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# Others-related motivation in decision making: computational and magnetoencephalographic correlates in humans

Laure Bottemanne

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**Titre :**

**Influence de la motivation liée à autrui sur la décision: corrélats computationnels et magnétoencéphalographiques chez l'Homme**

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## ***Résumé :***

L'homme est un animal social. La majorité des décisions que nous prenons se font dans un contexte social et dépendent d'autrui, ce qui implique des calculs cérébraux complexes qui incluent tous les facteurs contextuels et environnementaux. La majorité des études ultérieures de la prise en compte d'autrui dans la décision ont utilisé des tâches de partage de récompenses entre soi et autrui. Les choix possibles amènent le décideur à considérer autrui, mais dans le but de gagner soi-même une récompense ; donc dans un contexte où les récompenses liées à soi et les récompenses liées à autrui sont confondues. Le travail présenté dans cette thèse avait pour but une meilleure compréhension des mécanismes cérébraux soutenant l'intégration d'autrui dans la prise de décision, sans que la récompense pour autrui n'interfère directement avec soi.

Nous nous sommes appuyés sur le cadre théorique de la décision perceptuelle et des modèles de diffusion pour l'étude i) des modifications du processus décisionnel induites par une récompense monétaire allant à autrui et ii) de l'impact de l'effet d'audience (le fait de se sentir observé) sur la décision. Nos résultats computationnels montrent qu'une récompense pour autrui, par rapport à une récompense pour soi, et une audience, par rapport au secret, modifient le taux de dérive de la variable de décision. En magnétoencéphalographie, nos résultats indiquent que les décisions pour soi et pour autrui diffèrent pendant, mais aussi après, la prise de décision dans des zones cérébrales associées avec la transformation sensori-motrice, l'ajustement du compromis entre rapidité et justesse et avec la cognition sociale. Ainsi, le cortex temporal montre des différences de -1170 millisecondes (ms) à -1023 ms, de -993 ms à -915 ms et de -343 ms à -188 ms en amont de la réponse. Ce qui suppose une influence sur l'intégration

des preuves sensorielles. Après la décision, les régions frontales ont également montré des différences entre soi et autrui, de 153 ms à 303 ms post-réponse, suggérant une différence entre soi et autrui dans l'ajustement du compris entre justesse et rapidité. Le bénéficiaire de la récompense associée à la décision modifie les paramètres décisionnels et les corrélats cérébraux de la décision perceptuelle, démontrant l'importance du contexte social dans l'implémentation de la prise de décision chez l'Homme. Ce travail appuie également l'utilité des modèles mathématiques tels que les modèles de diffusion dans la compréhension des processus décisionnels, même de ceux découlant de la cognition sociale.

**Mots clés :**

Cognition sociale, autrui, prise de décision, décision perceptuelle, modèles de diffusion, récompenses.

## ***Résumé substantiel :***

Depuis plus d'un siècle, les chercheurs explorent les différents aspects de la cognition sociale chez l'homme. L'homme aspire à l'équité et a une tendance naturelle à la coopération et à l'altruisme ; traits cognitifs caractérisés en économie comportementales et en neuroéconomie. Ces caractéristiques de la cognition humaine viennent interagir avec la pragmatique de maximisation des récompenses individuelles. Dans un contexte de partage ou d'attribution de récompenses monétaires, les structures engagées par les décisions économiques (basées sur la valeur des choix possibles) et par l'apprentissage par renforcement basé sur la récompense sont en effet impliquées dans les comportements sociaux. Dans un contexte social, les mécanismes tels que la théorie de l'esprit (la capacité à se représenter les états mentaux d'autrui) ou l'empathie sont également engagés. Ainsi, la cognition sociale implique non seulement le système dopaminergique, en particulier le striatum ventral et le cortex préfrontal ventro-médian, mais aussi le cerveau social, comprenant notamment le cortex frontal ventro-médian, la jonction temporo-pariétale et les lobes temporaux. Une question qui reste à éclaircir est l'intégration d'autrui dans la prise de décision ; lorsque la décision impacte le bien-être autrui, sans conséquence directe pour soi. En s'appuyant sur le cadre conceptuel des modèles de diffusion, nous avons conduit des expériences étudiant comment autrui influence la mécanistique de la prise de décision et ses corrélats cérébraux en magnétoencéphalographie chez l'homme.

Bien que les décisions perceptuelles puissent paraître d'un faible intérêt d'un premier abord, elles peuvent – de par leur simplicité – procurer une fenêtre d'observation et d'analyse de

l'influence d'autrui dans la prise de décision. Ce cadre théorique offre en effet deux principaux avantages : les corrélats cérébraux des décisions perceptuelles sont largement documentés et ce cadre permet l'application de modèles computationnels d'estimation des paramètres décisionnels. D'après les modèles de diffusion, une décision dépend des preuves sensorielles disponibles au décideur, de leur intégration au cours du temps avec un taux de dérive donné, et du seuil décisionnel fixé pour faire un choix. Ainsi, une décision est prise quand la variable de décision atteint un seuil de décision. Le temps nécessaire à la décision dépend alors de la vitesse d'intégration des preuves sensorielles (le taux de dérive de la variable de décision) et de la distance entre le point de départ de la variable de décision et le seuil décisionnel. L'encodage perceptuel primaire du stimulus et l'exécution motrice de la réponse comportementale, ainsi que tous les autres processus ne faisant pas partie intégrante de l'accumulation des preuves sensorielles jusqu'au seuil décisionnel, sont compris dans ce qui est appelé le temps non-décisionnel ; ce temps s'ajoute au temps de réaction mesurés. Dans toutes nos expériences, nous avons utilisé le paradigme expérimental du nuage de point. Cette tâche, largement utilisée dans la littérature, consiste à présenter aux participants des stimuli visuels contenant des points ayant pour partie une trajectoire aléatoire et pour autre partie une trajectoire cohérente entre eux (ici, vers la droite ou vers la gauche). La tâche demandée aux participants est de déterminer la direction des points ayant une trajectoire cohérente entre eux et de répondre par l'appui d'un bouton quant à la direction des points. Nous avons appliqué les modèles de diffusion sur les données recueillies afin d'identifier quel(s) paramètre(s) décisionnel(s) varie(nt) lorsqu'une décision est prise en prenant autrui en considération.

Nous avons mené trois expériences comportementales et une expérience en magnétoencéphalographie (MEG). Dans la première étude comportementale, nous avons demandé aux participants d'effectuer la tâche dans le but de gagner – et d'éviter de perdre – une récompense monétaire, soit pour eux-mêmes soit pour un autre participant (inconnu et sélectionné aléatoirement). Cette première étude a montré que le niveau de récompense/punition influence le temps non-décisionnel mais aussi le taux de dérive de l'accumulation des preuves sensorielles. Cependant, le bénéficiaire de la décision n'a eu aucune influence sur les processus décisionnels. Dans la seconde version, nous avons retiré la possibilité de perdre de l'argent et changé qui était autrui: nous avons cette fois-ci demandé au participant de prendre leur décision pour un proche qu'ils avaient choisi préalablement. Cette seconde étude a montré une influence du bénéficiaire de la décision, modifiant le taux de dérive de l'accumulation des preuves sensorielles. Nous avons donc mené cette même étude en MEG. Les données cérébrales enregistrées en MEG nous ont permis non seulement de retrouver les corrélats électrophysiologiques de la décision perceptuelle déjà mis en évidence en électroencéphalographie (EEG) dans la littérature mais surtout de montrer des différences entre soi et autrui pendant et après la prise de décision. Plus précisément, nous avons montré des différences au niveau du cortex temporal et -frontal au moment de l'accumulation des preuves sensorielles (pendant le processus décisionnel) et des différences au niveau du cortex frontal après la décision. Dans un axe parallèle, nous avons mené une étude comparant les décisions perceptuelles sous observation (audience) et sans être observé. Cette recherche a montré qu'être observé modifie également le taux d'accumulation des preuves sensorielles.

En conclusion, ce travail de thèse est une preuve supplémentaire de l'étendue de l'impact de la cognition sociale dans la prise de décision. Il apporte une explication mécanistique à l'influence du bien-être d'autrui et du regard d'autrui dans la prise de décision, par une modulation du taux de dérive de la variable de décision. En outre, il est en faveur d'une théorie unifiée de la prise de décision, avec l'utilisation des modèles de diffusions aussi bien dans le domaine perceptuel que dans l'étude de mécanismes cognitifs économiques et sociaux intégrés dans le processus décisionnel.

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# ***Others-related motivation in decision making: computational and magnetoencephalographic correlates in humans***

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## ***Abstract :***

Humans are inherently social: most of human's decisions are within a social context and depend on others. For more than a century, researchers explored aspects of social cognition. Aiming to understand human behavior in social contexts, neuro-economic research showed that taking others into account involve complex brain computations that include all environmental and contextual factors. However, most of the work was carried out using money allocation tasks; mixing self-affecting and other-affecting rewards into the decision making process. The present work intended the understanding of the brain mechanisms underpinning the integration of others into the decision making process for decisions that include others and do not interfere with self-rewards.

Taking advantage of mathematical models from the drift diffusion model framework, we conducted experiments investigating how others influence the mechanisms of perceptual decisions and their correlates in the human brain. We showed that taking rewards for others into account and being observed by others influences the drift rate of the decision variable. The drift rate is higher in front of an audience than in secret and higher for self-rewards than for other-rewards. These results indicate that others are integrated into the accumulation process together with the evidence available for making a decision. At the brain level, we found

differences between self and other decisions over the anterior temporal and centro-frontal cortices during decision making. This suggests that the beneficiary of a decision modifies sensory-motor transformation processes. In addition, self- and other-affecting differences were distinguishable over the medial frontal sensors after the decision making process, indicating a variation in the speed-accuracy tradeoff adjustment process.

