SIT explained the ingroup bias through the “*minimal group situation*” experiments (Tajfel, 1970; Tajfel et al., 1971; Tajfel and Billig, 1974), which demonstrated how with a single different category, participants were able to understand intergroup difference and, therefore, develop a bias towards discrimination and competition against the others. The importance of SIT is undisputed (Brown, 2020), and not only has inspired research in many aspects of human psychology (such as inter-group relations, identity, leadership, norms, among others), but also in many other disciplines.

However, the present thesis is devoted to study the dynamics of the interaction, and here, perhaps the most successful attempt to describe the social forces and influences to conform, comes out from the *Social Impact Theory* (SIT; Latané, 1981; Latané and Wolf, 1981; Latané et al., 1995; Latané, 1996). In this framework, social influence is characterized as a force, similar to a physical force such as gravity or electro-magnetism, that acts on the individual’s decisions in three different dimensions related to the magnitude of the influence: (1) *persuasiveness*, which is related to different aspects that mediate in the strength or status of the source of influence (e.g., age, expertise...); (2) *immediacy*, related to the space-time proximity to the observer; (3) *supportiveness*, related to the number of people the observer is exposed to. Nevertheless, subsequent replications of this theory found difficulties and controversy to explain the extent of the magnitude of the two first factors (Mullen, 1985; Jackson, 1986), whereas there is enough evidence supporting the effects related to group size.

In summary, these proposals describe different contingency “force-fields” that individuals psychologically might sense (and play a role in their action selection) in an interaction. However, none of these theories tries to address the relationship between these factors and the basic functions underlying human behaviour (learning, decision making, reward processing...). In this sense, these accounts are of limited utility to describe the basic cognitive functions which might explain social interactions and their related neural mechanisms. Indeed, from an experimental point of view, and consistent to the views of Thibaut and Kelley and interaction psychologists like Robert F. Bales, in

his handbook *Social Interaction Systems*, psychological interactions happen under systematic contexts, and, therefore, they are measurable and predictable (Bales, 2001). Therefore, it is also understandable people need different cognitive mechanisms that can measure and predict “what is going next” in an interaction, to adjust their behaviour to others according to the different constraints described in SIT or any other socio-structural norms (as well as other personal and internal traits serving as contingents). Prosocial decision-making and interactive cooperation are a sequence of behavioural adjustments happening between two or more than two people in interaction. Considering a functional perspective, the way we adapt to others and select the most cooperative course of action requires, first, different types of (social) rewards, predictive learning capacity, and conflict monitoring mechanism that allow the tracking of the prediction errors (PE, difference between own’s and others’ view) and the behavioural adjustments needed to adapt to the others- In addition, all these different functions might be driven by different neural mechanisms. Unfortunately, the way how neuroscience has mainly studied social cooperative dynamics and actions in decision-making has also its own flaws, primarily because it has come out of research in non-social settings. Until recently, and mainly due to technical constraints, social adjustments and cooperation have been studied in the field of cognitive sciences and neurosciences from a single-subject perspective and, hence, without taking into account the interaction. Hopefully, in recent years this has begun to change with the rise of the second-person neuroscience. Although we will address this question in higher detail in following sections, we will start by introducing the different social networks in the brain. Despite the apparently poor ecological validity of single-person settings to understand social cognition, the truth is that evidence coming out of single-person neuroscience has been incredibly useful. Throughout the years, researchers have designed brilliant social paradigms that have delivered great evidence on the regions involved in social cognition and, more specifically, cooperation. In the next section, we will address the evidence from these studies and introduce the brain networks involved in the processing of different social stimuli in the brain.

## 2.2. Social cognition: brains in interaction

As commented on the previous section, there are multiple reasons why a person decides to conform and converge to the views of others, and this seems to be a result of different cognitive mechanisms. When people adjust to others, one needs to consider other's mental states. This is a key ability to humans which enables to predict, explain, and evaluate other's actions and intentions. Social interaction is a highly evolved mechanism that requires not only the consideration of one's aims but also the others. This complex process has been identified in neuroscience literature as "theory of mind" (ToM) or also mentalizing. Understanding what another human being might be thinking involves making inferences about their interests or preferences, beliefs, goals, and intentions as well as how it responds and processes emotions.

In terms of neuroanatomy and the location of different regions in the brain, functional magnetic resonance (fMRI) has been a main ally in the field of neurosciences in the mapping of the different brain networks involved in the different cognitive processing. fMRI uses blood-oxygen-level dependent (BOLD) contrast to identify the activations happening in the different parts of the brain.

If we want to understand the mechanisms behind social adjustments, we will need to distinguish the several computations that are involved in such a complex behaviour. We will start by introducing the general social regions and networks in social cognition.

### 2.2.1. Brain networks for a social nature

There is an increasing body of evidence (Redcay and Schilbach, 2019) suggesting the involvement of distinct core neural systems in social interaction. On the one hand the mirror neuron system (MNS), consisting of primary motor and sensory cortex as well as language regions and parietal cortex, responsible to the imitation process needed in joint action, seems to be involved in this processing (Redcay and Schilbach, 2019). On the other hand, the mentalizing system (MS), which has been identified in a network comprising the temporo-parietal junction (TPJ) and prefrontal cortex (PFC), including dorsolateral, ventrolateral, and orbitofrontal cortex is also a critical component of social interaction. Evidence (Gallagher et al., 2002; Frith and Frith, 2003; 2012) suggests each core area not only holds a different computation in mentalizing but also is sensitive to inputs of different nature. Coherent to this idea, recent evidence (Koster-Hale et al., 2017) found spatial and functional dissociation of the computation of another person's beliefs in right TPJ (rTPJ) and the valence of these beliefs in the ventromedial PFC (vmPFC) shedding light in the distinctive roles of each of these regions in social cognition. Extensive research has demonstrated the role of vmPFC in the computation of values (Clithero and Rangel, 2014), value integration (De Martino et al., 2013) and the encoding of confidence (Lebreton et al., 2015) in the decision-making process. Coincidentally, in a recent experiment with transcranial direct current stimulation (tDCS) in a conformity experiment found the cathodal stimulation of the vmPFC inhibits the informational conformity (Li et al., 2020). In other words, mentalizing, the ability to understand other people's mental states, requires a significant number of different reality representations that do not necessarily reference in the immediate physical reality. For instance, consider action valuation as an example: one can evaluate the action of how someone is doing something based on many different indicators (representations of reality): cooperative interests, self-interests, future-interests and so on. Furthermore, this mentalizing process demands simultaneous computations as well as the integration of information coming out of different brain regions.

However, especially when analysing social decision making, we cannot understand interaction without mentioning the reward-affective system comprising the amygdala (AMG), ventral striatum (VStr), orbitofrontal cortex (OFC) and anterior cingulate cortex (ACC) among other areas. At the end, people guide their social actions based on an intention to maximize their social reinforcements. The advantage of social interaction is learning happens with self-experience but also with observational learning. Due to its own importance to the present thesis, we are reviewing learning mechanisms in detail below (see section *Learning to adjust to others*) but first, we will introduce the networks involved in different aspects social cognition.

Literature on social cognition has used the concept empathy to describe the affective route needed to understand others and the MS or ToM, to describe the cognitive representation of other person mental states. However, these are used as umbrella terms that relate to a variety of different processes that not necessarily converge (Schurz et al., 2021). In fact, the same authors, based on an extensive meta-analysis, propose a hierarchical level derived from a clustering that better represents the findings of previous fMRI studies. The meta-analysis found three distinctive clusters that the authors called "*Cognitive*" and "*Intermediate*", which would correspond to what classically has been associated to ToM and "*Affective*" to results close to the "empathy" concept. *Figure 2.5* shows the activation

related to these clusters and the tasks and paradigms that fall inside these different processes.

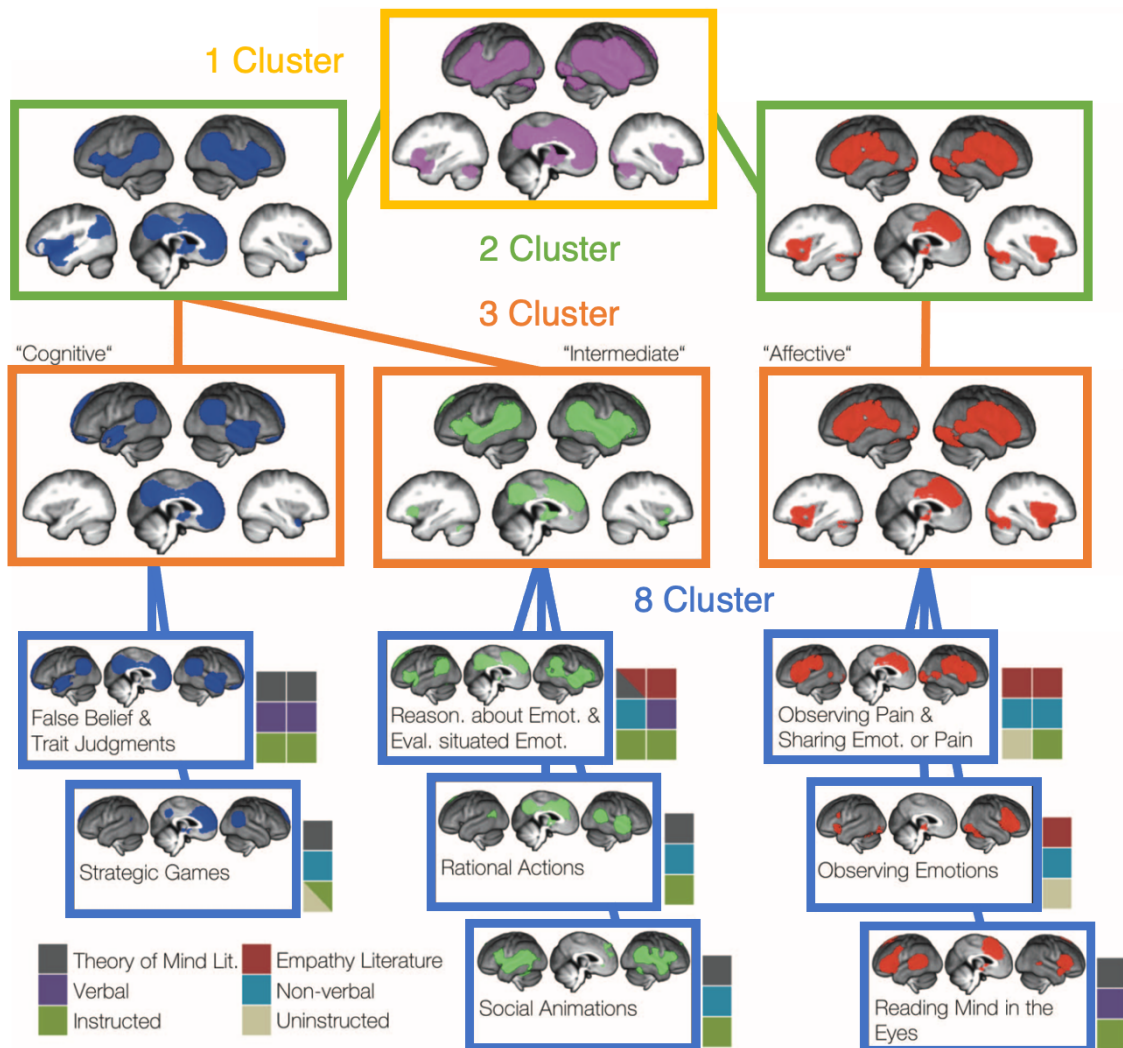


Figure 2.5 Average brain activations from pooled meta-analyses (separate per clusters). Analyses were thresholded voxel-wise of  $p < .005$ . 1 and 2 clusters are shown for illustrative purposes, whereas the 3-cluster separation is the more accurately distinctive which holds the different subcategories of networks related to different tasks. The diagram shows 3 distinctive clusters, identified as “Cognitive” (blue), “Intermediate” (green) and “Affective” (red). At the lowest level of the dendrogram, authors present an 8-cluster solution indicating each exemplary stimulus and task categorization (adapted from Schurz et al. 2021).

*Cognitive* cluster activations comprise cortical midline and temporoparietal areas. They have its strongest activations in the ACC and medial PFC, which extends along the cortical midline to the precuneus and midcingulate cortex. Then, the activation extends to bilateral temporoparietal areas (right posterior superior temporal gyrus, right supramarginal gyrus, left posterior middle temporal gyrus and inferior parietal lobule) and bilateral anterior temporal cortices as well as smaller subcortical areas (caudate). Interestingly, the authors found these networks to overlap (56% of voxels) to what has been identified as the default mode network (DMN; for a review Mak et al., 2017). According to previous claims, the self-generated cognition that is not referenced on the physical world, for instance inferences on what others might be thinking, is related to the DMN. In line with this claim, other research has identified ToM to be involved in a set

of cognitive processes with a social origin, which include intentions, beliefs, preferences, traits, desires, and other higher order inferences about other people's mental content (Frith and Frith, 2012).

On the other hand, the *Affective* cluster, close to the concept of empathy, represents the other extreme of the mentalizing spectrum. Here, the activation includes the right frontal cortex to the inferior frontal gyrus, and expanding into the right insula and temporal pole, precentral as well as postcentral gyri and the supramarginal gyrus. Other activations were also found in the left inferior frontal gyrus, insula, temporal areas and supramarginal gyrus. Other large areas were found in the supplementary motor area and the adjacent medial frontal gyrus and midcingulate cortex. Finally, two other smaller activation areas were found in the left inferior occipital gyrus and left cerebellum. This network mainly overlaps to what has been defined as the ventral attention network (26% of voxels; for a review Vossel, Geng and Fink, 2014), somatosensory network (16%) as well as the DMN (16%) although significantly less than in the *Cognitive* cluster. Authors identify activation patterns of these areas to be associated to the prediction of affective and emotional states of the others.

Finally, the *Intermediate* cluster, combines elements of the other networks. Activations are found in large parts of the bilateral temporal lobes, from the posterior superior temporal gyri to the anterior temporal lobes. Overlapping activations to *Cognitive* cluster include the bilateral temporoparietal cortex and precuneus. On the other hand, overlaps with *Affective* cluster include the left insula and the inferior frontal gyrus. The largest overlapping comes from the DMN (43%) and the ventral attention network (18%). Interestingly *Intermediate* as well as *Affective* clusters both showed high activations in language related regions which authors relate to the importance of human language to the organization of the motor system and vice versa.

These clusters depict a spectrum of social cognitive and affective processes, and the large number of regions involved in them, separated whether they are more *Cognitive*, *Affective* or *Intermediate*. However, even when this is a good start, we will dive a little deeper in the different processes inside these clusters which are relevant to the present research. We will start with the more cognitive one, that tries to explain the regions involved in learning to reach a convergence with others.

### 2.2.2. Learning to adjust to others

The process of reaching a consensual decision making by a group of people involves a mixture of inferences on oneself, others, and the context processing in different brain areas. Firstly, one must encode the other's prior decision which according to research (Suzuki et al., 2015) has been described to be linked to activity in Posterior Superior Temporal Sulcus (pSTS) and its neighbour area, the TPJ. These areas are active in the computational encoding of learning signals needed to predict what others will do (Kilner et al., 2007).

Learning is, indeed, an important aspect of social behaviour. We do not only learn from our own experience but also by transference or observation coming out from social sources. For instance, we can adjust our uncertainty on the environment not only based on the evaluation of our own experience but also on observation, instruction, and other types of learning. Learning or tracking the value of actions in a social environment that leads to maximization of rewards (socials or otherwise), explains how most of the regions involved in associative learning are also present in social cognition. In fact, reward system has a very important presence in social processes in the brain, and this seems to be the case not only in humans but also other social species. Therefore, in animal studies there is evidence from rodent studies (Dölen et al., 2013; Hung et al., 2017; Nardou et al., 2019; *for a recent review* Grimm, Balsters and Zerbi, 2020) that relate releasing of the Oxytocin (OT) hormone, as an activator of reward processing areas of the brain, in rewards associated with social learning. The segregation of OT has been long linked to positive social interaction in mice (Uvnäs-Moberg, 1998; Uvnäs-Moberg et al., 2005) as well as humans (Kumsta and Heinrichs, 2013; Althammer, Jirikowski and Grinevich, 2018). More recent studies (Hu et al., 2021), suggest a joint circuitry between the AMG and the hypothalamus (HPT), specifically with a population of GABAergic neurons on medial AMG, which would be promoting a positive reinforcement in social interaction beyond the classic striatal mesolimbic systems. There is also evidence that suggest an active modulatory role in social behaviour and reward caused by the action of certain projections from the cerebellum to the ventral tegmental area (VTA), which would influence the dopamine (DA), and subsequently, the reward circuitry (Carta et al., 2019). Other recent research (Noritake, Ninomiya and Isoda, 2018) with local field potentials in macaques, suggest social reward might be mediated by a cortex-to-midbrain pathway, rather than in the other direction, with a specific set of neurons in the mPFC that would be gating the action-selection.

Incidentally, one of the most metabolically demanding regions of the PFC is the mPFC. There is evidence on the participation of mPFC in many other computations such as ingroup favouritism (Volz, Kessler and Von Cramon, 2009), which has been previously linked to the representation of self (Wagner, Haxby and Heatherton, 2012) and self-referential processing (Kurczek et al., 2015), in ToM (Saxe and Powell, 2006; Sebastian et al., 2011), reasoning (Shamay-Tsoory, Tibi-Elhanany and Aharon-Peretz, 2006), reputation representation and status (Izuma, Saito and Sadato, 2010), abstract self-evaluation (Beer, Lombardo and Bhanji, 2010), intentions (Den Ouden et al., 2005).

Humans, as well as non-human animals, observe others to learn about the environment and make better models of the world that guide their actions. Consequently, humans need a mechanism to drive a self-referenced learning. It has been proposed that PEs, which



result from calculating the difference between the expected and received payoff, would be an ideal mechanism for such learning. In other words, to adapt to others, a person needs to evaluate the observed behaviour in other agents, compute the difference with their predictions, and adjust accordingly valuing in the decision-making contingencies of different nature, external and internal, to select and, finally, perform the adjusted action. In fact, the identification of the neurobiological substrate of this computation through the involvement of dopaminergic neurons (Schultz, Dayan and Montague, 1997), is probably one of the most important success stories in computational neuroscience. In fact, this topic, due to its relevance to the research in the present thesis, will have their own space in this introduction in the section *Action monitoring, prediction, and learning*.

### 2.2.3. Social Value Orientation (SVO) in the brain

In recent years, some studies have uncovered the underlying mechanisms that have an influence on our decision-making process and, in the previously mentioned, SVO (Messick and McClintock, 1968). Previously in the text we introduced how individual differences in preferences can lead to distinct objectives by people when interacting with others. For instance, the competitive type people focus on the outcomes that benefit them in the first place at the expense of their partners, while cooperative type people process not only outcomes that benefit them but also to their partners (Fehr and Karjibich, 2014). Other studies have also identified distinct neural correlates associated to individual differences in SVO (Haruno and Frith, 2010) which suggests people cooperate based on different preference weights and priorities. In fact, fMRI research has shown decisions that involve a social factor are promoted by SVO dependant reinforcement learning (RL) system anatomically distinct to self-value learning (Christopoulos and King-Casas, 2015). Although we will review models based on reinforcements and its value in the study of RL in a later section of this introduction (*Models of Reinforcement Learning*), this study suggests there are two distinct computational pathways happening depending on the difference in SVO, whether they are the cooperative or the competitive type. This study found SVO modulates learning through the difference in value representations when making decisions that affect others. Hence, while a cooperative individual experiences a certain result as an unexpectedly good outcome, positive PE, it is possible a competitive individual considers the same as a bad outcome, negative PE.

Anatomically, the social signals related to oneself within the social context are processed in parts of the frontal cortex that contribute to mPFC as well as dorsolateral PFC (dlPFC). Interestingly, evidence from recent research (Wittmann et al., 2016) suggests that, while the perigenual ACC (pgACC) seems to represent own performance history in the dorsomedial frontal cortex not only tracks other's performance, but it also carries what authors call self-other *mergence* representations, how people estimate the ability of others based on other's as well as one's own performance.

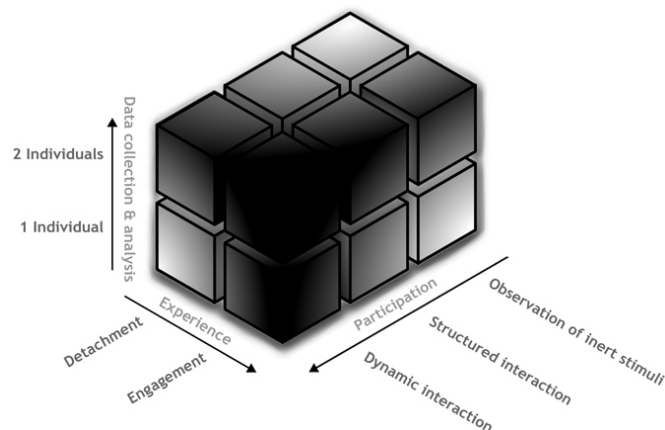
However, even though the level in the use of regions or the prioritization weights associated to the different sources of information might vary, evidence suggests there is a common network associated to process social roots in decision-making regardless of the level of SVO. At the end, evidence states (Schurz et al., 2021) social cognition is a multilevel and multi-layered phenomenon which mixes a different set of values coming out from affective, reward-related, cognitive, and other intermediate processes.

However, before going any further in the specific functional aspects of learning and cognition in the human brain, which will be reviewed extensively later in this introduction, and because this research is based on a two-person setting, we will introduce the state-of-the art coming out of research in two-person neuroscience.

#### 2.2.4. Single-person vs. Second-person Neuroscience

Most of the studies reviewed in the previous section have been developed using experimental paradigms involving one participant being exposed to some social stimuli (such as faces or apparently social reviews) or playing with or against (supposedly) other participants in other rooms (which in most cases were just bots or controlled by experimenters). This approach is based on classical paradigms used in cognitive neuroscience which have been successful to the definition of different important networks involved in different stimulus processing of social nature. However, some authors have suggested these findings could be strongly influenced by its prerogatives (Schilbach, 2010). A single-brain approach has mostly analysed neural correlates of the presence or absence of a specific stimulus or pattern of stimuli via the available neuroimaging techniques in healthy and pathological brains. However, while it is true that this research has allowed the understanding of the correlates or the circuitry of the so-called social cognition, it has been mapped through the absence of a real social stimulus. For instance, a picture of a face, an allegedly public review, a previously recorded audio, or video (commonly used as social stimuli, even though it is not encapsulated in an ecological social interaction). The problem with this approach is that social influences on our cognition do not happen in this kind of context in the real world and are, thus, suitable to cause a bias on the conclusions that might elucidate from this research. In other words, what we can learn from one person designs is restricted to a person as an observer of socially assumed stimuli.

Some researchers (Pfeiffer et al., 2013; Schilbach et al., 2013) propose a representation of the research landscape in social neuroscience based in three vertices *Figure 2.6*: (1) if the data has been collected from one or more than one individuals, (2) if the experience requires detachment or engagement and (3) if the participation is observational and passive, an structured interaction or a dynamic interaction. According to this depiction the authors identify the darker areas (as a metaphor of the unknown “dark matter” in space) as the more unexplored and the ones that suppose a higher challenge in the field.



*Figure 2.6: Depiction of experimental landscape of research of social domains in neuroscience; shader grey areas indicate more unexplored areas in this landscape (adapted from Pfeiffer et al., 2013)*

The cognitive perspective of social processes stipulates a passive view of cognition, which means an individual automatically processes information as it is coming, and this processing may be blurred and distorted by certain biases and influences, some of them in the social domain (Schilbach et al., 2013). The authors state this consideration can even have philosophical implications for the highly reduced understanding of the brain and its complexity.

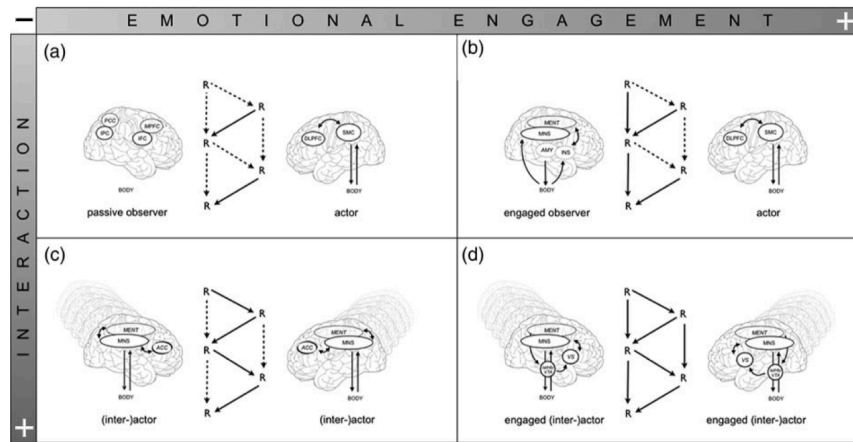
In fact, other views of the human mind like the ones in the theory of embodied cognition emerges from the sense that this approach is, in fact, uncomplete. According to linguists George Lakoff and Mark Johnson (1980), who established the foundations of this perspective, mentalization is a highly metaphorical process, meaning it involves a second-order modelling of the sensed experience which construes reality with both abstract and more concrete analogies. In fact, Lakoff and Johnson (1999) agree with the classic Aristotelian view when claiming there cannot exist an independent faculty of reason that is separate from bodily capacities such as perception and movement.

Later, Margaret Wilson (2002) postulated six claims that expand the meaning of the concept of embodied cognition: (1) cognition is situated and takes place in a context of real-world environment which involves perception and action, (2) cognition works under the pressure of real-time interaction, (3) there is an off-load of cognitive work to the environment which held or manipulate so we harvest it back later in a need-to-know basis, (4) the environment is part of a cognitive system where there is a flow between mind representations and the world, (5) cognition guides action and memory, and perception serves to deliver a situation-appropriate behaviour and (6) when cognition is decoupled from environment, activity is grounded in body based mechanisms such as sensory processing and motor control.

Based on these presumptions, Schilbach et al. (2013) claim there is an essentially different social cognition when an emotional engagement is present compared to an attitude of detachment. In other words, cognition is different when it happens in real-life interaction compared to when someone is a simple observer (*Figure 2.7*). According to the authors, four different scenarios can be drawn by means of emotional engagement and type of social interaction between two people (dyads) that will presumably elicit different computational systems involving distinct aspects of social processing.

Despite all these issues, experimental designs devoted to understanding social processing knowledge have traditionally been performed using settings where there is little or no emotional engagement nor the responsiveness to real people's actions (*Figure 2.7.A*). The lack of involvement of the affective networks and their influences in the system defines this social cognition to the mere observation of social cues. This has been changed with experimental settings that promote an engaged observer (*Figure 2.7.B*), which elicits sensory processing to valence networks, with engagement of AMG and insular regions, but still represents an observational engagement to social stimuli. On the contrary, experimental settings with interaction between dyads or groups of persons can be separated according to their emotional engagement. In the first case, where no emotional engagement is present (*Figure 2.7.C*), error and conflict monitoring systems, like ACC, engage to social control mechanisms as MS and MNS, as we already introduced in the previous section and will, due to its significance to the present thesis, explore further in its dedicated section (*Cognitive control and conflict monitoring theories*). Finally, when

interaction as well as emotional engagement is present (*Figure 2.7.D*), reward centres such as VStr and lateral habenula complex (LHb) participate in the processing.



*Figure 2.7: Identification of different mechanisms involved according to different types of social interactions and emotional engagements. In the centre of each type of interaction, there is a schematic depiction of contingencies for different situations. (A) no (or little) social interaction and no (or little) emotional engagement, (B) no (or little) social interaction, but emotional engagement of person A with person B, (C) social interaction, but no (or little) emotional engagement, and (D) social interaction and emotional engagement. Abbreviations: R: (re)actions performed by agents; MENT: mentalizing network including (IFC) inferior frontal cortex and (IPC) inferior parietal cortex; MNS: mirror neuron system; SMC: primary sensorimotor cortex; DLPFC: dorsolateral prefrontal cortex; ACC: anterior cingulate cortex; AMY: amygdala; INS: insular cortex; LatHb: lateral habenula complex; VTA: ventral tegmental area; VS: Ventral Striatum (adapted from Schilback et al., 2013).*

Summarily, for the study of social interaction and because it comprises a different set of regions in action, second-person neuroscience, that is, involving two participants in a real social interaction in the design of the experiment, provides a more naturalistic approach to how interaction and its influence happens in real life.

However, there is another crucial aspect that justifies the use of settings with two or more people. Brain connectivity between different participants engaged in a social interaction setting has been classically inferred from the aggregation of two independent observations to a statistical model where behaviours are associated to neural activation. However, in the following section we will introduce the importance of synchrony in the study of social interactions.

### 2.2.5. Brains in synchrony

As commented before, neural computation underlying social interaction is composed by a myriad of different order subprocesses happening sequentially or at the same time. For instance, a simple choice of action in a social context encompasses a certain conscience of past, present, and future computations, with other type of affective and valuation influences and weights, which will play a role in the action selection. The definitory complexity of social contexts demands many layers of parallelized processes that two or more individuals need to align at the same time.

The first recording of two interacting persons date back to 2002 (Montague et al., 2002), when they tried to correlate different regions of the brain of two different persons recorded simultaneously in two fMRI, in a simple game of deception to which followed a vast number of other fMRI studies (for a review: Mu, Cerritos and Khan, 2018; Misaki et al., 2021), and other electroencephalography (EEG) and functional near-infrared spectroscopy (fNIRS) ones (for a review: Mu, Cerritos and Khan, 2018; Wang et al., 2018; Misaki et al., 2021) in a variety of different paradigms. Since then, different types of experiments have tried to further explore the distinct mechanisms of social interaction with multiple brain measures. The measurement of simultaneous recording of more than one brain at the same time, is known as “hyperscanning” technique. This term has been popularized to identify second-person neuroscience methods and studies.

There has been controversy on whether the use of inter-brain synchrony adds value to single-person neuroscience approach. However, fMRI studies (see e.g., Symoni et al., 2016; Yoshioka et al., 2021; Xie et al., 2021; for a review Misaki et al., 2021) have shown the added value of measuring inter-subject functional correlations, with correlated regions across brains. For instance, in a recent three simultaneous participant fMRI study playing a Pictionary game, authors found evidence of synchronization of the TPJ during collaboration, which was higher with better joint performance (Xie et al., 2021).

Other evidence coming from fNIRS studies (Jiang et al., 2012) found inter-brain synchrony in speech coordination tasks in inferior frontal regions, which were described to be of higher importance in face-to-face interactions. Later, the same group explored leader-follower dynamics in communication (Jiang et al., 2015), also with fNIRS, to describe that synchrony was higher in leader-follower than in follower-follower, in line with the idea of other speech coordination mechanisms (Kawasaki et al., 2013). These findings in fNIRS, authors argued, would not be possible without the use of an hyperscanning setting. Incidentally, these measures seem to have a higher sensitivity to real-life structure as they filter out other intrinsic neural dynamics and artifacts that consistently appear within the same brain but disappear when comparing the data between two brains (Jiang et al., 2015). In fact, there are different findings that come out of second-person neuroscience that allow us to learn more of other details of the systems defined in social cognition. For instance, recently has been described how MS is engaged simply by interacting with another person, without the explicit demand of the cognitive act of mentalizing (Warnell, Sadicova and Redcay, 2018).

However, nowadays there is an ongoing debate on the conclusions that can be extracted from the inter-brain synchrony to explain and find causality (Czeszumski et al., 2020; Novembre and Iannetti, 2021; Hamilton, 2021; Gvirts-Provolovski and Perlmutter, 2021;

Schirmer, Fairhurst and Hoel, 2021). Notwithstanding, there is a general assumption that interpersonal entrainment, as measured with interbrain synchrony (IBS), is representing some sort of social mechanisms that are still to be properly understood.

Nonetheless, even when this hyperscanning approach has been prolific using fMRI and fNIRS (for a review: Mu et al., 2018), the use of hyperscanning using EEG has provided important insight on the different inter-brain synchronic oscillatory dynamics. In the next section we will briefly describe the information that comes out of EEG in form of neuro-electrical temporal dynamics and later, we will continue reviewing some of the findings coming out of inter-personal studies, specifically from EEG.

### 2.2.6. EEG oscillatory brain activity

EEG is a non-invasive technique that measures, through small sensors in the scalp, changes in voltage from electrical signals produced by the neurons in the brain. A neuron is a type of cell that exchanges ions between its interior and the extracellular space, to propagate action potentials to other neurons or maintain a resting potential. The principal neuronal activity captured by the EEG is the one produced by Pyramidal neurons in the layers closest to the skull from the cortex, as they are aligned large populations of cells that fire in ensembles and in patterns. This explains some of the disadvantages of the EEG: while it has a high temporal resolution, it also has a poor spatial resolution. Signal recorded by EEG is, therefore, the summation of the electrical signal produced by the synchronous activity of thousands, and sometimes millions, of neurons that share a spatial orientation (Dickter and Kieffaber, 2013). Derived from this signal, event-related potentials (ERP) are the time-locked to an event, or stimuli processing, averaged EEG signal. Thanks to different experimental paradigms, this technique has produced lots of important dynamic descriptions of the brain processes in perception, memory, attention, learning and other cognitive activities.

The EEG was first used to record brain activity in 1924 by Hans Berger. In his prominent seminal experiments (Berger, 1929), Berger differentiated alpha and beta waves and related them to different mental states. In his first report, he described EEG signal as a “*continuing curve of fluctuations*” that could capture two types of waves: the larger ones, what he called “alpha waves” or waves of the first order, and to the smaller ones, the “beta waves” or waves of second order. Since then, different oscillations have been found in the brain, from low-frequency delta ( $\delta$ ; 0,5-4 Hz.) waves primarily seen on sleep, to different frequency ranges in theta ( $\theta$ ; 4-8 Hz.), alpha ( $\alpha$ ; 8-12 Hz.), beta ( $\beta$ ; 12-35 Hz.), and gamma ( $\gamma$ ; >35 Hz.).

Neural oscillations are the repetitive and rhythmic pattern of registered simultaneous action potentials from a large population of neurons in the brain. This phenomenon is interpreted as the macroscopic oscillations observed in EEG, which are produced at different frequencies, and have been related to different purposes such as information transference, coordination of neural circuits or motor-related pattern generators (for a review: Llinás, 2014; Herrmann et al., 2016).

In a recent review, Adam Kohn, and colleagues (Kohn et al., 2020) proposed that there might be several types of cortical communication systems or architectural designs also with different biological advantages and disadvantages. In addition, they assume some of them could be activated at the same time using different communication support systems. This assumption of different strategies working at the same time reinforcing and strengthening the communication between areas seems the most plausible and explains how areas communicate between them. Incidentally, the authors propose four different communication strategies: temporal coordination, referring to the simultaneous and synchronous activation of populations of neurons; communication through coherence, aligning the oscillations of large-scale neuronal activity of different regions in the brain; communication subspace, related to matching the patterns of activation of different neuronal ensembles in different regions of the brain; pulvinar mediated communication, which uses a gating process in the thalamus to modulate activity between different regions.



Nevertheless, even knowing how the cortex manages to transfer information between brain regions, another different issue is the function of the direction, what is known as the cortical streams. In fact, one of the biggest questions in neuroscience is how low-level and high-level cognition are modulated. Here, and due to the obvious difficulty of studying *in-vivo* brains at cortical layer level, evidence coming from animal models starts to shed some light on the mechanistic role different oscillatory frequencies play in this processing. What seems plausible is that the brain needs an updating mechanism which is likely related to distinct oscillatory dynamics. We call *top-down* modulation when this comes from anticipatory or endogenously produced sources, and *bottom-up* when the update happens due to stimulus or exogenous sources. There is important evidence that suggest that different layers use different communication streams from high-level cortical areas to lower-level areas using oscillatory synchronization (for a review: Bressler and Richter, 2015). For instance, as it has been demonstrated extensively in visual (Khan and Hofer, 2018) but also auditory modalities (for a review: Rimmele et al., 2018), attentional anticipatory mechanisms use top-down brain control to prepare sensory and motor systems for the execution of the task. Importantly for the present work, an important function that benefits from this top-down / bottom-up relationship is predictive coding, the ability to update the mental model of the environment, as we will further review in a later section (*Action monitoring, prediction, and learning*).

Incidentally, in recent years it is being reported significant evidence relating different oscillatory dynamics to these top-down and bottom-up streams. For instance, in an important experiment studying the visual cortex in non-human primates (van Kerkoerle et al., 2014), authors showed evidence suggesting that the different layers of the brain play a top-down (feedback) and bottom-up (feedforward) role between alpha and gamma frequency bands, respectively, between a higher level (V4) and lower level (V2) areas of the visual cortex. These authors propose the different oscillations explain an updating mechanism between different areas of the cortex and suggest it might be more general to other areas of the cortex (*Figure 2.8*). Even though this evidence must be taken carefully, and we cannot generalize these findings to humans yet, other experiments have supported evidence claiming identical or similar mechanisms, all pointing to the predictive updating capacity in the brain (Jensen et al., 2015; Marshall et al., 2018) suggesting this to be a more extended mechanism than a phenomenon exclusive to the visual cortex. In fact, recent evidence suggests there might be an adaptive logic that associate these cortical mechanisms to be somehow extendable to other areas in the brain (Bastos et al., 2020; Lundqvist, Bastos and Miller., 2020).

Although intracranial studies, as the ones presented, have offered important insights on the functional role of oscillatory activity, EEG and magnetoencephalography (MEG) have allowed understanding the relationship between brain rhythms and cognitive functions. In fact, throughout the years, practically every cognitive process has been associated to different event-related oscillation. However, there are many more different processes than the traditional five frequency bands and, hence, we cannot establish a straightforward association between them. EEG oscillations contribute to different cognitive functions depending on their amplitude, frequency, phase, and coherence. In a recent review (Herrmann et al., 2016), the authors propose 4 assumptions that support this notion: first, different brain regions perform different functions; second, whereas EEG oscillations in slow frequency may represent the cooperative activity of large-scale neuronal network, high-frequency oscillations reflect mainly the activity to nearby (to the

sensor in the scalp) neuronal populations; third, coherent oscillations on two different brain regions may reflect a functional cooperation between them (Siegel, Donner and Engel, 2012); finally, fourth assumption, high-frequency oscillations suggest cooperation between nearby cortical regions and low-frequency oscillations reflect the contrary, cooperation between distant brain regions.

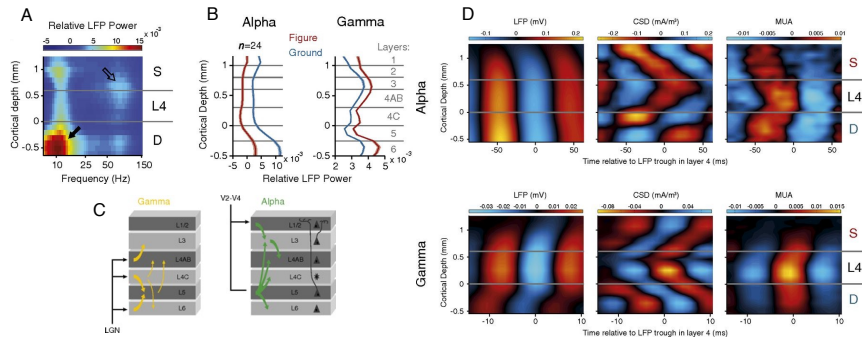


Figure 2.8: (A) Laminar profile of the increase in local field potentials (LFP) with lowest and highest multi-unit neuronal activity (MUA) response. (B) Laminar profile in alpha and gamma per layers and its depiction in (C). (D) shows laminar profile of cortical oscillation in the LFP, current-source density (CSD) and MUA responses in alpha and gamma (adapted from van Kerkoerle et al., 2014).