**Key-words :**

Social cognition, others, decision making, perceptual decisions, drift diffusion models, rewards.

## ***Part 1: Theoretical background***

## ***1.1. Chapter 1: In social settings, humans violate the Rational Choice Theory***

Humans are inherently social. Most of humans' decisions and actions are made in a social context. From birth (and probably even in-utero), we observe others, learn from others, act according to others and take others into account when making decisions. Others can be relatives, friends, every person we meet, every person we see; others may even be the mass formed by a society.

For more than a century, social psychology and, more recently, behavioral economy and social cognitive neuroscience has sought to understand the specificity of human social behavior, by studying the psychological, behavioral and brain activation changes induced by others. As such, research shows that decision making is modulated when taking others into account.

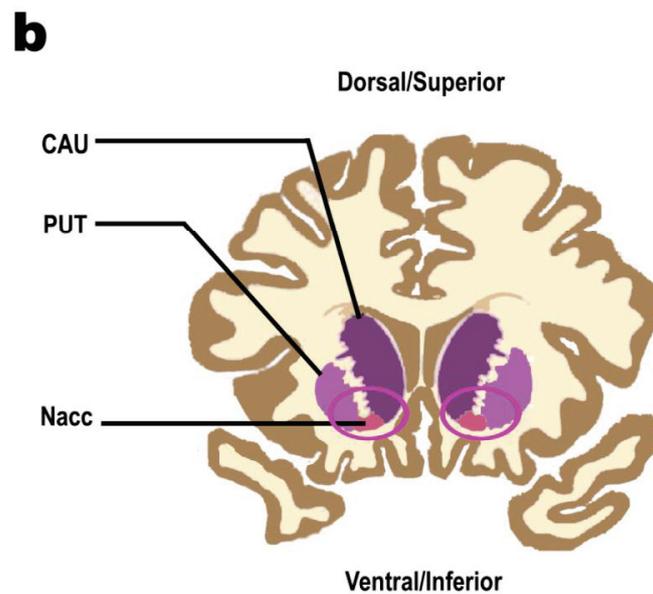
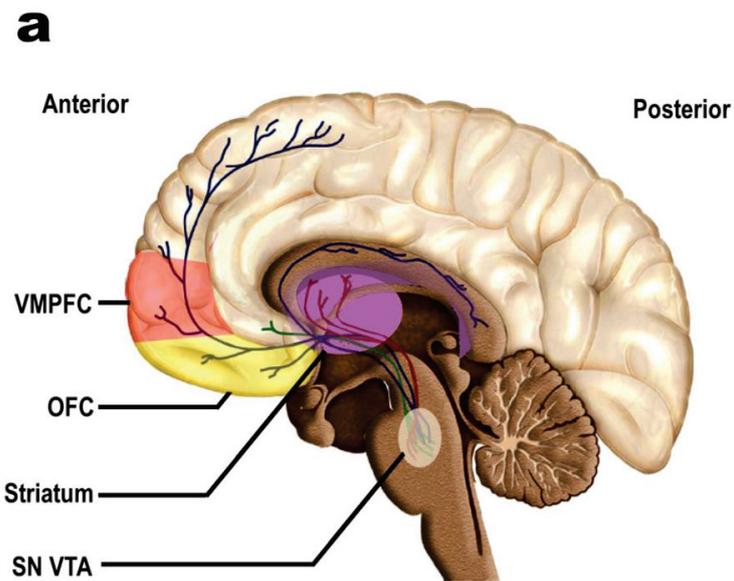
### ***1.1.1. Basics of reward processing***

The Rational Choice Theory assumes that humans act to maximize rewards and personal gain. Basically, decision making is based on the valuation of utility associated with each decision (D. Lee and Seo 2016). In its simplest computation, utility can be described as the value of the reward associated with the options available weighted by the probability of the option to be actually rewarded ( $Utility = Reward \times Reward\ Probability$ ).

The processing of rewards is sustained by the dopaminergic neuronal activity in the brain. This circuitry is responsible for mediating goal-directed behaviors (Schultz 2016; M. R. Delgado 2007). The dopaminergic systems involve two main pathways; both originate from the midbrain (**Figure 1**). The first originates from the ventral tegmental area (VTA), projecting to the ventral striatum and through the frontal lobe. The second originates from the substantia nigra (SN) and projects to the dorsal striatum (Arias-Carrión et al. 2010). The more ventral dopaminergic path (ventral tegmental area - ventral striatum - ventromedial prefrontal cortex/orbitofrontal cortex) is involved in processing rewards *per se*, responding to all reward types, their value and probability. The more dorsal path (SN- dorsal striatum-) is an essential component of reinforcement learning and information updating (Declerck, Boone, and Emonds 2013).

Neural activity in the ventral striatum and the orbitofrontal cortex scales linearly with the subjective value of a wide variety of reward types (Schultz 2004). The ventro-medial prefrontal cortex (VMPFC) is an action-outcome predictor, encoding goal-values and the comparison of these values in a common currency (Rangel and Hare 2010; Chib et al. 2009; Montague and Berns 2002). Reward information is further fed to brain structures involved in the organization of behavior, such as the dorso-lateral prefrontal cortex (DLPFC) – involved in cognitive control - and the dorsal anterior cingulate cortex – involved in conflict monitoring.

The dopamine (DA) signal is also involved in reinforcement learning, encoding a (positive or negative) prediction error. As such, a better reward than expected (and unexpected rewards) elicits DA activation, while lesser rewards than expected induce DA depression. The prediction error is a teaching signal that indicates such differences between the actual and the predicted rewards (Schultz 2016).



**Figure 1: Overview of the major components of reward system in the human brain. a) Sagittal view. Dopaminergic neurons are located in the midbrain structures (white): the substantia nigra (SN) and the ventral tegmental area (VTA). Their axons project to the striatum and the prefrontal cortex. The striatum (purple) and the orbito-frontal cortex (OFC -**

yellow) respond to rewards. The ventro-medial prefrontal cortex (VMPFC - red) sustains the comparison of values. Image adapted from (Arias-Carrión et al. 2010). **b)** Coronal section of the brain displaying the different parts of the striatum: the caudate nucleus (CAU), putamen (PUT), and nucleus accumbens (Nacc). The ventral striatum (pink circles) responds to reward and reward anticipation. Image adapted from (Sanfey 2007)

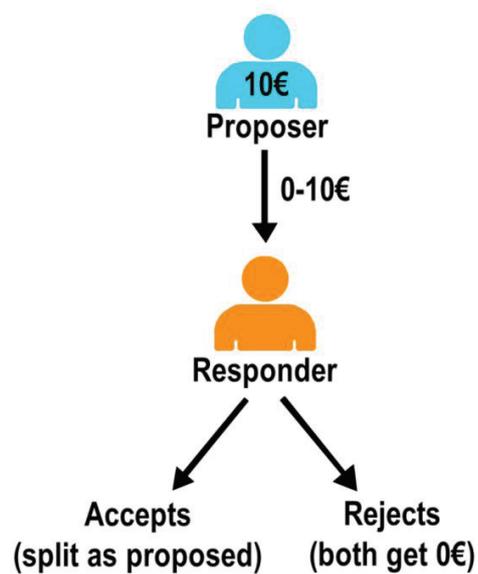
In social settings, humans violate the model established by the Rational Choice Theory, exhibiting altruistic behavior, fairness and cooperation during social interaction instead of acting as pure gain maximizer (D. Lee and Seo 2016). Social Cognitive Neurosciences emerged from the need to provide neurobiological and computational account of human decision making in a social context, using mainly Public Good Games combined with neuroscientific explorations (Stallen and Sanfey 2013; Declerck, Boone, and Emonds 2013; Rilling and Sanfey 2011; Rilling, King-Casas, and Sanfey 2008; D. Lee 2008; C. D. Frith and Singer 2008; Blakemore, Winston, and Frith 2004).

### **1.1.2. Public Good Games**

Public Good Games formalize situations in which the decider(s) faces money allocation tasks, in interaction with at least one other person (Stallen and Sanfey 2013). To investigate segmented parts of social value-based decision making, the protocol of the exchange constrains the set of possible choices.

**The ultimatum game (UG)** provides nice illustrations that humans violate the model established by the Rational Choice Theory, exhibiting altruistic behavior during value-based decision making in social interaction. The UG is a money sharing tasks between a proposer and a receiver (**Figure 2**). The proposer is given an amount of money and makes a sharing proposal to the receiver. The proposal can vary from sharing nothing to sharing the total initial endowment. This interaction then has two possible outcomes: i) the receiver accepts and it is split according to the proposal; or ii) the receiver refuses, which results in both protagonists getting nothing from the endowment. So, if the receiver were to calculate his decision only based on rational payoff maximization, he should accept any proposal higher than zero. However, offers where the receiver receives less than with less than 30% of the total shared amount (e.g. less than 3€ out of 10€) meet rejection (Han et al. 2018; G. Tabibnia and Lieberman 2007; C. D. Frith and Singer 2008). They are rejected (both payoff = 0€) even if accepting it would to a better self-payoff (self-payoff = the proposed split, e.g 2€ out of 10€) because they are considered to be

unfair, demonstrating that humans have an aversion for inequity. Even more, humans share their resources even if they don't have to. Indeed, in *the Dictator Game*, an UG alternative game in which the receiver has no choice but to accept whatever split the proposer makes, the proposers still share at least 20% of the pots.



**Figure 2: Ultimatum Game.** One player, the proposer, specifies how to divide an amount of money. The other player, the responder, then has the option of accepting or rejecting this offer. If the offer is accepted, the amount is divided as proposed. If it is rejected, neither player receives anything. Figure from (Stallen and Sanfey 2013)

***The Prisoner's Dilemma*** comes from the metaphorical situation of two prisoners being interrogated. The police do not have enough evidence to convict the prisoners for the totality of their crime. A bargain is offered to the prisoners: testify (defection) or remain silent (cooperation). It is important to say that the prisoners cannot communicate with each other in anyway during the decision making process. Three outcomes are possible: i) Both interrogated prisoners testify (defect), they both get 5 years of prison; ii) Only one of them defects, he is set free and the other gets 20 years. iii) Both remain silent (cooperation) and each gets 1 year in prison.

In the laboratory, years of imprisonment are replaced by monetary payoffs (**Figure 3**). Deciders are endorsed with funds and have to decide to invest part of their funds (cooperate) or not (defect). The monetary gain for each player depends on the combination of the decisions of both players. Critically, the payoff matrix is arranged so that it embodies a tension between individual rationality and group rationality. Defection from a cooperative partner leads to the most individually rewarding outcome. If players cared only about their own payoffs, both players should defect, but humans often choose to cooperate in the Prisoner's Dilemma games.

***The trust game*** is an iterated version of the prisoners' dilemma, in which the players make their decisions one at a time. The investor can invest part of his funds, which will be multiplied. The trustee then decides if he cooperates and splits the money or defects and keeps all the money from the investment. The decision of the investor is then how much he trusts player will respond with reciprocity and altruism and not as a pure payoff maximizer.

		<b>Player B</b>	
		Cooperate	Defect
<b>Player A</b>	Cooperate	Player A: 5 Player B: 5	Player A: 0 Player B: 8
	Defect	Player A: 8 Player B: 0	Player A: 2 Player B: 2

Both given 2€

**Figure 3. Example of a Payoff Matrix in the Prisoner’s Dilemma.** Two players (A and B) simultaneously choose to either cooperate or defect. The four possible combinations are: (1) both players cooperate, (2) player A cooperates and player B defects (3) player A defects and player B cooperates, or (4) both players defect. The largest payoff to a player occurs when he defects and the other cooperates (self: 8 €; other: 0 €). Defection from a cooperative partner is the most individually rewarding choice, thereby creating a temptation to defect. The worst individual payoff occurs when cooperating with a defector (self: 0 €; other: 8 €), creating a risk of being duped. Mutual defection provides a low amount to each individual (2 €) and for the group (self and other: 4€). Mutual cooperation yields a modest payoff for both players (5€), and the highest total for the two players taken together (total: 10 €). Figure: (Robson et al. 2019).

## ***Cooperation and generosity are fit strategies***

In the social dilemmas created in the Public Good Games, reciprocity is one of the keys of the emergence of cooperation (Clark and Sefton 2001). The idea behind reciprocity is that, in a group or a society, if I help you, you might help me later. This promotes the survival of each individual in the group and thus the survival of the group. The average wealth of a population of cooperators is higher than would be a population of defectors. A computer simulation experiment showed that tit-for-tat<sup>1</sup> is actually a good strategy to get great outcomes in the Prisoner's Dilemma (Axelrod 1980). Reciprocity can also be a successful rule for an individualistic pragmatist, motivated by an economical rational strategy (Declerck, Boone, and Emonds 2013). Cognitive skills are positively correlated with cooperation, such that people with higher cognitive abilities cooperate more (Chen et al. 2013; Burks et al. 2009; Jones 2008) as well as people with lower delay discounting<sup>2</sup> (Harris and Madden 2002). However, if pragmatic reciprocity was the only key to cooperation, then people should not cooperate in one-shot games (where players encounter each other only one time) – which they do (D. Lee 2008; Blakemore, Winston, and Frith 2004; Sally 1995; Batson and Moran 1999; Cooper et al. 1996). While cooperation is enhanced in iterative games, the fact that people cooperate in one-shot games shows that other phenomenon are at stake.

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<sup>1</sup> Tit-for-Tat" consists here of cooperating in the first round of the iteration, and then doing whatever the opponent did in the previous round.

<sup>2</sup> Delay discounting describes that people tend to weigh rewards in inverse proportion to its delay: long term benefits and rewards are less valued than the immediate ones. Low delay discounting means that this effect is moderated, such that long term rewards are also well-valued.

Even in computer simulation, with the objective to find the best strategy in the Prisoner's Dilemma to get the best possible outcome, it has been shown that niceness (not being the first to defect) and forgiveness (the propensity to cooperate after the other defected) play a crucial role (Axelrod 1980; Doebeli and Hauert 2005). Generosity (cooperate more than the partner) has also been pointed out as more effective than tit-for-tat in a noisy environment (Wu and Axelrod 1995; Bendor, Kramer, and Stout 1991). Personality traits and Social Value Orientation (SVO) indeed play a role in the tendency to cooperate (Kagel and McGee 2014; Emonds et al. 2011; Hirsh and Peterson 2009; Kassinove et al. 2002; de Dreu and van Lange 1995; Greenhalgh and Gilkey 1993).

It is to be noticed that in iterative Prisoner's Dilemma games, cooperation tend to decrease over time if defection is not punished (Stallen and Sanfey 2013; C. D. Frith and Singer 2008; Doebeli and Hauert 2005) and punishment is more effective than rewards for promoting cooperation – some authors underlined that the fear of super-natural punishment is highly promotive of cooperation (Johnson and Bering 2006)

Sanctions increase the cost of defection, thereby increasing the value of cooperative behaviors. This cognitive control exerted by the threat of punishment is sustained by the lateral prefrontal cortices (Declerck, Boone, and Emonds 2013). The dorsolateral prefrontal cortex (DLPFC) exerts a control on the selfish impulse (V. K. Lee and Harris 2013). Indeed, repetitive

Transcranial Magnetics Stimulation (rTMS), impeding the activation of the targeted brain area, on the dorso-lateral prefrontal cortex (DLPFC) lead to to higher acceptance of unfair offers.

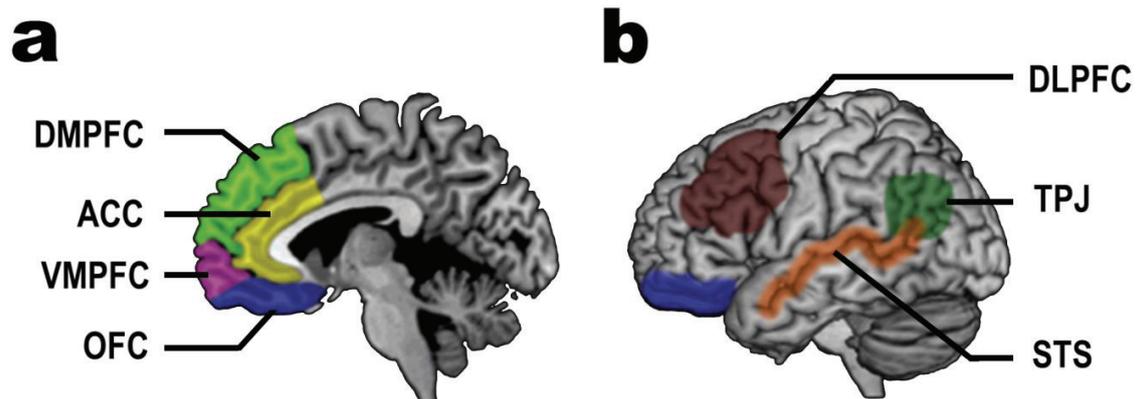
***Prosocial behaviors have an intrinsic value.***

Several studies now have demonstrated that the structures engaged in value-based decisions and reward-based reinforcement learning processes are also involved in social behaviors (**Figure 4**) (V. K. Lee and Harris 2013; Stallen and Sanfey 2013; Declerck, Boone, and Emonds 2013; C. D. Frith and Singer 2008).

The reward-related system responds during positive social interactions. Reciprocity and fairness are computed similarly to monetary outcomes in the reward-related system, suggesting that prosociality has an intrinsic value (G. Tabibnia and Lieberman 2007). The decision to act prosocially engages the OFC (Zaki and Mitchell 2011) and the dorsomedial prefrontal cortex (DMPFC) and predicts both monetary donations to others and time spent helping others (Waytz, Zaki, and Mitchell 2012). There seem to be a ventral-dorsal gradient for self-other rewards in the MPFC (Sul et al. 2015).

Reciprocated cooperation induces the activation of the ventral striatum (vSTR) and the ventro-medial prefrontal cortex (VMPFC) (Rilling et al. 2004b; 2002). Self-reported happiness in

response to fair offers has been correlated to activity in the vSTR and the VMPFC as well (Golnaz Tabibnia, Satpute, and Lieberman 2008). After an iterated Prisoner's Dilemma, viewing the faces of previous intentional cooperators, but not for those assumed to be following an assigned (cooperative) script, activated the vSTR and the orbito-frontal cortex (OFC)(Singer et al. 2004). Even smiling faces and monetary rewards - their value and magnitude encoding – overlap in the VMPFC (Lin, Adolphs, and Rangel 2012).



**Figure 4. Brain areas activated during cooperation. a)** Medial view. DMPFC: dorsomedial prefrontal cortex; ACC: anterior cingulate cortex; VMPFC: ventromedial prefrontal cortex; OFC: orbitofrontal cortex; **b)** Lateral view. DLPFC: dorsolateral prefrontal cortex; TPJ: temporo-parietal junction; STS: superior temporal sulcus. Note that the striatum, not represented in this figure, is also activated during cooperation. Figure from (Stallen and Sanfey 2013).