Despite this introduction on oscillations and their possible role in the context and prediction updating of the brain, in next sections we will dive a little deeper into these predictive signals and the possible role different oscillations have in them. Nonetheless, first, as announced in the previous section, we will review some of the findings coming out of inter-personal EEG research.

### 2.2.7. Inter-brain studies in EEG

The examples of paradigms used in EEG hyperscanning are incredibly diverse including deceptive games (Fallani et al., 2010), card games (Babiloni et al., 2007), hand movements (Dumas et al., 2010), flight simulation games (Astolfi et al., 2011) and even Leonardo DaVinci's bridge model building (Sciaraffa, 2021) among many others. Some of the first studies on the topic used joint action paradigms. These studies started soon to report different aspects of dual brain connectivity in coupled activities, such as a finger rhythmic movement, finding oscillatory components (Tognoli et al., 2007) that were differentiable between synchronized and not-synchronized conditions and whose source was the MNS (Rizzolatti and Craighero, 2004). Studies conducted with a pair of simultaneous guitar players (Lindenberger et al., 2009) detected an oscillatory phase alignment when musicians were preparing their tempo setting with their metronome and when they were playing coordinated, which suggested that oscillatory couplings might have a causal role in the initiation and maintenance of interpersonal action coordination. Later, studies by the same research team described that phase locking, phase coherence and structural properties of hyperbrain networks explained interpersonal action coordination (Sänger, Müller and Lindenberger, 2012) between two persons. They also defined there was a distinctive association depending on the role of the musician, whether they were leading or following (Sänger, Müller and Lindenberger, 2013). Later evidence in a finger-tapping task (Kovalinka et al., 2014) supported this distinction registering a frontal alpha suppression while leading the action, that was due to a higher allocation of cognitive resources which was in line to previous findings (Naeem et al., 2012). More recently, a new study with a duet of pianists (Gugnowska et al., 2022) found evidence on inter-brain synchrony to be not only an epiphenomenon of shared sensorimotor information but also an endogenous cognitive process phenomena important to behavioural synchrony and successful social interaction.

Another set of studies have focused on paradigms in which participants have to work together. In these settings, a couple needs to coordinate their attentional load. This joint attention paradigms show how two participants direct their attention simultaneously to a certain stimulus. Some studies have used a flight simulation paradigm to extract the level of cooperation (Astolfi et al., 2012) in different task phases (Astolfi et al., 2011). They concluded there was a high frontal alpha interbrain connectivity in conditions of maximal cooperation whereas this connectivity disappeared when the task was independent. Later developments of this paradigm in real world flight operations (Toppi et al., 2016) registered the same patterns of connectivity in phases with high coordination demands.

Second, other paradigms have explored shared or joint attention, where couples shifted together their attention while following partner's gaze (Lachat et al., 2012). These studies have described shared attention phases to have a decrease of power in alpha 2 oscillations (11-13Hz) over a large set of lateral centro-parieto-occipital electrodes. In another study held in a naturalistic environment of a classroom, the authors encountered shared attention to have a "tuning" of neural oscillations in alpha band to the temporal structure of what was happening around participants (Dikker et al., 2017). In fact, the authors reported how individuals who were less engaged showed lower synchrony levels with the rest of the group. This finding is crucial, as it states there is a certain oscillatory tuning

that happens when two persons cooperate independent to the task, only because of attentional coupling.

In recent, years studies, have tried to pinpoint higher level mechanisms that lead to mental coordination in the alpha band between participants. It has been proposed that this activity is favoured by the OT hormone (Mu, Guo and Han, 2016), that, as stated above, has been widely described to be part of a social regulatory mechanisms that modulate cognitive and neural processes (Meyer-Lindenberg et al., 2011; Bartz et al., 2011). In a later development of their study Mu, Han and Gelfand, (2017) described that, under a threat, the oscillatory couplings happened in gamma band, which has also been described to be associated to the processing of threat in single-person paradigms (Luo et al., 2007). This result would suggest gamma activity is used to coordinate in a more efficient way when people find themselves under threat.

Speech coordination research have also explored the synchronic coordination in the context of communicative interaction. First, studies find inter-brain synchronizations at theta/alpha frequency bands (Kawasaki et al., 2013) interpreting inter-brain synchronization as an index of mirror processing for other's speech rhythms. A later phase synchronization study in turn-taking interactions (Ahn et al., 2018), using EEG and MEG, found interbrain synchrony not only in alpha but also in gamma bands during the interaction.

However, despite the increase in this research in the last years, in a recent review Liu et al., (2018) argued that although most inter-brain studies report synchronic activity of some sort, little is known about the generative sources of such synchrony. The idea behind such claim is important and highlights the need to search from other sources of comparison, for instance using mathematical models, combining signals, etc.

To date, there have not been any inter-brain experiments on conformity and although there have been studies addressing this social adjustment, as we will review in the last section of this introduction (*Research paradigms for Conformity*), there is still room to understand further the different correlates surrounding such behavioural adaptation.

### 2.3. Action monitoring, prediction, and learning

As we already mentioned, when we adapt to align with others, as it happens in conformity, error and conflict monitoring systems are required to engage with social control mechanisms, such as MS and MNS. When we conform to others, we need to learn to predict our counterparts and engage our control mechanisms to adapt our behaviour to the context. Even when research from second-person neuroscience explaining these processes is still scarce, these cognitive systems have been extensively studied in single-person neuroscience and its literature serve us well to understand the different processes that could be involved in conformity. In the following sections we will dive through these findings which will be used as the theoretical foundation of our research.

### 2.3.1. Predictive signals in the brain

As introduced in a previous section, the brain needs to make its guesses about the environment, using previously acquired or learned patterns and regularities. All these systems are coordinated to send a “best guess” of what is going to happen in the endogenous anticipatory model of the environment. Then, this signal is sent to a control system which then monitors the discrepancies between the expected and the observed and sends that conflict signal as a PE that serves to update and optimize the model for future guesses. In a way, the brain is continuously trying to reduce the uncertainty and surprise in the environment through the update of its own models of the world.

One of the first EEG signals linked to the predictive capacity of the brain was studied through mismatch negativity (MMN) Event-Related Potential. This component was first registered by Risto Näätänen and colleagues (Näätänen, Gaillard and Mäntysalo, 1978). In the classical oddball paradigms used in this research, participants are exposed to deviant stimuli embedded in trains of repetitive standard tones. MMN appears as a frontocentral negative component 150-200 ms after deviant compared to standard stimuli and was considered by the authors as a form of “primitive intelligence” (Näätänen et al., 2001). This response is thought to be a by-product of a form of automatic learning formed by regularities and can be statistically modelled as a Bayesian learning foundation that has the capacity to detect deviant events (Gijzen et al., 2021).

MMN can be understood as an evoked sensory signal carrying a PE (Garrido et al., 2009) which served as integrated justification of predictive coding theory, where PE drives perceptual inference and changes so that PE is suppressed by learning (Garrido et al., 2008). Predictive coding theory is presented as a general framework to understand underlying mechanisms that follow an automated hierarchical filtering of variations in terms of complexity (Friston, 2008). Fundamentally, it postulates that to minimise the consumption of brain energy, MMN should be the response of minimising neural signal “surprise” about sensory states and proposes this should follow a continuous processing of the expectation, which is explained by change-detection, adaptation, and model-adjustment by means of a neurobiological mechanism of perceptual optimisation (Garrido et al., 2009). In other words, predictive coding states MMN signals are described as a specific type of automatic processing type for error signals. Therefore, in the predictive coding framework, the brain is considered to have an inferential nature, and hence it is sort of a Bayesian prior actualization machine, trying to build the best model of the world possible, in order to minimise surprise and following, what is called as free-energy principle (Friston, 2010). This explanation tries to be extendible to all living systems, which would try to minimise a free energy function of their internal states and models of the world. This formal statement assumes a system tries always to minimise entropy and uncertainty by updating and sophisticating their model of the world. Hence, the brain is an “inference engine”, which through perception and action (i.e., *active inference*), minimises or corrects the (internal) model of the world, using the difference between the internal model and the actual hidden (external) model of the world. Under this framework, the free energy is the complexity minus the accuracy, energy minus entropy or the minimisation of surprise (average of entropy) when this is diverging with the internal model.

However, the predictive coding theory is not only useful when describing low-level brain functions but might also have important application in the study of social interactions. In this sense, recent accounts have used this framework to try to explain interpersonal processes (Bolis and Schilback, 2017; 2020a) and even culture (Veissière et al., 2020). The understanding of the brain as a prediction-making machine might explain the way different sources of information, from interceptive and exteroceptive inferences (*Figure 2.9*) balance their value and complexity (Fotopoulou and Tsakiris, 2017; Bolis and Schilback, 2017; 2020a). In other words, people in social interaction first deal with their own different high-level inferences regarding distinct sources of predictive mental frameworks, which are simultaneously interacting with motor control and autonomic control (salience network). This later constitute an explicit response also perceived by other agents, and results into an interaction that updates the environment. This idea assumes that socio-cultural interchange, with an emphasis in social interaction, as well as learning or sensorimotor activity can be all considered as mutually interacting adjustments between a species and the environment they interact with (Bolis and Schilback, 2018). Of course, all these layers, as well as the information in them, loop back to the higher-level layers, updating the prior models of reality where new active predictions are consequently coded (Bolis and Schilback, 2020b). The authors call this a “*dialectical attunement*” (Bolis and Schilback, 2018), and this constitutes a conceptual basis where constructs of “self” and “other” connect in a dialectical interconnection between and interdependent modulation between internalization and externalization (Fotopoulou and Tsakiris, 2017; Bolis and Schilback, 2017; Bolis and Schilback, 2020a).

Other recent explanations of predictive coding framework on social influences and culture follows the same principle (Veissière et al., 2020). These authors call this *Thinking through other minds*. Here, predictive coding and active inference explain the force of the individual in a species within a circular causality framework where the individual has the power to adjust reality as they adjust itself. In other words, the agent learns the patterns and regularities of the environment, but this environment learns the agents’ beliefs through repeated interaction in return. Note here “environment” is understood as a general exogenous reality that can be social (other agents) or simply physical. The authors of the dialectical attunement hypothesis (Bolis and Schilback, 2018) have recently remarked in a comment the similarities between the two views (Bolis and Schilback, 2019) claiming internalization is explained as a construction of the model of the world by the individual, referred as predictive coding, and externalization is considered the joint transformation of the environment by the agents (active inference).

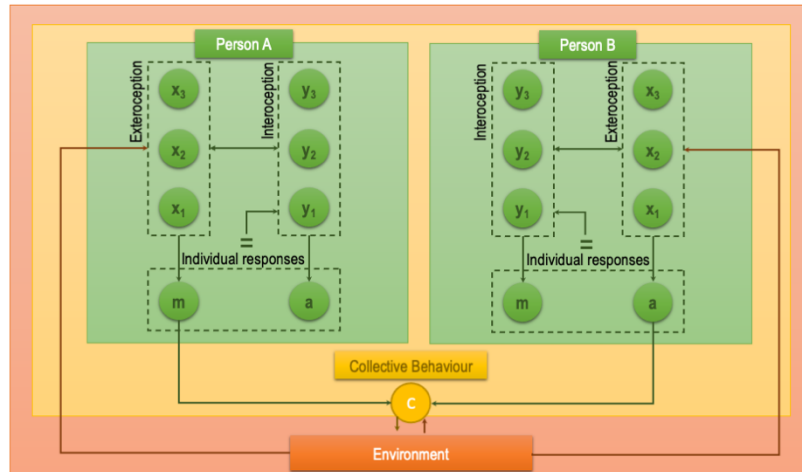


Figure 2.9: Bayesian framework for the study of interpersonal process during social interaction. Each individual, in red, has its own generative model, tracking two distinct models, interoceptive and exteroceptive tracking bodily and environmental phenomena respectively. Autonomic (*a*) and motor control (*m*) individual responses source are probabilistic translations from previous predictions, and then collective behaviour is seen as a non-linear fusion. Finally, environment serves as a provider of modulatory influence back to each individual's model of the situation (adapted from Bolis and Schilback, 2017).

Importantly, the view of the brain as an inferential machine that proposes predictive coding framework, has its foundation in the use of computational models to explain how the brain makes such inferences. In the domain of learning, one of the most used modelling frameworks is RL, which we are about to review in the next section and is one of the main topics of the present work. Predictive coding is consistent to certain principles of RL (Sutton and Barto, 1998; Dayan and Daw, 2008), where agents update the states of the environment. The difference is while in predictive coding, the Bayesian updating process is influenced mainly by the reduction of surprise, the RL proposes the update happens because of valuation of rewards, in order to choose the right course of action. In fact, given that both frameworks conceptualize similar phenomena, it is likely both computational models will merge soon at some point with the proposition of different modifications to the computational models (Friston, 2018). For instance, this is already happening in computer sciences using a predictive coding as a way of weighting rewards in RL (Lu, Tiomkin, Abel, 2019).



### 2.3.2. Models of Reinforcement Learning

RL is one of the most influential frameworks capable of describing how agents interact with the environment, and how this relationship is guided by reward. RL is centred on the mechanistic nature of behaviour based on learning-related parameters. Indisputably, using mathematical models to describe learning and learned outcomes is a very smart way of making predictions about how an agent, human or non-human, will behave. RL serves to that purpose, and its variety of algorithms allow capturing different reward-driven cognitive phenomena.

Until today, RL has demonstrated to be an incredibly useful way of operatizing certain reward-related computations in humans, and its use to explain certain aspects of decision-making is still the source and the tool of fascinating science. The purpose of this section is a general introduction to the framework of RL and its algorithmic construction that we believe is necessary to have a general understanding of the different implementations inside our research. This is critical in current thesis, as RL will be applied to explain the expectations on others' behavior. Indeed, there is evidence suggesting social reward plays a role on shaping the value-based attention in sensory processing (Anderson, 2016) and even fast-learning (Goldstein and Schwade, 2008). In addition, there is a growing body of research claiming an existence of a spatial-temporal signal overlapping or a common neural circuitry that processes monetary and social rewards (Izuma, Saito and Sadato, 2008; Oumeziane, Schryer-Praga and Foti, 2017; Kim and Anderson, 2020). Under this assumption, the mechanisms underlying learning in social situations could be described using similar approaches (e.g., RL) than those applied to other reinforcers such as money.

Very basically, RL is learning to maximize reward. Most of RL methods follow a Markov Decision Process (MDP; Howard, 1960) that try to learn the best action to take given the current state of the world. The model is understood by the following tuple or list of components  $\{S, A, P, R\}$ :  $S$  is the set of states ( $s$ ) that the process can move through.  $A$  is the set of actions ( $a$ ) that an agent can take in each  $s$ .  $P$  is the transition function ( $P: S \times A \times S \mapsto \mathbb{R}$ ) that describes the given current  $s$  and  $a$ , and the probability of reaching the next  $s$  ( $s'$ ).  $R$  is the reward function ( $R: S \times A \mapsto \mathbb{R}$ ) that describes the reward received when an  $a$  is taken in  $s$ . Both  $P$  and  $R$  functions, do not depend on information coming prior to the current  $s$ , which means any prior information must be included in the current  $s$  representation.

Of course, the agent can choose a particular course of action. In RL this is the same as saying choosing a policy ( $\pi: S \times A \mapsto \mathbb{R}$ ) that describes the probability of choosing  $a$  in  $s$ . When these policies ( $\pi$ ) are deterministic ( $a$  determined by  $s$ ), we can express the  $\pi$  function as  $\pi: S \mapsto A$ .

Finally, we denominate  $Q$  to the state-action value function ( $Q: S \times A \mapsto \mathbb{R}$ ), which represents the value of  $a$  in  $s$ , which is influenced by two distinct components. First, the reward ( $r$ ) received after performing  $a$ . Second, the predicted future  $r_{t+1}$  that the agent expects after the resulting state. It is important to note that sometimes values are expressed only in terms of the state-values ( $V: S \mapsto \mathbb{R}$ ), which can relate to the  $Q$  value as the maximum state-action value of the current state-value. That is to say,  $V(s) =$

$\max_a Q^\pi(s, a)$ . Therefore,  $Q^\pi(s, a)$  would return the state-value  $V(s)$  given a certain  $\pi$  that tries to maximize its  $r$  in next state.

Consequently, two components, the  $r$  received from  $a$  and the  $r$  expected in the future from the resulting  $s$ , can be seen in the following equation, known as the Bellman equation (Bellman, 1957), which assumes a deterministic policy, and is controlled by a discounting factor ( $\gamma \in [0,1]$ ) that prevents the expected values from going to infinity (since the agent keeps accumulating reward). We can adapt the equation using  $V^\pi(s)$  :

Equation 2.1

$$V^\pi(s) = R(s, a) + \gamma \sum_{s'} P(s, \pi(s), s') V^\pi(s')$$

As well as using  $Q^\pi(s, a)$ :

Equation 2.2

$$Q^\pi(s, a) = R(s, a) + \gamma \sum_{s'} P(s, a, s') Q^\pi(s', \pi(s'))$$

Thus, we consider the optimal  $\pi$  would be the chosen  $a$  selected that maximizes the  $Q$  value. However, here we encounter a vicious cycle:  $\pi$  depends on the  $Q$  function, and the  $Q$  function depends on  $\pi$ . As mentioned before, sometimes the best  $\pi$  will be *exploration*, when the environment is unknown, whereas when environment is relatively certain or sufficiently known, *exploitation* can be the optimal policy.

By means of searching an adequate  $\pi$ , Howard (1960) proposed what is known as a “policy iteration”, where the agent computes the new policy for all states with the following equation:

Equation 2.3

$$\pi(s) = \arg \max_a Q(s, a)$$

This is widely known as a *greedy policy*, as the agent simply selects the highest valued  $a$  possible at every  $s$ , and if  $\pi(s) \neq \pi'(s)$  the agent will always try to increase the  $Q$  value.

Equation 2.4

$$Q^\pi(s, \pi'(s)) > Q^\pi(s, \pi(s))$$

Sutton and Barto (1998) proposed another method, “value iteration”, which turns the Bellman equation into an update rule over all actions.

Be that as it may, determining  $\pi$  might not be as straightforward in humans and, also, we are assuming  $R$  and  $P$  are known. In other words, Bellman equation assumes the agent knows all the consequences of the actions taken ahead of time, while this is rarely the case. For instance, imagine a social setting, where humans constantly update their beliefs and expectations based on the change in the environment (by  $a$  of the other agent). In this situation (and in fact, in most of real-life settings) there is a high degree of uncertainty on

how reward will change on time and whether new states will appear. Therefore, we assume that what is known is  $s$  and the chosen  $a$ , and then the observed new  $s'$  for the received  $r$ .

One alternative to this is the model-based RL (Sutton and Barto, 1998) where the agent builds an explicit model of the world. However,  $P$  can become a very large and complex function, sometimes requiring an impractical amount of exploration to have a competent model. Because of this, an alternative is the *model-free* approach, also called unsupervised learning, or temporal difference learning (TDL), which estimates the value of  $s$ ,  $a$ , and  $(s, a)$  inspired to what was done in the classic associative learning Rescorla-Wagner (1972) iterative model. A learning rate guides proportionally the effect of a PE (difference between observed and predicted outcome  $\delta = r - V(s)$ ). The simplest of this model is called the “delta-rule” and only considers the immediate reward as the outcome. If  $V_t(s)$ , the value of the  $s$  in the  $(s, a)$  pair at time point  $t$ , the next iteration update  $V_{t+1}(s)$  will be defined as:

*Equation 2.5*

$$V_{t+1}(s) = V_t(s) + \alpha\delta_t$$

Furthermore, with the intention of tracking sequential dependencies and future outcomes, TDL can also use not only the reward outcome, but the predicted value of the next state, temporally discounted ( $\gamma$ ).

*Equation 2.6*

$$\delta_t = r + \gamma V_{t+1}(s) - V_t(s)$$

Going back to the Bellman equation (*Equation 2.2*), in the model-free RL, instead of learning  $R$  and  $P$ , the agent approximates the  $Q$  state-action function directly. In other words,  $Q$ , having an implicit relationship to  $s$  and  $a$ , straightforwardly represents the values that would be calculated if  $R$  and  $P$  were known.

For clarity, in *Figure 2.10* we aimed to depict a graphical representation of the already explained different parameters of a simple  $Q$ -learning iteration that will serve us to understand better the TDL. Here, we see how we are only defining the relationships to an agent, its actions and the information coming from the environment, and the observable outcomes from  $s$  and  $a$  by means of a  $R(s, a)$  function that come from after  $a$ . The agent’s computation starts with this  $R(s, a)$  that follows a PE affected by a learning rate that is used to compute a  $Q(s, a)$  that will lead to the next  $a$  given a policy  $\pi(s, a)$ . Importantly, even if *Figure 2.10* might give the impression PE as an independent component to  $r$ , in TDL it is not, as  $\delta$  is defined as the reward prediction error (RPE), the discrepancy between the reward prediction and the new information that causes a change in the prospect of reward  $Q_t(s, a)$ .

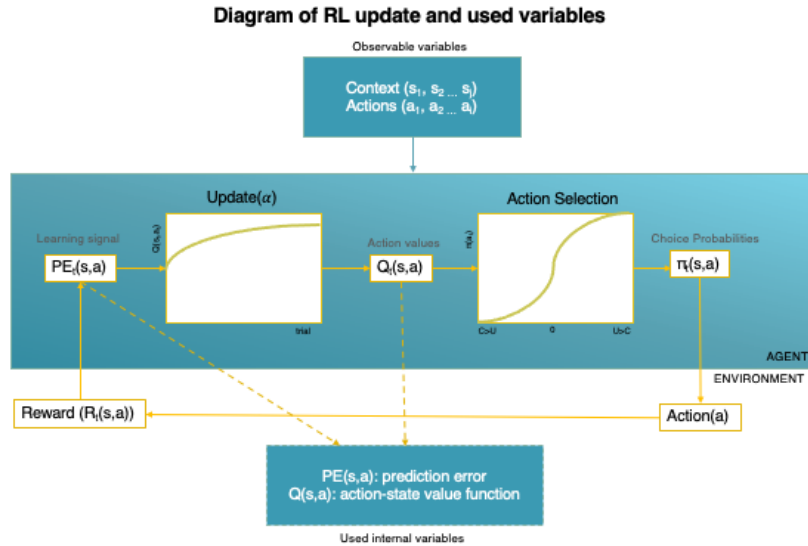


Figure 2.10: Summary diagram of the different aspects of RL framework in a simple update (author's own creation).

To calculate  $Q$  with given observations of  $s$ ,  $a$ ,  $s'$  and  $r$ , we can break down the function into two components, the immediate and future reward, considering  $a' = \pi(s')$ . Note  $Q^\pi = Q$  for clarity:

Equation 2.7

$$Q(s, a) = r + \gamma Q(s', a')$$

Thus, the delta rule translates into the same equations with the  $Q$  function.

Equation 2.8

$$\delta_t = r + \gamma Q_{t+1}(s', a') - Q_t(s, a)$$

$$Q_{t+1}(s, a) = Q_t(s, a) + \alpha \delta_t$$

Similarly,  $Q(s, a)$  is calculated after every decision and take an average over successive calculations (Rummery and Niranjan, 1994), in what is now known as SARSA algorithm.

Equation 2.9

$$Q_{t+1}(s, a) = Q_t(s, a) + \alpha \times [r + \gamma Q_t(s', a') - Q_t(s, a)]$$

Here, the updating of  $Q$  depends on the current  $s$  of the agent, the  $a$  the agent chooses, the  $r$  the agents get for choosing the action, the  $s'$  the agent enters after taking the action and, finally, the next  $a'$  selected based on policy  $\pi$ . However, this algorithm, and its focus on exploration, can slow down the learning process. Exploration means going with what could be classified as sub-optimal actions in order to have a better knowledge of the state space. An agent will have  $Q$  values learned based on its observations after a limited exploration. In SARSA, the value of the next state ( $V(s')$ ) is approximated by a sample

$Q(s', a')$ , and even though these two values will tend to converge over time (if we assume  $\pi$  tends to be optimal), there will be times where  $V(s') \neq Q(s', a')$ , and they will be based on incorrect estimates any time  $a' \neq \underset{a}{\operatorname{argmax}} Q(s', a')$ .

A common approach to allow the exploration is the soft-max algorithm, where the agent follows the following policy:

*Equation 2.10*

$$\pi(s, a) = \frac{e^{Q(s,a)/\tau}}{\sum_{a_i \in A} e^{Q(s,a_i)/\tau}}$$

Note we are denoting by  $i$  the iteration. In this equation, temperature ( $\tau$ ) is a parameter that controls the randomness of the exploration. Common practice is to initialize with high values of  $\tau$  to gradually decrease it over the course of learning, so the agent can focus on later times more on the high-value actions given by  $Q$  values. As far as  $\tau$  decreases over time and approximates to zero ( $\tau \approx 0$ ), which will tend to greedy policy.

*Equation 2.11*

$$\tau \approx 0 \Rightarrow \pi(s, a) \approx \underset{a}{\operatorname{argmax}} Q(s, a)$$

It is also common practice in neuroscience (Wilson and Collins, 2019) to use the inverse temperature parameter  $\beta$  rather than the  $\tau$ , which would indicate the level of stochasticity in the choice. Therefore,  $\beta$  ranges from  $\beta = 0$  when it is random responding and, on the contrary,  $\beta = \infty$  when it is deterministically the highest value option.

Despite all the policy-based updates, Watkins and Dayan (1992) proposed an off-policy learning, called  $Q$ -learning that assumes the agent will follow the optimal policy in future states. SARSA will remove the assumption waiting for the observation of the action that takes place.

*Equation 2.12*

$$Q_{t+1}(s, a) = (1 - \alpha)Q_t(s, a) + \alpha \times [r + \gamma \max_{a'} Q_t(s', a')]$$

Interestingly,  $Q$ -learning lacks representation of state-value estimates and is therefore insensitive to passive states, when acting like conditioned reinforcers. It is important to note that SARSA and  $Q$ -learning will produce the same results if the agent is acting optimally in respect to the  $Q$  values.

One of the most used architectures in neural modelling is the Actor-Critic (AC). Here, there is a separation between the action values associated to environmental responses, identified as the “critic”, and the agent’s used policy, the “actor”. Contrary to  $Q$ -Learning or SARSA, where the policy is directly based on the action values (see *Equation 2.3* and *Equation 2.10*), in AC the agent learns two distinct functions independently, the first one mapping from *states to values* ( $C: S \mapsto \mathbb{R}$ ) and the other one, mapping *states to actions* ( $K: S \times A \mapsto \mathbb{R}$ ). Nonetheless, the output of the critic is used to update both  $C$  and  $K$ .

$$\Delta K(s, a) = \Delta C(s) = \alpha \times [r + \gamma C(s') - C(s)]$$

Even though in reality there will be essentially the same result as in SARSA, because in AC the  $\Delta C(s)$  is calculated with the states the agent is visiting, and the end outcome of  $K$  will be a function (same as  $Q(s, a)$ ) that will track the preferable actions in each state.

However, in neuroscience, sometimes having two distinct functions have its advantages, because even though it is a learning process, having the possibility of two distinct learning rates ( $\alpha_c \neq \alpha_k$ ) can sometimes add explanatory power.

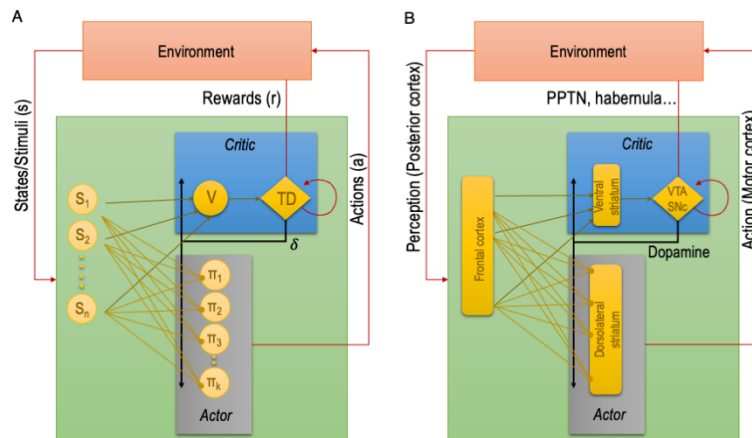


Figure 2.11: (A) Classic actor-critic algorithm, where environment provides two signals into the system, the current state,  $s$ , and the current reward,  $r$ . The actor maps between  $s$  and action probabilities  $\pi(a|s)$ , the critic maps between  $s$  and values,  $V$ . The value of  $s$  provides input to temporal difference (TD) module that integrates  $s_t, s_{t-1}$  (highlighted in the feedback red arrow), and the current  $r$ , to compute the prediction error signal ( $\delta$ ). (B) Proposed mapping of the different architectural modules in neural substrates in the cortex and the basal ganglia, assuming the prediction error is computed in the ventral tegmental area (VTA) and the substantia nigra pars compacta (SNc) dopaminergic nuclei, based on  $s$  values incoming from ventrostriatal efferents (habenula, PPTN). (adapted from Takahashi, Shoenbaum and Niv, 2008)

Even if this set of algorithms were originally conceived for computer science and machine learning, the use of different models to predict the activity of different regions in the brain has been incredibly successful since the discovery of the dopaminergic neurons tracking the RPE at the end of the last century (Schultz, Dayan and Montague, 1997). The study of brain activity with RL models have made outstanding progress to explain different learning processes happening in the brain.

In fact, some authors have established similarities between the actor-critic algorithm and the interdependence of different regions of the cortex. For example, Figure 2.11.A shows the basic actor-critic algorithmic architecture from RL and Figure 2.11.B maps these same modules of the algorithm to the different brain regions (Niv, 2008; Takahashi, Shoenbaum and Niv, 2008). A recent review suggests how different state and action representations processed by different, anterior as well as posterior, regions of the brain

seem to interact with striatal reward circuits (Averbeck and O’Doherty, 2022). For instance, recent evidence has identified dissociated action and state value representations in the cortex while projecting the calculation of both distinct RPE to the dorsal and ventral striatum (Colas et al., 2017). Another recent evidence even suggests a functional hemispheric asymmetry regarding learning driven by a PE (Santo-Angles et al., 2021). Interestingly, social neuroscience studies have consistently showed evidence relating cooperative behaviour with brain areas involved in reward-based learning (Decety et al., 2004; Rilling et al., 2002; Rilling et al., 2004). Precisely, this has also been the case with conformity, where a PE has been related in terms of norm-learning deviation (Klucharev et al., 2009).

The framework of TDL assumes there is an adjustment on the way we learn that is linked to how the reward system works, as we as learners tend to seek the maximum cumulative reward (Cohen and Ranganath, 2007). Depending on the outcomes, some behavioural patterns are reinforced while errors or unexpected outcomes call for adjustments in behaviour. This is what TDL assumes as a PE. Agents update their beliefs and behaviours depending on the outcomes which deliver a rewarding information or an error signal which calls for adjustment. Research using TDL have identified the update in the beliefs is also related to an update in the value of the future events. Negative RPE induce conflict and a trigger for a state that calls for adjustment. In the social domain, or more concrete, in conformity, which is the phenomenon studied in the present thesis, the computation to adjust to others requires three different substrates. First, a shared norm about the expectation; second, a control system that calculates deviations to this norm; and, finally, the capacity to imagine this from the other person’s perspective (Montague and Lorenz, 2007). Therefore, in order to adapt our behaviour to others, the brain requires not only signals linked to reward systems to compute value (Zaki, Schirmer and Mitchell, 2011) but also need certain signals related to conflict monitoring and a way to integrate such information. In fact, there is evidence that suggest people compute deviations to the norm, similar to what the RPE does in a learning model (Klucharev et al., 2009). However, there is also evidence suggesting the way we process social stimuli is not only based on reinforcement but is also mediated by value associations mediated by emotional preferences (Evans et al., 2011).

Therefore, as predicted by RL and its similarity to conformity mechanism, agreement increases the activity in the striatum (Campbell-Meiklejohn et al., 2010), which, as already shown, is related to the reward system. Thus, a more recent meta-analysis (Wu, Luo and Feng, 2016) gives a more detailed insight on the anatomy of implicated areas: Agreement and predictable behaviour coherent to norm activates VStr while disagreement, deviations from group norms as well as unfairness, engage dorsal posterior MFC (dpMFC) with anterior insula (AI). Interestingly, there is evidence using TDL relating mid-frontal theta activity (generated in PFC) in conflict and PE (Mas-Herrero and Marco-Pallarés, 2016). This study suggests theta activity might serve to temporally encode different valuations and unsigned prediction errors as well as variations in learning rate (Mas-Herrero and Marco-Pallarés, 2014).

In the present thesis we propose to use a TDL to understand the predictive learning associated to the behaviour of others in a conformity scenario. The same way RL framework delivers a great explanatory capacity on reward guided learning, we will review in the next section different theories trying to explain conflict monitoring and

cognitive control, which are, as we have already argued, crucial in the behavioural adjustment associated with conformity.



### 2.3.3. Cognitive control and conflict monitoring theories

As introduced in the previous section, the conscious adaptation to conform relies not only in a reward guided learning process, but also in a conflict monitoring system that also influences action selection. However, the way of how the brain addresses such computations is yet an ongoing debate.

Jonathan Cohen (Cohen, 2017) discusses in the book *The Wiley handbook of Cognitive Control* how everyone seems to agree that the fundamental function of cognitive control is the reduction of interference from different processing streams that might be in conflict. In other words, control is engaged in presence of competing processes because the allocation of control to one process inevitably involves an opportunity cost for others. The author states humans have a remarkable flexibility to rapidly configure and execute a diversity of behaviours if they can be relevant to reach a certain goal. This ability requires a variety of activation of control representations which serve as internal context and, also, handling the processing of other parts of the system to produce goal-relevant behaviour (Cohen, 2017). These context representations are agreed to be the function of the PFC (Miller and Cohen, 2001). As we already mentioned in a past section, this region includes dorsolateral, ventrolateral, and orbitofrontal cortex, and regarding cognitive control, a recent review (Menon and D'Esposito, 2022) identifies that it plays a key role in different mechanisms such as the comparison between sensory input and self-referential thinking and monitoring (e.g., internal goals), top-down and bottom-up reorienting and strategy updating processes, the suppression of inappropriate action selection or as an integration hub to shift, coordinate and accommodate resulting computations from different networks.

An important meta-analysis of fMRI studies showed evidence to functional interactions between the monitoring activity of the posterior medial prefrontal cortex (pmPFC) and the regulatory processes happening in lateral PFC (lPFC) which serve to performance adjustment mechanisms. In an important meta-analysis review (Ridderinkhof et al., 2004), the authors identify different areas that relate to different experimental paradigms such as pre-response conflict, decision uncertainty, response error and negative feedback.

In another recent large-scale (289 studies) meta-analysis (Wu et al., 2020) of fMRI studies exploring executive control, working memory and decision making, some networks were described to participate in the *Cognitive Control Network*:

- a) *frontoparietal network* that includes the frontal eye fields, the dlPFC, the intraparietal sulcus extending to the superior parietal lobule, the supplementary motor area (SMA) extending to the ACC, and the anterior insular cortex (AIC).
- b) *cingulo-opercular network* that includes ACC/SMA and AIC.
- c) the *striatum*. The same study relates the activation of this network to the level of uncertainty in the environment.

For instance, taking the psychological feedback processing, Kiehl et al. (2000) as well as Menon et al. (2001) found there is a correlated activation on ACC in presence of error or incongruent stimuli. This evidence has motivated the consideration of ACC as the main generator of an error signal (Botvinick et al., 2001). In fact, the first proposal of the neuroanatomical function of the PFC in cognitive control comes from this finding.

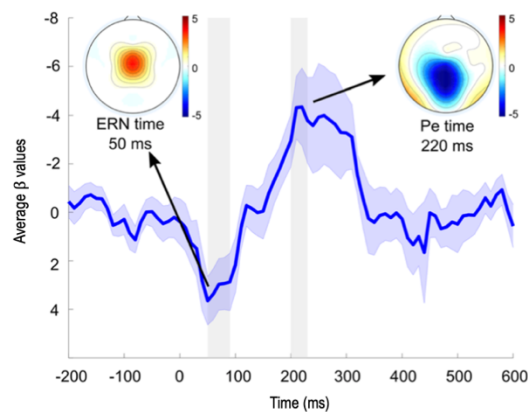
*Cognitive control theory* (Botvinick et al., 2001) refers to the ability to guide actions and thoughts and link them to intentions, throughout two distinct processes: regulation and evaluation. On the one hand, regulation requires a top-down control to adjust to task demands, allocate the necessary attention, monitor the maintenance of the task to rules in the context and prepare to override inadequate responses. On the other hand, evaluation includes a performance monitoring that alarms on mistakes or conflict, signalling the urgency to change and providing feedback about the need for control. In its first seminal paper, Botvinick et al. (2001) used computational models to describe an ACC-mediated conflict monitoring system, which is evaluative. In their proposal, ACC evaluates current control demands and signals when more control is needed, as in high conflict situations.

However, even though fMRI provides important information on the different regions involved in distinct functions of cognition, its temporal resolution is low, in the order of seconds. In contrast, EEG and MEG techniques provide a much better perspective on the time and frequency related dynamics. As we know from a previous section, ERP are localized patterns of activity happening at the continuous presence of a stimuli (i.e., event). The signal registered in an ERP constitutes a waveform which can reflect the ongoing synaptic activity relative to the mental processing happening under a particular experimental condition. The joint venture between these two techniques, EEG and fMRI, has been incredibly fruitful recognizing different aspects of performance monitoring and feedback related processing that we will try to address in this section.

Neural components of error have been described broadly in EEG signal (Falkenstein et al., 1991; Gehring et al., 1993). The most well-known one is the as error negativity (Ne; Falkenstein et al., 1991) that later was known as error-related negativity (ERN) (Gehring et al., 1993; Bernstein, Scheffers, Coles, 1995; Holroyd and Coles, 2002), a negative deflection in the voltage of EEG signal in the commission of an error. In fact, ERN is defined as a response-locked mismatch signal. Studying this response, Michael Coles, and Clay Holroyd (Coles, Scheffers and Holroyd, 2001) proposed that there had to be a system devoted to error detection that, when engaged, elicited the ERN. This theory was called *mismatch theory* and assumed a response-selection model of the ACC, considering it a filter that learns to what control mechanism transfer the authority to control. Based on this theory, Holroyd and Coles, (2002) proposed a reinforcement learning ERN RL theory in which the basal ganglia (BG) in the brain oversee monitoring the information coming from the sensory system and from self-generated action and compares this information to what has previously learned. Here, the theory assumes learning follows a TD error that updates weights between candidate responses. This context update provokes consequently an acquired expectation which might elicit, or not, a reinforcement. Put in other words, when information comes from external and internal sources and is congruent to what was expected, it produces a reward response through the DA streams from midbrain's VTA to VStr. In this scenario, when DA neurons signal worse than expected event, ACC inhibits their action and, hence, the ERN signal appears.