## ***Reputation***

The tendency to cooperate relies on the probability of reciprocation (Baker and Rachlin 2001). It requires a strategic sophistication to attempt to predict what the partner will do, to decide accordingly. This prediction is highly driven by the personality traits gathered about the other player, such as trustworthiness (Declerck, Boone, and Emonds 2013), and depends on the incentives of both players (Capraro 2013; Costa-Gomes, Crawford, and Broseta 1998). The ability to predict the choices of others and their underlying cognitive processes plays an important role during social interactions.

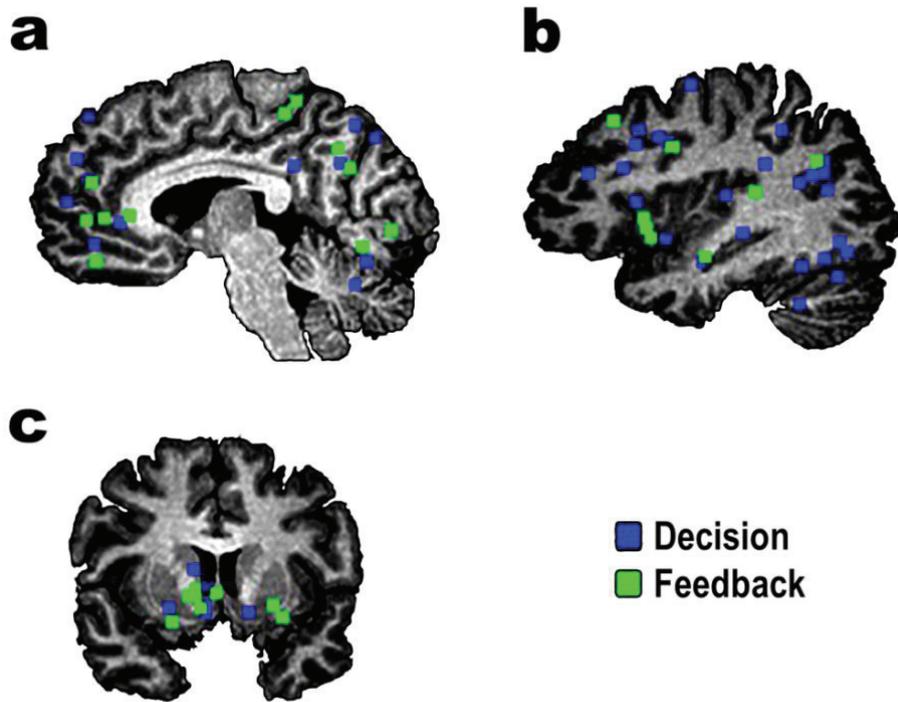
Trustworthiness can be inferred from previous behavior, learned and dynamically updated through experience (L. J. Chang et al. 2010). Or it can be primed (i.e. gossips). If primed (through labels or descriptions) in believing that the other player is likely to cooperate, then cooperation is promoted (Stallen and Sanfey 2013; C. D. Frith and Singer 2008; Boone, Declerck, and Suetens 2008; G. Tabibnia and Lieberman 2007; Oda 1997). The studies have shown that the medial prefrontal cortex (MPFC) is specifically engaged in making inference on personality traits (i.e. trustworthiness) and prediction about the behavior of another human.

Reputation also concerns oneself via impression management: cooperators are seen as more moral (Krueger and Acevedo 2007). Acquiring a good reputation (being labelled trustworthy) activates the striatum, as monetary rewards do (Keise Izuma, Saito, and Sadato 2008) and donating to a charity as well (Keise Izuma, Saito, and Sadato 2010). Impression

management is related to the image we want others to have of us. Reputation and impression management requires a second order of mentalizing. Interestingly, social reputation could be uniquely human (Keise Izuma 2012; C. D. Frith and Frith 2012; Adolphs 2003) and would be missing in people from the autism spectrum (K. Izuma et al. 2011; U. Frith and Frith 2001).

### ***There is something special about interacting with a human***

Researchers have compared decisions made in interaction with a presumed human agents to decisions made with a computer, using Public Good Games (Rilling et al. 2004a; McCabe et al. 2001; Krach et al. 2008), rock-paper-scissors games (Gallagher et al. 2002) or poker games (Carter et al. 2012). These have shown that human behave differently when facing a human and when facing a computer. Participants experienced more fun and competition playing against an alleged human than against a computer. Moreover, they rejected more unfair offers coming from a human than unfair offers coming from a computer, cooperated more and tried to bluff more with alleged humans than with computers. Using functional magnetic resonance imaging (fMRI), they revealed that some brain structures were more activated when interacting with a human than when interacting with a computer (**Figure 5**). The medial prefrontal cortex (MPFC), the temporo-parietal junction (TPJ) and the posterior superior temporal sulcus (pSTS) were preferentially activated when playing against a human.



**Figure 5. Brain regions showing an effect of human agent compared to non-social control.** The differences occur during decision making (blue) and at feedback processing (green). **a)** Medial view showing activity in the medial prefrontal cortex as well as in posterior cingulate cortex and the precuneus. **b)** Lateral view exhibiting activation in the dorsolateral prefrontal cortex, the temporo-parietal junction and the superior temporal sulcus. **c)** Coronal view displaying the implication of the striatum. Figure from (V. K. Lee and Harris 2013)

## ***1.2. Chapter 2: To interact with another human being is special***

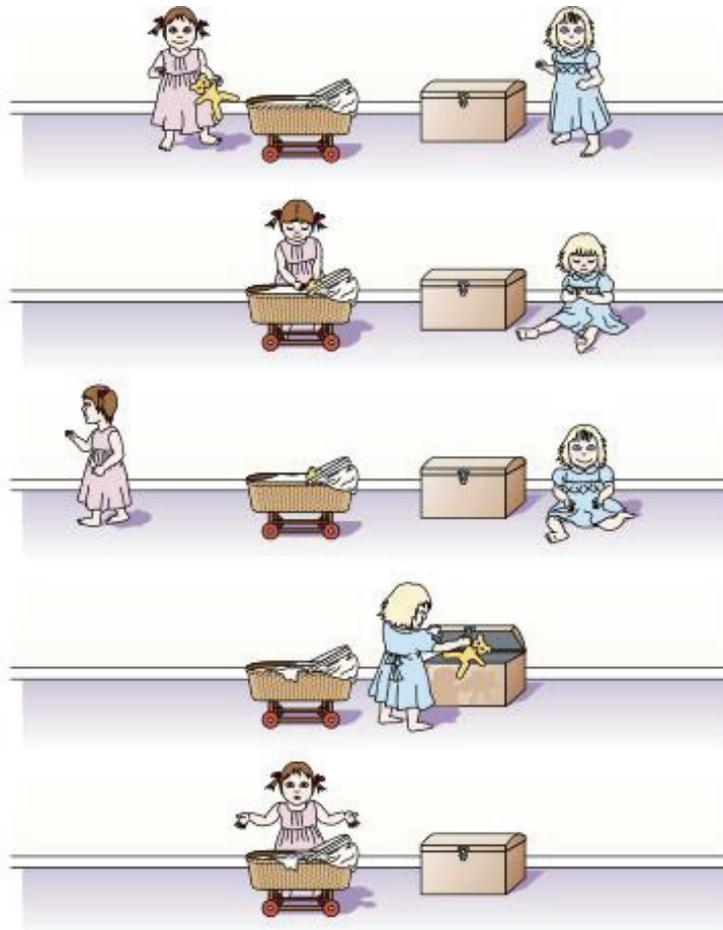
### ***1.2.1. The Theory of Minds***

The human brain is wired for taking others into account (V. K. Lee and Harris 2013; C. D. Frith and Singer 2008; Adolphs 2003). As such, nine-month old babies are able to learn new sounds, a new language, only if these sounds come from a real person and not from a tape or a video. In the same line, eighteen-month old infants perform imitation of humans, but not of robots (Blakemore, Winston, and Frith 2004).

More importantly, humans automatically assign animacy, action goals and intention to stimuli (Adolphs 2003). This ability is even engaged when reading stories, looking at cartoons or watching simple animation (C. D. Frith and Singer 2008; Blakemore, Winston, and Frith 2004). The cognitive ability to represent the intentions and thoughts of another is named Theory of Minds (ToM) or *mentalizing* (U. Frith and Frith 2001). The ToM has been the focus of extensive studies in social psychology and social cognitive neurosciences; it is a basis for social cognition (Preckel, Kanske, and Singer 2018).

A typical experiment for testing the emergence of such aptitude is the False Belief Task, in which we must recognize that people have differing sets of knowledge about a scenario depending on what they see (**Figure 6**). In this task, children are requested to watch a series of pictures, or a movie. Firstly, these depict a scene where a character (Sally) put an object in a given place (i.e. a pram) and leaves. Then, a second character (Ann) takes the object where Sally left it and changes its location. Finally, the child is asked where Sally will be looking for the object. The child knows the object was moved by Ann, he saw it happen. But if he can represent what Sally thinks (through ToM), not knowing that the object's place was changed, he will answer that she will look for it where she put it (in the pram). However, if the child does not perform ToM, he will answer that Sally will look where Ann put it afterward. Studies using this kind of paradigm showed that ToM appears between the age of four and seven (Van Overwalle 2009; Adolphs 2003).