Error detection systems work by means of a PE and a monitoring system (Holroyd and Coles, 2002) that uses distinct signal deflections, both positive and negative, as a way of connecting different pathways involved in the attention, memory, and valuation processing of the stimuli. Therefore, if a prediction is correct, it will be followed by an associated reward (Proudfit, 2015; Sambrook and Gosling, 2015; Holroyd and Umemoto, 2015; Walsh and Anderson, 2015; Wischniewski and Schutter, 2019; Kirchner et al., 2020), and when a mismatch is present, the error detection system will elicit a PE

(Holroyd and Coles, 2002; Holroyd, Pakzad-Vaezi and Krigolson, 2008; Walsh and Anderson, 2015; Kirchner et al., 2020) (*Figure 2.12*). Yeung, Botvinick and Cohen (2004) proposed another explanation on error signal and ERN that supposed an innovation, as well as a distinction from previously explained theories. They proposed ERN was not an error signal elicited by the presence of conflict, as previously theorized, but almost the opposite. According to this theory, there is a continuous monitoring of the stimulus and ERN reflects the moment immediately after the detection of error. In other words, ERN is associated to the input, and not the output, of a process of conflict monitoring and error detection system. This conceptualization allowed the authors to relate ERN with the anterior N2 component (i.e., negative wave that peaks at 200-350ms post-stimulus found in anterior scalp locations).



*Figure 2.12: Modulation of error related EEG activity by error awareness and confidence in accuracy judgment. Note the scale is in regression beta values and not voltage. (adapted from Kirchner et al., 2020)*

Furthermore, more recent research also points towards a general N2 negativity elicited by general task-relevant events (Holroyd, Pakzad-Vaezi and Krigolson, 2008) autonomous of them being correct or incorrect. In this same study, authors propose the correct feedback related to positivity to be identified as reward positivity (RewP), an EEG index of a neural process that reduces the amplitude of the N2 that is supposed to reflect an evaluative process irrespective of its valence. This observation is consistent to evidence suggesting that the feedback ERN (fERN) amplitude is modulated significantly more in correct feedback than in error feedback (Eppinger et al., 2008; Hewig et al., 2008; Holroyd and Coles, 2008; Potts et al., 2006). In other words, the authors suggest RewP reflects an appraisal of information that predicts future reward. These authors propose, therefore, that feedback related to fERN and N2 are the same component, and they should be generated in the same brain region, most likely in the dACC (Holroyd, Pakzad-Vaezi and Krigolson, 2008).

Before going any further to the more recent theories of cognitive control, it is important we pause here to explain about a specific signal that is especially relevant in our studies about conformity. In any social interaction, also in conformity, we adjust our behaviours based on what we observe and, hence, we integrate not only our actions but also the actions we are witnessing from others which obliges us to adjust accordingly. Throughout the years, expert researchers in cognitive control have been very interested in the way our brain processes information during the observation when it requires the encoding of a PE.

Consistently, the trace in the EEG signal related to such computation, visible in ERP studies, is identified as a feedback-related negativity (FRN), which appears around 250ms after negative feedback onset (Miltner, Braun and Coles, 1997; however, see above for an interpretation of FRN as an N2, Holroyd et al 2008). FRN would be elicited by feedback while ERN is considered response locked. However, some authors (Holroyd, Pakzad-Vaezi and Krigolson, 2008) suggest both ERN and FRN share a similar distribution, time course, morphology and functional dependencies and propose this negative deflection to be the same phenomenon. Interestingly, in a study where researchers compared the component structure of a response-related ERN with a reward prediction violation or stimulus-related FRN share a common central factor, most likely the ACC generator, and might suggest certain overlapping, whereas FRN would contain a second more anterior factor (Potts et al., 2011). This component was pinpointed to be part of a RPE and represents a valuation of the outcome (Holroyd and Coles, 2002). Incidentally, these same authors (Holroyd, Pakzad-Vaezi, and Krigolson, 2008) describe, right after the FRN, a correct-related positivity, a positive deflection happening when feedback is aligned to expectation.

In a recent meta-analysis (Sambrook and Gosling, 2015) the authors distinguished between a component responding to valence (FRN) and another component signalling the volume and the size of the RPE (named RPE-FRN). This later component would appear at 270-300ms latency and would capture the strongest effects of magnitude and likelihood.

In terms of oscillatory dynamics, in the time range of both, ERN and FRN, a theta band enhancement has been consistently found associated to the activity in mPFC (Marco-Pallarés et al., 2008; Cavanagh, Cohen and Allen, 2009). In fact, evidence identified the role of theta band in the interaction between the error processing system in mPFC, with the cognitive control systems in IPFC (Cavanagh, Cohen and Allen, 2009). The role of theta in this interaction was detailed later as carrying information on the degree of negative as well as positive RPE (Cavanagh et al., 2010). Later, using a RL model, evidence was found implying midfrontal theta and FRN was modulated by the absolute value of RPE (probably associated with surprise), and variations of this component were associated with participants' learning rate (Mas-Herrero and Marco-Pallarés, 2014).

Back to the different explanations of cognitive control, recently some of the authors of cognitive control theory proposed the *expected value of control* (EVC) theory (Shenhav, Botvinik and Cohen, 2013). They suggest dorsal ACC estimates a value, the EVC, that determines the net amount of control a task demands using the information trade-off between reward and costs.

In another recent development, an evolution of the mismatch theory or response-selection model (Coles, Scheffers and Holroyd, 2001) has been proposed: the *response-outcome* (PRO) theory (Alexander and Brown, 2010). This proposal takes the performance monitoring from response-selection model and turns it into an actor-critic architecture, that we already explained in the previous section. Here, predictive signals drive approach or avoidance behaviour while discrepancy updates action plans. However, PRO models learn to predict the outcome given a planned response, regardless of valence, and indicates discrepancies. Importantly, PRO theory refers to the mPFC (Alexander and Brown, 2011) as an action-outcome predictor, and the role of ACC is detecting the

discrepancies between the actual and the predicted outcomes or, as the authors identify, stimulus-action-outcome predictor. Very recently this proposal has been amplified with the addition of the expectation of effort and reward (PRO-Effort) observed in mPFC and dlPFC to propose a hierarchical error prediction that explains the interaction between those regions (Vassena, Deraeve and Alexander, 2017). Also, another recent addition has been proposed that identifies the ACC as computing error and prediction signals that elicit proactive and reactive control (PRO-Control; Brown and Alexander, 2017). Additionally, the same authors have presented evidence in favour of PRO model over EVC in a comparative study (Vassena, Deraeve and Alexander, 2020) and they have claimed it is more open to integrate new developments and that accommodates the higher amount of evidence (Vassena, Holroyd and Alexander, 2017). However, to this date it seems the choice of the best explanatory model of the cognitive control is still an ongoing debate and far from being over.

#### 2.3.4. Performance Monitoring System and associated EEG components

Evidence suggests a non-overlapped difference between PE brain mechanisms, inside performance monitoring (PM) systems, which are associated to the FRN and the following initiation of other distinct endogenous responses such as processes inside the P300 component, sensitive to goal relevance (Walentowska et al., 2016) or outcome value (Luque et al., 2017). P300 is one of the most widely studied endogenous components on ERPs, that is, potentials which are modulated not by the attributes of the stimulus *per se* but by the reaction to it. This component is a positive deflection of the voltage at a latency starting around 300ms and going through the 500ms and beyond. This component can be identified equally as P3 or P300 and was first described in the early sixties (Chapman and Bragdon, 1964), linked to attention (Kahneman, 1973) and being segmented in two subcomponents, P3a and P3b (Gazzaniga, 2000; Polich, 2003). These two components present different topographic distributions and latencies (Polich, 2007), as we will address in detail later in this section.

In *Figure 2.13* we have a representation of the evolution of the interpretation of this component and the brain representation of the attention/memory relationship of P300 and its subcomponents. Incidentally, recent research shows evidence of an individual difference variability in this signal related to the style of the decision maker whether they inhibit or not the processing of new information rather than relying on previously memorized resources (Achtziger et al., 2014).

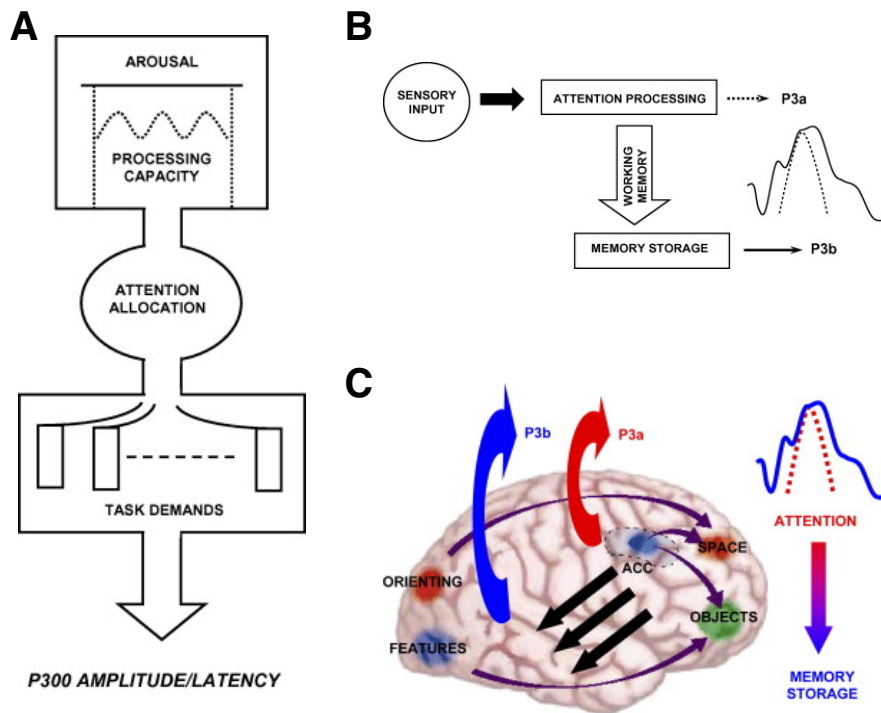


Figure 2.13: A is a schematic figure representing the framework that was used to understand the effect of attentional resources to P300 (Kahneman, 1973), which relates arousal levels to the amount of processing capacity available to the allocation of attention to the ongoing tasks. B represents the update of the framework by Polich (2003) Where sensory input is processed from attention-driven working memory changes producing the signal component of P3a while the memory updating operations in temporal/parietal lobes sourced the P3b. C illustrates a representation of brain activation patterns that are associated to the different subcomponents of P300, starting at fronto-central P3a and evolving into a parieto-temporal P3b (adapted from Polich, 2007).

Back to the definition of the different subcomponents of the P300, the novelty related component, P3a, presents a fronto-central distribution and shows a higher amplitude the higher the novelty of the stimuli. It is related to the attention allocation. On the other hand, the context-updating processing and memory storage of this novelty-induced changes is signalled by the parietal P3b, which after feedback, has been found to be related to motivation to engage in the activity (Riepl et al., 2016). Higher P3b amplitudes are related to the target identification inside the working memory (WM) updating process (Rac-Lubashevsky and Kessler, 2019). In addition, the P3b has also been related to goal-relevant information (Gray et al., 2004).

In a meta-analysis conducted across 75 studies, van Dinteren, et al., (2014) hypothesized that P300 amplitude might reflect an index of cognitive capacity while P300 latency might index brain speed or efficiency. Incidentally, San Martin et al., (2013) differentiated this component from FRN, stating that in contrast to FRN, P300, and its subcomponents predict behavioural adjustment on subsequent trials. In fact, there is evidence suggesting the P3a to be involved in strategy switching in decision making processes (Zhang et al., 2013). It is important to note these components, in conjunction to the previously explained FRN, index a performance monitoring system inside the brain's cognitive control that encompasses stimulus processing, response generation and feedback evaluation. In Figure 2.14, Ullsperger et al., (2014) present not only P300

components, but earlier components introduced in previous sections providing an integrative vision of their individual topographies and latencies.

According to evidence (Ullsperger et al., 2014), first, stimulus processing starts with a negative deflection in frontal areas that is followed by a P3 component different when it is frontocentral (which computes perceptual decision making prior to response) than when it is parietal (which associates value to the decision-making process). Secondly, error in response generation presents, first, an ERN followed by frontal (early Pe) and later parietal (late Pe) error positivity. Lastly, the feedback evaluation process starts with an FRN and followed by a P3a related to attention and ending with a P3b in what is understood to be a fronto-parietal network related to executive functions (Sauseng, et al., 2005). Incidentally, interesting evidence using RL suggests FRN indexes PE only when the learning is active, and not when learning is merely observational. In other words, the proposal suggests in P3a, linked to attentional reorienting, the effect in active and observational learning is comparable whereas the earlier FRN and the late P3b, related to stimulus value update, are significantly larger only when learning is active, requires action selection, but not when it is merely observational (Burnside, Fischer and Ullsperger, 2019).

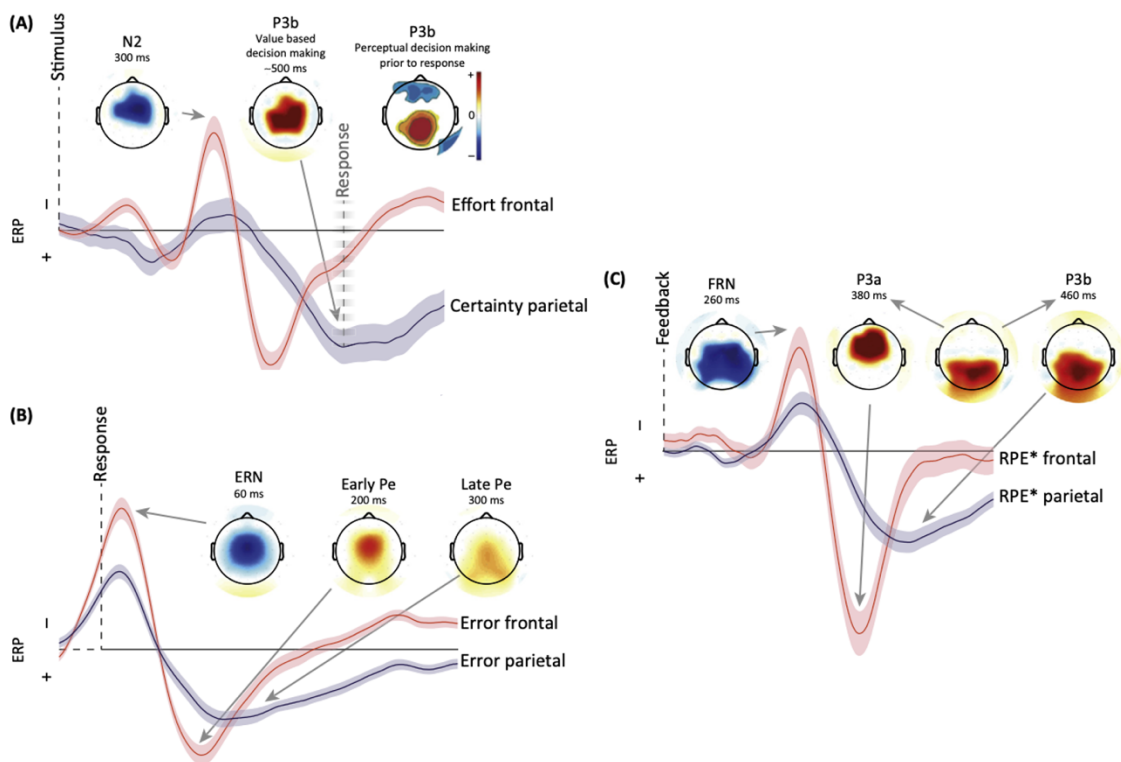


Figure 2.14: (A) depicts the schematic representation of stimulus processing and its topographic location followed by the subcomponents of the different P3b according to its location; (B) represents the response generation which starts at an early error related negativity (ERN) followed by Error Positivity (Pe); (C) illustrate feedback evaluation and P300 components which start frontal and end up parietally positive (adapted from Ullsperger et al., 2014)

In summary, as reviewed in this and the previous section, the brain utilizes different PE mechanisms that activate executive functions ingrained in a fronto-parietal network used to process, respond, and evaluate one's actions and its outcomes.



As we already mentioned in this introduction, these cognitive control and performance monitoring systems have a fundamental role in any social environment, where the uncertainty of other's actions requires a constant update of the representation of the environment. Consistently, conformity also requires an adaptation to the environment, represented by a partner's choices, and the integration of different sources of information and value functions that will, correspondingly, result in a behavioural adaptation. ERP gives us precise temporal information on the relationship of stimuli and response and its topography on the scalp. For instance, in a recent ERP experiment relating the previously mentioned components, the authors (Guo et al., 2019) studied conformity using the induction of an error in an online review evaluation task. The task induced a comparison between a participant's own review to what allegedly was other reviewer's ratings. The evidence showed incongruence with majority in participants elicited a more negative FRN and a less positive P300. These findings suggest cognitive computations in conformity could follow patterns described in feedback related processing as well. However, as we already discussed in previous sections of this introduction, in this research participants are assumed that feel the presence of an actual counterpart and, hence, the social influence is merely induced. We will dive deeper into the limitations of such experimental paradigms in the last section of this introduction.

## 2.4. Research paradigms for Conformity

In previous sections of the introduction, we have addressed different important aspects that define the theoretical foundation of the studies that we are presenting in this thesis. Given the diversity of the questions covered until now and the wide conceptual framework used, we will start this final section by briefly summarising the different topics that we addressed in previous sections.

In the first part of this introduction, *What is Cooperation?*, we started by introducing the concept of cooperation diversely addressed by a myriad of disciplines. From an evolutionary point of view, and from a darwinist view, cooperation represents an anomaly. The first paradigm that was used to study cooperation were dilemmas, such as PD. Here, researchers had the chance to elevate the simplistic darwinist view and began to mathematically observe different evolutionary advantages of cooperation which resulted in the demonstration of our intrinsically biased tendency towards it, even when conditions are not rationally favouring this behaviour. Afterwards, we described how cooperation involves a set of individual compromises in favour of a common goal. One of these compromises is called conformity, which its neural correlates constitute the main interest in this thesis. Conformity has been experimentally studied from the nineteen-thirties by social psychologists and behaviourists which described broadly the different motives and influence sources behind such adjustment. This framework serves us to understand this as a complex interaction that requires the integrated function of different neural mechanisms that relate to social processing.

In the second part of this thesis, *Social cognition: brains in interaction*, were we address the most common brain networks for social stimuli processing. Here, we have identified how in order to conform to others, our brain requires the presence of different computations at the same time. To be able to conform, we need a self-referenced learning mechanism, such as PE, as well as the activation of different monitoring and control systems that enable us to encode value functions that result in an action selection that corresponds to the execution of the behavioural adaptation of conformity. Unfortunately, most of the literature that we can use to better describe such phenomena come from individual experimental paradigms which constitute a definitory limitation, as we are studying social experiences in unsocial settings. The simultaneous recording of inter-brain activity is relatively new but has been prolific in the recent years. We addressed different findings from studies coming from different neuroimage techniques that would not be possible without the ecological value of social interaction.

Later, the third part of this introduction tries to explain the different signals that are important in *Action monitoring, prediction, and learning*. We detailed and explored the RL framework and its relevant validity to make predictions about how someone interacts with an environment. Here we present evidence relating the computations happening in a TDL to interrelated activity of specific regions in the brain, such as different regions in the cortex and some subcortical nuclei in the striatum. Afterwards, we linked RPE to other computations that are guided by other PE in cognitive control and conflict monitoring as well as in performance monitoring. Research in neuroscience describing these different systems have been prolific and explained in detail different ERP components that certainly are very likely to be present in conformity such as FRN and P300 components. Importantly, very few studies have been devoted to understanding the role of learning,

prediction, and action monitoring (and their above-mentioned associated neurophysiological components) in conformity. One of the main problems when addressing this topic has been the paradigms used until now to study the brain correlates of conformity. In this last section of the introduction, we will review the research paradigms that have been used to study conformity.

Conformity has been studied in cognitive sciences using a variety of paradigms since the seminal experiments in social psychology, discussed earlier, where participants were put in settings to influence their rationality and manipulate them to conform. However, while these influential studies (Sheriff, 1935; Asch 1956) on the cognitive and perceptive distortions happening under social influence focused on the adjustment under explicit social forces (the participation of other participants in the experiments), the goals of the researchers evolved with time. Therefore, since Freedman and Fraser (1966) foot-in-the door experiment (showing that agreeing on a small request increases the likelihood to conform to larger requests), studies were focussed on other aspects of social influence (Cialdini and Goldstein, 2004). This led some authors (Cialdini and Goldstein, 2004) to develop experiments to describe the different goals behind conformity such as the goal of accuracy, the goal of affiliation, and the goal of maintaining a positive self-concept.

Be that as it may, when trying to study the neural computations behind cognitive, attentional, or learning processes in conformity, being aware of an explicit social force is key in the ecological validity of the findings. At the end, it is important to note that in the present work we are trying to uncover the neurophysiological correlates underlying such adjustment under social influences. Thus, recent paradigms from social psychology that study the source and subtleties of the social influences under the umbrella of conformity do not seem a plausible option to reach this goal. In fact, this is even more difficult when considering the needs of neuroimaging technique (e.g., large number of trials in event-related potential designs).

Luckily, conformity has been interesting to other fields where we also can get inspiration from. For instance, in the field of economics researchers (Banerjee, 1992; Bikchandani, 1992) have shown interest in this adaptation, that they call “herding”, in terms of the payoffs and trade-offs individuals get by deciding to use or ignore their own perceptive information or the “herd” information to make rational decisions. This research has been conducted mainly using voting paradigms (Anderson and Holt, 1997) that focus on the information cascades or inequality aversion. Consequently, this type of paradigm has also been translated into experiments in cognitive sciences in the form of reviewers (Guo et al., 2019). Other conformity paradigms in this field propose participants in a group to choose between options with different payoffs. Incidentally, these paradigms have shown that decisions are influenced by different perceptions of the context (McElreath et al., 2005), are tracked by probable popularity trade-off (Toelch et al., 2010) or served to categorize participants in terms of “mavericks” or “conformists” (Efferson et al., 2008). However, the problem here is similar to the one with the distinction of the goals, as experimenters are only addressing one type of preference of information, which in the brain would translate to different weighted valuation processes according to individual differences (Zaki et al., 2011). Even when this might be interesting from an experimental point of view, it would not be useful for our goals which are the study of the learning and adjustment mechanisms used by participants to value the situation.

In addition, in second-person neuroscience, and due to the technical challenges when measuring more than one brain activity at the same time, conformity paradigms have been mostly designed to use the indirect induction of group pressure, giving *a posteriori* information about previous or untrue apparent group decisions (Figure 2.15; Klucharev et al., 2009; Morgan et al., 2011; Shestakova et al., 2013; Schnuerch and Gibbons, 2015; H Zaki et al., 2011; Campbell-Meiklejohn et al., 2012; Xie et al., 2016; Liuzza et al., 2019; Overgaaw et al., 2019; Li et al., 2020; Duell et al., 2021) or in game theory paradigms such as ultimatum-games (Wei, Zhao and Zheng, 2013). These paradigms constitute to date the standard approach to study conformity in neuroimaging studies.



Figure 2.15: Conformity research paradigm for fMRI, as first proposed (Klucharev et al., 2009), and consequently replicated in most of recent studies of conformity, where participants were evoked a conflict with group ratings (adapted from Klucharev et al., 2009).

Similarly, in another study using EEG, group influence was induced in a visual discrimination task, where participants were given the opinion of the majority (Trautmann-Lengsfeld and Herrman, 2013).

As we already introduced in a previous section, game theory-based paradigms, such as PD or ultimatum game has been widely used in social psychology. These paradigms have been recently adapted to ERP studies (Bogdan et al., 2021). This study is a great proposal as people were forced to change their behaviour by an induced drift in their motivational framework. Unfortunately, participants were not in direct interaction, and they achieved such effect by alternating their role as responder or proposer.

Consistent to what we have argued in this introduction, to be able to study the cognitive processes under a social behavioural adjustment, we would assume social forces would be explicit. If a participant does not have the direct interaction with another person, how can we assure the cognitive adjustment that is made is framed inside a social computation? On the other hand, if we consider people make predictive models of other persons, how can one accurately make models and predict outcomes if they are not based on interactions between the agent and the environment (social interactions)? In the next section we will present the research aims of this thesis, which materialize these and other questions and defines the scope of the present research.





### 3. Research aims

### 3.1. Introduction

All the evidence presented in the previous introduction tried to cover the literature behind the behavioural adjustment of conformity, from its contextualization inside cooperation, to the first seminal experimental definitions and conceptualization, the neurological correlates behind this adjustment, the different aspects related to its neural anatomy, and the more specific components and computations that we can expect from EEG studies. In essence, it was reviewed how this behaviour, of social nature, is hypothesized to be organized and computed between different brain regions the brain according to what we know so far.

Briefly, as we already explained in the previous section, conformity is a behavioural adjustment referenced on the observation of another person's behaviour. This adjustment requires the prediction of other person's potential action as well as the trailing of expectancies in another person's mind. Accordingly, all this processing is guided by information coming from the environment where a tracking system is required to monitor conflict and deviation based on the anticipated behaviour. Certainly, for this purpose, the brain requires to allocate control and attentional resources on the one hand, and initiate learning guided by reward on the other, in order to end up adjusting the action selection which results on the level of conformity.

However, as also stated in the introduction, even when there is growing evidence supporting different aspects of conformity as a social computation, the hints coming out of research addressing the topic are not fully complete or have not been based on real social settings. The main goal of the present thesis is to study the neurophysiological mechanisms underlying the social behavioural adjustment of conformity and its modulation with repeated or pervasive interaction. Nonetheless, despite this general aim, we raised three specific questions that serve as pillars or research motivations in the present thesis.



### 3.2. Aim 1: To design a new experimental paradigm to study the neurophysiological mechanisms underlying spontaneous conformity and its evolution throughout repetition and learning

As previously stated, since the first paradigms in Social Psychology, especially in cognitive neuroscience, conformity has been fundamentally studied in artificial paradigms where the influence to conform is simply induced in belief (Klucharev et al., 2009). In other words, the social nature of an influence in participants is induced by the addition of an information from, apparently, social sources (i.e., a review score given by an unknown group of people). Still, although this setting proves to be an effective source of bias, is harder to defend its social nature, as it is not sourced in a real social interaction or structure. In the first specific subgoal of the present thesis we aim to develop a new experimental paradigm in which conformity appears spontaneously and evolves aided by the history of previous cooperation or lack thereof.

Because conformity is known to be driven by different reasons, the task will require, first, to be encapsulated into a naturally cooperative decision-making activity happening between more than one person at the same time, with the unbiased willingness to decide whether they want to conform or not. Therefore, our proposed task, as it is, cannot explicitly induce participants to conform in any case and needs to leave the door open for the behaviour to happen as it would happen out of the laboratory. Due to this constraint, we will use a pre-activation before the task that we believe will induce the cooperative tendencies of the participants, so we do not have to instruct them later to team-up or seek any goals.

Also, to capture learning or predictive updates of the process, the task will require to be pervasive, and feedback driven, allowing participants to have the chance to adjust their responses once they observe their partner's input. This fact is important, as we are interested in using as reference all the studies in neuroscience explaining different feedback related processing in the brain that was introduced in the previous section.

Because we are not using monetary, food, or other type of classic conditioning rewards in our task, we consider the social interaction experience to be a self-sufficient rewarding drive. In fact, we sustain our task in a strong hypothesis: Convergence between humans is so inherently rewarding that we will not have to induce it or condition it by any means. Hence, we are using only the convergence in the responses between participants in a communication bottleneck (they will be physically divided by a screen or a wall that impedes them seeing each other) as the indicator of conformity. Correspondingly, this and no other force will drive the participants chance to adjust their predictions about the other person at their will.

Summarising, the questions that rise from this objective are the following: Is convergence an unconditioned social reward? Is cooperation a precursor of convergence? Will people tend to converge even if they are not explicitly instructed to do so? Will our task capture neural signals of conformity? Will the pervasive design of our task capture signal differences in cognitive and learning activity in the brain?

### 3.3. Aim 2: To study the neural electrophysiological correlates underlying conformity between two people.

Because we are interested in the simultaneous data acquisition of the brain activity of two participants, we will focus our research on EEG signal analysis. Therefore, the second aim in our research comes from the exploration of different neural correlates behind such behavioural adaptation. As we already explained in the first part of this thesis we expect, first, different neural signal components related to cognitive control and conflict through feedback monitoring and valuation. The study of the ERP will provide a chance to measure how differences related to feedback impact in cognitive control as well as cognitive load, and also if we can capture role related differences regarding the level of conformity in a trial. In concrete, we will analyse the different moment in which participants have their and their partner's information (feedback). This will be the moment of awareness of the consequences of their own actions, the moment of inference and integration of their partner's intentions, and the moment when the next action selection will be computed and later executed. In fact, the use of a 2-person paradigm will provide the opportunity to study simultaneous activity between the two participants as they are interacting in their dyads. This will raise some important questions: Are the ERP different when people conform more compared to their partners? Are there any expected oscillatory dynamics happening during feedback? Does this feedback processing follow similar patterns and pathways as others already identified by research in performance monitoring?

On the other hand, another interesting opportunity provided by *hyperscanning* will be the study of oscillatory coherent activity at different phases. As we already explained in the introduction, oscillatory coherence in the brain is the way neuronal populations propagate, through spiking, and “communicate” with each other (Kumar, Rotter and Aertsen, 2010). Hence, we hypothesize exploring such oscillatory coherent phases will broaden our understanding on different activity layers happening when people engage in a conforming behaviour.

### 3.4. Aim 3: To study changes in conformity due to previous experience as a learning process using RL models

Even though we have already discussed the multi-layered nature of conformity (and any other social process), we hypothesize part of it, as it is dependent on learning and reward processing, will be able to be modelled with a RL computational framework. The use of behavioural models in neuroscience opens the door of exploring where does it operate in the brain and under which neuronal codes, such as oscillatory rhythms.

Conformity has an implicit learning involved. The way people conform to others is preceded by the interaction with the model that people created on other's behaviour. Having a predictive model requires the action of learning through observation. The pervasiveness in the interaction between the agent and the information coming out of the environment improves such model and reduces surprise or uncertainty. Learning is so ingrained in our brains we start with such process before we are born (see James, 2010 for a review). Luckily, as we already said, experimental psychology has studied many ways to operationalize learning and nowadays there is important knowledge on how this acquisition happens in the brain.

For this purpose, we will use a simple TD routine using participants' responses to generate expectancies that will be updated on the bases of PE. Firstly, we are interested in exploring any differences on predictability associated to cooperativity which would be tracked by means of a learning model. Our hypothesis is people who have previously cooperate will have an enhanced tendency to conform and, hence, converge in their responses. In addition, they will have an increased predictive capacity towards their partners and, thus, their actions will be tracked to a greater extent by the model. On the other hand, we also expect parameters inside RL models, such as Q-value and Prediction Error, to give us important hints about how the brain treats such computations in the brain when people are conforming. As already stated in the introduction, RL has been successfully applied in cognitive neuroscience to understand how the brain tracks learning and makes useful predictive models that are used in the action selection. We expect RL models, and more specifically their parameters which track prediction errors (PE) and predictions (Q), will give us certain hints about the oscillatory dynamics operating in these layers of computation. Importantly, we are considering here as well a hypothesis that comes from previous aim, that considers convergence among dyads is a sufficient reward and, as such, can guide a reward-referenced learning process.

Consequently, we want to respond to the following questions in this aim: Will the reward and, more specifically, reward prediction error drive a learning process that we can track with a computational model? Would cooperation induce increased predictive models to participants? Will a computational model track different dynamics associated to learning in the brain?



## 4. Results



4.1. Study 1: Spontaneous convergence in cooperating dyads as explained by a reinforcement learning model of conformity

#### 4.1.1. Summary

The aim of the current research is to create an experimental paradigm where cooperation emerges naturally, so we can study it in the most ecological way out of judgement task or game theory competition/cooperation frameworks. We asked participants to perform a set of activities, individually (I) or cooperatively (C), before registering their answers in a dyadic decision-making design in order to compare whether the grouping factor would be a predictor related to the level of convergence in their responses. We also model our results with a Reinforcement Learning (RL) algorithm to find differences between groups. Our results showed a significantly higher level of convergence in C group. In addition, participants in this group reported a more trusting, satisfactory, rewarded, and synched overall experience. Also, RL Temporal Difference algorithm showed higher learning rate and explained better the convergence behaviour of the C group compared to the I group. Our study validates a new proposal to study conformity spontaneously appearing under cooperation.

#### 4.1.2. Introduction

Compared to other apes, humans are a very proactively prosocial species with a high intrinsic prosocial motivation (Jaeggi, Burkart and Van Schaik, 2010). This tendency has an easy evolutionary explanation given our biological nature of working and thriving together. To cooperate, people need to influence each other's reflections and perceptions in the vicinity of a practical alignment that benefits a joint efficacy. In addition, humans often need to precisely coordinate their interaction to be effective with one another, and they usually tend to partially sacrifice one's view to seek convergence with their partner. Arthur Jeness (1932) was the first to describe people's natural tendency to group convergence, and described group discussion acted, in fact, as an enhancer of such impulse. Later, Muzafer Sherif (1935) conducted his famous "Autokinetic Effect Experiment" and demonstrated how this tendency to converge in humans made them bias their own perception. This behaviour coined the name of conformity and was later experimentally described by Asch in his seminal line-judgement study (1951) in which a significant amount of people was indeed able to choose an obviously incorrect choice to conform to a majority of confederates. Since then, several studies have been devoted to study this phenomenon under different perspectives (see, e.g., the foot-in-the door experiment, Freedman and Fraser, 1966; preference for consistency in ambivalence, Newby-Clark et al., 2002; free choice dissonance paradigm, Bator and Cialdini, 2006). However, in the field of Social Psychology most of research has focused on the subtleties of conformity and the different sources of influence (Cialdini and Goldstein, 2004).

From an experimental perspective, conformity has been mainly studied under the mathematical framework of game theory (Von Neumann and Morgenstern, 1944), trying to understand the rationale behind human cooperation on the bases of intrinsic or extrinsic reward mechanisms. This framework has importantly allowed evolutionary biologists to explain cooperation from the point of view of strategical equilibrium (Smith, 1972; Axelrod and Hamilton, 1981). Nonetheless, from a psychological point of view, game



theory framework mainly focuses on the rationality, the losses, and its aversive variables whereas it might fail to reflect other influences in beliefs or other consequences coming out of social learning (Colman, 2003). However, there is also evidence that models coming out from game theory explaining social or group behaviours lose explanatory power when data is analysed disaggregated, because as it is commonly the case in other areas such as physics, the aggregate behaviour of a system does not have a direct correspondence to the behaviour of the average individual inside the same system, and therefore, individuals do not learn and act as they are predicted by the models as the variability increases (Hichri and Kirman, 2007). This does, in fact, rise a question on whether competitive-cooperative games can capture the cooperative mechanisms that imply a conscious behavioural adjustment, such as conformity, as this opposition is effectively capturing cognitive dynamics associated to self-interest trade-offs and representations, as defined in social exchange theory first proposed by Homans (1961), but reduces its validity to study cooperation alone. Besides, cooperation in real-life situations appears spontaneously or uninduced most of the times and can be modulated by previous experience (Jenness, 1932; Freedman and Fraser, 1966). This suggests that conformity might act as a prosocial reinforcing itself and not just as an opposition to non-cooperative circumstances or as a consequence of mere rational thinking. Interestingly, previous studies have suggested that people reduce value of their own vision (Campbell-Meiklejohn et al., 2010) when it is in conflict to the group so they can reduce discrepancy and conform to the norm (Klucharev et al., 2009). This idea induces several assumptions: first, conformity is an adjustment guided by learning (i.e, group norms and/or other's behavioural predictive modelling), and second, that this learning is likely influenced or induced by reward prediction error (i.e., discrepancies between expected behaviour and real one).

Human decision-making requires a quick adaptation to changes in the environment, and it needs a framework to associate stimuli with action. Because of this, reward related learning modelling and operationalization has been a primary field of interest since the annals of behaviourism. Ultimately, mathematical models are efficient ways of capturing the systemic structure or functional representation in any type of data. However, it was not until the beginning of the 70's that Rescorla and Wagner (1972) modeled associative learning. Under this approach, a reward error tracks the predictive strength of a conditioned stimulus and gets updated at every occurrence, where a learning rate weights the error in the previous prediction and constitutes the update to get the current prediction. Although this model was excellent, it was unable to capture all classical conditioning phenomena such as latent inhibition, quick reacquisition, or spontaneous recovery. Since that, Reinforcement Learning (RL) framework has been used to explain how humans learn the value of choices led by rewards. Here, different algorithms explain learning problems of agents interacting with environments through rewards and/or punishments received based on the adequacy of their actions. Among these algorithms, the ones capable of working without a model of the environment are the model-free RL algorithms, where predictions are estimations of the values of states, or state-action pairs, and are updated at each iteration by a reward prediction error. One of these algorithms is Temporal Difference Learning (TDL), which models learning by bootstrapping from the current prediction to decide the next action. This algorithm was introduced to psychological and brain sciences from computer science field by Richard Sutton and Andrew Barto (1998), and it provides a complete framework to model prediction and behaviour in a reward-based learning process. RL algorithms have been successfully applied to model individual decision making (see, e.g., Niv, 2009), but their application

in the study of social interactions has been scarce. Among the few, some studies have used RL algorithms in cooperative tasks (Klucharev et al., 2009; Levorsen et al., 2021), but they have been based on the change in judgement due to the influence of other people in a forced single-person task alone, where social influence has been simply induced or faked. Application of RL in real social settings might, therefore, help in understanding the mechanisms underlying cooperation. Indeed, being able to predict others behaviour might be reinforcing as it helps in reducing the cognitive effort required to converge with others (Kahnt et al., 2010). Therefore, convergence seems to be a natural mechanism to maximize social reward between people. Therefore, the goal of the present research is to study whether conformity appears spontaneously as a form of social reward when there is social interaction and whether the social convergence behaviour might be explained by means of RL. To reach this goal we developed a new dyadic task where behavioural convergence appeared spontaneously, and not by opposition to competition or induced by imagination. In brief, in the task two people perform an estimation task (indicating the position of a point using two references) and, after being exposed to their peers' estimations, can adjust their results in two more opportunities. Importantly, before the task, one group of participants solve a set of activities cooperatively, while the other group solve them individually. We hypothesize that, even when not explicitly instructed, participants will converge in their responses along the repetitions and that people who have previously cooperated will present higher convergence rates. In addition, according to previous evidence (Mobbs et al., 2009; Kahnt et al., 2010), we hypothesize that the expectancy or convergence of the peer will be better explained by a RL-TDL model in the cooperative than in the non-cooperative group.