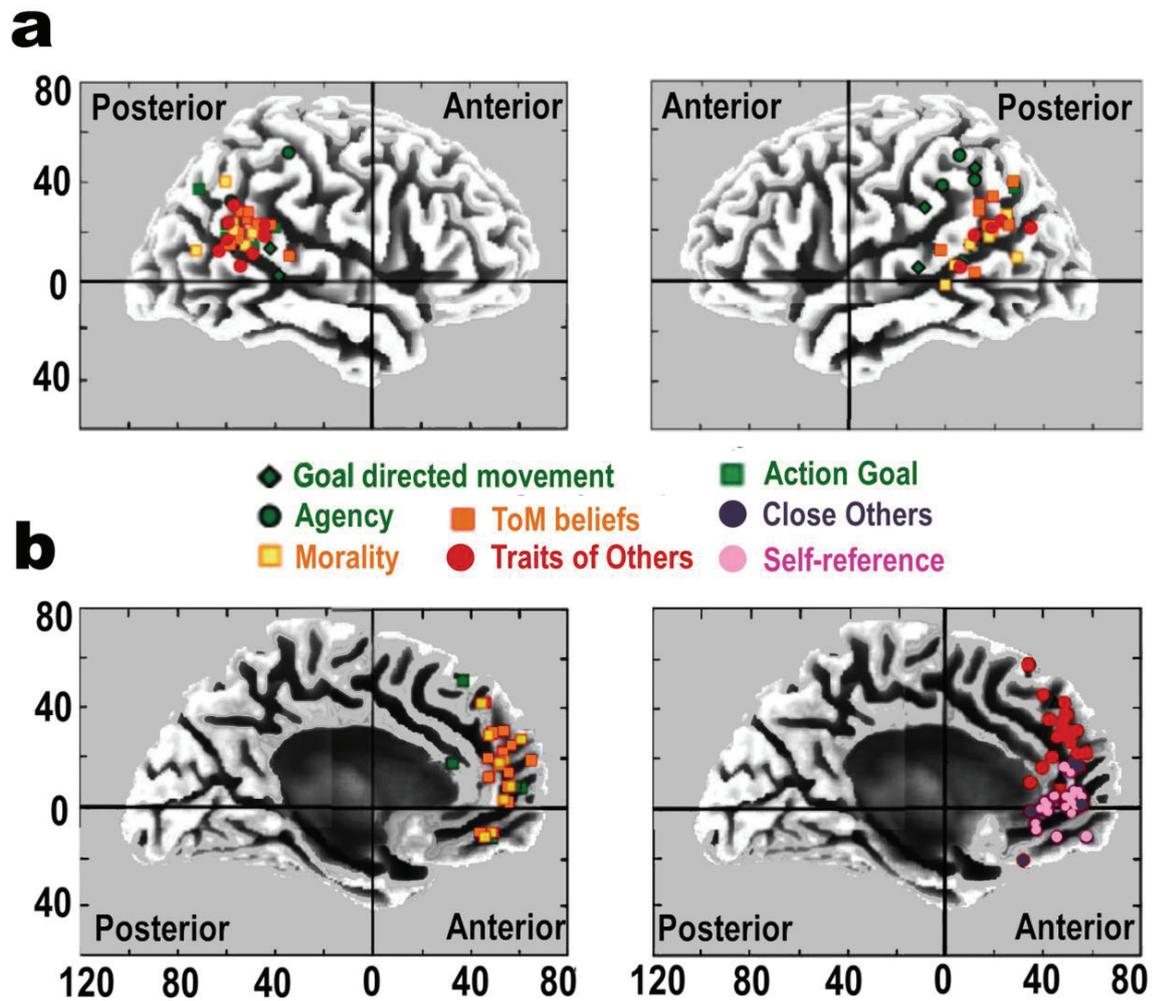
The use of fMRI showed that some brain regions were consistently activated during ToM paradigms (Preckel, Kanske, and Singer 2018; C. D. Frith and Frith 2012; Van Overwalle 2009; Amodio and Frith 2006; U. Frith and Frith 2001). Evidence suggests a neural ToM network involving the posterior superior parietal sulcus (pSTS), the temporo-parietal junction (TPJ), the medial prefrontal cortex (MPFC) and the temporal poles (**Figure 7**). A recent connectivity analysis, using Dynamic Causal Modeling on the data of 5 ToM studies, showed that the interplay between bilateral TPJ and their forward connection with the (ventral and dorsal) medial prefrontal cortex play a crucial role when forming impressions about other people (Van Overwalle, Van de Steen, and Mariën 2019).



**Figure 6. Schematic of the scenario used to assess Theory of Minds abilities in children (Sally-Anne task).** Sally has a pram and Anne has a box. Sally puts a toy into her pram, and then she goes out for a walk. While she is outside, Anne takes the toy from the pram and puts it into her own box. When Sally comes back, where will she look for the toy? Normal children of four years of age and older answer that Sally will look inside her pram, because that is where she (falsely) believes the toy is. Image from (Adolphs 2003).

When performing ToM, forming an impression about a person and attributing personality traits to others, the superior temporal sulcus (STS) is involved in the perception of visual motion, eyes and mouth movement and facial expression; processes partly mediated by mirror neurons – neurons that fire both when performing an action or feeling an emotion and when observing the same actions or emotions (Gallese, Keysers, and Rizzolatti 2004). Direct electric stimulation of the fibers connecting superior temporal gyrus and the dorsolateral prefrontal cortex in patients undergoing surgery confirmed the implication of this network in face-based mentalizing (Yordanova, Duffau, and Herbet 2017). This information is presumed to be integrated in the temporo-parietal junction (TPJ), further involved in the attribution of action goal and mental states, presumably in an automatic/implicit manner, at a relatively perceptual level. The VMPFC is engaged in ToM and in the integration of social information at a more abstract level, sustaining its representation to guide behavior (Van Overwalle 2009).

The different mentalizing brain processes sustaining ToM are presumably involved in a variety of disorders (Herold et al. 2015), such as the Autistic Spectrum Disorders (Rosenblau et al. 2015; Rice et al. 2015; Schuwerk et al. 2016) and Schizophrenia (Bliksted, Ubukata, and Koelkebeck 2016; Koelkebeck et al. 2018; Karpouzian et al. 2016; Booules-Katri et al. 2019), but also borderline personality (Van Heel et al. 2019; Duval et al. 2018) and eating disorders (Redondo and Luyten 2018). Numerous tests have been developed to study ToM and mentalizing at different orders of reasoning and whether each particular process involved in mentalizing is implicit or explicit, resulting from automatic cognitive processes or resulting from high-level reasoning (Brown et al. 2019; Turner and Felisberti 2017).



**Figure 7. Activation in the brain during mentalizing tasks. a)** Implication of the Temporo-Parietal junction and the posterior superior temporal sulcus. **b)** Involvement of the medial prefrontal cortex. The representation is placed in the stereotactic atlas. Ordinates represent the anatomical z-axis, abscises represent the y-axis; the x-axis is not shown. Adapted from (Van Overwalle 2009)

### ***1.2.2. The mere presence of others***

#### ***Eating a lot or eating alone***

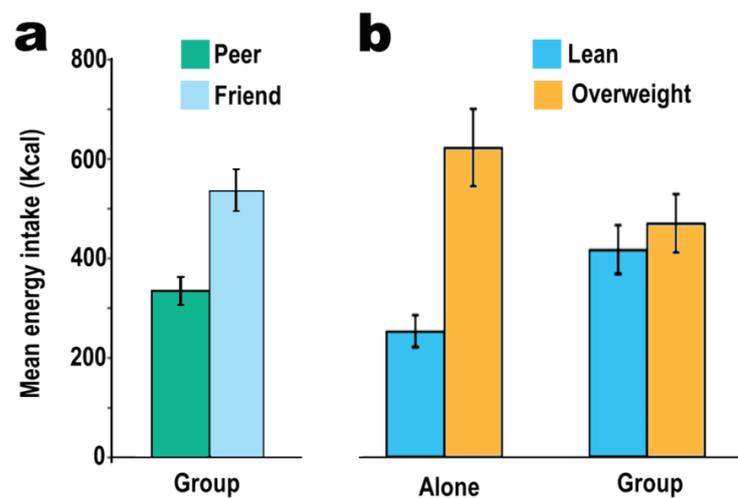
Considerable evidence shows that people have larger food intakes during meals with others than alone (Herman 2015; de Castro 1994; Clendenen, Herman, and Polivy 1994), linked to a longer time spent eating with others than eating alone (Pliner et al. 2006; Feunekes, de Graaf, and van Staveren 1995). People eat more when eating with other people, and eat more with a friend than with a stranger (Salvy et al. 2009; Hetherington et al. 2006) (**Figure 8**). This could be partly mediated by the distraction conveyed by others during the meal, as compared to watching T.V. or to listening to stories (Hetherington et al. 2006; Bellisle and Dalix 2001). All those effects are true in co-action, especially with friends, and when the other is also eating. But this is not true when eating under observation: with an audience, the food intake tends to dramatically diminish (Herman, Roth, and Polivy 2003).

Crucially, these effects are not true in overweight people<sup>3</sup>, who, on the contrary, eat more alone than with others, except if the others are also overweight (Salvy et al. 2007) (but see (Edelman et al. 1986)). This points-out the importance of impression management, the fact that we want to project a proper image of ourselves to others in behavior (Herman 2015; Vartanian,

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<sup>3</sup> As indicated by the Body Mass Index (BMI)

Herman, and Polivy 2007). The image we want others to have of us modifies such a primitive behavior as eating. Overweight people could fear to be blamed when eating in front of non-overweight others<sup>4</sup>. This could also explain why people eat more with friends than with strangers. When with friends, we let our guards down and feel free(r) to be ourselves. There is less, or no, fear of judgement.