#### 4.1.3. Methods

##### 4.1.3.1 *Participants*

80 psychology students (40 randomly assigned dyads) from the University of Barcelona participated in the study. They were also randomly assigned in two different groups. Participants signed an informed consent prior to the experiment and received a point-based reward in their grades. The study was approved by the Bioethical Commission in the University of Barcelona (UB). All sessions were recorded in audio and video under all participants' consent.

Our sample consisted in 17 men participants and 63 women (30 women and 10 men in "Cooperative" group; 33 women and 7 men in "Individual" group). The dyad composition was random with the only limitation that participants were not acquainted prior to the experiment.

##### 4.1.3.2 *Pre-Task*

Dyads were randomly assigned into two different groups. These groups were named "Individual" (I) and "Cooperative" (C). All participants were required to complete the

same set of problem-solving tasks with the only difference that if the dyad was in the “Cooperative” group, they were sitting in a table next to each other (*Figure 4.1.A*) in order to maximize their cooperative interaction (Sommer, 1959) while if they were assigned to the “Individual” group the space was separated so, they could not see or interact between them while solving the exercises (*Figure 4.1.B*). The set of tasks was inspired by the cooperative dimension of the circumplex model (McGrath, 1984) and tried to emulate the different kind of tasks that are normally performed in groups, in order to re-create a task-oriented group experience that might lead to a pre-activation of cooperation for the C dyads. All participants had a maximum of 60 minutes to solve the pre-task, and they were given the instruction to move forward if they were not able to solve it in the estimated time of completion (*Table 4.1*).

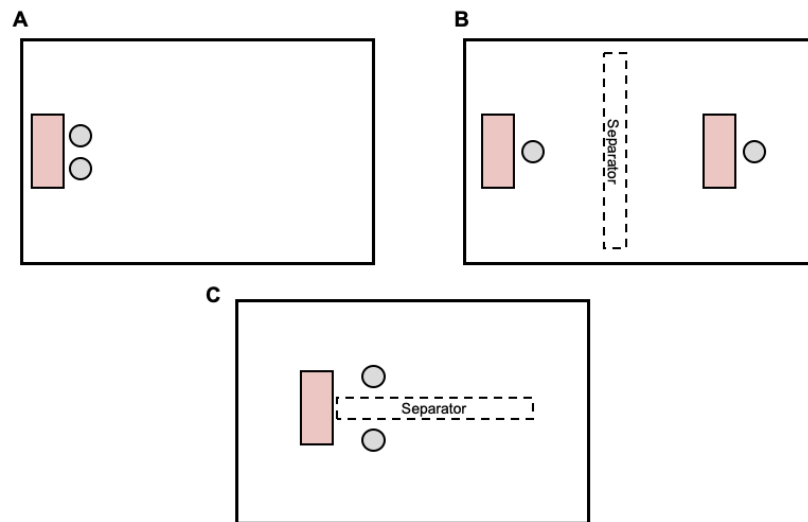
*Table 4.1: Pre-Task Assignment Structure and Classification. Total ETC is set to 60’.*

Type of Assignment	Classification of the type of Task	ETC
Estimation Questionnaire	Intellective Task	10’
Puzzle Solving	Performance/psychomotor Task	20’
Team Profiles	Planning Task	7’
Logo Creation	Creativity Task	7’
Faces: Setting a level of judgement	Intellective Task	7’
Estimating time	Performance/psychomotor task	4’

#### 4.1.3.3 Task

Both groups performed the second part of the experiment, the experimental task, in the same setting of the room (*Figure 4.1.C*). The design of the task was inspired by the classic autokinetic effect experiment by Sherif (1936). In every trial we present our dyads a line with two numbers informing about the limits and a highlighted point (in red) dropping somewhere over the line. The limits of the line were randomly assigned by the computer program with a minimum difference of 40 and maximum of 80. The program also randomly presented the orientation (vertical or horizontal) and the location of the point.

Every trial started with the presentation of the figure. Participants were asked to input their guess about the position of the point with a keypad. After both participants entered their input, participants saw their input and their peer's input (*Figure 4.2*). Then, the same procedure was repeated two more times with the three figures and participants had to enter their estimation again, which could be modified by the observation of the other's value. Importantly, participants were not explicitly instructed to do anything in their responses other than guessing the number of the point over the line to the best of their abilities. Therefore, they were not explicitly instructed to try to converge with their peers' estimations.



*Figure 4.1: Disposition of the lab for the different group configurations. A) corresponds to a "Cooperative" dyad setting and B) to an "Individual" dyad setting and C) to a task setting in both groups (author's own creation).*

The experiment consisted in 4 blocks of 40 trials each (three repetitions of the same figure in each trial), for a total of 480 observations in each experiment.

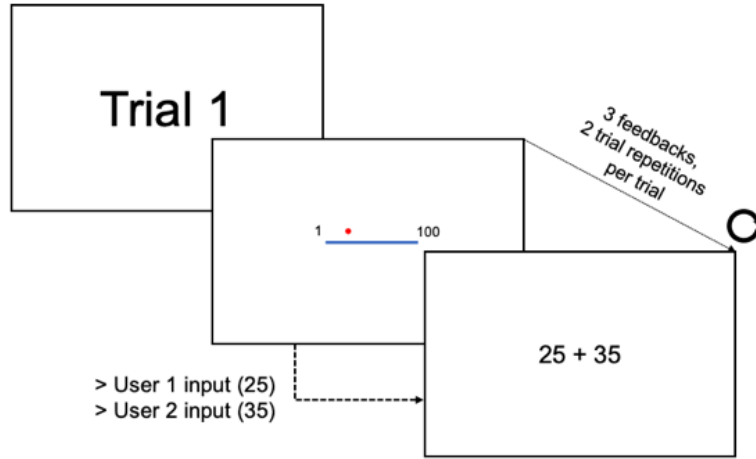


Figure 4.2: Task depiction that dyads were requested to do after the pre-task at both groups (author's own creation).

#### 4.1.3.4 Post-task Questionnaires

After the task, every participant completed a custom-made questionnaire requesting information about the general perception on the experience of the experiment. Here, we asked 4 questions to measure the perceptive and subjective experience in terms of likeability, synchronicity, trust, and reward. The questions were **AB**) “Did you feel synched with your partner?” which we called “Synchronicity”, **C**) “Did you find you could trust your partner?”, which was called “Trust” and **D**) “Did you find rewarding working with your partner?” which was called “Reward” They had a Likert type scale, starting from 1 (lower) to 5 (higher).

#### 4.1.3.5 Statistics

In order to measure the difference between groups, we used a linear mixed-effects model (LMEM) framework that serves to represent the nature of the nested structure of the data coming out of our experimental design. The dependent variable is the difference in answers ( $ResDiff_{ijk}$ ) between groups. Our aim was to calculate a varying slope for every trial with the 3 repetitions so we could compare the effects between groups. To do so, we defined a random error structure ( $\varepsilon_{ijk}$ ) that included the nested participants ( $b_{ij}$ ) inside dyads ( $u_i$ ) error dependency.

Equation 4.1

$$ResDiff_{ijk} = \beta_0 + \beta_1 Group + u_i + b_{ij} + \varepsilon_{ijk}$$

The outcome variable in our model is a variable that refers to the absolute value of the difference in responses between the two participants. The fixed effects are the interaction between Group factor (I, C) and Trial Repetition (1<sup>st</sup> repetition, 2<sup>nd</sup> repetition, 3<sup>rd</sup> repetition). We used Cohen’s *d* to quantify effect sizes. We also performed a t-test and a Wilcoxon rank-sum test for testing the model fit and alpha differences in RL respectively. We used a simple analysis of variance (ANOVA) for post-experiment questionnaire result analysis.

As we expected a non-parametric distribution in the questionnaire responses, to measure these responses and the difference among groups, we used a Wilcoxon rank-sum testing the hypothesis where the alternative hypothesis specifies that C group is greater than I group.

#### 4.1.3.6 RL Model

To test our task with a RL algorithm, we used a Temporal Difference Learning (TDL) where the agent responds a certain action (*a*) in different states (*s*) representing each of every trial. We kept the model as simple as possible, as we were merely interested in a model fit comparison by groups. We scaled the responses by the two participants together for every trial ( $a \in [0,1]$ ). The reward (*r*) was considered the absolute differences of scaled responses by the partner from the first partial state (1<sup>st</sup> repetition) to the last (3<sup>rd</sup> repetition) in the trial. The future state was calculated with what is known as “delta rule” or simplest form of RL, where in order to get the current value of state ( $V(s_t)$ ) we added to the previous estimate the prediction error ( $\delta_s$ ) multiplied by a learning rate ( $\alpha$ ). The prediction error was calculated by extracting to the reward the previous trial value of previous state  $V(s_{t-1})$  following the classic delta-rule equation:  $V(s_t) = V(s_{t-1}) + \alpha\delta$  where the prediction error was updated as  $\delta = r - V(s_{t-1})$ .

For each participant we found the corresponding individual learning rate. To do so, the value state (*V*), which in this case represented the normalized predicted change of the peer (where 0 would indicate no change and, alternatively, 1 would imply a total change towards the estimation of the participant in the first repetition) was compared to the change performed by the partner (*C*). Therefore, using the distance in responses between the two participants as a parameter of fit relates to the actions jointly taken in a given state where convergence is reward. For instance, if the participant had a perfect estimation of the change of the peer in the three trials, and if the goal of the participant was to try to converge with their peer,  $V + C$  should be closer to 1. Consequently, we computed the model fit of each participant as:

Equation 4.2

$$fit = - \sum_i \log(1 - Vi - Ci)$$

When  $Vi + Ci \sim 1$  (that is, if the participant had a good prediction and changed their estimation to converge with their peer), the fit was higher. Thus, individual learning rates were estimated by maximizing this fit. Additionally, when dyads coincided in their responses, which resulted in  $(1 - Vi - Ci) = 0$ , we replaced the 0, that would return in the undefined  $\log(0)$ , with 0.001.

#### 4.1.4. Results

The first model fitted was the simple divergence by trial repetition, which serves as a baseline to consider the strength in the effect sizes of the rest of the models and contrasts. Here, we consistently found a decrease in the divergence with more trial repetitions, from an initial difference in the predicted value in first trial repetition of 6.4033 ( $\beta=6.4033$ ;  $SE=0.2444$ ) and decreasing by -2.6325 ( $\beta=-2.6325$ ;  $SE=0.1282$ ) in the second trial repetition, and by -3.3492 ( $\beta=-3.3492$ ;  $SE=0.1282$ ) in the last repetition.

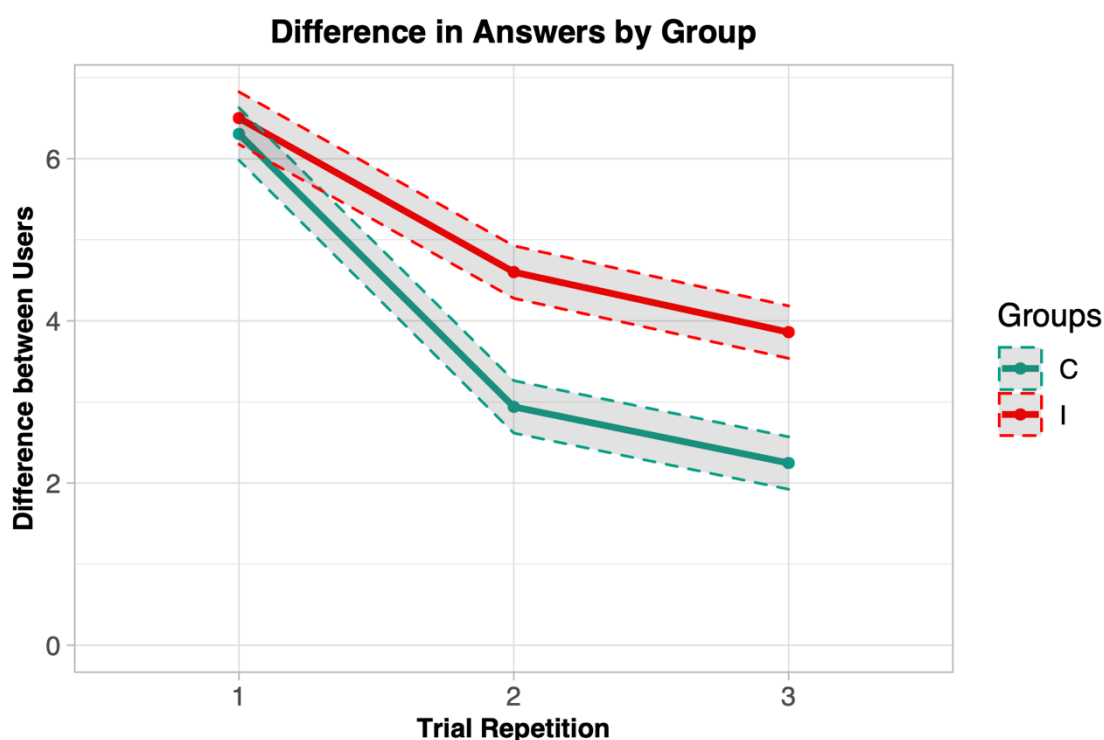


Figure 4.3: Plot of the differences in the convergence, extracted from the differences in answers among dyads, between groups at every trial repetition. Closer to zero means more convergent answers (author's own creation).

Then we fitted the main interaction model that represented the differences in group together with trial repetition. Intercept represented C at stimulus onset (1<sup>st</sup> repetition). The baseline (intercept) at first repetition and Group C in inter-personal divergence was predicted to be 6.3056, and the expected increase in value was 1.4669 ( $\beta=1.4669$ ;  $SE=0.2562$ ) in 2<sup>nd</sup> trial repetition and 1.4191 ( $\beta=1.4191$ ;  $SE=0.2562$ ) in the 3<sup>rd</sup> trial repetition in Group I compared to C, which according to the change in trial repetitions can be considered a strong evidence of this difference in results between participants.

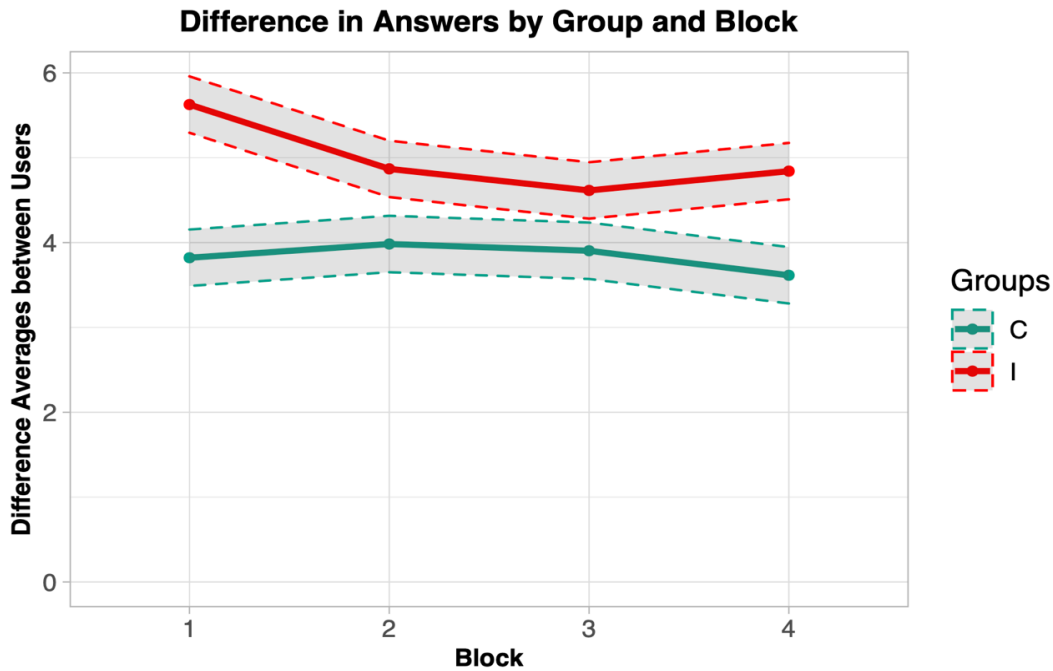


Figure 4.4: Average differences between dyads among blocks (author's own creation).

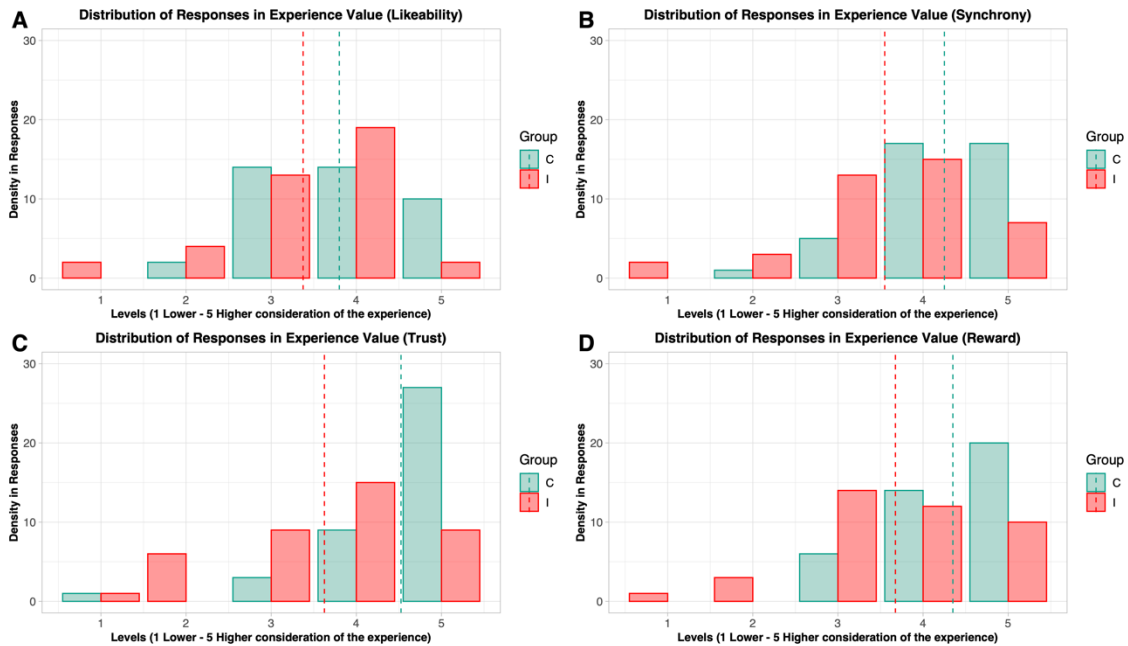
Figure 4.3 shows that both groups decreased the difference between the estimations (increased convergence) with repetitions, but C showed a higher decrease. To measure whether the effect size was significant, we calculated the mean over the absolute divergence in the final trial repetition result of each dyad which returned a Cohen's  $d$  of  $d=-1.147$ , that is, a mean decrease in group C over I of more than one standard deviation, which, according to common interpretation, is considered a very large effect size.

Then, we fitted the interaction model of Block and Group (Figure 4.4), where we hypothesized would reflect engagement and tiredness related effects. With the intercept, or baseline value of the inter-personal divergence at 1<sup>st</sup> block in group C, being 3.8213, we found differences in Group I to be decreased by 0.92 ( $\beta=-0.92$ ;  $SE=0.2988$ ) at block 2, by 1.0946 ( $\beta=-1.092$ ;  $SE=0.2988$ ) at block 3 and by 0.5779 ( $\beta=-0.5779$ ;  $SE=0.2988$ ) at block 4, showing therefore a strong evidence in the 2<sup>nd</sup> and 3<sup>rd</sup> block and a weaker in block 4. However, when performing a Tukey pairwise contrast, we only found strong evidence suggesting differences between groups at 1<sup>st</sup> block ( $\beta=-1.80$ ;  $SE=0.209$ ) as well as in the differences in Group I between the 1<sup>st</sup> and 2<sup>nd</sup> block ( $\beta=0.7579$ ;  $SE=0.209$ ).

Regarding the post-experiment questionnaire, as seen in Figure 4.5, in all responses there was a significant increase in the more positive subjective experience in the C group. The effect was significant in the question "Did you like the experiment?", ( $F(1,78) = 4.418$ ;  $p = .038$ ; Figure 4.5.A). The other three questions showed similar behaviour. In question 2, "Did you feel synched with your partner?" the results ( $F(1,78) = 11.69$ ;  $p = .001$ ) showed significantly higher perception of synchronicity in partners who have previously cooperated (Figure 4.5.B). In the third question, "Did you find you could trust your partner?" the answers were considerably higher, as they are visually appreciable in the corresponding depiction (Figure 4.5.C) and the ANOVA results also showed this significance ( $F(1,78) = 17.23$ ;  $p < .001$ ). Finally, in the last question, which addressed



the rewarding value of the experience (“Did you find rewarding working with your partner?”), people who had previously cooperated valued the experience significantly higher ( $F(1,78) = 11.49; p < .001$ ; *Figure 4.5.D*).



*Figure 4.5: Plots that depict the differences in responses to questions by Group: A) “Did you like the experiment?”, B) “Did you feel synched with your partner?”, C) “Did you find you could trust your partner?” and D) “Did you find rewarding working with your partner?” (author’s own creation)*

In addition, we compared the difference between the responses given by the participants with the real position of the point. To do so, we took the centred difference at the end of the trial, 3<sup>rd</sup> repetition, between both participants and compared it to the actual point getting an accuracy value per trial. We also dropped the results out of 1<sup>st</sup> and 99<sup>th</sup> quartile to remove outliers that were most likely caused by typing errors (*Figure 4.6*). The effect-size analysis showed difference between groups was negligible ( $d = -0.1316$ ).

#### 4.1.4.1 RL Results

Results on the RL model show a significant difference between groups both for the model fit ( $t(78) = -5.24, p < .001$ ) and also for the alpha learning rate ( $W = 559; p = .02$ ). As we can see in *Figure 4.7.A* boxplot, the C group had a significantly lower model fit score than the participants in the Individual group, indicating that the fit of the model was better for participants of the C group compared to the I group. On the other hand, boxplot in *Figure 4.7.B* show a higher average alpha for the C group than for these in I group, although with a high dispersion, which would account to the dependency of the constant learning rate in a trial-by-trial basis.

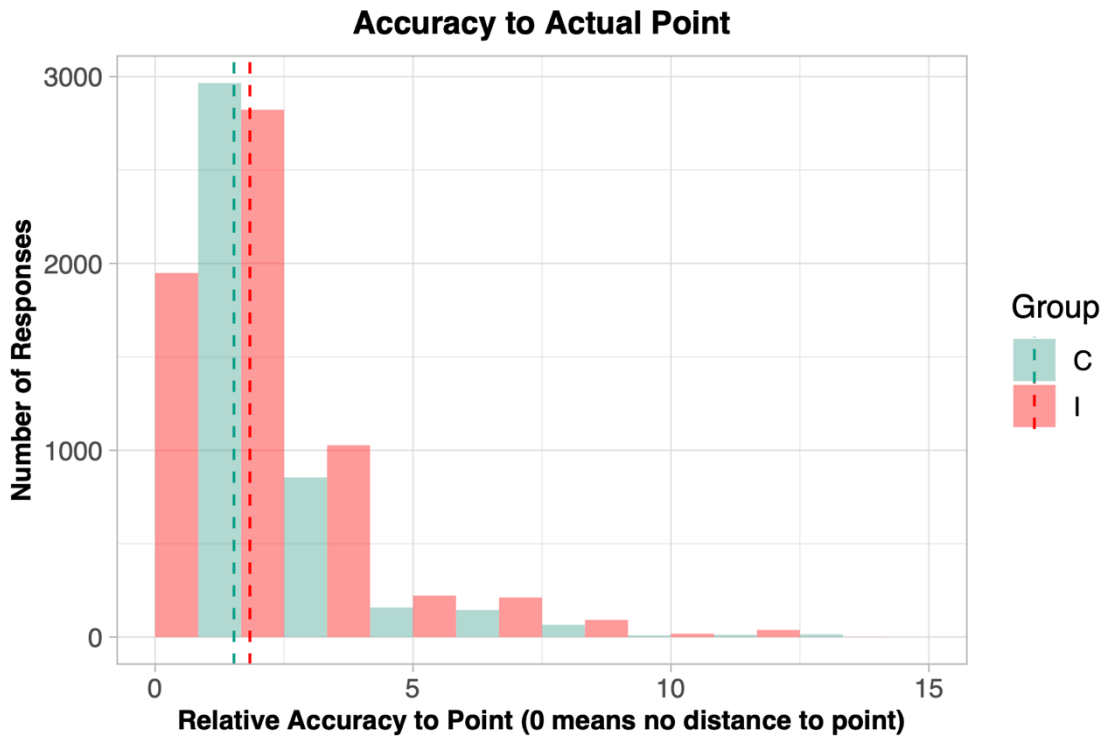


Figure 4.6: Accuracy between groups to the actual point. Dashed line represents the mean. Precision reflects the difference between the average response by dyads in the 3rd trial and the actual point, where 0 is a match and higher values show higher discrepancies. We limit the x-axis, which relates to response distance, to 15, rejecting other outliers (keyboard typos) (author's own creation).

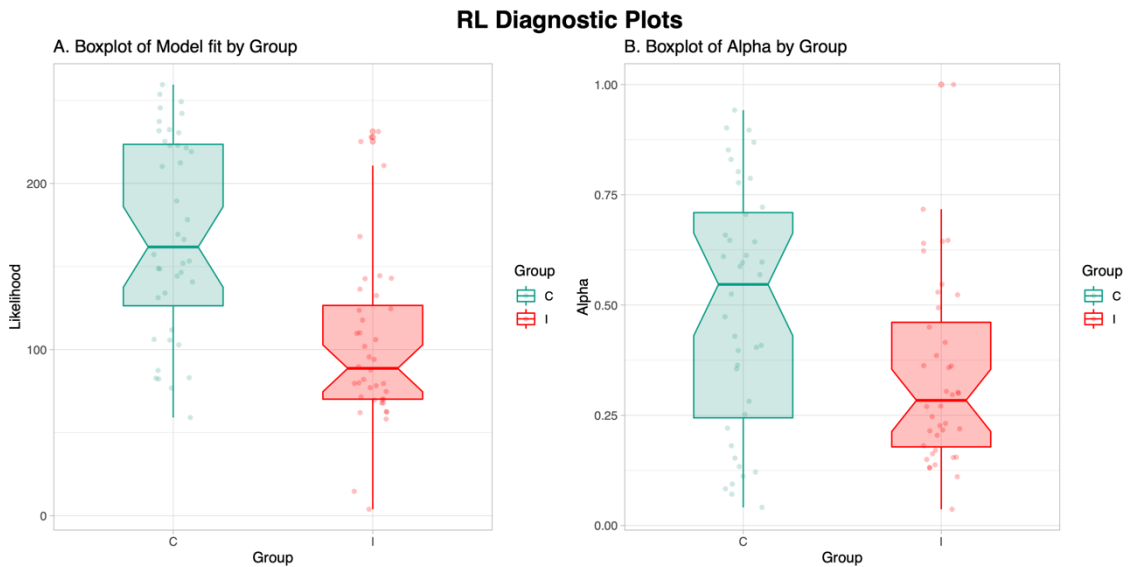


Figure 4.7: Diagnostic plots of RL analysis by Group. (A) Boxplot showing the per subject distribution of the model fit by Cooperative and Individual group, more negative numbers meaning a higher level of data explained by the model. (B) Boxplot with the alpha learning rates, the higher alphas meaning a lower dependency of the model and a higher dependency to the immediate learning rate from the trial (author's own creation).

#### 4.1.5. Discussion

In the present study we developed a new experimental paradigm to study spontaneous behavioural convergence. As hypothesized, participants showed natural tendency to converge even if they were not explicitly instructed to do so and independently whether they had previously cooperated. Results clearly showed a decreasing curve in the divergence in responses in every dyad, even in those who had not previously worked together. Nonetheless, as also hypothesized, people who previously cooperated reached higher convergence than those who did not. Finally, RL model better described the behaviour of participants of the C group compared with the I ones, showing larger learning rates, indicating that those participants were more consistently using information from previous trials to update their predictions on other's behaviour.

The first main result is that, even if it was not explicitly instructed nor rewarded, participants converged in their responses. This is in line with previous experiments that claimed conformity was mediated by a reward-driven learning (Klucharev et al., 2009; Levorsen et al., 2021). Also, we believe the evidence presented in the present work supports the use of our task proposal to study spontaneous social convergence or conformity. Importantly, as we hypothesized, the C group showed higher convergence than the Individual group. Previous studies have suggested that cooperation leads to a certain cognitive facilitation that promotes the genesis of normativity (Kleiman-Weiner et al., 2016) and that people who previously cooperated should show a higher tendency to reach common ground. Our results clearly support this explanation as the differences between groups clearly state there is a higher proactivity to convergence in C from the beginning of the task. In fact, although our results suggest a significant difference in the interaction between Groups and Blocks, the pairwise comparison in our data only shows a significant decrease between groups in the 1<sup>st</sup> block and in the I group from the 1<sup>st</sup> to the 2<sup>nd</sup> block. These results might suggest people tend to converge naturally, even though they have not previously cooperated, and they tend to look for ways to converge in their responses as trials go by. Interestingly, while dyads in the C group presented more convergence at the beginning of the task (block 1), there were no significant differences between groups from the second block on. However, and supported by the reports of the participants in the post-experiment questionnaire that show higher ratings in the overall experience for the C group, it is reasonable to assume cooperation acts as an intrinsically rewarding experience and, because of this, it is likely people who have previously cooperated are also increasingly predicted by a reward-based learning model. Indeed, previous evidence suggests cooperation acts as an intrinsic reinforcer (Balconi and Vanutelli, 2017).

Based on the previous assumption, one of the main novelties of the present study was the use of a RL algorithm to explain the adjusting behavioural estimation in our participants. The model showed a higher predictive capacity in group C compared to group I, as shown by the increase in the model fit indicating higher similarity between the prediction of the model about peer's behaviour and participant behaviour. In other words, our data shows group C participants behaviour can be better explained using a RL learning model to predict their partners than group I participants. On the other hand, data also shows higher alpha rate in group C, and, thus, these participants would rely more in their immediate

trial-by-trial course of action. However, as is also clearly observed in our data, previous evidence (Gershman, 2015) has reported that there is a high asymmetry in alpha learning rate, a measure that normally hides a high variability between individuals. We believe our results sail in favour of the same claim, and even if members of group C might seem more dependent on this parameter, the high dispersion of the learning rate across participants invites us to be cautious with the conclusions.

Our proposed algorithm, which uses the information on the observed partner as the update parameter to predict one's actions in a TDL, is a straightforward computation that demonstrates the prioritization of the information incoming from social sources, and the influence it has on the update of one's decision boundaries. We believe the first set of activities prior to the task, when solving them dyadically, serves as a preactivation of the social prioritization, which makes C participants actions more predictable by our model. Our results are consistent to the literature suggesting that social norms are a way of reinforcing behavioural predictability on individuals inside groups (Klucharev et al., 2009) and support the classic principle that claims when people cooperate and socialize, social influence contingency mechanisms, such as norms, arise in order to structure activity, which increase certainty within groups. This claim is nothing but new, and it has been a topic of interest since the early 50's by George Homans (1950) who explained this group dynamic as a uniformity mechanism that required a certain amount of maintenance effort by members in groups. We believe our results might shoot in favour of this same idea, although given our data we cannot state that norms are the aim of the reinforcement, and we can only interpret such influences as being affected by social reinforcements in general.

The present experiment also has some limitations. First, the participants of the two groups were very homogenous in different characteristics such as education, cultural background, and age. Therefore, the generalization of the present results to the general population must be taken with caution. In addition, the variability in the alpha learning rate points out to important individual differences which should be further explored. Another limitation of the present study is the simplicity of the RL model used. This selection was intentional, as we wanted just to capture the global effect across repetitions, but only considering the difference between the 1<sup>st</sup> and the 3<sup>rd</sup> repetition (ignoring the 2<sup>nd</sup> adjustment) minimizes the explanatory power of the whole phenomenon and we understand this choice does not allow a complete description of the convergence process. However, the use of such simple model was sufficient for the goals of the present behavioural experiment. Besides, future studies could explore the use of more complex RL algorithms taking into account all the adjustments in the task and/or using other adjustment parameters.

In conclusion, in the present experiment we presented a new experimental paradigm that reliably and spontaneously induced behavioural convergence between people and that this converge was higher in those people who cooperated before it. In addition, we showed that convergence (especially in the cooperative group) can be by means of a reinforcement learning task, supporting the idea that convergence is a form of social reinforcement. Future developments of this task can help in disentangling some aspects of this behaviour by, e.g., identifying differences between roles inside the dyads (e.g., people that conforms more or less) or through the study of brain mechanisms underlying it by using electrophysiological signals or functional magnetic resonance imaging.





4.2. Study 2: Do you conform, or you don't? Neurophysiological correlates of conformity in an interactive decision-making task in dyads

#### 4.2.1. Summary

Conformity is a fundamental cooperative behaviour which helps people to adjust their mental frameworks to reach a common goal. However, while conformity has been extensively studied in social psychology, little is known about the neural mechanisms underlying this behaviour. To study this, we registered the electroencephalographical (EEG) activity of 36 participants in a cooperative decision-making paradigm in which dyads had to make a perceptual estimation in three consecutive trials and converge in their decisions without an explicit request or reward to do so. Event-related Potentials (ERP) revealed signal differences related to response adjustments in three different intervals. In addition, ERP results showed different levels of cognitive engagement associated to the level of conformity and derived to the type of adjustment in dyads. Time-frequency analysis showed evidence in theta, alpha and beta relating to cognitive-control, attention, and reward processing.

#### 4.2.2. Introduction

Cooperation is a type of prosocial behaviour (Batson and Powell, 2003) which involves the willingness to engage in an interdependent activity with another person, or group of people, for a common goal that will likely result in a common benefit. Evolutionary psychologists frame the cause of human pervasiveness in cooperation in reciprocity and conformity (Henrich, Chudek and Boyd, 2015; Richerson et al., 2014; Henrich and Boyd, 2016). Research trying to understand why people have such prosocial behaviour has identified different variables involved in it, ranging from individual differences in personality to prosocial motivations, social influence, and identity (Penner et al., 2005).

One of the key mechanisms involved in human cooperation is influence. Seminal social psychology experiments showed that people tend to match each other's behaviour (Asch, 1956) and perception (Sherif, 1935; 1958) as part of an automatic psychosocial mechanism. Therefore, as a mechanism that promotes and facilitates cooperation, conformity is a type of prosocial behaviour that happens when a person changes their own judgements and decisions to match those of another person or group. Conformity is crucial in cooperation and involves the adjustment of one's own view or behaviour in favour of a shared framework with others to reach a synergic goal. Interestingly, people show a tendency to adjust their behaviour to others' even when there is no explicit instruction or reward to do so. This adaptation seems to be almost automatic, and it has been demonstrated as a power force in shifting people's decision-making, even by positive contagion (Nook et al., 2016). However, despite the vast literature on this topic from a social psychology perspective, little is known about the neural mechanisms underlying this automatic processing. In contrast, several studies have been devoted to studying the brain processing of behavioural adaptation due to other sources, such as changes in the environment (i.e., changes in the contingencies between actions and rewards, Mas-Herrero and Marco-Pallarés, 2014) or in an agent's internal states (i.e., after an error commission or due to conflict in the stimuli, Marco-Pallarés et al. 2008). Therefore, the brain mechanisms responsible for the adjustments performed in social conformity situations should be associated with those involved in the adjustment of



behaviour due to environmental contingencies. Adjusting behaviour in the face of external signals, social or otherwise, requires at least two crucial steps: first, detecting a discrepancy between the performed actions and other sources of information; and second, allocating the necessary cognitive resources to take the appropriate actions to correct or adapt this response.

The detection of discrepancies with previous stimuli has been traditionally related to different electrophysiological brain responses. Despite there is still an ongoing debate on the model that best represents the conflict monitoring computational schema in the brain (Holroyd, Pakzad-Vaezi and Krigolson, 2008; Shenhav, Botvinick and Cohen, 2013; Shenhav, Cohen and Botvinick, 2016; Vassena, Holroyd and Alexander, 2017; Vassena, Deraeve and Alexander, 2020), there is a consensus that this error systems work by a monitoring driven by means of a prediction error (Holroyd and Coles, 2002). Previous studies have reported that after negative feedback, a negative frontocentral deflection appears, peaking 250-300 ms after feedback onset, the so-called Feedback Related Negativity (FRN, Miltner, Braun and Coles, 1997). This ERP is sensitive to the magnitude of the loss as well as to the likelihood of the negative feedback and has been proposed to be related to reward prediction errors (Sambrook and Goslin, 2015). Some authors have suggested the feedback-locked, as well as the response-locked negativity associated to errors (Error-Related Negativity, ERN) have a similar distribution, time course, morphology, and functional dependencies (Holroyd, Pakzad-Vaezi and Krigolson, 2008). Interestingly, this subcomponent of ERP signal has been already associated to social conformity based on subjective norm-related measures such as attractiveness rating (Shestakova et al., 2013; Schnuerch et al., 2015). However, even though these might simulate conditions of conformity, the behavioural adaptation is induced, and its sociality assumed *de facto*. Another important component related to adjustment of behaviour is the P300 ERP (Polich, 2003; 2007). A number of studies have consistently reported the P3 ERP associated with attentional changes needed to allocate the attention to relevant changes in the environment and to the required targets (Polich, 2003; 2007). The P3 has traditionally been divided into two main components. P3a is related to attentional processes driven by context (Katayama and Polich, 1998) or emotional value (Delplanque, et al., 2006) among many others. This component has been associated with behavioural adjustments and switching (Polich, 2003; 2007). The P3b subcomponent, on the other hand, is related to cognitive engagement operations as well as a memory-storage mechanism coming after such engagement (Kropotov, 2010). Higher P3b amplitudes are related to target identification in the working memory updating process (Rac-Lubashevsky and Kessler, 2019) which might be relevant in higher-level adjustments associated with social convergence. In addition, decision-making studies have also revealed a crucial role of theta oscillatory activity in cognitive control (Cavanagh et al., 2010; Cavanagh and Frank, 2014), conflict (see Polich, 2007 for a review), and computation of surprises or prediction errors (Alexander and Brown, 2011; Cavanagh et al., 2012; Mas-Herrero and Marco-Pallarés, 2014). This oscillatory activity plays a key role in the engagement of diverse prefrontal cognitive mechanisms crucial in action-selection (Cavanagh, Zambrano-Vazquez and Allen, 2012) and should be, therefore, critical in the adaptation processes underlying social convergence/conformity. Finally, frontal alpha suppression has also been identified as possibly being important in influence dynamics related to attention as well as prediction (Klimesch, Sauseng and Hanslmayr, 2007; Sadaghiani and Kleinschmidt, 2016).