**Figure 8. Co-eating and food intake. a)** Eating with a friend induces a larger food intake than eating with a (stranger) peer. **b)** Lean persons eat more in group than alone, while overweight person eat less in group than alone. Adapted from (Salvy et al. 2007; 2009).

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<sup>4</sup>The direction of this effect might only be true in the social context of our societies, where the social norm is to have a low BMI.

## ***Performance under observation***

The mere presence of others is by essence what makes our environment into a social one. The impact of the presence of others on performance, also called social facilitation, has been the focus of extensive research in the field of psychology, for at least one hundred and thirty years (further details in(Stroebe 2012)). This topic is merely divided in two types of presence: i) another one performing the same activity as the subject: 'co-action', and ii) another one observing the subject performing the activity: 'audience'.

Many studies investigated how the presence of others impacts task performance and brought controversial findings: audience and co-action can either improve or worsen performance (see the meta-analyses (Bond and Titus 1983; Uziel 2007)). The Drive Theory was suggested as an explanation of this effect depending on complexity. The theory advances that the presence of others amplifies arousal, which in turn induces the emission of a dominant response, the response with the stronger habit (Zajonc 1965). This dominant response would be erroneous in a non-learned – complex - task but would be correct in a well-learned – simple - task<sup>5</sup>.

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<sup>5</sup> Refinement of the Drive Theory were further provided, suggesting that the plausible threats represented by others, evaluation apprehension and self-awareness could be the causes for an elevation in arousal. Attentional distraction was also proposed as alternative explanation.

However the Drive Theory suffers from many caveats. For example, why would a dominant response in a non-learned task be automatically erroneous? And how could there even be a dominant response, a so-called response associated with strong habits, in a task that was never performed before? In addition, several studies measuring self-rated arousal, skin conductance, cardiac-frequency or cortisol levels failed to support the hypothesis that physiological arousal directly mediates the effects of an audience (Laughlin and Wong-McCarthy 1975; Rousseau and Standing 1995; Ukezono et al. 2015; Brennan and Enns 2015). The presence of a conspecific could even reduce stress (Davidson and Kelley 1973) and improve healing processes (Detillion et al. 2004).

Moreover, not all complex tasks see their achievement being impaired by an audience or co-action. Already in 1983, Charles Bond and Linda Titus denoted in their meta-analysis that performance was not worse in presence of others for about 40% of the complex tasks (Bond and Titus 1983). In this framework, complexity is often defined by the novelty of non-learned tasks. Comparing the results of two different tasks, trained tasks and novel tasks, is tedious. Dissimilar cognitive processes actually sustain *learning* a task and *performing* this task. A study precisely emphasized this dissimilarity between learning and performing and how these processes are distinctively affected by an audience and co-acting peers (Gagné and Zuckerman 1999). In order to account for the effect of the presence of others, experiments should thus involve a unique task in which the difficulty can be objectively manipulated.

Finally, social behavior in humans is highly tuned, with much inter-individual variability. Everyone is unique. A recent meta-analysis highlights the importance of personality traits (Uziel 2007). The results suggest that the effect of the presence of others on performance could be explained by the social orientation and personality traits. People with a positive social orientation or a high extraversion score would perform better in co-action/audience than alone, independently of the complexity of the task. In contrast, people with negative orientation or high neuroticism would get worse when observed than when alone.

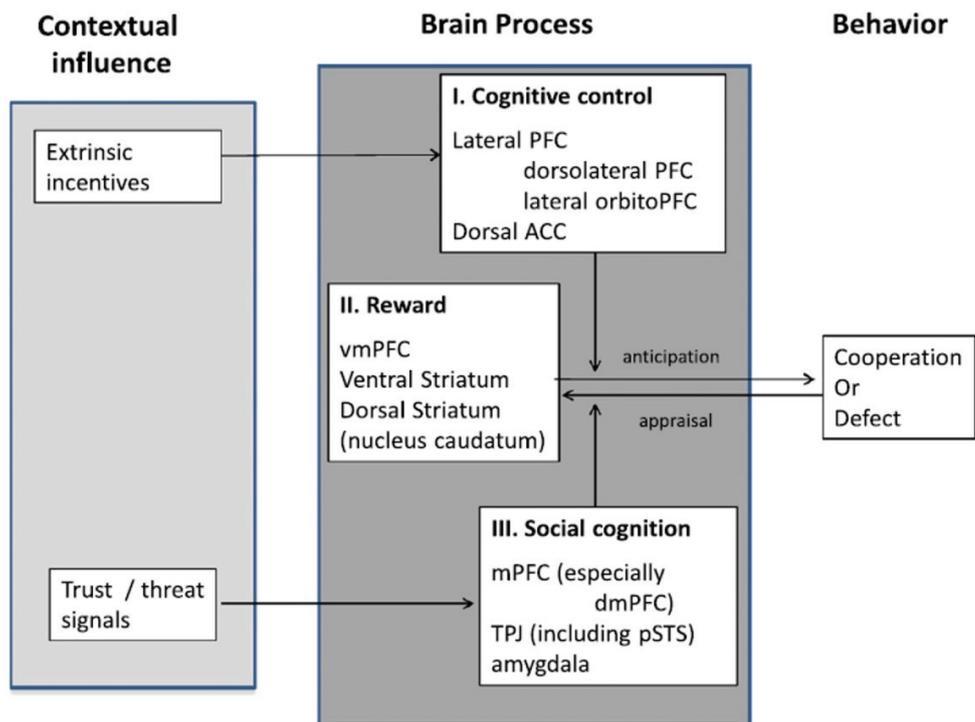
Further research should focus on decomposing the effects among task types (learning or performing goals, motor or cognitive tasks) and between cognitive tasks and analyze its interaction with personality traits for a better and complete understanding of the effect of the mere presence of others. Much work is needed to fully understand how the mere presence of others shapes individuals' behavior. The presence of others affects a wide range of behaviors, actions, tasks and decisions, even down to the basic activity of eating, and the mechanisms are still not clear today.

### ***1.2.3. Looking for the computational correlate of others***

Social cognition is very large and encompasses several mechanisms (**Figure 9**) among which: value-based decision making (to associate values with each possible choice), learning, cognitive control, trait inference and theory of minds (to predict how the other might behave). Public Good Games and their derivatives are elegant paradigms which provide great insight on how social cognition affects value-based decision-making. Although individuals value personal monetary payoff, they also experience prosociality, fairness, cooperation and gaining in reputation as a reward; through the same dopaminergic brain circuitry. It suggests that decision making is at least partially driven by preferences for prosociality in the human brain and reinforced in the reward learning system. However, Self- and Other- affecting payoffs are tied together during such money allocation tasks. Cooperating and being fair is also rewarding in terms of personal direct benefits (monetary or reputational). This helps to understand how humans decide to *share* (monetary) resources, but not how decisions impacting others well-being, and only theirs, are made. One alternative to study prosociality came from charity donation paradigms, where participants receive an initial endowment which they can decide to use in order to make a donation (Kwak, Pearson, and Huettel 2014; K. Izuma et al. 2011; Hare et al. 2010; Carter et al. 2009). In charity decision tasks, the decider is endowed and can choose to give part of this endowment to a charity at his own expense. It is a design elaborated to probe human's altruism. But, again, decisions directly affect the participant's own payoff. To decipher

how decisions are made when they concern only others' well-being, we should make self and other benefit separately.

A direct observation of the brain mechanism underlying ecological (naturalistic) social decisions is tricky with the existing non-invasive recording techniques in humans. Although very simple decisions do not appear to be the most interesting on their own, they could - through their simplicity - provide a way to observe and test how others are considered in decision making. This is why we decided to take advantage of the perceptual decision making framework and perceptual decision making paradigm in all of our experiments. It offers two main advantages: the underlying brain mechanisms are well-documented and computational models can be applied to estimate which stage of the decision process is modified.



**Figure 9. Theoretical framework identifying the neural networks recruited to solve social dilemmas.** ACC: anterior cingulate gyrus; PFC: prefrontal cortex; mPFC: medial prefrontal cortex. Figure from (Declerck, Boone, and Emonds 2013)

### ***1.3. Chapter 3: Perceptual Decision Making***

The perceptual decision making theory describes how information gathered from sensory systems is combined and used to influence how we behave in the world. The ability to flexibly translate sensory inputs into behavioral responses is fundamental. It requires the comparison and integration of sensory evidence to generate a behavioral response. Addressing this question has been termed perceptual decision making.

Typical experiments consist of judging differences in perceptual features of stimuli (H R Heekeren et al. 2004). The historical, and probably best known, experiment employs the random-dots-motion task, where subjects decide whether visually presented dots move either to the left or right. Although this task appears to be a severe reduction of the question of how the brain maps its continuous stream of high-dimensional sensory input to one of the many possible categories, it has provided a wealth of insightful findings about the neurobiological mechanisms underlying decision making (Glimcher 2003; Gold and Shadlen 2007a).

One key feature of the random-dots-motion task is that the stimuli are rendered extremely noisy. This high noise level makes the task difficult so that subjects have to sample the sensory input for hundreds of milliseconds before they can commit to a decision. This long observation period is motivated by the experimental aim to delay decisions, in order to differentiate the mechanisms of evaluating the sensory input and those of making a decision.

### ***1.3.1. Drift diffusion Models and the brain correlates of perceptual decision***

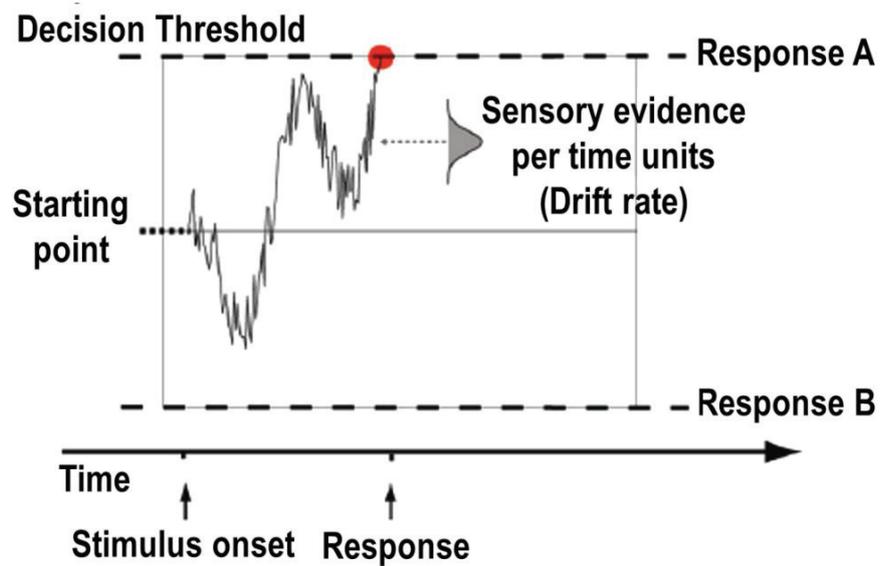
Perceptual decision making can be accounted for by Drift-Diffusion Models (DDM), a class of decision-making models that assume a stochastic accumulation of evidence over time (M. J. Mulder, van Maanen, and Forstmann 2014; Smith and Ratcliff 2004; Ratcliff and Rouder 1998). DDM comprise a large variety of similar models and were developed in psychophysics to uncover the cognitive processes underlying typical perceptual decision. They have been successfully applied on many behavioral data, i.e. reaction times and accuracy. Their area of applications has also included a wide range of other categorization and memory retrieval tasks (Voss, Nagler, and Lerche 2013) and is now extending to economical set ups (A. Harris, Clithero, and Hutcherson 2018; Philiastides and Ratcliff 2013; Summerfield and Tsetsos 2012).

DDM define a decision variable implemented through a continuous stochastic process, during the period of time during which a stimulus is presented (**Figure 10**). The underlying assumption is that the brain extracts, per time unit, a constant piece of evidence from the stimulus disturbed by noise. The accumulation process stops when one of the decision variables reaches a decision boundary for one of the alternatives at hand. The rate of the accumulation process is derived from the representation of the stimulus and is closely linked to information

quality. A better quality of evidence enables a more efficient evidence accumulation, represented by a larger drift rate, and a faster and more accurate response. The noise in the evidence and the variability in the path followed by the decision variable results in decisions that terminate at different times (producing Reaction-Time distributions) and sometimes at the wrong boundary (producing errors). The components of processing outside the decision process, such as primary sensory encoding and motor response output, are combined in the model in a single parameter: the non-decision time.

### Box 1. Drift Diffusion Models

The drift diffusion model (DDM) assumes that two-choice decisions are made by a noisy process that accumulates information over time from a starting point ( $z$ ) toward one of two choice criteria or boundaries (here, corresponding to left and right response decision, respectively). When one of the boundaries is reached, a response is initiated (**Figure 10**). The starting point ( $z$ ) and the decision boundaries are separated by distance ( $a$ ). The evidence that drives the accumulation process, the drift rate ( $v$ ), is derived from the representation of the stimulus. The better the quality of the evidence, the higher the drift rate toward the appropriate decision boundary, and the faster and more accurate the response. The components of processing acting outside the decision process itself, such as encoding and response output, are combined in a single parameter: the non-decision parameter ( $T_{er}$ ). Across-trial variability in drift rate is assumed to be normally distributed with standard deviation  $\eta$ . Across-trial variability in the starting point (equivalent to across-trial variability in the boundary positions) is assumed to be uniformly distributed with range  $s_z$ , and across-trial variability in the non-decision component is assumed to be uniformly distributed with range  $s_t$ .



**Figure 10. Schematic representation of the drift-diffusion model.** The model assumes that two-choice decisions are based on the accumulation of noisy evidence over time. The process has a starting point and ends at a decision threshold. Drift rate represents the amount of evidence accumulated per time unit. Figure from (Martijn J. Mulder et al. 2012)

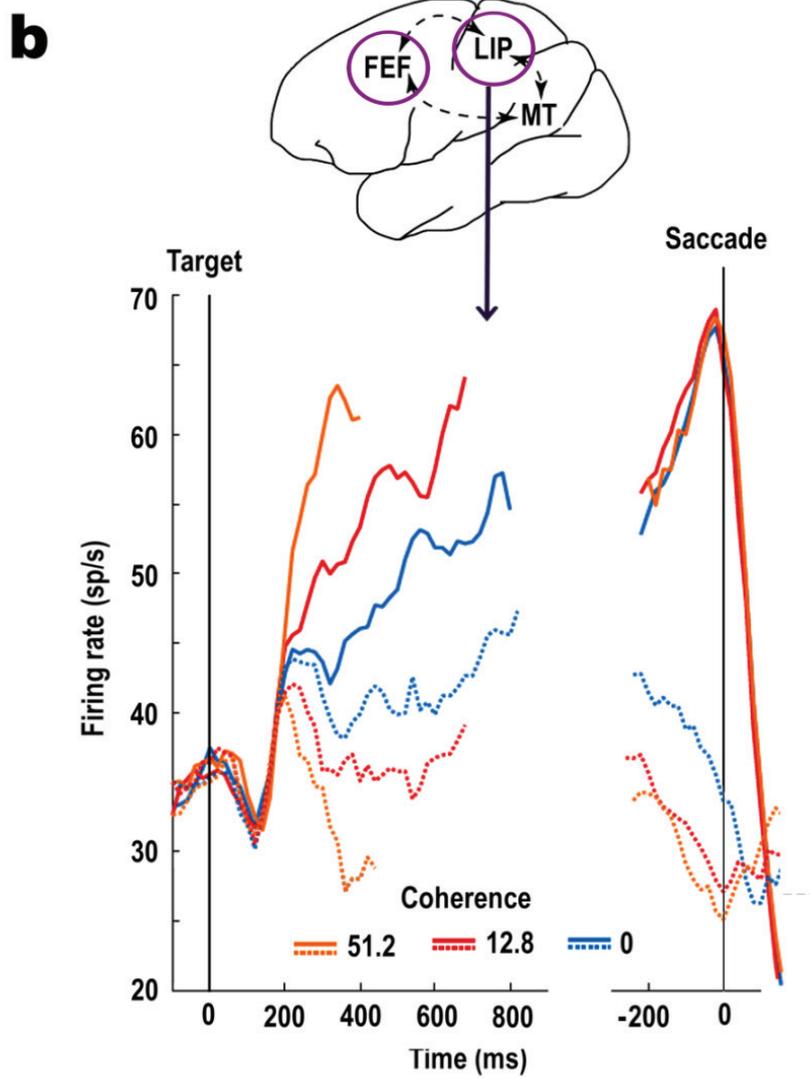
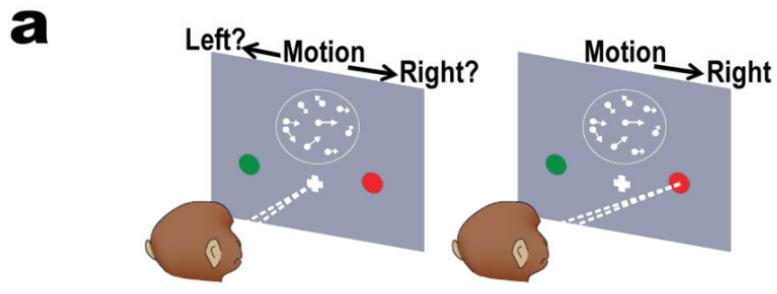
### ***1.3.2. Cerebral correlates of perceptual decision making***

Led by the DDM, researchers found neural correlates of the decision parameters. The experiments were firstly performed on non-human primates, using the motion-dots paradigm. Monkeys had to look at the dots stimuli and give, with a saccade, their decision about their direction (**Figure 11a**). While the task was performed by the animals, neural activity was recorded inside of different brain areas. The researchers were able to find activity that exhibited crucial features of the mean trajectories of perceptual decision making as described by the DDM.