Although neuroscientific prosocial behaviours have been traditionally studied using simulated social paradigms rather than real social interactions (see Stallen and Sanfey, 2015 for a review), in recent years it has been possible to design dual-brain simultaneous approaches (also known as hyperscanning, Balconi and Valutelli, 2017; Redcay and Schilbach, 2019), in which two (or more) people are simultaneously recorded during social interactions (Balconi and Valutelli, 2017; Zhang et al., 2018; Zhang et al., 2019; Kelsen et al., 2020; Hamilton, 2020). Hyperscanning creates an opportunity to step out of individual cognitive processes to study neurophysiological mechanisms underlying social interactions in a multi-brain setting (Zhang, 2018). Also, dual-person neuroscience opens the door to study role-related differences between participants in social-interaction dynamics. However, the domain of cooperative decision-making has been dominated by experimental paradigms inspired in the game theory such as the prisoner's dilemma (see Liu et al., 2018; Redcay and Schilbach, 2019 for a review), which usually simplifies cooperation as being contrary to competition. Importantly, to the best of our knowledge, no previous studies have been devoted to the study of the neurophysiological brain correlates of behavioural adjustments to reach social conformity in real social scenarios involving simultaneous registers of two people.

The goal of the present experiment was to study the mechanisms behind conformity in a cooperative decision-making task. To reach this goal we designed a new experimental paradigm with two parts. In the first one, participants naturally cooperated resolving different tasks as a team and with no constraints other than time to activate and predispose participants to cooperation. The second part was the main EEG experimental session and was inspired by the norm related seminal study of autokinetic effect by Sherif (1936). In the current paradigm, the two participants had to simultaneously determine the position of a point on the screen. They had three attempts for each decision and were informed after each decision about the response of their partner. Even not explicitly stated/instructed, we hypothesized that participants would tend to converge in their responses. In addition, we aimed to study the neurophysiological correlates of social conformity in the moment participants were informed about the decision of their partners. We hypothesized that the brain responses which have traditionally been related to discrepancy (theta activity) and attentional demands (P2 and P3) would be related to the automatic adaptation of behaviour in this social context and would be modulated by the degree of adaptation performed by participants. Additionally, we are analysing all data from a single-trial perspective that facilitates the study of other cognitive process differences associated to participant's responses (i.e., their intra-personal or inter-personal adjustments) as well as role-related differences regarding their level of conformity in the trial.

#### 4.2.3. Methods

##### 4.2.3.1 *Participants*

44 participants (24 females and 20 males, age: 19-58) were randomly assigned to pairs (dyads) with the only criteria being not knowing each other before the experiment. Four

dyads were excluded from the experiment due to technical problems, resulting in a final sample of 18 dyads (36 participants: 20 female and 16 male, Age Median: 24, range: 19-53). The experiment was approved by the ethical committee of the University of Barcelona and all participants signed an informed consent prior to their participation. Participants received a monetary payment of €30 for their participation in the experiment. The experiment took an average of three hours.

#### 4.2.3.2 Design

The experiment consisted of two main parts. In the first part (pre-task), participants were asked to jointly solve a set of different challenges and activities designed to simulate different types of tasks and activities that naturally happen in groups (Table 4.2), inspired by the cooperative dimension inside the circumplex model (McGrath, 1984). The goal of these activities of joint action and cooperation was to emphasize synchronicity and social bonding before the main task in order to predispose participants to cooperation.

After the pre-task, an EEG headcap was mounted to each participant, and then they went together to the same room with a separator between them so they could not see each other during the task. Participants sat in a comfortable chair and responded via a numeric keypad. Before the beginning of the task, participants were asked to relax for 3 minutes by listening to a pre-recorded guided meditation. After that, two training trials were presented and then the main task started.

Table 4.2: Pre-task answer sheet task design structure, type of task and estimated time of completion. Participants had a maximum of 60' to complete the entire answer sheet.

Type of assignment	Classification of the type of task	ETC
Estimation questionnaire	Compensatory/discretionary task	10'
Puzzle solving	Conjunctive task	20'
Team profiles	Decision-making task	7'
Logo creation	Creativity task	7'
Faces: judgement	Categorization task	7'
Estimating time	Time synchronization task	4'
Imitation of postures and faces	Joint action task	5'

Note. ETC abbreviates *estimated time of completion*

#### 4.2.3.3 Task

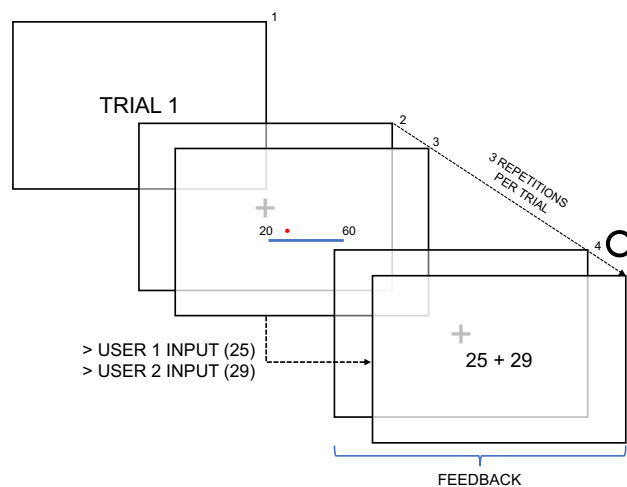
The task consisted of 100 trials. In each trial, a vertical or horizontal line appeared on the screen, with two numbers at each end indicating the arbitrary limits of the line. In addition, a red point appeared at a random position along the line. Participants were required to write the position they estimated for this point as a number. After the users

had inserted their inputs, a cross was displayed on the centre of the screen for 0.5s and then participants saw the two inputs (own and partner's) so they could evaluate the difference and adjust, or not, the estimation as they willed. The line with two limits and the red dot was presented on the screen until the moment both participants pressed the intro button, and then they were shown their respective feedback. After this, the next trial started when the two participants had pressed the intro button. The same figure was presented three consecutive times, so participants could change their estimation. However, and very importantly, participants were neither explicitly nor implicitly encouraged nor rewarded to coincide in their estimations (*Figure 4.8*).

The task was programmed using Python 2.7. The experiment was divided into 4 blocks of 25 trials per block with 3 repetitions of the same stimuli per trial. At the end of every block, participants could rest before moving forward to the next block (both participants had to press their enter button) whenever they were ready.

#### 4.2.3.4 EEG Processing

EEG was recorded using an ANT Neuro ASALab EEG amplifier at 1024 Hz using two different elastic caps from 27 scalp electrodes (Fp1/2, Fz, F3/4, F7/8, Fc ½, Fc5/6, Cz, C3/4, Cp1/2, Cp5/6, Pz, P3/4, P7/8, Poz, Oz, M1/2). Eye movements were registered with an electrode at the infraorbital ridge of the eye associated with the participant's dominant hand. The electrode impedance was kept below 5kΩ during the task.



*Figure 4.8: Example of a single trial in the task. (1) Trial numeration. Participants had to press enter to go to next screen. (2) Attentional cross in the middle of the screen automatically displayed for 0.5s. (3) Main input screen with the horizontal or vertical line, the random limits and the red dot randomly falling somewhere on the line. (4) Automatic attentional cross for 0.5s. (5) 1st feedback with their respective inputs. They have to press enter to go forward. Note steps (2) to (5) are repeated for a second and third time, referred to as 2nd and 3rd feedback (author's own creation).*

The electrophysiological signal was bandpass filtered, with cut-off frequencies of 0.1 Hz to 30Hz, and re-referenced to the activity of the two mastoids. Epoch events were extracted from -2 to 2 seconds after the stimuli showing the estimated position of each participant (feedback). Independent Component Analysis (ICA) (Makeig and Onton,

2011) was used to discard artifacts and, afterwards, epochs exceeding  $\pm 100 \mu\text{V}$  from -100ms to 1000ms were automatically rejected. Time-frequency analysis was also computed by convolving single trials with 7 cycle complex Morlet wavelet for frequencies ranging from 1 to 30 Hz. Changes in power was normalized respect to baseline (-400ms to -100ms) for each electrode, trial, and condition.

#### 4.2.3.5 Bayesian Multilevel Modelling

We used Bayesian Multilevel Modelling (BMM) due to its stability (Baayen, Davidson and Bates, 2008) in experimental designs where repeated measures and multiple comparisons are present (Ara and Marco-Pallarés, 2020), using all the available data by trial. BMM gives an objective alternative to frequentist corrections in multiple comparisons (Berry and Hochberg, 1999; Gelman, Hill and Yajima, 2012), as we use priors centred at 0, and we inform custom hierarchical priors when a hierarchical model requires it, which makes Bayesian inference highly conservative (Gelman, Hill and Yajima, 2012). Separate intercepts and slopes were used for each dyad. To define the random slope model, we defined a nested random term (participants nested in dyads) defined by our experimental design. In other words, by defining this factor in the random term, we let our model calculate co-dependent intercepts by dyad. We used the same modelling structure for both ERP and time-frequency analysis. Informative priors were used in the intercept and slope (normal,  $\mu = 0$ ,  $\sigma = 1$ ) and in the varying effects (gamma,  $\alpha = 1$ ,  $\beta = 10$ ) for the simplest *signal~FB* and *signal~Discrepancy<sub>FB1</sub>* model, and a hierarchical prior in every other interaction model for higher consistency (Gelman and Hill, 2006). For the *signal~Discrepancy<sub>FB1</sub>* model we scaled the dyads divergences, took the first feedback (enhanced novelty effect) and used the median to make a categorical variable that classified it as highly adjusted (high adjustment) or loosely adjusted (low adjustment).

Posterior samples were computed using the outcome of 4 independent chains, and all the partial variabilities added according to the model. After the modelling, the inference was computed using the Highest Density Interval (HDI) of 95% (Kruschke, 2014) to check the inclusion of the null hypothesis in the posterior models, and hypotheses were tested as proposed in Kruschke (2018) and Kruschke and Lidell (2018). In addition, we used, as suggested by Kruschke (2018), a decision rule considering, together with the HDI, the region of practical equivalence (ROPE) around the null value. The ROPE range was adjusted to every contrast multiplying the variability,  $SD_y$ , by  $\pm 0.05$ , so we ended up having an approximate, highly conservative,  $\pm 0.5$  ROPE range. In time frequency analysis, because reductions in power data are in a much lower scale than voltage data, and so is its variability, we reduced the ROPE range to  $\pm 0.01$ . It is also important to note whereas voltage models follow a student's  $t$  distribution, power models follow a *Gamma* ( $\gamma$ ) distribution with a *log* link. The reason why we chose this link function to the  $\gamma$  is that contrary to what happens with the canonical link, the log link produces a multiplicative model on the original scale, which allows a straightforward interpretation of its results. We are reporting  $SD_y$  maximum ( $SD_{y_{max}}$ ) and minimum ( $SD_{y_{min}}$ ) limits after commenting results of every model. Furthermore, we are reporting as credible only the results with the HDI+ROPE decision rule, where the entire HDI falls outside the ROPE. Posterior distributions were computed with four Markov chains initialized at zero with 10000 samples, where the first 1000 were discarded as warmup. According to the type of parameters for sampling algorithms, target acceptance rate or parameter "adapt\_delta"

was set to 0.9. The No-U-turn sampler (NUTS) algorithm maximum treedepth parameter was set to 10 in all the modelling to maximize the depth of the trees at each iteration (Bürkner, 2017). All models converged with those parameters, according to split-R-hat criteria (Gelman et al., 2013). Our models were built based on the intercept and subparts (differences) extracted from posteriors. Voltage (or power in case of time frequency) was the dependant variable in our model ( $y$ ) and the rest are treated as predictors, alone or in interaction. We intentionally permuted the contrasts (FB1-FB2  $\rightarrow$  FB2-FB1), to match the sign of the HDI to the reduction (-) or augment (+) in voltage (or power) at feedback and have a clearer interpretation of results.

The ERP analysis was focussed on three central electrodes (Fz, Cz and Pz) and four different time ranges (225 to 275ms, 275-350ms, 350 to 500ms, and from 500 to 700ms) corresponding to the three different components found in the ERPs (*Figure 4.10*). Statistical analysis of time-frequency data was performed in theta (4-8Hz), alpha (8-12Hz) and beta (12-30Hz) bands. We treated the range from 180 to 500 as the region of maximum difference in activity in all the different frequencies and divided it in two different subregions, the first between 180 and 230ms, and the second, from 230 to 500ms.

#### 4.2.3.6 *Intra-Difference and Conforming Interaction Factor (CIF)*

To ascertain whether components found were related to the degree of change in the decision (that is, whether a participant in a particular trial tried to converge more or less than their peer) we added an addition predictor by computing the change in the same persons behavioural response (estimation on the position on the point). In other words, we scaled the difference in the participants responses at every trial and used it as it represents a measure of their own adjustment.

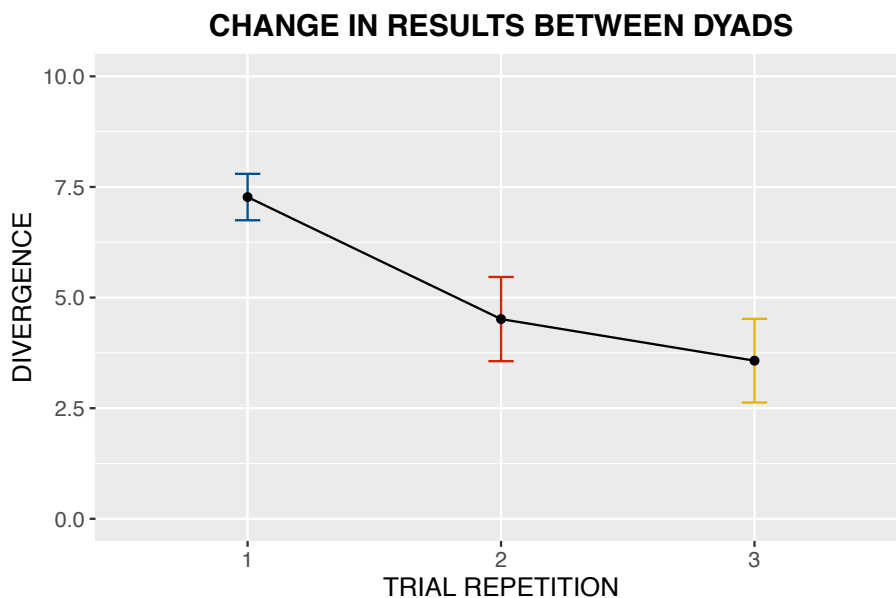
We also fitted a model using the divergence in responses between the pair of participants at every feedback scaled and used it as an independent variable predicting their respective signals.

Finally, we also used the differences in the responses by participants and compared them to those of their partners to ascertain, in each trial, if participant was non-conforming (NC, that is, they changed less than their peer estimation) or conforming (C, they changed more than their peer estimation). However, there is a third possibility, when both participants change the same or coincide. This condition will be referring as Equally Conforming (EC). These three conditions represent the different levels of the factor in the model. Also, we are identifying this contrast as Conforming Interaction Factor (CIF).

#### 4.2.4. Results

##### 4.2.4.1 Behavioural Results

Results of the estimation given by the two participants showed that the divergence between peers (the absolute value of the difference between the values provided by each participant) decreased during the three repetitions of the same trial (*Figure 4.9*) even when participants were not explicitly required to do so. A repeated measures ANOVA between divergences (we normalized this value as response divergences are dependent of different range scales) in results between dyads and the trial repetition showed a significant change between conditions ( $F(2,51) = 855.54; p < .001$ ).



*Figure 4.9: Divergence of results with trial repetition. Difference in the estimation of the position of the point between participants decreased when they observed the value given by their peer (author's own creation).*

##### 4.2.4.2 ERP Results

*Figure 4.10* shows the average ERPs for the three presentations of the estimation (feedback) at the Fz, Cz and Pz electrodes (*Figure 4.10.A*) as well as its topographic representations (*Figure 4.10.B*). *Figure 4.10.A* reveal all electrodes apparently present a reduction of amplitude with trial repetition. The topographical maps of the four studied time ranges (*Figure 4.10.B*) suggest a clear frontocentral activity at first interval (225-275ms) and second interval (275-350ms), more centro-parietal at 350-500ms and clearly posterior at 500-700ms, which is reduced in the second and third FB compared to the first one. Consistently, BMM revealed this signal reduction in the HDI (see *Table 4.4* in *Supp.*) but we did not find the strongest credible evidence (HDI+ROPE) of such reduction until the third interval in the second adjustment (FB3-FB2) in all electrodes (HDI(95%): 350-500ms: Fz: [-1.81 – -0.96]; Cz: [-1.58 – -0.74]; Pz: [-1.66 – -0.84]). In the fourth studied time interval, we found strong evidence of decrease in voltage in the first adjustment in

Cz and Pz, (HDI(95%): FB2-FB1: 500-700ms: Cz: [-1.12 – -0.56]; Pz: [-1.26 – -0.60]) and in the second adjustment in all electrodes (HDI(95%): FB3-FB2: 500-700ms: Fz: [-1.97 – -1.12]; Cz: [-2.19 – -1.34]; Pz: [-2.50 – -1.63]). Variability of this model, used for ROPE, ranged from  $SDy_{min}=9.50$  to  $SDy_{max}=11.87$ .

Next, the second model we want to address referred to the divergence between participants in the first FB in relationship to the level of behavioural adjustment, which, as stated above, refers to high adjustment (when the difference between participants is lower than their corresponding median) and low adjustment (when the difference is higher). Therefore, firstly, we wanted to test if there was a credible relation in high/low adjustment in certain ranges with a difference in voltage in the signal on first FB. Notice divergences in responses can be consistently higher in FB1 compared to differences in responses between participants from second or third FB, where they already had the chance to adjust. Note in this model lower discrepancy or higher adjustment represents the intercept. Strong credible dependencies in signal to the adjustment in the first range (225-275ms) was not found at none of the electrodes. The rest of intervals showed credible negative signal differences when there was a higher divergence (lower adjustment): 275-350ms (HDI(95%): Fz: [-2.29 – -1.08]; Cz: [2.28 – -1.10]); 350-500ms (HDI(95%): Fz: [-2.43 – -1.22]; Cz: [-3.18 – -1.95]; Pz: [-2.92 – -1.74]); and 500-700 ms (HDI(95%): Cz: [-2.36 – 1.16]; Pz: [-2.04 – -0.84]). Variability of this model ranged from  $SDy_{min}=6.68$  to  $SDy_{max}=8.98$ .

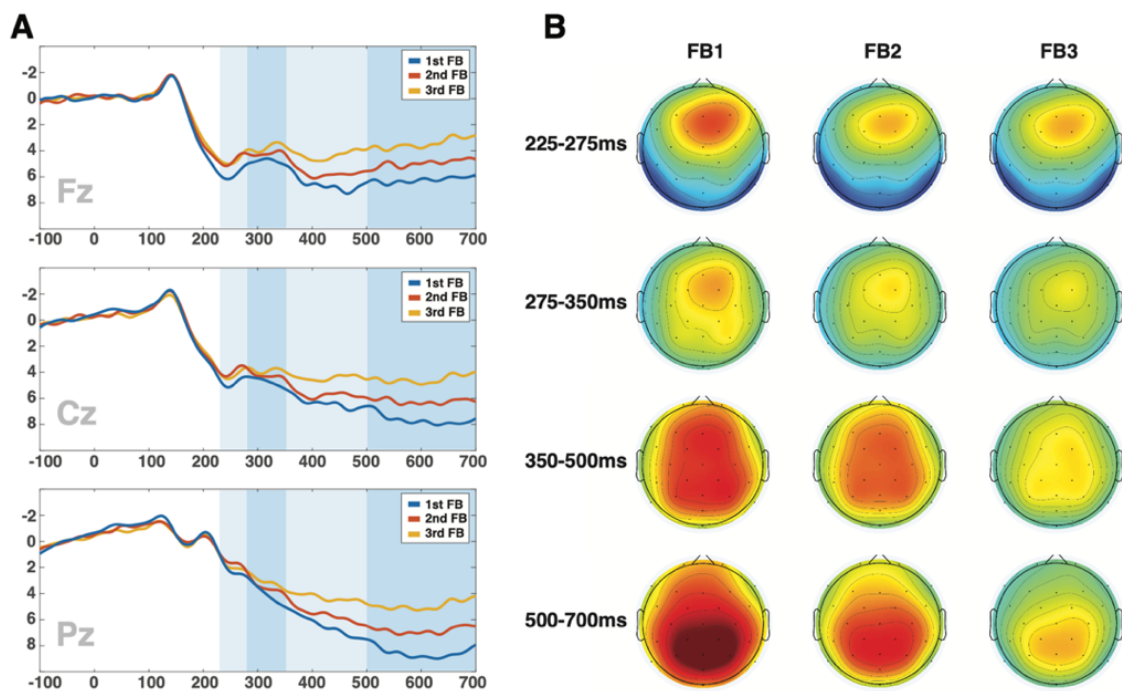


Figure 4.10: (A) ERPs at the central electrodes (Fz, Cz, Pz) for every feedback and the identification of the different ranges of interest over signals (225-275ms, 275-350ms, 350-500ms, 500-700ms). (B) Topographies at three feedback conditions through the interval (author's own creation).

Then we explored the intra-difference interaction factor, that is, the relationship between single trial changes in EEG responses and changes in participants' responses at each trial. We found a credible relation in the first interval (225-275ms) in FB2-FB1 in Fz and Pz (HDI(95%): : Fz: [0.91 – 3.12]; Pz: [0.96 – 3.15]). In the next intervals and in the first



adjustment, the difference related to response was credible in the three electrodes: 275-350ms (HDI(95%): Fz: [0.89 – 3.22]; Cz: [0.83 – 3.19]; Pz: [1.23 – 3.33]); 350-500ms (HDI(95%): Fz: [1.24 – 3.30]; Cz: [1.22 – 3.29]; Pz: [1.45 – 3.58]); 500-700 ms (HDI(95%): 500-700ms: Fz: [1.46 – 4.17]; Cz: [1.44 – 4.10]; Pz: [1.32 – 4.26]). In addition, in this last interval, a credible relation between activity and behavioural change was also found in the second adjustment (FB3-FB2) in the Pz electrode (HDI(95%): [0.56 – 2.55]). Variability of this model ranged from  $SDy_{min}=9.50$  to  $SDy_{max}=11.87$ .

Table 4.3: Summary table for CIF (Conforming Interaction Factor) posterior distribution with credible evidence results.

Dyadic Behaviour	Adjustment Operation	Electrode	Time interval (ms)			
			225-275	275-350	350-500	500-700
NC	2-1	Fz				
		Cz				
		Pz				
NC	3-2	Fz			[-2.32 - -1.20]	[-2.18 - -1.01]
		Cz			[-2.20 - -1.09]	[-2.48 - -1.30]
		Pz				[-2.69 - -1.47]
NC	2-1	Fz			[0.62 - 1.62]	
		Cz			[0.82 - 1.84]	
		Pz				
NC	3-2	Fz				[-2.18 - -0.98]
		Cz			[-2.05 - -0.87]	[-2.51 - -1.31]
		Pz				[-2.65 - -1.41]
EC	2-1	Fz	[-3.17 - -1.34]	[-5.27 - -3.43]	[-7.50 - -5.63]	[-5.99 - -4.18]
		Cz	[-2.51 - -0.66]	[-5.43 - -3.62]	[-7.85 - -6.01]	[-7.29 - -5.50]
		Pz		[-4.67 - -2.89]	[-7.56 - -5.76]	[-7.66 - -5.88]
EC	3-2	Fz				
		Cz				
		Pz				

Note. Presented results comply HDI(95%) with ROPE rule. The contrasts are purposefully permuted to match negative results to drops in signal voltage (-mV) and, alternatively, positive results to increases (+mV).

Additionally, we did not find any credible evidence relating signal differences to the response divergence in dyads at neither of the four intervals or any of the electrodes.

In addition, we also analysed the CIF which divided the situation of each participant in each trial based on their behaviour as “non-conforming”, “conforming”, or “equally conforming”, according to the role in the trial of each participant in the dyad. For clarity, and because we are comparing the differences between three different situations, we summarized in Table 4.3 all the results from this model. In addition, we show the results for the first adjustment in Figure 4.11 (see second adjustment plots in Supp. Figure 4.13).

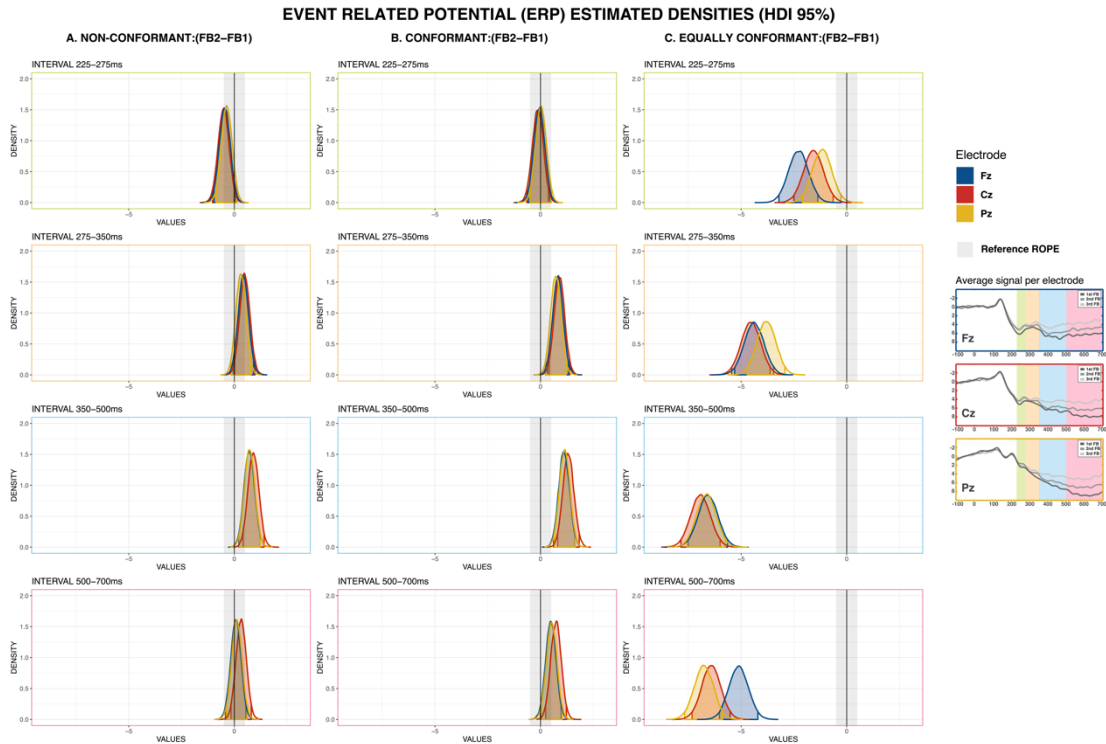


Figure 4.11: Estimated densities of different hypotheses regarding the: (A) differences between 1st and 2nd feedback in participants non-conforming in the trial; (B) differences between 1st and 2nd feedback in participants conforming in the trial; and (C) trials where both participants were equally converging. Note the dimmed area is an approximate ROPE range used as reference. As explained in the methods sections, all the ROPE ranges were adjusted considering individual variability. Hence, we use a standard  $-0.5 - 0.5$  range here as visual reference (author's own creation).

We first analysed the first adjustment (FB2-FB1). In the first time range (225-275 ms) we only found credible differences in the EC condition at Fz and Cz (HDI(95%): Fz: [-3.17 - -1.34]; Cz: [-2.51 - -0.66]) but neither in NC nor in C conditions. This was similar in the next time range (275-350 ms), with differences in the three studies electrodes in EC (HDI(95%): Fz: [-5.27 - -3.43]; Cz: [-5.43 - -3.62]; Pz: [-4.67 - 2.89]), but not for NC nor C. In the third interval (350-500ms), we found strong credible evidence in the first adjustment in C, with a positive shift in signal in Fz and Cz (HDI(95%): : Fz: [0.62 - 1.62]; Cz: [0.82 - 1.84]) and, again, a still incrementally negative difference in EC (HDI(95%): 350-500ms: Fz: [-7.50 - 5.63]; Cz: [-7.85 - -6.01]; Pz: [-7.56 - -5.76]). Finally, in the last interval, we again found a strong negative change in signal in the first adjustment in EC (HDI(95%): 500-700ms: Fz: [5.99 - -4.18]; Cz: [-7.29 - -5.50]; Pz: [-7.66 - -5.88]).

In contrast, when analysing the second adjustment (FB3-FB2), we did not find any credible interval in the first two studied time ranges (225-275ms and 275-350 ms). The first differences were found in the 350-500 ms in NC in Fz and Cz (HDI(95%): 350-

500ms: Fz: [-2.32 – -1.20]; Cz: [-2.20 – -1.09]), an in C in Fz (HDI(95%): 350-500ms: Fz: [-2.05 – -0.87]). In the last time range (500-700 ms), differences were found in all electrodes in NC (HDI(95%): Fz: [2.18 – -1.01]; Cz: [-2.48 – -1.30]; Pz: [-2.69 – -1.47]) and C conditions (HDI(95%): Fz: [2.18 – -0.98]; Cz: [-2.51 – -1.31]; Pz: [-2.65 – 1.41]). Importantly, we also contrasted the differences between NC and C at first and second adjustment at every interval and we did not find any strong credible evidence to sustain that their signal changes were different. Variability of CIF model ranged for the three different dyadic behavioural types were: NC ( $SDy_{min}=9.38$  –  $SDy_{max}=11.58$ ), C ( $SDy_{min}=9.47$  –  $SDy_{max}=11.73$ ) and EC ( $SDy_{min}=9.73$  –  $SDy_{max}=12.50$ ).

#### 4.2.4.3 Time frequency analysis

Figure 4.12 shows the time-frequency analysis for the three studied electrodes and the three feedbacks. Results showed a clear enhanced of theta activity in the first feedback with a clear decrease at every feedback repetition. The BMM revealed consistent evidence for this reduction in the first studied time range (180-230 ms) only for the second adjustment (FB3-FB2) in Pz (HDI(95%): Pz: [-0.069 – -0.014], and in the next time range (230-500 ms) in the first adjustment (FB2-FB1) for all three electrodes (HDI(95%): Fz: [-0.070 – -0.013]; Cz: [-0.070 – -0.025]; Pz: [-0.075 – 0.029]). No strong evidence was found for differences in this time range in the second adjustment.

In addition, alpha activity change showed no strong credible change in the first studied time range. In contrast, in the second interval (230-500ms) there was a consistent reduction in the alpha band in the three electrodes in the first (HDI(95%): Fz: [-0.070 – -0.014]; Cz: [-0.094 – -0.038]; Pz: [-0.082 – -0.029]) and second adjustment (HDI(95%): Fz: [0.004 – 0.065]; Cz: [0.034 – 0.094]; Pz: [0.017 – 0.074]).

Finally, regarding beta activity changes throughout the trial, we find credible evidence in the first interval (180-230ms) of a decreased activity in the first adjustment (FB2-FB1) in the three electrodes (HDI(95%): Fz: [-0.068 – -0.021]; Cz: [-0.063 – -0.017]; Pz: [-0.062 – -0.015]). However, this decrease was not sustained in the next interval nor in the second adjustment. Variability of these models (theta, alpha and beta) ranged from  $SDy_{min}=0.52$  to  $SDy_{max}=1.32$ .

Then, in the adjustment model, that is, when comparing the changes in power in the first adjustment with behavioural changes, we only found credible evidence of a decrease in power when there was a higher divergence in participant results at FB1 in  $\beta$  frequency, in the second time interval and in every electrode of interest (HDI(95%): 230-500ms: Fz: [-0.077 – -0.023]; Cz: [-0.069 – -0.017]; Pz: [-0.064 – -0.010]). Variability of this model ranged from  $SDy_{min}=0.53$  to  $SDy_{max}=1.35$ .

Finally, we studied the CIF model, that is, the relationship of changes of power depending on the behaviour of participants in each trial. In the theta frequency we found a credible decrease in EC in the second adjustment (FB3-FB2) in all electrodes and in the two time intervals (HDI(95%): 180-230ms: FB3-FB2: Fz: [-0.009 – -0.012]; Cz: [-0.010 – -0.018]; Pz: [-0.010 – -0.014]; 230-500ms: Fz: [-0.010 – -0.016]; Cz: [-0.011 – -0.028]; Pz: [-0.011 – -0.027]). In the alpha frequency band, in the 230-500ms interval we found a credible decrease in Cz in the first adjustment in NC (HDI(95%): Cz: [-0.008 – -0.015]) and C (HDI(95%): Cz: [-0.008 – -0.011]), as well as a credible increase in the second

adjustment only in C (HDI(95%): Cz: [0.001 – 0.101]). However, we did not find strong evidence to assume credible differences in alpha activity between C and NC in any of the studied time ranges nor adjustments. Finally, in the beta frequency we found C had higher power than NC in FB1 in the three electrodes at first interval (HDI(95%): Fz: [0.002 – 0.089]; Cz: [0.002 – 0.083]; Pz: [0.001 – 0.080]).

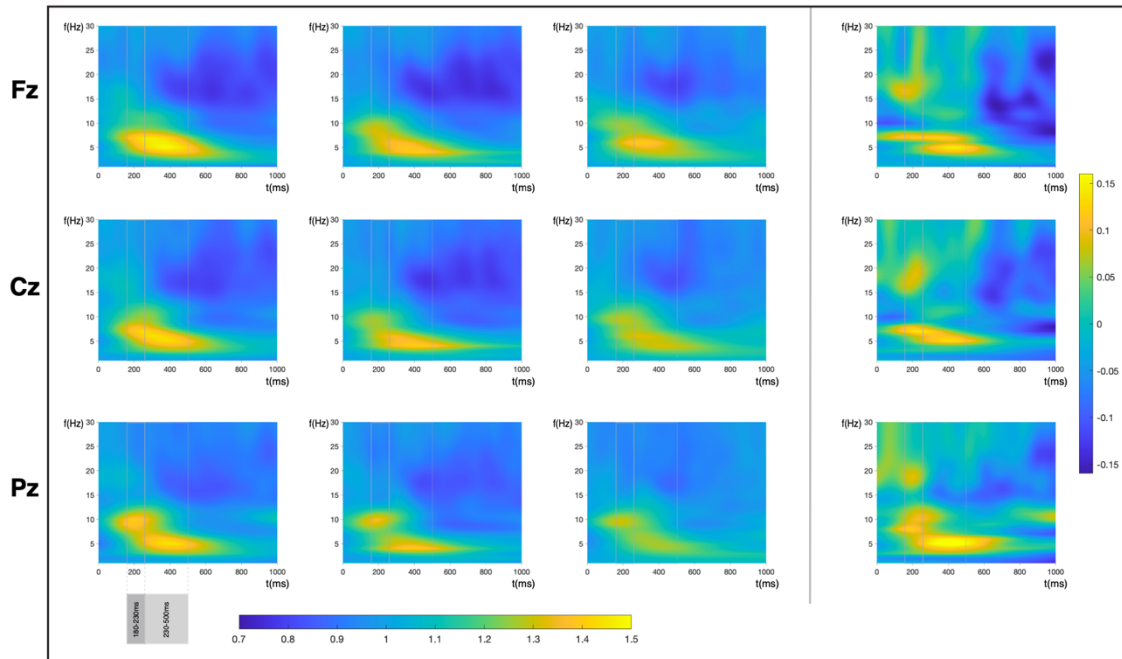


Figure 4.12: Time-frequency plots depicting the three feedback power changes per electrode and the difference between the 1st and the 3rd feedback power (author's own creation).

#### 4.2.5. Discussion

In the present paper we used a new experimental design to study the neurophysiological mechanisms of social conformity. Results showed, first, that participants tended to converge in their decisions even when this was neither explicitly stated nor rewarded. Second, we showed that ERPs were different as the convergence unfolded but that they did not signal with credible strength differences in the level of conformity between C and NC. Finally, time-frequency analysis revealed credible changes in the theta, alpha and beta bands, with some activity being related to the CIF factor. These results show the complex nature of neural mechanisms underlying conformity as a psychological phenomenon in a novel way. Indeed, previous research in the neural correlates of conformity has been studied by means of the social distortion in judgement (Wei et al., 2013), obedience (Xie et al., 2016) or the violation of norms (Shestakova et al., 2013; Schnuerch et al., 2015; Huang et al., 2019), but not as a spontaneous phenomenon emerging in an unaltered cooperative task.

Additionally, other main results of the present study were the credible differences found between the ERPs associated to the different feedbacks in the four studied time ranges (225-275ms, 275-350ms, 350-500ms and 500-700ms). In accordance with previous literature showing the involvement of different components in different stages of stimulus processing, especially for those trials with novel or important information (Polich, 2007). Indeed, and even if it was not explicitly stated nor rewarded, participants converged in their estimations (Figure 2). In order to do so, they needed first to detect the differences between their own and their peers' estimations and, afterwards, evaluate these differences against the previous representation allocated in working memory and the new context (Donchin, 1981). Finally, participants had to decide whether to change their estimation (and to what degree) and take the necessary actions to implement such change, or to stay with their current decision (Donchin, 1981). In the next paragraphs we will try to unfold these different processes with the evidence in our study.

An interesting result of present study arises from the relationship between brain responses and discrepancy between estimations of the participant. Therefore, according to results from *signal~Discrepancy<sub>FB1</sub>* model, voltage in the second interval (275-350 ms) was more negative when the discrepancy between the two participants was higher compared to when it was lower, especially at frontocentral electrodes. This is compatible with the Feedback-Related Negativity, which has been proposed to appear after negative feedbacks (Miltner et al., 1997) and to be modulated by the prediction error (Sambrook and Goslin, 2015). Therefore, given that the discrepancy in this model has been dichotomized as higher or lower than the median, increase in the negativity of this component associated with high discrepancy trials would indicate “worse than expected” agreement in initial estimation of the two participants, yielding to higher FRN. An alternative account proposed by Holroyd et al. (2008), would consider that the negativity in the 275-350ms would be the standard response, and that positive feedback would superpose a positive response to it (Reward Positivity, RewP), decreasing its negative amplitude (Holroyd, Pakzad-Vaezi and Krigolson, 2008). Present results would be compatible with these two interpretations. However, it is important to note that this response would appear latter in time than the traditional FRN/RewP, which normally peak around 250-300ms after feedback onset. A possible explanation for this delay would be the complexity of the feedback that, in contrast to traditional symbolic feedbacks used in learning or monetary paradigms (ticks, crosses, etc.), requires of further computation (processing of two numbers, comparison among them).

In addition, results in the model exploring direct differences in response changes by participant also found credible evidence associating positive relationship of the voltage difference FB2-FB1 with the absolute change of the estimation between the two presentations. These differences were credible in all the studied intervals, affecting all the electrodes but Cz in the first interval. This result shows, therefore, given that the difference FB2-FB1 is generally negative, the lower the adjustment, the higher the amplitude difference between feedbacks. In other words, in those events in which the change in the estimation between presentations is small, the ERPs associated to the first and the second trials is more different than in those trials in which the behavioural change has been large. Hence, in those trials in which the change has been large, probably corresponding to trials in which the participant is willing to adjust the behaviour to their peer, people need a higher allocation of cognitive resources to track the changes and reach an agreement. These cognitive resources might include fronto-parietal networks related

to performance monitoring system (Ullsperger et al. 2014) as well as attentional resources (Polich et al. 2007) among others. In contrast, when changes are small (either because convergence was reached in the first trial, initial estimations were close or participant does not want to converge), only the first trial is relevant, yielding to higher differences in the two feedbacks.

Regarding the role related differences model, we studied the CIF that divided participants' behaviour in each trial (NC, C, EC). Although we expected differences between NC and C, using our strict HDI+ROPE criteria, and contrary to our initial beliefs, we did not find strong credible evidence to support this claim. However, we found a credible positive signal increment in first adjustment in C in fronto-central areas that was not replicated in NC. These differences would be related to higher attentional and cognitive demands required to reach convergence in the C conditions, which require more adjustment than NC ones. Both NC and C show higher decreases in signal in the second adjustment in the third (300-350ms) and fourth (500-700ms) interval. Nonetheless, as stated above, when we contrasted the in-between differences, results did not reveal credible evidence to support such claim. On the contrary, when participants were EC, that is, when they did or did not change their responses, as they have already reached a desirable convergence, there is credible evidence of strong decrease in signal in the second feedback compared to the first one in all studied time ranges. In relation to the P3 components (Polich, 2007), previous studies have found this ERP to be relevant in the categorization and interpretation of stimuli, as well as the allocation of attentional resources needed to perform a certain task. In the current experiment, the first feedback contained most of the information regarding the degree of discrepancy between participants and the need for adaptation of behaviour. Therefore, as expected, participants showed increased P3 for the first feedback compared to the other ones. Attending to where the differences are more credible in our results, we see how to adapt their behaviour, participants require higher attentional and cognitive resources engaged for a longer time in the trial. Therefore, while participants when EC reduce credibly their cognitive load in the first adjustment, NC and C keep their engagement through the next adjustment and drop it consistently at the end of the trial (2<sup>nd</sup> adjustment, FB3-FB2). As we already mentioned, it is also worth noting that, in the first adjustment, and contrary to what happens to EC, when participants are C, they credibly increase their signal positivity in the third interval (350-500ms) in frontocentral electrodes in what we interpret to be a preparation required when aiming convergence. Finally, it is interesting to note that previous studies have related the P3b component to social mentalizing processes generated in temporoparietal junction (TPJ) and medial prefrontal cortex (mPFC; see Overwalle and Vandekerckhove, 2013, for a review). Indeed, in the present study, participants used mentalizing strategies to, e.g., predict the degree of change of the estimation of the peer or infer the willingness to converge. However, this was not controlled in the experiment and no manipulation was performed on this process, making it impossible to disentangle the role of mentalizing in the P3 generation. Future modifications of the present experiment manipulating the degree of social mentalizing could help in better disentangling possible cognitive and mentalizing contributions to the P3 ERP.

The second main electrophysiological finding of the current experiment is the increase of theta oscillatory activity for the three electrodes in the 230-500ms interval in the first feedback compared to the activity from the second and third ones. Theta activity has consistently been associated with cognitive conflict, prediction error and surprise among

many other functions (see Cavanagh et al, 2014, for a review), with its main generators located in the Anterior Cingulate Cortex (ACC, Mas-Herrero and Marco-Pallarés. 2016). In addition, it has been proposed that this component plays a key role in the top-down cognitive control necessary for the behavioural and strategic adjustment necessary in the decision-making process after an unexpected result (Cavanagh et al., 2010) or the adaptive control under uncertainty (Cavanagh et al. 2012). In addition, the CIF model shows in EC a consistent disengage of theta in the second adjustment, which would be in line of a higher cognitive control component needed in those conditions in which participants converged more, therefore allocating higher cognitive resources. Alpha activity showed a different behaviour, with decrease of activity in the first adjustment increase in the second one. The role of alpha in cognitive control functions have been described as a signal to alertness (see Sadaghiani and Kleinschmidt, 2016, for a review). The role of alpha as a top-down physiological inhibitor has been also studied in non-human animal studies suggesting alpha oscillations increase when neuronal activity of the brain region decreases (Haegens, et al., 2011). Our results would suggest a certain coherence to this interpretation, as attentional engagement is still required, or even required to be enhanced, in the first adjustment, whereas these requirements drop in the second as participants are closer to their goal. Finally, results in the beta band suggest an early activity decrease in the first adjustment for the three electrodes. Moreover, the CIF model also finds an increased early beta activity in C when compared to NC. However, this early activity was not previously hypothesized and is far from the scope of the present research. Further studies manipulating attentional demands of similar conformity tasks could help in interpreting the functional role of these oscillatory components. On the other hand, previous studies have suggested an association of beta bands and reward processing (Mas-Herrero, et al., 2015), which would suggest it to act as motivational signal that could mediate different cognitive processes (see Marco-Pallarés et al., 2015 for a review). In our study, even if we expected convergence between participants would act as a natural reinforcer, we had no clear evidence to declare such relationship would, in fact occur. Withal, we understand the evidence from the discrepancy model regarding beta activity supports such claim and is coherent to the interpretation relating beta as a motivational value signal across the brain.

Therefore, the present results support the idea that the proposed paradigm is valid to study the neural correlates of convergence mechanisms and goes beyond previous experimental paradigms that have focused on segmented parts of the conformity process, allowing the study of this phenomenon in a more holistic way. Future directions on the use of this task would imply not only the verification and extension of the cognitive processes mentioned in the current research but also the study of other group processes happening under different conditions, such as threat, social-categorization, polarization processes and so on. In addition, future implementations of the task could involve increasing the number of the people working together, a fine-grain control of the intimacy levels of the dyads or how personality traits affect behavioural adjustments or the use of the paradigm in different populations different neuropsychiatric condition affecting social cognition.

#### 4.2.6. Supplementary Materials

In the present supplementary materials, we are presenting additional detailed results on what has been already discussed in the main article. All these materials are accordingly addressed and commented in the main text.

*Table 4.4: Results from model signal~FB*

Interval	Electrode	Contrast	ROPE_low	ROPE_high	ROPE_%	Equivalence	HDI_low	HDI_high
225	Fz	2-1	-0.55	0.55	0.00	Undecided	-1.08	-0.54
225	Fz	3-2	-0.54	0.54	0.93	Undecided	-0.67	0.16
225	Cz	2-1	-0.53	0.53	0.00	Undecided	-1.04	-0.52
225	Cz	3-2	-0.52	0.52	1.00	Accepted	-0.39	0.43
225	Pz	2-1	-0.48	0.48	0.02	Undecided	-0.97	-0.45
225	Pz	3-2	-0.48	0.48	0.95	Undecided	-0.23	0.58
275	Fz	2-1	-0.58	0.58	0.18	Undecided	-0.93	-0.38
275	Fz	3-2	-0.57	0.57	0.59	Undecided	-0.94	-0.10
275	Cz	2-1	-0.57	0.57	0.19	Undecided	-0.92	-0.35
275	Cz	3-2	-0.56	0.56	0.87	Undecided	-0.77	0.07
275	Pz	2-1	-0.51	0.51	0.08	Undecided	-0.93	-0.38
275	Pz	3-2	-0.50	0.50	0.65	Undecided	-0.84	-0.01
350	Fz	2-1	-0.60	0.60	0.14	Undecided	-0.98	-0.45
350	Fz	3-2	-0.59	0.59	0.00	Rejected	-1.81	-0.97
350	Cz	2-1	-0.59	0.59	0.17	Undecided	-0.94	-0.40
350	Cz	3-2	-0.58	0.58	0.00	Rejected	-1.58	-0.74
350	Pz	2-1	-0.54	0.54	0.05	Undecided	-0.97	-0.45
350	Pz	3-2	-0.53	0.53	0.00	Rejected	-1.67	-0.84
350	Fz	2-1	-0.56	0.56	0.00	Undecided	-1.09	-0.55
350	Fz	3-2	-0.56	0.56	0.00	Rejected	-1.97	-1.13
350	Cz	2-1	-0.56	0.56	0.00	Rejected	-1.13	-0.56
350	Cz	3-2	-0.55	0.55	0.00	Rejected	-2.19	-1.35
350	Pz	2-1	-0.53	0.53	0.00	Rejected	-1.26	-0.60
350	Pz	3-2	-0.53	0.53	0.00	Rejected	-2.50	-1.63



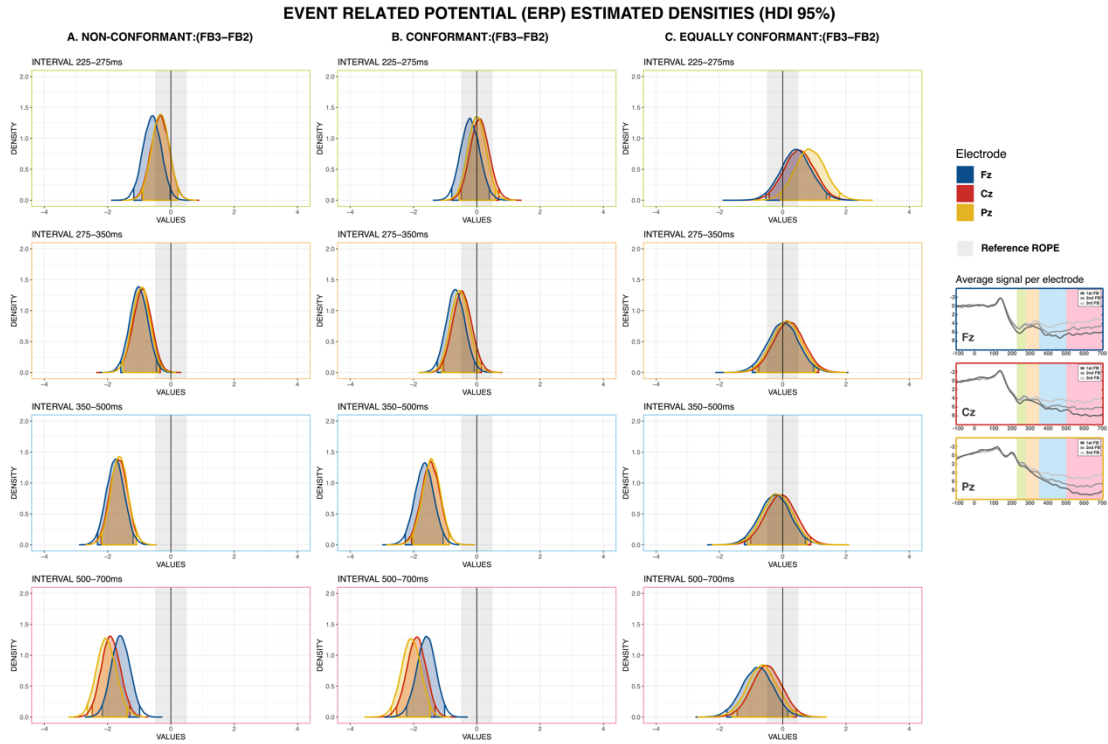


Figure 4.13: Estimated densities of different hypotheses regarding the: (A) differences between 2nd and 3rd feedback in participants non-conforming in the trial; (B) differences between 2nd and 3rd feedback in participants conforming in the trial; and (C) trials where both participants were equally converging. Note the dimmed area is an approximate ROPE range used as reference. As explained in the methods sections, all the ROPE ranges were adjusted considering individual variability. Hence, we use a standard -0.5 - 0.5 range here as visual reference (author's own creation).



4.3. Study 3: Inter-brain synchrony oscillations underlying the behavioural adaptation of conformity

#### 4.3.1. Summary

There is a natural tendency in humans to synchronize their behaviour to other people which is a key ability in any type of prosocial behaviour. However, although it happens almost automatically, the adjustment of behaviour and the conformity to others is a complex phenomenon whose neural mechanisms are still yet to be understood. The goal of the present experiment was to study the oscillatory synchronization mechanisms underlying the automatic convergence of behaviour in an EEG hyperscanning experiment. 36 people performed a purely cooperative decision-making task in dyads in which they had to guess the correct position of a point in a line. Intra- and inter-connectivity among electrodes was assessed using intersite phase clustering (ISPC) in four main frequency bands (theta, alpha, beta and gamma) using a two-level Bayesian Mixed Modelling approach. Results showed that, although they were neither instructed nor rewarded to do so, participants converged in their estimations about the position of the point after knowing the estimation provided by their peers. We found two different dynamics related to attention and executive functions in alpha and reinforcement learning tracked by theta. We also find other inter-brain coherence in beta related to low adjustment trials.

#### 4.3.2. Introduction

Conformity is a social adaptation where people adjust their vision and behaviour in favour of cooperation. This behavioural adjustment is a complex phenomenon which requires tracking different intra-personal and inter-personal levels of representation of reality and other computations such as conflict monitoring, providing different values in action selection, prediction and learning while integrating information from executive functions, reward circuitry, as well as mentalizing. More importantly, conformity is a behavioural response happening when a person makes a conscious choice to converge in their view of the world to their partner, by means of an intrinsically social reward and integrating information from different sources.

One approach that can consider rewards (of social nature in this case), and its effects in one's model of the world to make decisions is the reinforcement learning (RL) framework. This operationalization of learning considers a value being iteratively updated by means of a prediction error (PE) coming out of a reward (or lack thereof). In other words, a RL model can provide an estimation of a learning process in a participant's brain by means of an iterative learning rule, where participants, make constant predictions ( $Q_{t+1}$ ) that constitute an influence over their own actions based on their partner's observed behaviour and update these predictions tracking a PE. Importantly, social conformity has been explained by reinforcement learning (Klucharev et al., 2009). This study proposes an interpretation of norms and their learning acquisition, as the explanation to why people sacrifice their vision by means of a common goal. This explanation has been widely accepted in the interpretation of different findings regarding social conflict (Zubarev et al., 2017). However, recent evidence suggests this explanation to be rather simplistic (Levorsen et al., 2021), because it assumes PE is the same as social conflict, while it has been proposed they could be unrelated (Izuma and Adolphs, 2013). Therefore, RL might be useful in providing insights in the study of conformity, but only at computational level under a multi-layered complex psychological phenomenon. Accordingly, although an RL

model alone cannot explain all the adaptation phenomenon, we believe it could be valid to track the learning computational component.

As a complex phenomenon, conformity involves the interaction of different factors (e.g., states, traits, agents, and environment), which, are driven, in fact, by computations occurring in a reduced temporal scale in different areas of the brain. A neural mechanism which has been proposed to integrate information from different temporal scales and brain regions is brain oscillations (Varela et al. 2001). These oscillations have been identified as facilitators of dynamic temporal and spatial neural activity coordination mechanisms (Varela et al., 2001; Fries, 2005; 2009; Canolty et al., 2010) and are thought to reflect distinct communication systems between areas in the cortex (Kohn et al., 2020). Particularly in the field of social neuroscience, in recent years, neural dynamics and, more specifically, synchronic oscillations in interacting individuals, have been studied using a two-person approach, in what has been identified as *hyperscanning* settings. Here, it has been claimed oscillatory coupling between persons is a form of organizing collective behaviour, especially effective for additive tasks like joint-action or temporal motor synchronization (Sänger, Müller and Lindenberger, 2012; Astolfi et al., 2020) but also observed in verbal interaction (Pérez, Carreiras and Duñabeitia, 2017), shared attention (Dikker et al., 2017) or intention (Barraza, Pérez, Rodríguez, 2020), creativity (Lu et al., 2019) or decision making (Hu et al., 2018). In fact, despite the ongoing dispute on the validity of hyperscanning to interpret causal evidence in inter-personal interaction (Czeszumski et al., 2020; Novembre and Iannetti, 2021; Hamilton, 2021; Gvirts Provolovski, H. Z., and Perlmutter, 2021; Schirmer, Fairhurst and Hoel, 2021), there is evidence suggesting inter-brain phase synchronization to be an indicator of collective performance (Szymanski et al., 2017) better than other self-report measures (Reinero, Dikker and Van Bavel, 2021). Recently, it has been suggested the connectivity of the cognitive processes between the interactors in a social interaction is distinct than during social observation (Schilbach et al., 2013). The growth of this new research has been key to identify two distinct core neural systems as a key part of social interaction (see Redcay and Schilbach, 2019 for a review). On the one hand the Mirror Neuron System (MNS), consisting of primary motor and sensory cortex as well as parietal cortex, responsible to the imitation process needed in joint-action paradigms. On the other hand, the Mentalizing System (MS), which has been identified in a network comprising the Temporo-Parietal Junction (TPJ) and prefrontal cortex (PFC). Such findings suggest there is a logical interest on substantiating different hypotheses coming from single-person neuroscience into dual-person settings.

The multi-layered nature of social cognition is undisputed, and so it is the understanding of the brain as a system continuously searching for reducing its own uncertainty. Social agents seek information in the environment (or other agents) to optimize their models of the world reducing entropy, aiming to better adapt their action strategies. In fact, how biological systems act towards a minimization of future surprise by means of a Bayesian prior actualization, has been proposed to explain how the brain infers its environment and acts accordingly (Friston, 2010; 2018, Bastos et al., 2012). This theory, and its translation into the neuronal action (Bastos et al., 2012), has been shown in different brain areas and functions such as auditory cortex (Heilbron and Chait, 2018), sensory processing (Arnal and Giraud, 2012; Kok and de Lange, 2015), visual cortex (Van Kerkoerle et al., 2014; Alamia and Van Rullen, 2019; Strube et al., 2021), spatial working memory (Zhang et al., 2019), natural speech (Hovsepyan, Olasagasti and Giraud, 2020) or frontal cortex activity (Alexander and Brown, 2018). In recent years, research in

predictive coding has tried to relate different oscillatory dynamics with the reduction of surprise suggested by the theory. For instance, recent findings in non-human primates suggest gamma and beta dynamics are associated to predictive coding (Bastos et al. 2020). Therefore, beta oscillations would be related to predictions and gamma would be linked to prediction errors (Bastos et al., 2020) in a continuous information updating process. These findings are in line with previous evidence that have related the role of high (gamma) and lower (alpha/beta) frequency oscillations with feedforward (bottom-up) and feedback (top-down) trace respectively in the oscillatory dynamics of primate visual cortex (Van Kerkoerle et al., 2014; Jensen et al., 2015) and selective attention (Marshall et al., 2018), with some authors suggesting this could be a general mechanism extensive to other areas of the cortex (Bastos et al., 2020).

However, even when such explanation is compelling, it results in a rather reductionist principle, especially in the case of recording from the scalp by means of electroencephalography (EEG) or magnetoencephalography. EEG signal is produced by the simultaneous action of thousands of broadly distributed neurons. Therefore, the relationship between oscillatory component measured using EEG to and cognitive processes is of complex nature. However, the use of some instruments, such as computational models, might help in disentangling this problem. For example, the use of RL algorithms to model neural activity is nowadays common practice in neuroscience specially when studying value learning (Eckstein et al., 2021). In recent years, the use of these models in EEG has shed light on the action and expectation monitoring research, being frontal theta a candidate to track reward prediction errors (Cavanagh et al., 2010) or uncertainty and unexpectedness during exploration (Cavanagh et al., 2012; Mas-Herrero and Marco-Pallarés, 2014). These studies suggest theta activity could be a biophysical marker of predictive modelling and cognitive control (Cavanagh and Frank, 2014). In addition, a recent study on the MEG oscillatory dynamics of conformity (Zubarev et al., 2017) showed that mismatch opinions between an individual and a group were tracked by theta in both anterior and posterior cortices. Therefore, given its critical role in cognitive control and prediction error signalling, theta oscillatory activity is a key candidate to track the changes of the peers and implement the appropriate actions in conformity settings and social behavioural adaptation.

However, other oscillatory components could also play a role in conformity. For example, in the Zubarev et al. (2017) above-mentioned study, beta oscillations in anterior parts of the brain were engaged when opinions of the participant matched the group's one, supporting a role of this activity in reward processing (Marco-Pallarés, Münte and Rodríguez-Fornells, 2015). In fact, when we consider complex and multi-layered psychological processes, we are targeting functions that might be using different regions of the brain and different neuronal populations simultaneously. Given that the brain relies on multivariate information encoded in response patterns (Anzellotti and Coutanche, 2017), these different areas rely on connectivity to synchronize for a coherent outcome. There is evidence coming out from non-human primate studies suggesting information is repeatedly encoded in different areas of the brain at the same time (Siegel, Bushman and Miller, 2015). Most of these dynamics in electrophysiology influence phase-coupling, the relationship between oscillation phases in different regions, by means of a communication mechanism serving to coordinate distant cell assemblies in the brain (Canolty et al., 2010). A recent review suggests for this distant communication, there is not only one but different temporal coordination mechanisms that cooperate for this

multivariate purpose (Kohn et al., 2020). One of the most described mechanisms among these, mostly because it can easily be studied in frequency dynamics in the cortex with the use of EEG, is the *communication through coherence* connectivity strategy between structural and neuronal synchronization (Fries, 2009; see however Jaramillo, Mejias and Wang, 2019 or Bolkan et al 2017 among others for other sources of communication different than the cortex). This type of cortical communication assumes that neural oscillations are sourced in the excitability fluctuation of different ensembles of neurons and, hence, they can communicate when they share a similar excitability state. It is also assumed the lag between these oscillations to be explained by signal traveling speed between regions (Bastos et al., 2015; Fries, 2015). In addition, in recent years, oscillations in alpha band have been related to functional inhibition mechanisms, in what has been called *gating by inhibition* (Jensen and Mazaheri, 2010; see Van Diepen, Foxe and Mazaheri, 2019 for a review).

Recent evidence coming out of two-person neuroscience suggests simultaneous synchronic coherence in two different participants, might be related to distinct aspects of shared processing. Research has described temporally coupled brain-to-brain oscillatory patterns during social interactions in temporo-parietal areas (Kinreich et al., 2017) mainly coded by gamma oscillations. There has been also evidence (Schurz et al., 2014) coming from single-person neuroscience that supports the idea of this temporal parietal cluster of regions involved in social processing. More recent evidence in inter-brain studies suggests gamma-band oscillatory power to be the dominant marker of rapid bottom-up synchrony in mother-child interactions (Levy, Goldstein and Feldnamn, 2017), social coordination (Mu, Guo and Han, 2016; Mu, Han and Gelfand, 2017), action preparation (Bramson et al., 2018), prediction errors (Bastos et al., 2020), working memory (Gestopoulos, Whittington and Koppel, 2019), as well as in shared intentionality (Barraza, Pérez, Rodríguez, 2020). In addition, there is also evidence of synchrony of other frequencies (alpha and beta) in other paradigms such as in verbal interaction (Pérez, Carreiras and Duñabeitia, 2017). Moreover, in a recent massive (4800 people) sample experiment conducted outside a lab (Dikker et al., 2021), authors reported inter-brain coupling in beta-band to be associated with joint social attention.

Importantly, and to the best of our knowledge, no previous studies have been devoted to describing the role of oscillations in the intra- and inter-brain synchronization in social conformity. Indeed, cooperation, and in particular, conformity is difficult to study in the lab, because it has a certain degree of freedom, spontaneity, and unpredictability by default. Therefore, to study this social adaptation, we propose a cooperative task between two participants who have the chance to naturally adjust their responses to converge at their will (and without any explicit instruction nor reward to do so), at three different repetitions of a stimuli. To study such interactions, we will explore coherence dynamics in phase-based connectivity both intra- and inter-person. We designed a task that captures the inter-dependence and conflict between two distinct state representations: first, participants' own internal views and guesses, and second, the adjustment in action due to an intrinsically social valuation. To do so, participants need to learn about their partners to predict their intentions, which will be important specially in the 2<sup>nd</sup> and 3<sup>rd</sup> adjustments at every trial, where the prediction and its error will play a role. *Figure 4.14* explains the general processes we expect to be present in the different phases of the experiment. Here reward is represented by means of cooperativity of participants, when they are spontaneously willing to converge in their responses. We are, therefore, performing a strict exploratory analysis, with the use of a two-level Bayesian Mixed Modelling, that

probes the simultaneous phase-coherent activity at different frequency bands between the different scalp electrodes from a single person or in dyads at different time windows. We will also use a RL model to relate the oscillatory activity with the different value and prediction parameters obtained using the RL algorithm.

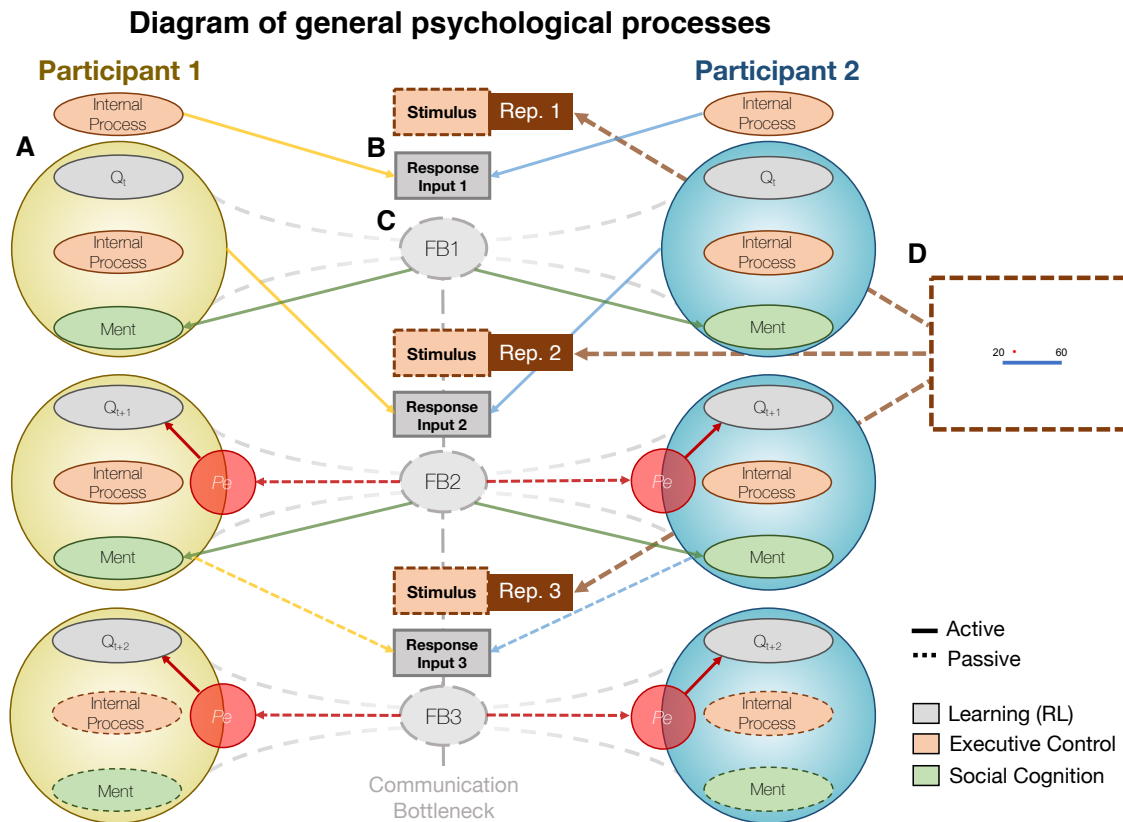


Figure 4.14: Depiction of the major processes involved in a pervasive cooperative task, where participants have two chances to adjust their behaviour in the presence of a feedback of a shared state, where they can see each other's responses (C), with their partners. The circles (A) indicate the three different epochs (by each participant) at every trial that we are using as data in this research. At first repetition (FB1) of the stimulus (D) participants only use their own views to respond (B), once they have their first feedback, they start the mentalizing and reinforcement learning processes to try and predict what the partners intentions are based on the observed information. In second repetition (FB2) different levels of processing interact to give a second response, with a prediction based on learning from previous trials. At last repetition (FB3) the previous prediction error ( $Pe$ ), difference between expected ( $Q_t$ ) and observed (FB) value, has influenced the subsequent  $Q$ -value ( $Q_{t+1}$ ). Finally, third and last feedback will have an influence in learning that will be inherited in the next trial. Note the stimulus remains the same throughout the trial. We categorized the three different groups of internal processes: Learning, Executive Control and Social Cognition, and differentiate between dashed lines, that imply passive processes and solid lines which indicate an active process. (author's own creation)



### 4.3.3. Methods

#### 4.3.3.1 *Participants*

36 participants in 18 dyads (20 women and 16 men; age Median: 24, range: 19-53) took part in the experiment. All participants were volunteers, signed an informed consent before starting the experiment and were rewarded 30 euro for participating in the experiment. The experiment was approved by the Bioethics Committee of the University of Barcelona.

#### 4.3.3.2 *Instructions and Procedure*

The experiment consisted in two parts. First, dyads had to finish some activities printed in a paper involving different cooperative tasks inspired by the cooperative dimension in the circumplex model (McGrath, 1984) with a time limit of one hour in order to pre-activate cooperative tendencies. Then EEG was prepared to record the dyads brain activity in the main task.

The experimental paradigm consisted in a decision-making paradigm where participants had three chances to adjust their guess in an estimation task. A line (vertical or horizontal) was presented on the screen simultaneously to the two participants and a randomized range of numbers marked at both edges of the line. Over the line, they were able to see a red dot falling somewhere over it. They had to introduce the estimation on the position of the dot in a keypad, and they were showed feedback with their own and their partners' responses. After introducing their responses, they were exposed to their and their partners responses as seen in *Figure 4.8*. The moment of feedback constituted our trigger of interest at every repetition. This stimulus was shown two more times per trial so participants could, at their will, adjust their responses, although this not specifically instructed. The experiment was divided in 4 blocks of 25 trials in each block with 3 trial repetitions per trial.

#### 4.3.3.3 *EEG Data Collection*

EEG was continuously recorded using an ANT Neuro ASALab EEG amplifier from 27 scalp electrodes (Fp1/2, Fz, F3/4, F7/8, Fc 1/2, Fc5/6, Cz, C3/4, Cp1/2, Cp5/6, Pz, P3/4, P7/8, POz, Oz, M1/2) and 3 external electrodes: two (horizontal, vertical) registering eye movement, one in the nose. The electrode impedance was kept in less than 5k $\Omega$ . We did not apply any filters at data collection, and it was digitized at a sampling rate of 1024Hz.

#### 4.3.3.4 *Pre-Processing*

We used EEGLAB in MATLAB for pre-processing. The data was bandpass filtered from 1 to 42Hz. Epochs from  $-2$  to 2 seconds were extracted in each trial and Independent

Component Analysis (ICA) was applied to remove the ocular artifacts. Surface Laplacian (Cohen, 2014) spatial filter was applied to the data, a strategy to mitigate volume conduction for electrode-level connectivity, to the data prior to angle extraction. We then subtracted to each single trial the ERP to ensure frequency dynamics are task-related but are not driven by the ERP and after that, each trial was convolved with a complex Morlet wavelet. Angles of the wavelet coefficients were extracted for each single trial time-frequency data point and used to compute the synchronization between electrodes by means of inter-site phase clustering (ISPC) procedure (Cohen, 2014) for each frequency. Then we averaged them over frequency ranges ( $\theta$ , 4-8Hz;  $\alpha$ , 8-13Hz;  $\beta$ , 13-25Hz;  $\gamma$ , 38-42Hz) and in two time-ranges: first, from 0 to 500ms and second, from 500-1000ms. This division is based in previous studies on the mirror neuron system (MNS) that have identified the 500ms approximate midpoint as the moment where there is a significant event-related desynchronization (ERD) when the exogenously activated signal integrating loops start (Simon and Mukamel, 2016; 2017), that is when sensorimotor regions (as part of the MNS) switch from automatic to controlled processing.

#### 4.3.3.5 Two-level Analysis

Our statistical procedure is inspired by the two-level analyses from fMRI studies (Friston et al., 2005). In the first level analysis, we included ISPCs as dependent variables in a mass-univariate generalized linear model (assuming beta-distributed values) and extracted their relation to the *FB* repetitions (per dyad in the interpersonal analysis and per participant in the intrapersonal analysis) using maximum likelihood estimation with the R package *glmmTMB*. Next, we used the R package *lsmeans* to compute the least-squares means of the parameters of interest and extract their estimates and associated standard errors.

Subsequently, we used these first-level data to carry out null-hypothesis credibility testing (NHCT) in a second-level analysis. This was done by including the first-level data from all connections -excluding the mastoids (i.e. 625 connections in dyadic data, 300 connections in intra-personal data)- in a hierarchical Bayesian meta-analysis (BMA; Marsman et al., 2017; Kruschke, J.K. and Lidell, T. M., 2018) assuming normality ( $\mu$ : identity; prior on  $\sigma$ : student-t,  $\mu = 0$ ,  $\sigma = 2.5$ ,  $\nu = 3$ ) and with weakly informative priors over the intercept (normal,  $\mu = 0$ ,  $\sigma = 10$ ) and over connections as varying effects (gamma,  $\alpha = 1$ ,  $\beta = 10$ ) using the R package *brms* (Bürkner, P. C., 2017; 2018). For NHCT we consider posterior distributions credibly different than zero when the totality of a Region of Practical Equivalence (ROPE) around the null hypothesis ( $H_0: \beta_0 = 0$ ) consisting in the range  $\pm 0.01 * SD_y$  -where  $SD_y$  is the standard deviation of the dependent variable- completely falls outside 95% of the posterior's Highest Density Interval (HDI) (Kruschke, 2014; 2018; Kruschke, J.K. and Lidell, T. M., 2018). For completion, we also display the results without a ROPE around the  $H_0$  95% of the posteriors' HDIs in the supplementary materials, although we are sticking to the HDI+ROPE rule for discussion.

For the interaction analysis and the extraction of other contrast of interest from the model (i.e., adjustments FB2-FB1 and FB3-FB2), we always took the estimates and standard deviations from first level to the second. This means that contrasts and interaction terms were always calculated at the first level, so we only took the estimates and the standard deviations to the BMA for a sample-level analysis.

Contrasts were calculated analysing the relationship between the ISPC and feedback repetition ( $FB_{rep}$ ). We also analysed the effect of type of adjustment ( $Adj$ ;  $FB_{rep} \times Adj$ ), being the later a dichotomic consideration on *High*, (*high-high*, coming highly adjusted from the first opportunity to change their responses and continuing this way to the second) and *Low* (*low-low*) adjustment, depending on the level of behavioural adjustment towards convergence effort in the trial compared to the median of all response adjustments by each participant in all trials.

It is worth noting we intentionally permuted the order in the differences (i.e., for differences between FB1 and FB2 we use FB2-FB1 contrast instead of FB1-FB2, and, of course, the same applies to differences between FB2 and FB3). The reason for this is the sign in the HDI to directly relate to what is going on in the activity from one feedback to another. Hence, we consider a relationship positive when the activity is increased in relation to its reference, e.g., a positive relationship in the contrast FB2-FB1 would indicate an increase in the synchronization of FB2 compared to FB1. A negative relationship would be interpreted in the opposite way.

#### 4.3.3.6 Reinforcement Learning analysis

A RL algorithm was used to model the adjusting of behaviour done by participants on the bases of previous trials. At each time

( $t$ ), the algorithm updated the subsequent Q state-action ( $s, a$ ) value with a prediction error obtained from the subtraction of the previous Q to the actual reward:

*Equation 4.3*

$$Q_{t+1}(s, a) = Q_t(s, a) + \alpha \times [r - Q_t(s, a)]$$

In essence, the Q function was updated by the reward, but represented a state where the agent acts. With the intention to maintain the state representation in a simple way, we considered a dichotomic option per action choice: we considered a cooperative (C) choice in the case the participant decided to preserve their response if this was, in fact, converged to their partner's or the participant decided to change their response in pursue of convergence with their partner; and an uncooperative (U) choice in any other case. Then, we defined a reward value ( $r$ ) of 1 in case of cooperative situation and  $-1$  in case of uncooperative one.

For all the values the learning rate  $\alpha$  was set to 0.5. Internal variables were analysed in relation to the signal with the feedback repetition in interaction with the prediction error ( $FB_{rep} \times PE(s, a)$ ) and the Q update ( $FB_{rep} \times Q(s, a)$ ).

#### 4.3.4. Results

##### 4.3.4.1 Contrast analysis in trial-by-trial results

In the results section we will only describe in detail those results with strong evidence using a combined  $\text{HDI}_{\text{NHCT}}(95\%)+\text{ROPE}$  approach. However, to complement present data, we provide the results of the inference with the HDI rule but without the ROPE interval in the supplementary material which has also been proposed to be used in Bayesian inference although it clearly supposes a significantly less conservative approach (Kruschke, 2018).

Intra-personal contrasts in the first adjustment (FB2-FB1) (*Figure 4.15*) showed a credible change in the first time range (0-500ms) associated with positive or increased activity in alpha frequency band (Positive: 114 out of 300 connections in  $\text{HDI}_{\text{NHCT}}(95\%)+\text{ROPE}$ ). In dyadic data (*Figure 4.16*), inter-brain connections in the first adjustments were credibly related negatively to beta (Negative: 9 out of 625 connections in  $\text{HDI}_{\text{NHCT}}(95\%)+\text{ROPE}$ ). We found no sufficiently credible evidence on activity change related to any frequency bands for the second adjustment (FB3-FB2).

## Intra-personal frequency coherence plots

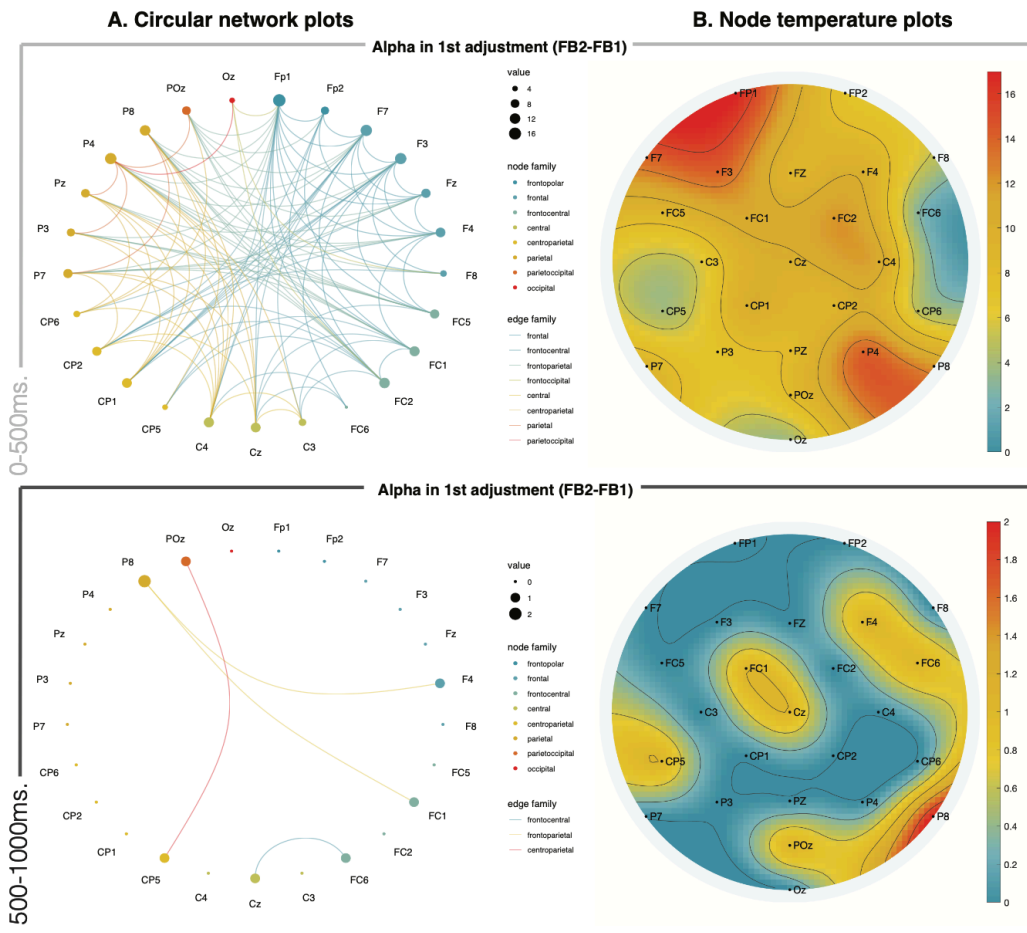


Figure 4.15: (A) Circular network plots show specific electrode credible connections (HDI+ROPE rule) framed light at 0-500ms and dark in 500-1000ms. The size of the node shows the degree of connections at each node which is later shown with higher detail in the plot (B), where the same connections are depicted in a topographical colormap always start at 0 and goes high as the maximum number of edges in an electrode node (author's own creation).

In the second time range (500-1000ms), results also showed credible intra-personal frequency coherence related to a positive change in the first adjustment in alpha (Positive: 4 out of 300 connections in  $HDI_{NHCT}(95\%)+ROPE$ ), and in inter-brain data, also an increase in alpha (Positive: 2 out of 625 connections in  $HDI_{NHCT}(95\%)+ROPE$ ). Here, again, the second adjustment did not show a credible change with any of the studied frequency bands.

Lastly, we performed an analysis based on the adjustment ( $FB_{rep} \times Adjustment$ ) made by participants, differentiating lowest adjustment trials (*low-low* contrast from FB3-FB2, for first and second adjustment) and the highest adjustment trials (*high-high* contrast from FB3-FB2, for first and second adjustment). We only used the second adjustment contrast because FB2-FB1 was the reference in the identification of the adjustment level of the trial. Results did not reveal any credible or strong enough evidence related to the adjustment model ( $FB_{rep} \times Adjustment$ ) in any of the studied frequencies with the ROPE+HDI rule.

### Inter-Brain frequency coherence plots

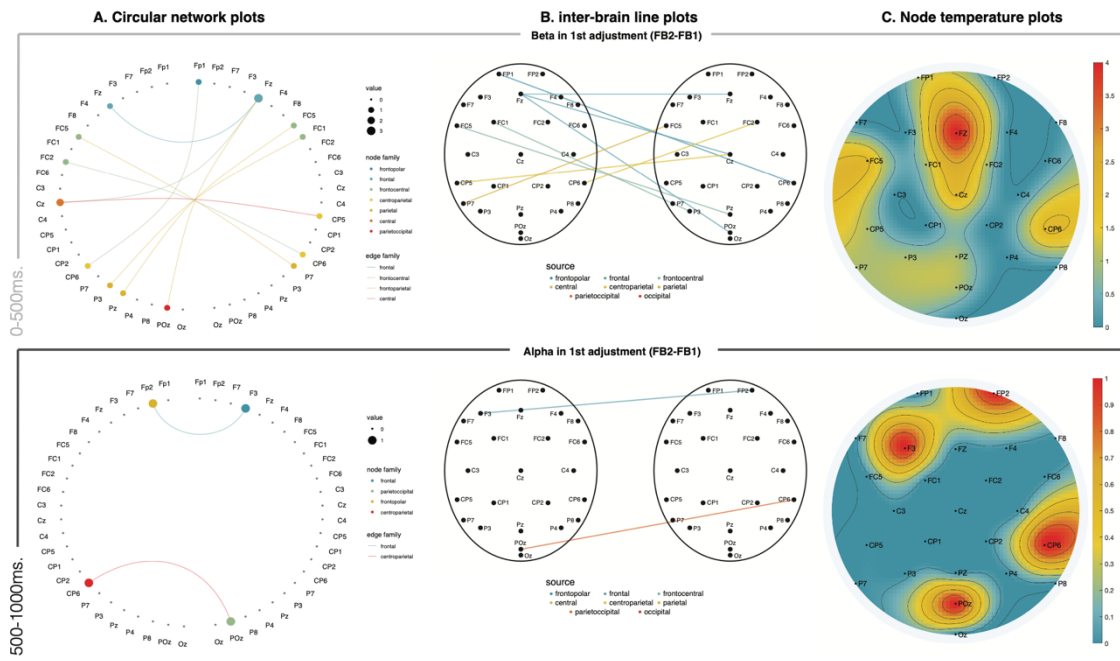


Figure 4.16: Inter-brain or brain-to-brain coherence plots, depicting (A) circular network plots and line plots (B) shows different representations of the same connections, with connections on one brain in every side. Lastly, node temperature plots (C) show the degrees of electrode nodes in a colormap starting from 0 to the highest number of edges in an electrode (author's own creation).

#### 4.3.4.2 Reinforcement learning analysis

RL parameters revealed credible relationship with brain synchronization only in the first time-interval (0-500ms), and we did not find any credible connections in the second phase (Figure 4.17). Additionally, all the credible activity change in feedbacks related to RL variables ( $FB_{rep} \times PE(s, a)$  and  $FB_{rep} \times Q(s, a)$ ) was associated with theta frequency band and only in the second adjustment (FB3-FB2) condition PE increased theta connectivity mainly in frontal areas (Positive: 25 out of 300 connections in  $HDI_{NHCT}(95\%)+ROPE$ ) with the addition of a centroparietal cluster. In addition, Q-value which indexed the prediction (Negative: 134 out of 300 connections in  $HDI_{NHCT}(95\%)+ROPE$ ), showed credible connectivity decrease in frontal and parietal areas. Therefore, our data showed a strong tracking of the PE increased at next feedback repetition and a decreased theta activity related to Q-value reduced at FB3.

## Plots from RL model parameters

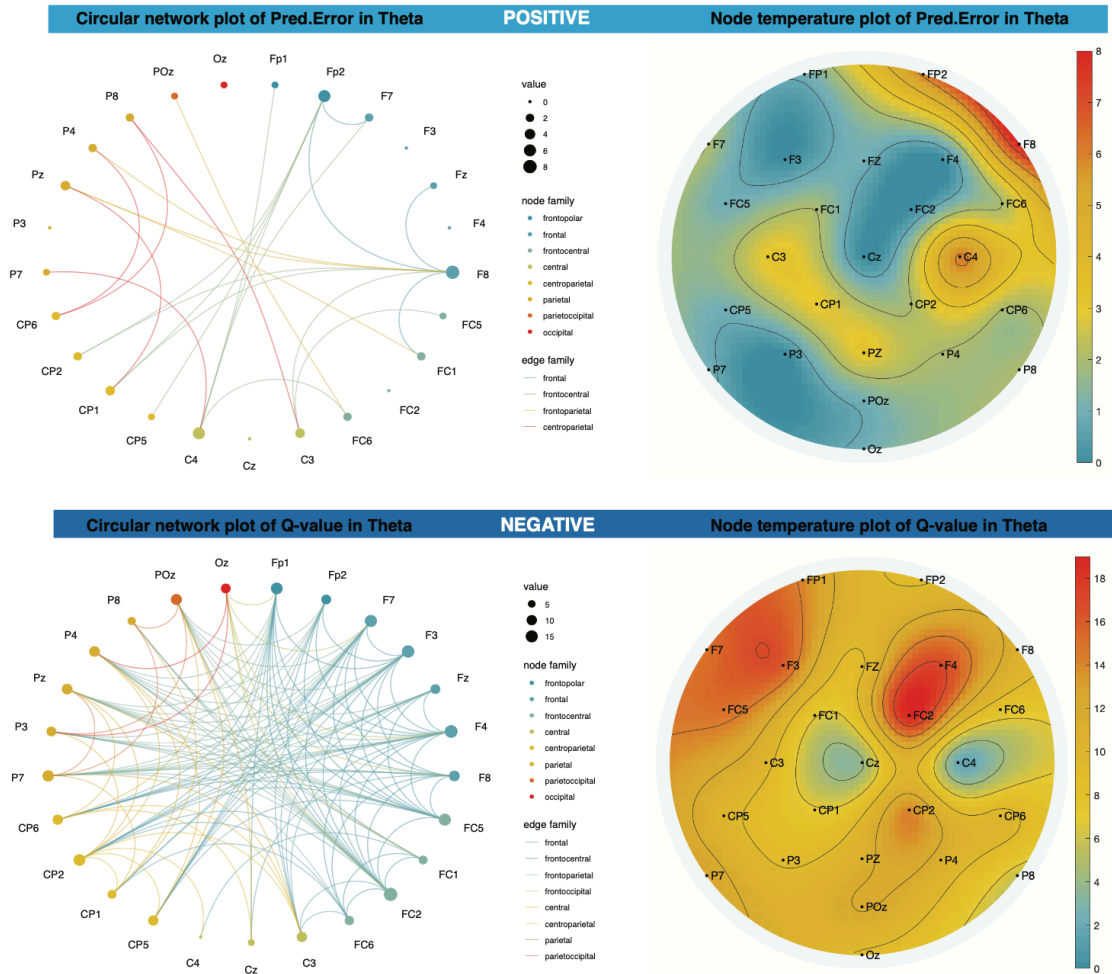


Figure 4.17: Tracking of RL parameters in FB2-FB3 in the  $FB_{rep} \times PE$  and  $FB_{rep} \times Q$  interactions.  $Q$ -values represent the prediction and the PE represent the error in these predictions compared to observed state (author's own creation).

### 4.3.5. Discussion

In the present study we explored the intra- and inter-brain oscillatory phase-based connectivity in dyads during spontaneous behavioural adaptation in a conformity paradigm. Our results (*Table 4.5 Supp. Materials; HDI+ROPE*) showed, first, distinctive mechanisms underlying local and distal neuronal population connectivity in alpha frequency band and, second, a theta band tracking learning mechanisms inside conformity. On the other hand, we found inter-brain synchrony change in the dyads in beta band. Contrary to our initial hypothesis, we did not find any frequency phase coherence related to the type of adjustment. Lastly, we also found credible differences in intra-personal oscillatory phase-based connectivity in alpha in the whole studied time range.

Firstly, credible increased intra-personal brain frequency coherence changes in the 1<sup>st</sup> adjustment (FB2-FB1) were mainly and widely tracked in alpha in the first time-range (0-500ms), and a solid remanent still in alpha in the second time range (500-1000ms). We interpret this alpha synchronization change as caused by the broad inter-regional communication needed in a multi-layered valuation process happening when people conform. In fact, the difference in the phasic coherence being especially prominent before the 500ms midpoint would suggest its association with attention and cognitive control computations. Indeed, alpha band plays a role in cognitive control functions (see Sadaghiani and Kleinschmidt, 2016, for a review) and working memory (Wianda and Ross, 2019) among many other functions. Alpha band involvement has also been reported in social neuroscience studies to be associated to social cognitive processing (Perry et al., 2010; Naeem et al., 2012) and in interactive decision making (Jahng et al., 2017; Hu et al., 2018). Recent evidence suggests alpha coherence as a large-scale rhythmic communication between brain-regions (Chapeton et al., 2019). Therefore, our results are in line of a key role of alpha in the orchestration of the different neural mechanisms underlying the processing of converge with others.

In contrast, in inter-personal synchrony, results showed mainly the involvement of beta frequency band, especially in fronto-central and centro-parietal areas, in the first adjustment (FB2-FB1), in the first time-range. Interestingly, one of the biggest samples hyperscanning (two-person neuroscience) studies ever made (Dikker et al., 2021), integrated in a neuroscience-art installation, reported evidence related to joint attention in beta band. In this installation dyads were requested to look at each other while trying to put their minds “in sync” while having immediate visual feedback on their level of correlated brain synchronic activity. Here, dyads who shared a higher synchrony in their brain activity showed this higher phase-coupling in beta frequency band. In our experiment, participants needed the highest level of joint attention to the stimulus at first adjustment and first interval. However, this interpretation must be taken with caution as we forced a communication bottleneck in our setting. Participants could not stare at each other or even communicate as there was a wall between them. Therefore, although beta connectivity related to joint-attention seems a plausible explanation, the conditions are different than in previous studies, and more in-place manipulations are needed to support this claim.

Besides, we also found a clearly distinct tracking of frequency dynamics related to a learning model in lower frequencies in the 2<sup>nd</sup> adjustment (FB3-FB2). According to previous evidence (Christie and Tata, 2009; Cavanagh et al., 2012; Mas-Herrero and Marco-Pallarés, 2014; van de Vijver et al., 2018) we were expecting to have a certain coherence tracking prediction error parameter change in theta, but theta connectivity was not only related to PE, but also with the prediction value update ( $Q_t$ ). While the PE showed an increase in theta synchronization in 2<sup>nd</sup> adjustment, the Q-value parameter showed the opposite effect (see *Table 4.6* and *Table 4.7* for HDI ranges with detailed order of credible evidence in connections). The role of theta has been identified to track complementary information related to different high-level computations in reinforcement learning (Holroyd and Yeung, 2012; Hajihosseini and Holroyd, 2013) as well as than low-level aspects such as relative uncertainty (Cavanagh et al., 2012) and PE computation (Cavanagh et al., 2010). Our results are, therefore, in line with evidence relating an



increased theta that is associated to the presence of error or conflict (as in the PE) and a decrease as predictions are fulfilled or for high Q values (Weismüller et al., 2019).

In our initial hypothesis, and based on previous literature, we expected a role of gamma band in the synchronization of different brain areas in social-related tasks ensembles (Fries, 2009; Friese et al., 2016; van Pelt et al., 2016; Bonnefond, Kastner and Jensen, 2017; Zhang et al., 2019). However, our results did not reveal any credible strong evidence related to such interplay (although we do find some evidence of it when only taking the HDI as reference as it can be seen in *Table 4.5 Supp. Materials; HDI*). Also, we believe this to be associated to the frequency window we chose for gamma beforehand (25-42Hz), that covers lowered frequencies than the gamma ranges typically studied in the literature (Friese et al., 2016). In addition, and contrary to our initial hypothesis, we did not find any synchronic oscillatory phase activity related to behavioural adjustment other than some residual evidence (HDI only, see *Table 4.5 Supp. Materials; HDI*) in gamma in *low-low* condition.

In conclusion, we are presenting evidence of phasic coherence happening in a conformity task both intra- and inter-subject affecting different brain regions, time ranges and frequency bands. We understand our study relates different frequencies to activity of different layers of computation, being theta primarily related to learning and cognitive control, alpha to other control and communication strategies of distal regions of the brain. We would like to acknowledge some of the interpretation in this discussion can sound highly speculative, especially from the evidence associated to inter-brain dynamics as we understand the field of 2-person neuroscience is still in its first steps. We think our results constitute a starting point addressing phase coherence changes happening in a conformity experiment. The introduction of different manipulations and changes in the paradigm could help us examine further causal relationships in the presented evidence.

#### 4.3.6. Supplementary Materials

As stated in the methods section, we are reporting also the credible evidence out of the HDI Null Hypothesis Significance Test (NHST) alone. An important aspect in Bayesian inference is the need to adjust the inference to the posterior estimated densities coming out of the BMM. We used ROPE rule to only report strong effects, and not only spurious connectivity coherence. Nonetheless, we considered adding this supplementary material would also be of interest.

As seen in the additional figures, there was positive change evidence in intra-personal coherence related to alpha (Positive: 268 out of 300 connections in  $\text{HDI}_{\text{NHST}}(95\%)$ ). On the other hand, brain-to-brain dyadic connection was found negative in beta (Negative: 181 out of 625 connections in  $\text{HDI}_{\text{NHST}}(95\%)$ ). About the adjustment interaction, we found decreased gamma activity in brain-to-brain data and low-low condition (Negative: 9 out of 625 connections in  $\text{HDI}_{\text{NHST}}(95\%)$ ). Also in this interval, we tracked the RL model parameters with theta in PE (Positive: 32 out of 300 connections in  $\text{HDI}_{\text{NHST}}(95\%)$ ) and Q value (Negative: 174 out of 300 connections in  $\text{HDI}_{\text{NHST}}(95\%)$ ). Interestingly, in this case, the change in connections was less important with and without the ROPE addition to the decision rule, most likely caused by the extraction procedure of the ERP before the time-frequency decomposition explained in the methods section. As we believe it has valid interest, we are also showing a table with the HDI ranges of the RL parameters PE (*Table S6.2*) and Q (*Table S6.3*), as we can see the ones with the utmost credible evidence.

Moving into the next interval, we found in the first contrast evidence of coherent increased activity in intra-personal data in alpha (Positive: 41 out of 300 connections in  $\text{HDI}_{\text{NHST}}(95\%)$ ) and gamma (Negative: 1 out of 300 connections in  $\text{HDI}_{\text{NHST}}(95\%)$ ). Interestingly, we also found brain-to-brain coherence in both alpha (Positive: 210 out of 625 connections in  $\text{HDI}_{\text{NHST}}(95\%)$ ) and gamma frequencies (Negative: 15 out of 625 connections in  $\text{HDI}_{\text{NHST}}(95\%)$ ).

Locations to all these reported results can be found in the additional figures and summary tables.

Table 4.5: Summary of Results both in HDI+ROPE rule and HDI alone. Note for having a clearer interpretation, we are permuting the extraction so the sign can reflect what is happening to the activation from the previous state.

		THETA		ALPHA		BETA		GAMMA	
		HDI+ ROPE	HDI	HDI+ ROPE	HDI	HDI+ ROPE	HDI	HDI+ ROPE	HDI
<b>0-500ms</b>									
<b>(FB2-FB1)</b>	<i>DYADS (625)</i>					9	181		
	<i>INTRA (300)</i>			114	268				
<b>(FB3-FB2)</b>	<i>DYADS (625)</i>								
	<i>INTRA (300)</i>								
<b>Low-Low (FB3-FB2)</b>	<i>DYADS (625)</i>								9
	<i>INTRA (300)</i>								
<b>High-High (FB3-FB2)</b>	<i>DYADS (625)</i>								
	<i>INTRA (300)</i>								
		<i>PE</i>							
<b>RL MODEL (FB3-FB2)</b>	<i>INTRA (300)</i>	25	32						
		<i>QS</i>							
		134	174						
<b>500-1000ms</b>									
<b>(FB2-FB1)</b>	<i>DYADS (625)</i>			2	210				15
	<i>INTRA (300)</i>			4	41				1
<b>(FB3-FB2)</b>	<i>DYADS (625)</i>								
	<i>INTRA (300)</i>								
<b>Low-Low (FB3-FB2)</b>	<i>DYADS (625)</i>								
	<i>INTRA (300)</i>								
<b>High-High (FB3-FB2)</b>	<i>DYADS (625)</i>								
	<i>INTRA (300)</i>								

Negative (Decreased in relation to its reference)  
  Positive (Increased in relation to its reference)

  Negative (Decreased in relation to its reference)  
  Positive (Increased in relation to its reference)

Table 4.6: PE table (ROPE+HDI), in order from the most credible evidence in top (according to their HDI high furthest to 0) to the smallest in the bottom.

ROPE_EQUIVALENCE	HDI_LOW	HDI_HIGH	CONNECTION	ELEC1	ELEC2
Rejected	2,75624E+14	2,46529E+14	PE: Freq 4	Fp2:F8	Fp2
Rejected	2,82256E+14	2,45032E+14	PE: Freq 4	Fp2:CP1	Fp2
Rejected	2,59915E+14	2,37863E+14	PE: Freq 4	F7:C4	F7
Rejected	2,16658E+14	2,29205E+14	PE: Freq 4	F8:FC1	F8
Rejected	1,72489E+14	2,27315E+14	PE: Freq 4	F8:Pz	F8
Rejected	1,71302E+14	2,19206E+14	PE: Freq 4	F8:CP1	F8
Rejected	1,3069E+14	2,18697E+14	PE: Freq 4	Fp2:CP2	Fp2
Rejected	1,10555E+14	2,17854E+14	PE: Freq 4	F8:C3	F8
Rejected	1,16473E+14	2,16686E+14	PE: Freq 4	Fp2:F7	Fp2
Rejected	1,41159E+14	2,14962E+14	PE: Freq 4	FC1:Pz	FC1
Rejected	7,09881E+14	2,14609E+14	PE: Freq 4	CP6:P8	CP6
Rejected	1,06736E+14	2,13988E+14	PE: Freq 4	CP6:P4	CP6
Rejected	9,78968E+13	2,12804E+14	PE: Freq 4	CP1:Pz	CP1
Rejected	7,27263E+13	2,12789E+14	PE: Freq 4	Fz:F8	Fz
Rejected	7,1899E+13	2,0939E+14	PE: Freq 4	Fp2:C4	Fp2
Rejected	8,65267E+13	2,08353E+14	PE: Freq 4	C4:Oz	C4
Rejected	4,98528E+14	2,07669E+14	PE: Freq 4	FC5:C3	FC5
Rejected	6,75422E+14	2,06632E+14	PE: Freq 4	F8:P4	F8
Rejected	6,10303E+12	2,06364E+14	PE: Freq 4	Fp1:C4	Fp1
Rejected	4,99569E+13	2,06139E+14	PE: Freq 4	FC6:C4	FC6
Rejected	4,96076E+13	2,05847E+14	PE: Freq 4	C3:P8	C3
Rejected	4,63621E+14	2,05845E+14	PE: Freq 4	FC6:POz	FC6
Rejected	3,73553E+13	2,04555E+14	PE: Freq 4	F8:CP2	F8
Rejected	4,7279E+14	2,03765E+14	PE: Freq 4	C4:P7	C4
Rejected	2,79276E+14	2,01644E+14	PE: Freq 4	Fp2:CP5	Fp2

Table 4.7: QS table (ROPE+HDI), in order from the most credible evidence in top (according to their HDI low furthest to 0) to the smallest in the bottom.

ROPE_EQUIVALENCE	HDI_LOW	HDI_HIGH	CONNECTION	ELEC1	ELEC2
Rejected	-2.023E+12	-7.928E+14	QS: Freq 4	F4:POz	F4
Rejected	-1.966E+13	-4.847E+14	QS: Freq 4	Fz:P7	Fz
Rejected	-2.017E+13	-6.221E+12	QS: Freq 4	Fp1:F4	Fp1
Rejected	-2.032E+13	-1.035E+14	QS: Freq 4	F8:CP2	F8
Rejected	-2.039E+13	-9.85E+14	QS: Freq 4	Cz:CP6	Cz
Rejected	-2.07E+13	-1.19E+14	QS: Freq 4	P8:POz	P8
Rejected	-2.097E+13	-1.546E+12	QS: Freq 4	CP5:CP2	CP5
Rejected	-2.122E+13	-1.631E+14	QS: Freq 4	FC6:CP1	FC6
Rejected	-2.122E+13	-1.649E+13	QS: Freq 4	FC1:Oz	FC1
Rejected	-2.124E+13	-1.667E+14	QS: Freq 4	FC5:CP6	FC5
Rejected	-2.164E+13	-2.117E+14	QS: Freq 4	F3:CP1	F3
Rejected	-2.169E+13	-1.883E+14	QS: Freq 4	F3:CP5	F3
Rejected	-2.378E+13	-3.164E+13	QS: Freq 4	F4:P4	F4
Rejected	-1.97E+14	-5.821E+13	QS: Freq 4	CP1:P8	CP1
Rejected	-1.974E+14	-7.528E+12	QS: Freq 4	FC1:FC6	FC1
Rejected	-1.975E+14	-5.909E+13	QS: Freq 4	F7:P4	F7
Rejected	-1.983E+14	-5.088E+13	QS: Freq 4	F7:CP2	F7
Rejected	-1.985E+14	-8.087E+13	QS: Freq 4	FC5:FC2	FC5
Rejected	-1.986E+14	-5.591E+14	QS: Freq 4	CP6:POz	CP6
Rejected	-1.988E+14	-5.782E+14	QS: Freq 4	FC2:Oz	FC2
Rejected	-1.989E+14	-4.547E+14	QS: Freq 4	Fp2:CP5	Fp2
Rejected	-1.992E+14	-5.826E+13	QS: Freq 4	FC2:P8	FC2
Rejected	-1.992E+14	-5.976E+13	QS: Freq 4	FC5:P3	FC5
Rejected	-1.994E+14	-7.152E+12	QS: Freq 4	C3:CP6	C3
Rejected	-1.995E+14	-6.427E+12	QS: Freq 4	C4:CP2	C4
Rejected	-1.995E+14	-7.245E+13	QS: Freq 4	Fp1:F8	Fp1
Rejected	-1.995E+14	-5.696E+13	QS: Freq 4	FC5:P8	FC5
Rejected	-1.996E+14	-5.625E+14	QS: Freq 4	C3:P7	C3
Rejected	-2.001E+14	-4.233E+13	QS: Freq 4	F4:Oz	F4
Rejected	-2.002E+14	-6.454E+13	QS: Freq 4	F7:POz	F7
Rejected	-2.002E+14	-6.903E+14	QS: Freq 4	F4:P3	F4
Rejected	-2.002E+14	-7.586E+13	QS: Freq 4	Fp2:POz	Fp2
Rejected	-2.004E+14	-7.265E+12	QS: Freq 4	F3:P3	F3
Rejected	-2.004E+14	-6.6E+14	QS: Freq 4	FC1:POz	FC1
Rejected	-2.005E+14	-4.242E+14	QS: Freq 4	P7:P8	P7
Rejected	-2.005E+14	-8.528E+14	QS: Freq 4	FC2:P3	FC2
Rejected	-2.005E+14	-7.494E+13	QS: Freq 4	F8:FC6	F8
Rejected	-2.006E+14	-6.662E+13	QS: Freq 4	FC2:POz	FC2
Rejected	-2.007E+14	-6.083E+13	QS: Freq 4	FC1:C4	FC1
Rejected	-2.007E+14	-5.788E+12	QS: Freq 4	F3:Pz	F3
Rejected	-2.007E+14	-7.854E+14	QS: Freq 4	F8:P7	F8
Rejected	-2.009E+14	-7.467E+14	QS: Freq 4	FC2:FC6	FC2
Rejected	-2.01E+14	-4.966E+14	QS: Freq 4	Fp2:P4	Fp2
Rejected	-2.012E+14	-6.055E+12	QS: Freq 4	CP5:POz	CP5
Rejected	-2.012E+14	-7.339E+13	QS: Freq 4	F8:Cz	F8
Rejected	-2.013E+14	-5.111E+14	QS: Freq 4	CP6:Pz	CP6
Rejected	-2.015E+14	-5.283E+13	QS: Freq 4	F3:F4	F3
Rejected	-2.016E+14	-9.466E+14	QS: Freq 4	Fp1:P4	Fp1
Rejected	-2.018E+14	-5.187E+13	QS: Freq 4	F8:FC5	F8
Rejected	-2.019E+14	-8.076E+13	QS: Freq 4	P7:Pz	P7
Rejected	-2.022E+14	-4.744E+14	QS: Freq 4	F7:P3	F7
Rejected	-2.023E+14	-6.768E+14	QS: Freq 4	F4:CP6	F4
Rejected	-2.025E+14	-8.02E+13	QS: Freq 4	F3:P4	F3
Rejected	-2.025E+14	-6.924E+12	QS: Freq 4	Fp2:F3	Fp2
Rejected	-2.025E+14	-6.893E+13	QS: Freq 4	P3:Oz	P3
Rejected	-2.026E+14	-8.791E+14	QS: Freq 4	FC2:P7	FC2
Rejected	-2.027E+14	-7.573E+14	QS: Freq 4	P3:POz	P3
Rejected	-2.027E+14	-1.064E+14	QS: Freq 4	Cz:POz	Cz
Rejected	-2.027E+14	-7.55E+14	QS: Freq 4	Fz:CP5	Fz
Rejected	-2.029E+14	-7.234E+13	QS: Freq 4	Fp1:FC1	Fp1
Rejected	-2.03E+14	-8.502E+13	QS: Freq 4	FC5:CP5	FC5
Rejected	-2.03E+14	-4.608E+14	QS: Freq 4	F3:P7	F3
Rejected	-2.031E+14	-8.801E+13	QS: Freq 4	FC2:P4	FC2
Rejected	-2.033E+14	-9.859E+14	QS: Freq 4	F3:FC5	F3
Rejected	-2.034E+14	-9.946E+12	QS: Freq 4	FC1:P8	FC1
Rejected	-2.034E+14	-8.422E+13	QS: Freq 4	F4:P7	F4
Rejected	-2.036E+14	-9.044E+14	QS: Freq 4	F7:F4	F7
Rejected	-2.037E+14	-9.429E+14	QS: Freq 4	Fp2:P7	Fp2
Rejected	-2.04E+14	-9.952E+14	QS: Freq 4	F3:CP6	F3
Rejected	-2.04E+14	-6.977E+13	QS: Freq 4	F4:FC6	F4
Rejected	-2.04E+14	-8.196E+13	QS: Freq 4	CP5:Oz	CP5
Rejected	-2.042E+14	-9.766E+13	QS: Freq 4	F7:C3	F7
Rejected	-2.042E+14	-1.078E+14	QS: Freq 4	CP1:P4	CP1
Rejected	-2.044E+14	-8.931E+12	QS: Freq 4	F4:C3	F4
Rejected	-2.045E+14	-1.122E+14	QS: Freq 4	FC2:CP2	FC2
Rejected	-2.045E+14	-9.148E+14	QS: Freq 4	FC6:C3	FC6
Rejected	-2.046E+14	-1.06E+14	QS: Freq 4	Fz:Pz	Fz
Rejected	-2.047E+14	-8.714E+12	QS: Freq 4	F7:CP6	F7
Rejected	-2.047E+14	-1.342E+13	QS: Freq 4	CP1:CP2	CP1
Rejected	-2.05E+14	-9.985E+13	QS: Freq 4	Fz:POz	Fz
Rejected	-2.055E+14	-1.014E+13	QS: Freq 4	Fp1:F3	Fp1
Rejected	-2.055E+14	-1.436E+14	QS: Freq 4	C3:Pz	C3
Rejected	-2.056E+14	-9.142E+14	QS: Freq 4	F8:FC2	F8
Rejected	-2.057E+14	-1.071E+14	QS: Freq 4	FC6:P7	FC6
Rejected	-2.058E+14	-1.265E+14	QS: Freq 4	F7:P7	F7
Rejected	-2.058E+14	-1.19E+14	QS: Freq 4	Fp1:CP6	Fp1
Rejected	-2.058E+14	-1.276E+13	QS: Freq 4	F8:Oz	F8
Rejected	-2.066E+14	-1.425E+14	QS: Freq 4	F7:Oz	F7
Rejected	-2.069E+14	-1.166E+14	QS: Freq 4	FC2:Pz	FC2
Rejected	-2.07E+14	-1.185E+14	QS: Freq 4	F7:F3	F7
Rejected	-2.071E+14	-1.237E+14	QS: Freq 4	Fz:C3	Fz
Rejected	-2.072E+14	-1.158E+14	QS: Freq 4	FC2:C3	FC2

Rejected	-2.072E+14	-1.076E+13	QS: Freq 4	Fp2:Pz	Fp2
Rejected	-2.073E+14	-1.394E+14	QS: Freq 4	F3:F8	F3
Rejected	-2.077E+14	-1.085E+13	QS: Freq 4	CP1:P7	CP1
Rejected	-2.078E+14	-8.93E+13	QS: Freq 4	F4:FC2	F4
Rejected	-2.078E+14	-1.464E+14	QS: Freq 4	F7:FC2	F7
Rejected	-2.078E+14	-1.314E+14	QS: Freq 4	Fz:FC5	Fz
Rejected	-2.085E+14	-1.539E+14	QS: Freq 4	C3:CP2	C3
Rejected	-2.093E+14	-1.439E+14	QS: Freq 4	Fp2:FC5	Fp2
Rejected	-2.096E+14	-1.189E+14	QS: Freq 4	Fp1:CP2	Fp1
Rejected	-2.1E+14	-1.595E+13	QS: Freq 4	Fp1:FC2	Fp1
Rejected	-2.1E+14	-1.602E+14	QS: Freq 4	Fp1:FC5	Fp1
Rejected	-2.102E+14	-1.194E+13	QS: Freq 4	P4:Oz	P4
Rejected	-2.107E+14	-1.417E+14	QS: Freq 4	F3:C3	F3
Rejected	-2.108E+14	-1.696E+13	QS: Freq 4	Fp1:Cz	Fp1
Rejected	-2.108E+14	-1.556E+14	QS: Freq 4	Fp1:Oz	Fp1
Rejected	-2.11E+14	-1.759E+14	QS: Freq 4	CP2:P4	CP2
Rejected	-2.113E+14	-1.655E+14	QS: Freq 4	Fp1:P7	Fp1
Rejected	-2.12E+14	-1.358E+14	QS: Freq 4	F4:FC5	F4
Rejected	-2.125E+14	-1.45E+13	QS: Freq 4	Fp2:F4	Fp2
Rejected	-2.127E+14	-1.68E+14	QS: Freq 4	FC6:CP2	FC6
Rejected	-2.131E+14	-1.426E+14	QS: Freq 4	FC1:FC2	FC1
Rejected	-2.131E+14	-1.655E+14	QS: Freq 4	F4:CP5	F4
Rejected	-2.132E+14	-1.712E+13	QS: Freq 4	F8:CP6	F8
Rejected	-2.133E+14	-1.794E+14	QS: Freq 4	F7:F8	F7
Rejected	-2.134E+14	-1.164E+14	QS: Freq 4	Fz:FC2	Fz
Rejected	-2.142E+14	-2.054E+13	QS: Freq 4	Fp2:FC2	Fp2
Rejected	-2.147E+14	-1.677E+14	QS: Freq 4	F4:CP2	F4
Rejected	-2.148E+14	-1.621E+14	QS: Freq 4	CP2:P3	CP2
Rejected	-2.151E+14	-1.95E+13	QS: Freq 4	F7:CP5	F7
Rejected	-2.155E+14	-1.985E+13	QS: Freq 4	Fp1:P3	Fp1
Rejected	-2.156E+14	-1.766E+14	QS: Freq 4	CP2:Pz	CP2
Rejected	-2.16E+14	-1.78E+14	QS: Freq 4	FC5:CP2	FC5
Rejected	-2.175E+14	-2.095E+13	QS: Freq 4	Fz:CP1	Fz
Rejected	-2.194E+14	-2.037E+14	QS: Freq 4	F3:FC2	F3
Rejected	-2.196E+14	-2.094E+14	QS: Freq 4	FC5:P4	FC5
Rejected	-2.199E+14	-1.86E+14	QS: Freq 4	Fz:F4	Fz
Rejected	-2.205E+14	-1.938E+13	QS: Freq 4	FC5:Pz	FC5
Rejected	-2.205E+14	-1.909E+14	QS: Freq 4	F7:FC5	F7
Rejected	-2.207E+14	-2.035E+14	QS: Freq 4	F7:Pz	F7
Rejected	-2.212E+14	-2.106E+14	QS: Freq 4	F3:POz	F3
Rejected	-2.231E+14	-2.193E+14	QS: Freq 4	CP5:P4	CP5
Rejected	-2.289E+14	-2.439E+14	QS: Freq 4	Fp1:Pz	Fp1

# Intra-personal frequency coherence plots (HDI 95% $\neq$ Null)

## A. Circular network plots

## B. Node temperature plots

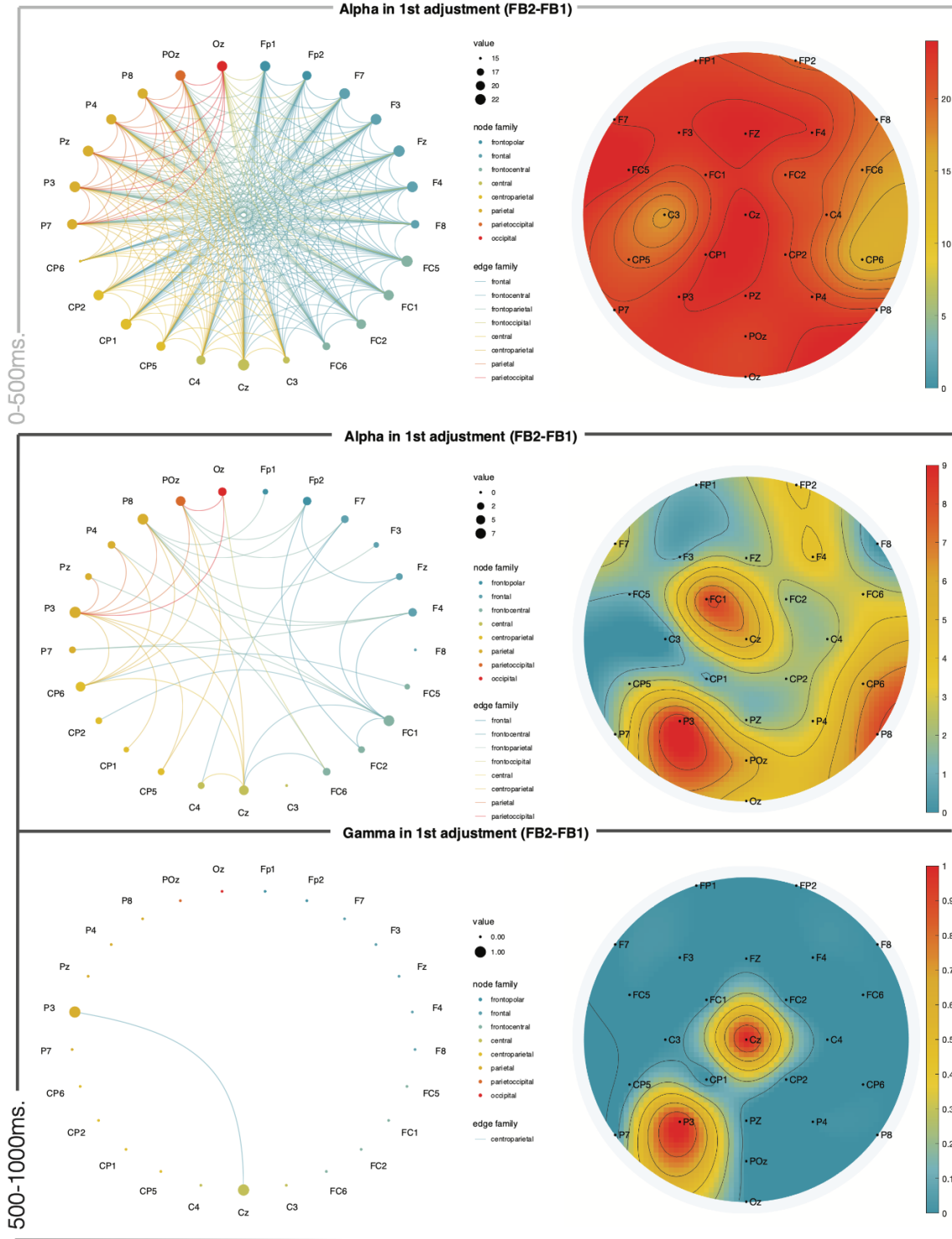


Figure 4.18: Intra-personal plots with circular plots (A) and node temperature plots (B) considering the HDI rule alone (author's own creation).

### Inter-Brain frequency coherence plots (HDI 95% ≠ Null)

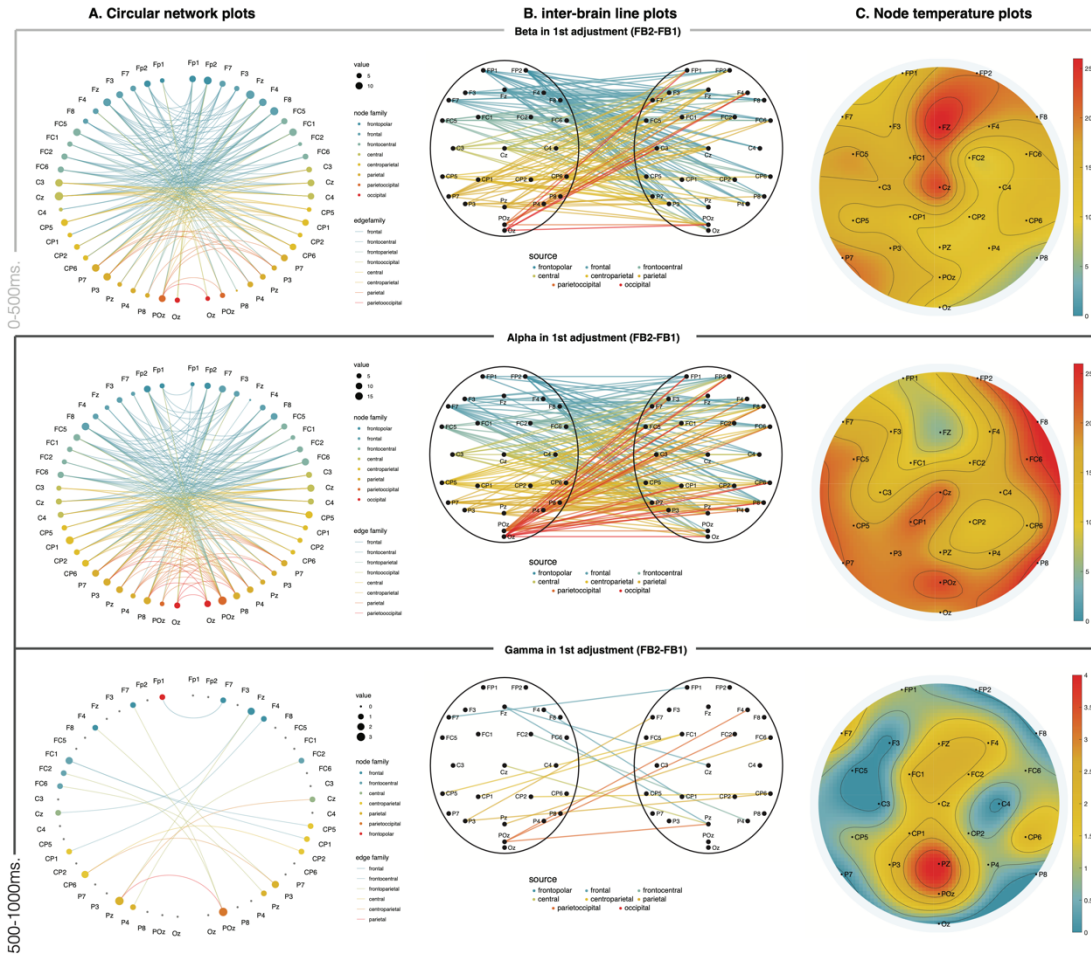


Figure 4.19: Inter-brain plots with circular network plots (A), inter-brain line plots (B) and node temperature plots (C) with credible evidence taking the HDI rule alone (author's own creation).



# Intra-personal frequency coherence plots (0-500ms; HDI 95% ≠ Null)

Circular network plots

Node temperature plots

Gamma positive frequency coherence in Low-Low condition

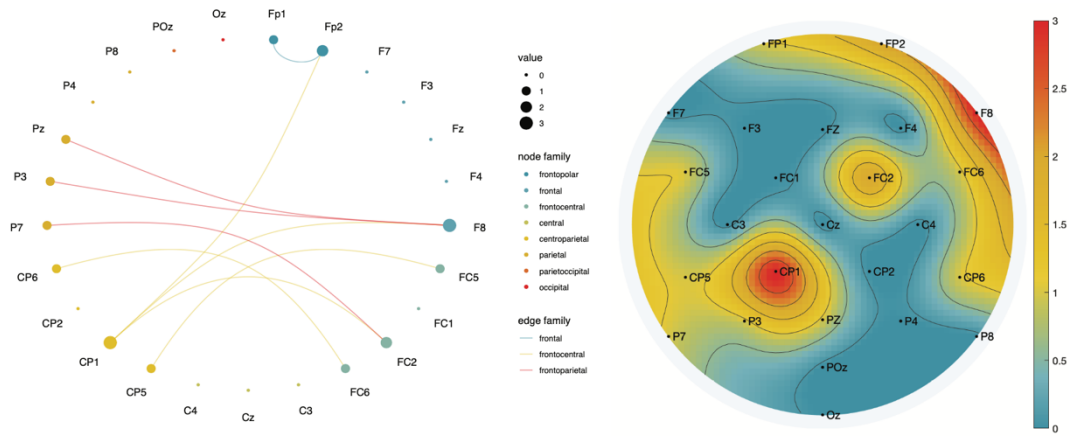


Figure 4.20: Adjustment interactions from intra-brain low-low condition in the HDI NHST alone (author's own creation).



## 5. General Discussion

## 5.1. Introduction

It has been a while since Sherif (1935) described how people conform. Individuals are willingly biased towards cooperation, decide even to change their own perception of the world. This behavioural adaptation has demonstrated to be crucial for cooperation as well as team performance (Kraiger and Wenzel, 1997; Mathieu et al., 2000; Schmidt et al., 2014; Santos, Uitdewilligen and Passos, 2015). The present thesis started with the aim of better understanding the social phenomenon of conformity. The choice of this behavioural adaptation over the others was very intentional. Indeed, conforming needs a certain degree of devaluation and sacrifice of one's individual thoughts and perceptions of the world to favour sociality. This adaptation is conscious and, thus, requires effort, self-regulation and is driven by reward. We could argue conformity is the quintessential or stereotypical example social behavioural adaptation with a social motive and relies on multiple layers of simultaneous social cognitive computation. To adapt to the other person, one needs to compare the social and individual benefit of the adaptation, seize the degree of conflict, take account of the other's degree of adaptability based on previous belief and update prior knowledge accordingly (which requires learning).

Conformity as a research object has been widely studied in the Social Psychology field but has received scarce attention and limited research in Neuroscience. In fact, this thesis represents one of the first examples of an experimental settings where conformity happens spontaneously and at will by the participants.

The first aim of the present thesis was to “*Design a new experimental paradigm to study the neurophysiological mechanisms underlying spontaneous conformity and its evolution throughout repetition and learning*”. As proposed, we designed a new task paradigm where conformity happened naturally, and this result has been replicated in two different experiments with 116 people. Importantly, the task was designed so conformity emerged without the explicit instruction to conform. As we already mentioned, we were seeking the natural behaviour, where people are naturally moved to conform by their own choice and preference. From this point of view, we believe our task has demonstrated to be a valuable setting to study conformity in the laboratory without an explicit influence that obliges to it, which we think is experimentally relevant.

In the next sections we will deep in detail to the general contributions of the results of this thesis in relation to the research aims presented and will propose an integrated view of the results of the three studies, the influences between them and their accumulated knowledge. We will finish this section with a brief comment on future directions of this research.

## 5.2. Convergence as a form of reward

In the first experiment, we wanted to empirically support, first, the idea that convergence is a natural tendency in humans that can be manipulated and enhanced; and second, that people cooperate acquiring predictive models of the behaviour of their partners. In this regard, we used previous cooperation or lack thereof, as a factor to differentiate how this factor affected convergence and the prediction on others' behaviour.

Results in Study 1 showed that predictions on others' convergence could be modelled by using a RL model, especially in the cooperation group. However, in this first experiment we did not have straightforward evidence because our experimental paradigm lacked a manipulation of reward processing (as we could have if using neuroimaging techniques which allow registering the activity of reward network). However, the RL learning model used in this experiment was based on the implicit reward associated with a correct prediction of the behaviour of the peer. Given that the model showed predictive capacity, we interpreted this as an indicator of coherence with previous literature (Klucharev et al., 2009; Zaki et al., 2011; Overgaaw et al., 2019; Li et al., 2020).

On the other hand, our data sails in favour of the idea that people tend to naturally converge in their responses even when they are not explicitly instructed to do so. This implicitly supports the claim that, even though there is a high variability in individual differences in social sensitivity (Crawford et al., 2020), there is also an intrinsic motivation in humans to prosocial behaviours or, at least, row in favour of what would be considered more socially acceptable or rewarding. Our task has consistently captured this social phenomenon in all the data collected throughout the research.

Moreover, our first experiment supported the claim that cooperation, by working together to solve different activities, preactivated the intrinsically social reward processing, by means of the convergence dyads reached in their common undertake later in the task. Here, the data from study 1 showed relevant differences between the compared groups, where some participants worked together before the main task and others performed individually. This different activity before the task materialized in the amount of convergence in cooperative group being considerably larger than in the non-cooperative one. Our results also suggest additional implications, as our evidence did not advocate for a difference in groups relatable to their precision or performance in the task or productivity related measures. We believe our results supports the claim that conformity is an intrinsic prosocial, and not necessarily transactional, behavioural adaptation which is intensified by social interaction.

Additionally, the use of the RL (and other) computational models which have been previously used in other areas of psychology and neuroscience, opens an opportunity in this domain to study how people adapt their behaviours to others and how they learn and predict on the bases of previous interactions. We hypothesized that the predictive model would better fit behaviour of people in the cooperation group and, therefore, would better fit a learning process. Here, as previously explained, we used a simple TDL model to capture these differences and, as expected, we found evidence supporting our initial hypothesis. Our data showed a clear distinction on the model fitting between the two groups, that is, the dyads who previously cooperated and the ones that did not. As expected, we found strong evidence which showed increased model fit in the dyads who

previously cooperated, indicating they followed a more predictable, and modellable, learning process than the other uncooperative dyads.

The results here responded importantly to some questions regarding conformity. First, conformity is a common tendency when people work together, regardless on their previous history of cooperation. People naturally converge as this behaviour is perceived as an intrinsic reward. Second, people who previously cooperate value convergence as an increased reward. Third, people who have previously cooperate fit better to a learning model based on reinforcement. Simply put, we suggest that the social interaction, which is the difference between cooperative and uncooperative dyads, promotes a qualitative difference in their mutual consideration, where dyads who previously cooperate categorize their peers with an enhanced valuation guided by intrinsic social reinforcements as well as an increased tendency to conform.

When studying oscillatory activity, instead of using a scaling of the responses of the participants in the task, we simplified it into a dichotomic variable, distinguishing between cooperative or uncooperative behaviour. When participants made a wilful effort to converge, this was considered cooperative, while when did not, it was considered uncooperative. The reduction of the scale of the representation into a simpler one, facilitated the tracking of the learning in the brain oscillatory activity. Even though our analysis showed the dichotomic variable was more effective on tracing a learning process of the partner, we still need to work further on this hypothesis, although it seems an interesting approach to test under different paradigms. Modifications of our task, introducing differently represented choices, or different blocks of cooperation vs. non-cooperation would help in tackling this approach. In fact, working under different manipulations of our task where not only state but also reward representations vary, is something we are very interested to explore in the future.

### 5.3. Event-related Potentials and the study of roles

The results of the first experiment were the foundations to “study the neural electrophysiological correlates underlying conformity between two people”, which corresponded to the second aim of the present theses. In this study we explored different questions: Does the pervasive nature of our task capture a difference in electrophysiological signals at every trial repetition? Is convergence really treated in the brain as a reward? Are there neurophysiological signals indexing whether a participant conforms more or less than their partner? Are there role related differences in the domain of frequency dynamics?

Table 1 summarizes the main results of the second study. Firstly, the study of ERP signals showed interesting differences that are closely related to different aspects of feedback related processing in the conflict monitoring literature. We measured the change among different feedbacks in the dyads in the EEG signals together with their behavioural adjustments. Our results suggest there is a bigger amplitude difference in the signals in the first, compared to the other two feedbacks, and these differences are specifically divergent from 350ms onwards. The time intervals of choice are typically associated to different neural mechanisms that might be linked to widely studied feedback components such as FRN, P200, P3a and P3b. FRN has been related to valuation of the outcome, and after this is component, a mainly fronto-central positivity happens which has been described to fluctuate according to expectation, where correct expectations relate to more positive fluctuations (Holroyd, Pakzad-Vaezi and Krigolson, 2008). Even when our results do not find strong evidence for early feedback related components as FRN (that normally appears in the 250-300ms time window), we find strong evidence supporting such claim from this point onwards, starting in fronto-central areas (275-350ms) and being modulated in time to more centro-parietal electrodes (500-700ms).

P200 is a sensory-evoked potential associated with attention selection or an early processing of the feedback, that allocates attentional resources to the neural representations to be made later in the brain. A frontocentral P200 has been related to be larger in novel stimuli (Luck, 2014), which is exactly what happens in our task at the beginning of every trial. It has been proposed the positivity of this component is, in fact, related to the unpredictability and risk-taking (Kiat, Straley and Cheadle, 2016). In our results, we find this positivity to be possibly at a later point and possibly overlapped with other later components from the 275ms inflection point.

On the other hand, in the P300 domain, what is widely considered an endogenous ERP, the P3a and P3b subcomponents also show significant differences among the three feedbacks, not only fronto-centrally but also parietally. These components have been classically related to “call to attention” or the interpretation and categorization of the stimuli respectively (Polich, 2007). In other words, the role of attentional resource allocation in memory processing is related to amplitude and latencies of P300 components. Moreover, we believe results in the second study could match the intuition behind context updating theory (Donchin, 1981). This neural dynamic is described to oversee processing of change in context among three different stages. First, the brain needs to detect what is different (sensory processing). Second, it needs to evaluate these differences with the previous representation allocated in working memory and the new context. Lastly, if there is no change, there is no need for further allocation of attentional

resources but, in case the change is present, the brain needs to reconfigure how to respond with the information at hand. Thus, there is a vast ground of literature that relates these stages in the P300 domain (Polich, 2007).

Based on the previous assumption, in Study 2 we hypothesized if we studied disaggregated data, there would be role differences associated to the level of conformity. According to the rationale presented in the previous paragraph, we could expect, when people were conforming, evidence would support higher resource allocation than when people were non-conforming. *Table 5.1* summarizes the results on this experiment relating ERP and Time Frequency signals. Interestingly, and contrary to our initial beliefs, even when we could ascertain some differences between roles, this evidence resulted not credible enough and, therefore, we could not conclude there were real differences depending on the role the participants were having in the trial. In fact, to the answer we raised in the research aims of “*Are the ERP different when people conform more compared to their partners?*” the answer would be not given with the strongest evidence at hand. Even when there are certain tendencies, our results fail to show reliable differences.

Nonetheless, there were other interesting results in this study that appeared when both participants coincided in their results. Importantly, here we could see a credible drop in signal from first to second feedback at all time intervals, being this more fronto-central at the earlier time-window and more general but moving into more parietal sites in the later time-windows. We interpret that this directly relates to cognitive control mechanisms being unengaged as convergence is achieved.

In the Time-frequency analysis, our data supports the role of theta as an index of discrepancy between the expectancy and the stimuli at hand. Due to the decrease in the discrepancy in the following repetitions in the trial, theta power also decreases (see Cavanagh et al, 2014, for a review). This is especially relevant when participants share the degree of conformity in EC, when they consider the trial is over, and the rest of the repetitions are simply unneeded, with a critical reduction in theta activity.



Table 5.1: Summary of results of Study 2

ERP Analysis	Time-Frequency Analysis
<p><b>Feedback (FB<sub>2</sub>-FB<sub>1</sub> and FB<sub>3</sub>-FB<sub>2</sub>)</b></p> <ul style="list-style-type: none"> <li>· Credible decrease in all electrodes in 350-500 in FB<sub>3</sub>-FB<sub>2</sub>.</li> <li>· Credible decrease in FB<sub>2</sub>-FB<sub>1</sub> in Cz and Pz in 500-700ms.</li> <li>· Credible decrease in FB<sub>3</sub>-FB<sub>2</sub> in all electrodes in 500-700ms.</li> </ul> <p><b>Adjustment (FB<sub>1</sub>)</b></p> <ul style="list-style-type: none"> <li>· Credible decrease in signal voltage related to higher divergence in Fz and Cz in 275-350ms.</li> <li>· Credible decrease in all electrodes in 350-500ms.</li> <li>· Credible decrease in Cz and Pz in 500-700ms.</li> </ul>	<p><b>Theta (<math>\theta</math>) frequency (4-8Hz)</b></p> <ul style="list-style-type: none"> <li>· Decrease in theta in Pz in 180-230ms and consistently in all electrodes from 230-500ms.</li> </ul> <p><b>CIF</b></p> <ul style="list-style-type: none"> <li>· Credible decrease in theta in EC in second adjustment.</li> </ul>
<p><b>Responses/Feedback</b></p> <ul style="list-style-type: none"> <li>· Increase in signal positivity when amplitude between responses is reduced in 225-275, FB<sub>2</sub>-FB<sub>1</sub> in Fz and Pz.</li> <li>· Increase in signal positivity in 275-350; 350-500; 500-700ms in the three electrodes in FB<sub>2</sub>-FB<sub>1</sub>.</li> <li>· Increase in signal positivity in second adjustment related to response in Pz in 500-700ms.</li> </ul>	<p><b>Alpha (<math>\alpha</math>) frequency (8-12Hz)</b></p> <ul style="list-style-type: none"> <li>· Reduced alpha activity in the first adjustment and increased activity in second adjustment for the three electrodes in 230-500ms.</li> </ul> <p><b>CIF</b></p> <ul style="list-style-type: none"> <li>· Credibly decrease in alpha for NC and C in first adjustment, and increase in second adjustment for C.</li> </ul>
<p><b>CIF (Conformity Interaction Factor)</b></p> <ul style="list-style-type: none"> <li>· Signal decrease in FB<sub>2</sub>-FB<sub>1</sub> in EC for Fz and Cz in 225-275ms.</li> <li>· Decrease also in EC in first adjustment in three electrodes in 275-350ms.</li> <li>· Increase in positivity for C in Fz and Cz in 350-500ms in FB<sub>2</sub>-FB<sub>1</sub> and decrease in second adjustment in Cz, and also in NC in Fz and Cz. Again, decrease in first adjustment for EC in the three electrodes.</li> <li>· Decrease in all electrodes in 500-700ms in first adjustment in EC and in second adjustment for C and NC.</li> </ul>	<p><b>Beta (<math>\beta</math>) frequency (12-30Hz)</b></p> <ul style="list-style-type: none"> <li>· Decreased beta in the first adjustment and first interval for the three electrodes in 180-230ms.</li> </ul> <p><b>Adjustment (FB<sub>1</sub>)</b></p> <ul style="list-style-type: none"> <li>· Related decrease in beta when adjustment is low.</li> </ul> <p><b>CIF</b></p> <ul style="list-style-type: none"> <li>· C start the trial with an increased power compared to NC.</li> </ul>

On the other hand, in alpha domain, our results revealed a suppression of alpha in the first adjustment and an increase in the second, being particularly pronounced both in NC and C. Alpha plays a role to signal alertness and as a top-down inhibitor (see Sadaghiani and Kleinschmidt, 2016, for a review). This is coherent in the present context, where attentional resources need to be engaged if the objective is still unreached after the first feedback, in order to reach to a consensus in responses. Finally, we also found beta activity related to the level of adjustment in what we interpret as a reward related neural coding (see Marco-Pallarés et al., 2015, for a review).

#### 5.4. Frequency dynamics and distinct oscillatory coherent pathways

As appointed in the *Research Aims* section, we were interested in exploring the frequency coherence dynamics happening in participants, and between dyads. Here, again, we used a reinforcement learning model to track learning dynamics into participant's thought process in conformity to see if we could see differences in differently layered brain processes happening in a social adaptation like this. We identified two distinct phases of interest, from 0 to 500ms and from there to 1000ms, and studied the synchronic oscillation happening both at intra-personal and inter-personal level.

Firstly, we find credible coherence changes happening throughout the task only in the first adjustment ( $FB_{rep1} - FB_{rep2}$ ), and primarily tracked by alpha, that we relate to inter-regional communication necessary in a multi-layered, attention and cognitive control computations behind a complex valuation process. We explained this evidence to recent hypothesis relating lower-higher frequency coupling dynamics being an indicator of feedback-feedforward communication systems in the cortex (van Kerkoerle et al., 2014; Jensen et al., 2015; Michalareas et al., 2016; Lundqvist, Bastos and Miller, 2020). Secondly, we found credible evidence of an inter-brain synchrony change in beta that might be related to different aspects of joint attention, although, as we insisted in the study, this interpretation must be taken with caution, as the previous evidence on this interpretation comes out from a face-to-face paradigm, and our dyads had a defined and intentional communication bottleneck in our task. In the second time range, we also found some evidence on alpha inter-brain synchrony change happening in the first adjustment. The interpretation of this activity as an inter-brain dynamics phenomenon must be cautious, as it could also be explained by simultaneous activity change happening in alpha oscillatory activity in each participant. Finally, and very relevant for the present thesis, in the second adjustment we found a relationship with the RL model, which was reflected by a tracking of the prediction error as well as the predictive update in change of theta oscillations compatible with previous literature on the neural oscillatory bases of reward prediction errors (Christie and Tata, 2009; Cavanagh et al., 2012; Mas-Herrero and Marco-Pallarés, 2014; van de Vijver et al., 2018). Indeed, as stated in the *Research Aims* section, we were very interested in tracking prediction error as a basic learning mechanism, and our results show strong evidence supporting the role of theta. In contrast, and contrary to our initial hypothesis, no other rhythms seemed to play a role in this computation. We believe this evidence supports the claim about a mechanistic distinction in the role of oscillatory dynamics and cognitive functions. Therefore, in this case, prediction errors associated with learning would be tracked only in the theta synchrony. In contrast, we did not find any role of the beta-gamma activity which has been proposed to be a reward value signal (Marco-Pallarés, Münte and Rodríguez-Fornells, 2015) and to be activated by positive feedback (Marco-Pallarés et al., 2008, Mas-Herrero et al., 2015) in RL. Nonetheless, we believe the tracking of convergence as a reward is more complex than simply a win-loss outcome in a monetary gain, as it requires an indirect pathway of region communication that is probably wider. On the other hand, previous activity on beta was captured between a specific timeframe between approximately 250-500ms, and we took a larger time range (0-500ms). Future studies could help in

determining whether beta synchrony activity plays a role in learning on the bases of social reward.

## 5.5. Integration of studies

After reviewing the different findings coming out of the studies in this thesis, we will now address how their results intertwine. First important result from Study 1 marks the rest of the research: prior cooperation inclined participants to converge to their peers and increased the reinforcing properties of dyadic convergence. In addition, we find this reinforcement guided learning to be traced not only in the low-frequency oscillatory activity in the brain (Study 3), both in the prediction and its error, but also in beta frequency in the ERP analysis (Study 2) in line to other evidence in the literature (see Marco-Pallarés et al., 2015, for a review). Hence, after the three studies our results support the notion of convergence as a form of social reward capable of guiding reward-based learning in the brain.

Moreover, results of time-frequency analysis in Study 2 show how the feedback related processing is also related to theta activity, supporting the idea that this oscillatory activity is involved in decision making as well as learning, that are fundamental to a social behavioural adjustment such as conformity. Interestingly, this interpretation is not only assumed but is also explained by the RL model in the analysis of oscillatory activity in Study 3 even when ERP activity is removed from the data. Therefore, combined evidence from Study 2 and Study 3 suggests that both cognitive control and learning computations happening in the social behavioural adaptation of conformity are signalled in theta frequency band.

In study 1 we demonstrated how cooperative interaction has a causal relationship to enhance conforming behaviours in dyads, result that has been replicated in all our data, including the one presented in Study 2-3. Results in Study 2 show how people when conforming need to allocate their attentional and cognitive resources for a longer period of time. This explanation would suppose the engagement of monitoring system that measures the adjustment and learning at the service of predicting and adjusting to how the partner acts are expected to be two important functional processes. Even if this might be true, there are still other aspects of the social cognition that are not covered by this explanation. As we stated in the introduction section, recent research in social neuroscience has focused on the importance of the MS in social behaviour. The need of having a model or reference framework of the other person involves the collaboration of multiple regions in the brain. Even though we have not found any conclusive evidence of such network, a candidate for such function according to previous evidence would be the alpha oscillatory phase synchrony found in the Study 3. This activity was found to be engaged in anterior and parietal electrodes, compatible with the locations proposed for MS and other social cognition functions. Therefore, as explained in the introduction, MS needs the collaboration of different regions in the brain such as the mPFC, TPJ and precuneus portion of the cortex as well together with MNS and other regions such as inferior parietal sulcus (IPS). Given the limitations of present studies, the proposal of a key role of alpha synchronization in MS, although suggestive, is only tentative. New experimental paradigms with the use of other neuroimaging approaches (e.g., combined EEG-fMRI, MEG or intracranial recordings) might help in shedding light in the role of the different oscillatory synchrony mechanisms underlying the wilful act of conforming.

## 5.6. Statistical framework

Although it was not one of initial aims, one of the main innovations of the present thesis is the use of a Bayesian framework which, even if it is an increasing trend in cognitive neuroscience, it is yet to be generalized in the field. Very briefly, in Bayesian framework we make probability statements from parameter  $\theta$  in its unobserved distribution ( $p(y|\theta)$ ) and  $y$ , related to an observed distribution ( $p(\tilde{y}|y)$ ) where its joint probability distribution can be written as a product of two densities coming out of prior ( $p(\theta)$ ) and sampling distribution ( $p(y|\theta)$ ):  $p(\theta, y) = p(\theta)p(y|\theta)$ . Additionally, with the conditioning of the known value of data  $y$  we can yield the posterior density following the Bayes rule:

*Equation 5.1*

$$p(y|\theta) = \frac{p(\theta, y)}{p(y)} = \frac{p(\theta)p(y|\theta)}{p(y)} \propto p(\theta)p(y|\theta)$$

In the last step, the probability of observed data  $p(y)$  is omitted and, with fixed  $y$  and treated as a constant (as it does not depend on  $\theta$ ), we can yield to an unnormalized posterior density. This simple explanation covers, in fact, the main technical foundation to Bayesian inference, that develops a model ( $p(\theta, y)$ ) to summarize  $p(y|\theta)$ . Hence, Bayesian framework inferences are conditional to the data, and they are exact, which evades the need to asymptotic approximations and provide high interpretable power.

In study 2 we used a Bayesian multilevel modelling (BMM) under the generalized linear model framework that allowed us to retain the maximum amount of information for modelling. BMM, forced us to do assumptions on the predictors and link them to the data. Multilevel models are also the usual choice when data is nested in aggregated units. In our case, data was nested not only by participants in dyads, but also in other grouping factors such as electrodes and time intervals. The main advantage of this approach when using it together with Bayesian framework compared to other procedures is it does not rely on summary statistics that might lose the explanatory power of the variance at individual level, resulting in a loss of statistical power of the corresponding inferences. In fact, there is evidence suggesting it to be the most trustworthy method for controlling error in multiple comparisons (Gelman, Hill and Yajima, 2012), as the null-hypothesis testing requires priors that result in shrinkage of the likelihood, making it more difficult for weak evidence to result non-zero. Additionally, we decided not to use flat or uninformative priors but make them high-tailed and hierarchic. Also, we used the highest density interval together with the region of practical equivalence rule (HDI+ROPE) that considers other parameters to constitute its range such as the type of scale in data, as well as the variance in the observed data. Taken together, we believe our methods present evidence of highly conservative consistency.

For study 3, we proposed a two-level analysis that is inspired in the analysis traditionally used in fMRI (Friston et al., 2005). However, even though we modelled the first level via frequentist statistics (extracting individual level estimation and variances), we modelled the second group levels to connection permutations using Bayesian modelling and used an HDI+ROPE rule. This approach maintained most of the advantages of BMM at connection level, that were used to compute more than 625 connection combinations (that would require a hardly manageable amount of time of computation) with the efficiency

of extracting individual level estimates and variances from the first level. To the best of our knowledge, this is the first time that is proposed an inferential approach like this in cognitive neuroscience.

In conclusion, we believe Bayesian framework offers several different advantages in exploratory studies where multiple comparisons are present and might constitute a leap forward in the of study neurological phenomena using the maximum amount of information at hand.

## 5.7. Future directions

We started this research trying to capture the behavioural adaptation of conformity in its spontaneous reality, and even if we did, there is an obvious need to apply different manipulations to our paradigm in order to strengthen our arguments and interpretations. For instance, we could induce manipulations such as changes in one's responses different than their initial intentions to measure control discrepancies that would explain detailed signal variances on such process. On the other hand, even if time resolution in EEG has resulted very useful to associate signal to different fronto-parietal systems, the use of MEG or fMRI would enrich our intuition with a greater spatial resolution as well.

From a more computational perspective, it would be interesting to explore the use of multi-agent RL paradigms, designing joint computational models such as those combining RL with working-memory models, dynamic causal modelling, as well as more sophisticated or complex algorithms (with increased number of parameters) to trace different aspects of learning. In fact, in recent years research with more sophisticated algorithms has bloomed showing how complex algorithms can explain multi-layered phenomenon in the brain (see Collins and Shenhav, 2022 for a review). Furthermore, recently the use of similarity analysis of neural signal with Deep Q-Network (DQN) models, that model Q state-space representations of a RL framework, convolutional neural networks (CNN), recurrent neural networks (RNN), or more sophisticated Long Short-Term Memory (LSTM) networks or Transformer models nowadays widely used in computer sciences, are successfully being implemented in perception models (Yasmins and DiCarlo, 2016) and decision making (Cross et al., 2021), and even explaining complex regions such as the PFC (Wang et al., 2018). Here, we have the intuition that a DQN might explain the Bayesian inferential high-dimensional dynamic of mentalizing that can only be assumed in the current job by conjecture.

There are also other interesting manipulations and additions we can make to our code. For instance, we could introduce context learning or other delayed learning processes, that would require a secondary model to track in a continuous matter at every trial, this would allow us to detail further the origin and evolution of each parameter. Also, it would be interesting to introduce the exploration of influence variables like threat conditioning or other socially induced drives such as status, fairness, certainty, autonomy of choice... As we commented in the introduction, research from social psychology has studied different reasoning behind the choice of conformity that we believe our experimental paradigm, as it induces a spontaneous conformity, could also further explore.

Finally, we could explore individual differences to increase the detail on the variability of the population regarding this social adjustment. In our introduction we presented evidence that related SVO with a personal bias towards cooperative or conforming tendencies. Similar to this idea, we might suppose certain traits, that enhance a particular decision bias to conform, could be associated to higher role related differences. In our results we did not find credible evidence in signal related to conforming or non-conforming behaviours. However, we might presume a sample balanced through personality traits related to social tendencies (such as SVO), as they might correspond to more stable individual differences in the brain, could end up capturing higher credible evidence in this arena. On the other hand, the use of different neuro-atypical populations

could give us a hint on the origin of certain social difficulties associated to specific psychiatric conditions.



## 5.8. Limitations

As any research, the present proposal is not without limitations. Even when they have been analysed in the discussion section of the different studies, we consider important to acknowledge them in a more integrated way. Firstly, even if the design of the task was purposefully unaltered as we wanted to capture the phenomena unbiased, it is also true the lack of manipulations limited the interpretation of some of the results, leaving them to a more speculative level.

Secondly, we acknowledge the number of dyads in our study is not very large, especially in the EEG studies. Nonetheless, we believe the use of Bayesian framework and its avoidance of asymptotic limits is helpful in this specific limitation. Yet, it cannot be ignored a higher number of dyads would contribute positively to the strength and generalization power of the presented evidence.

On the other hand, we believe the use of only one neuroimage technique, in this case the study of EEG signal, limits the explanatory possibilities of describing the neural networks involved in conformity. Even when we have used other social cognition literature to explain some of our findings, we understand this comes at price of directly linking our evidence to other important evidence in the field of single-person neuroscience.

Lastly, from a statistical point of view, the use of a Bayesian framework also carries certain disadvantages, especially in the selection of priors. Despite our efforts to reduce such bias with several different contingencies, Bayesian inferences are not absent of subjectivity as our inferences will always be induced by the priors. However, we believe we have chosen them with responsibility and diligence, and together with the highly restrictive rules applied to the inference, we understand we have controlled such influence. Also, we believe advantages overcome prejudice in terms of statistical power for all the benefits we have mentioned in previous sections, and we still believe is the best choice to analyse and make inferences on observed data.



## 6. Conclusion

From the beginning, the main aim of this thesis has been a better understanding of one of the most fascinating phenomena in social psychology: conformity. Here, the first important addition to this field of study is the proposal of a completely new, although inspired by classic behaviourists, experimental paradigm where conformity is not explicitly induced but appears spontaneously. In this regard, having a paradigm where conformity is not induced helps to study the mechanisms that dominate this behavioural adaptation.

An important question that was clear from the beginning was the use of non-induced two-person setting, where the behaviour could emerge spontaneously. As explained in the introduction of this thesis, conformity has been studied in neuroscience by forcing its appearance, and this could be criticized when trying to generalize its findings. However, in part thanks to hyperscanning techniques that permit the simultaneous recording of two brain signals, a new paradigm could be designed that could evade this limitation, and this was our first motivation. Furthermore, the dynamics described in this study are, to the best of our knowledge, the first documented electrophysiological recordings of such social adaptation in a two-person setting that does not induce the behaviour and treats cooperation as an intrinsic and sufficient reward. The challenge, in our case, has been to dive deep into the literature to find relatable evidence that could serve us to make prior hypotheses as well as posterior interpretations of our results.

Nonetheless, in this work, we relate the behavioural adaptation of conformity to cognition, attention, value-based decision-making and learning. Additionally, to explore the neural correlates of conformity, we had to bridge literature and evidence from feedback related processing, conflict monitoring and reward-based learning. This phenomenon, in fact, reinforces the idea or serves as an example of the complexity of social cognition: a multi-dimensional and multi-layered computation which obliges an eclectic general view of different fields inside the umbrella of cognitive sciences.

In this thesis we have first presented strong behavioural evidence supporting how people have a natural tendency to converge in their responses, and that this natural tendency is enhanced with cooperation. Secondly, we have shown how people who cooperate create more useful (in terms of predictability) models of their partners intentions. In other words, people who cooperate are more willing to predict their partner's responses and therefore increasingly engage their learning abilities.

Moving into the neurophysiological correlates found in the studies, an interesting finding was how conformity is an adaptation requiring the engagement of cognitive resources, that disappear when convergence is present. We found this control mechanisms to be mainly mediated by theta and attentional mechanisms in alpha. Also, we could state convergence does, in fact, act as a social reinforcer, and we found different time-frequency associations to this claim in beta power.

In the final study, where we were interested in synchronic coherence in phase-oscillatory activity in 1 second in two different phases of 500ms, we found other interesting conclusions. Firstly, we found alpha dynamics happening in what we interpreted as an inter-regional communication mechanism in participants related to different functions inside social cognition. Then, we looked how reinforcement learning model parameters, such as the prediction error and the prediction update, were traced only in theta frequency.

Finally, we found beta related inter-brain synchrony change in dyads, giving support to other evidence in literature that reported this inter-personal synchrony, in what has been interpreted as a mechanism of correlated joint attention.

Looking back at the initial aims of this research, we moved forward in the understanding of all the questions we proposed. Firstly, we designed a new experimental paradigm that did not put cooperation opposed to competition and where conformity happened without being induced or imagined but happening naturally and in a real social environment, which takes us to the next aim. Second, our research wanted to study the neural correlates of conformity in a 2-person setting, where we could study role-related differences as well as inter-brain dynamics. Lastly, we used a RL paradigm using convergence as an internal reinforcer to explain learning and predictive updates that happen when people conform and cooperate.

Conformity has been a social phenomenon of high interest from the first social and cognitive psychologists, who explained this adaptation and the drive behind it in multiple different ways. Our work proudly contributes to enlarge the understanding of this behaviour that pioneers like Jeness, Sherif, or Asch, many years ago commenced to experimentally describe.

Finally, we believe the evidence presented in this dissertation contributes to the advance on the understanding of conformity as a social behavioural adaptation which was, from the very beginning, the spot-on passion behind all these years of work.

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### 8.3. Abbreviation List

AC – Actor-Critic  
ACC – Anterior Cingulate Cortex  
AI – Anterior Insula  
AMG – Amygdala  
ANOVA – Analysis of Variance

BG – Basal Ganglia  
BOLD – Blood-oxygen-level dependent  
BMA – Bayesian Meta-analysis  
BMM – Bayesian Multilevel Modelling

C – Cooperative (only in Study 1)  
C – Conforming  
CIF – Conforming Interaction Factor  
CNN – Convolutional Neural Networks

DA – Dopamine  
dlPFC – Dorsolateral Prefrontal Cortex  
DMN – Default mode network  
DQN – Deep Q-Networks  
dpMFC – Dorsal Posterior Medial Frontal Cortex

EC – Equally Conforming  
EEG – Electroencephalography  
ERD – Event-related desynchronization  
ERN – Error-related Negativity  
ERP – Event-related Potentials  
EVC – Expected Value of Control

FB – Feedback  
fERN – Feedback Error-related Negativity  
fMRI – Functional Magnetic Resonance  
fNIRS – Functional Near Infrared Spectroscopy  
FRN – Feedback-related Negativity

HDI – High Density Interval  
HPT – Hypothalamus

LHb – Lateral habenula complex  
lPFC – Lateral Prefrontal Cortex

I - Individual  
IBS – Interbrain Synchrony  
ICA – Independent Component Analysis  
ISPC – Intersite Phase-clustering  
IPS – Inferior Parietal Sulcus

LMEM – Linear Mixed-effects Model  
LSTM – Long Short-Term Memory Networks

MDP – Markov Decision Process  
MEG – Magnetoencephalography  
MMN – Mismatch Negativity  
MNS – Mirror Neuron System  
MS – Mentalizing System  
NC – Non-Conforming  
NHCT – Null-hypothesis Credibility Testing  
NUTS – No-U-turn sampler

OFC – Orbitofrontal Cortex  
OT – Oxytocin

pgACC – Perigenual Anterior Cingulate Cortex  
PD – Prisoner’s Dilemma  
PE – Prediction Error  
PFC – Prefrontal Cortex  
PM – Performance Monitoring  
pmPFC – Posterior Medial Prefrontal Cortex  
PRO – Response-outcome theory  
pSTS – Posterior Superior Temporal Sulcus

RewP – Reward Positivity  
RL – Reinforcement Learning  
RNN – Recurrent Neural Networks  
ROPE – Region of Practical Equivalence  
RPE – Reward Prediction Error  
rTPJ – Right Temporo-Parietal Junction

SD – Standard Deviation  
SE – Standard Error  
SIT – Social Identity Theory  
SVO – Social Value Orientation

TDL – Temporal Difference Learning  
tDCS – Transcranial Direct Current Stimulation  
ToM – Theory of Mind  
TPJ – Temporo-Parietal Junction

vmPFC – Ventromedial Prefrontal Cortex  
VStr – Ventral Striatum  
VTA – Ventral Tegmental Area  
WM – Working Memory