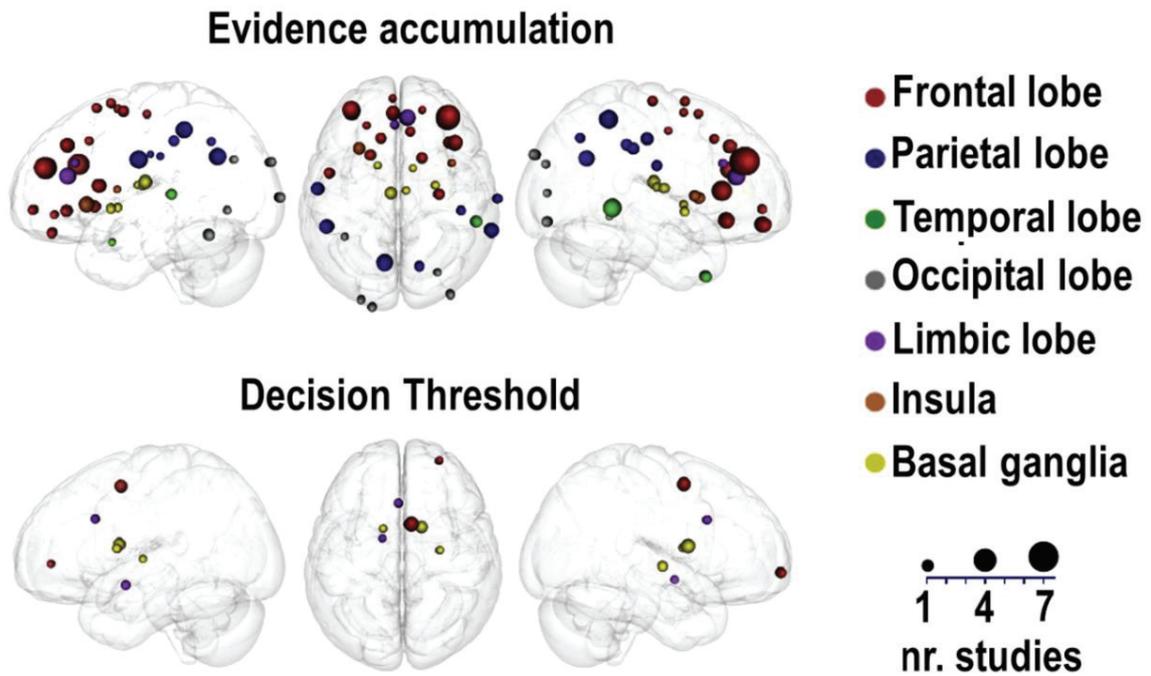
They found brain areas where neuronal activity closely related to evidence integration through time, at a rate depending on the availability of sensory evidence (**Figure 11b**). This activity peaked and stopped at the moment of the saccade execution, the decision being made when the signal reaches the decision boundary (Gold and Shadlen 2007a). As such, the neuronal activity in the lateral intraparietal cortex (LIP) and in the dorsolateral prefrontal cortex (dlPFC) were found to represent the accumulation of noisy sensory evidences over time. Even more interesting, the level of activity at which the saccade was executed always was the same, whatever the quality of evidence.(Gold and Shadlen 2007a; Huk and Shadlen 2005).

However, such direct invasive recordings are not possible in humans and the research for similar neural correlates of the DDM parameters in humans was first carried with fMRI. The studies confirmed the implication of a similar fronto-parietal network in human perceptual decision making (**Figure 12**). The timing of the decisions (the reaction-times) could be predicted with the blood oxygenation level dependent (BOLD) signal recorded in this fronto-parietal network (Domenech and Dreher 2010; Hauke R. Heekeren, Marrett, and Ungerleider 2008; H R Heekeren et al. 2004). The principles identified in single-unit recording studies in non-human primates thus seem to hold for the human brain. The representation of sensory evidence occurs in lower-level sensory regions of the human brain, accumulation and further comparison of sensory evidence for decision commitment occurs in regions related to higher-levels of cognition, such as the prefrontal cortex.

Nonetheless, functional MRI studies in humans suffer from one major caveat: temporal precision. fMRI results are based on the use of the mean of the BOLD signal, taken over a quite large time window (generally six or eight seconds) and make sub-components of the decision making process indistinguishable. Many parts of the perceptual decision making processes are confounded with each other in a large time-window and escape the eye of the researcher. The search for precise neural correlates of the DDM decision parameters in humans requires the temporal precision of electrophysiological techniques. Temporal precision is a crucial aspect in the decomposition of the different processes involved. Perceptual decisions are fast; otherwise they would lack sufficient efficiency to be useful.



**Figure 11. Perceptual decision making in non-human primates. a)** Random dots task. The animal is facing a screen where dots in motion appear. He has to decide if the dots move to the left or to the right direction. When the decision is taken, the animal makes an eye saccade toward that direction. **b)** Neural activity related to decision making. Patterns of neural firing that predict the time-course of behavioral decisions have been recorded in the frontal eye field (FEF) and the lateral intra-parietal area (LIP). As coherence strength in dot motion (target) increases, the firing rate increases as well. The decision (saccade) occurs when the neural activity reaches a threshold, this threshold being the same for all coherence strengths. Graph ordinate represents the firing rate in spike per second (sp/s); abscise represents the time, expressed in milliseconds (ms). MT: middle temporal. Adapted from (Hauke R. Heekeren, Marrett, and Ungerleider 2008; Gold and Shadlen 2007a; Smith and Ratcliff 2004)

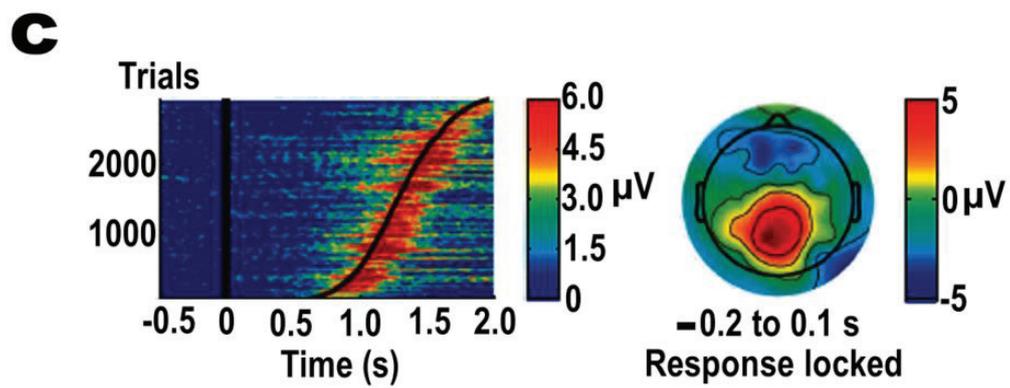
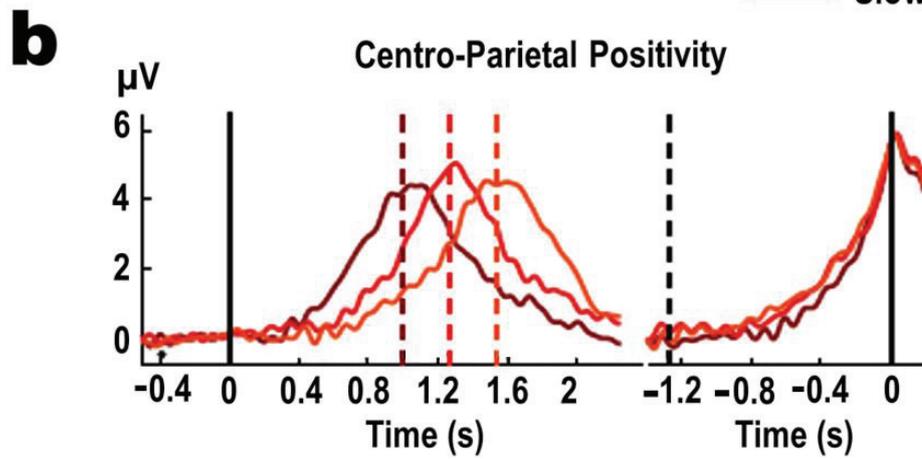
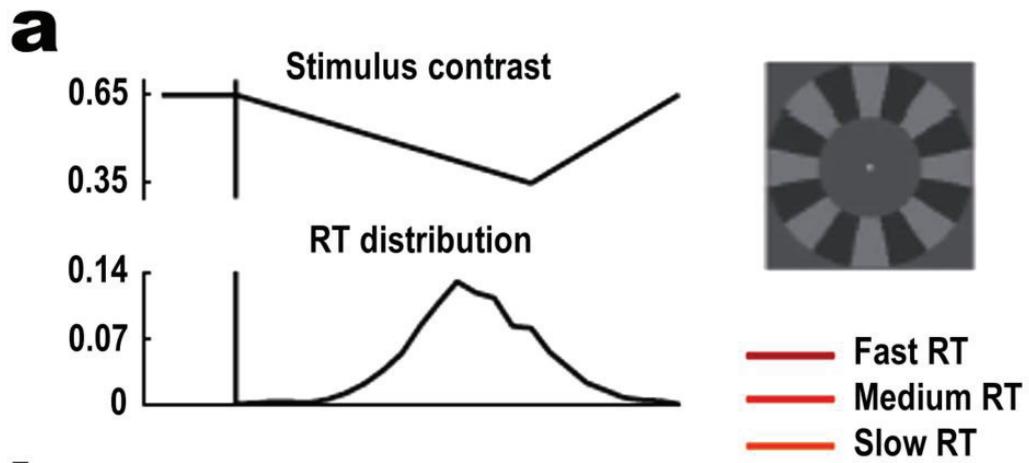


**Figure 12.** 3D renderings of the peak-coordinates reported by studies that include drift diffusion model parameters in fMRI analysis, in humans. Seven studies are included for evidence accumulation, two studies are included for decision threshold. Figure from (M. J. Mulder, van Maanen, and Forstmann 2014)

### ***1.3.2. The Centro-Parietal Positivity***

Simon Kelly and Redmond O’Connell were the first to find event-related potentials could be related to neural signatures of perceptual decision making such as described by the DDM. They revealed ramp-like activity resembling the one found in LIP and FEF in non-human primates, producing similar results (O’Connell, Dockree, and Kelly 2012). They asked the participants to look at a visual target of which the contrast was gradually changing over time (**Figure 13a**). They had to press a button as soon as they perceived this change. By simply averaging the single trial activity elicited by the targets stimuli (start of the contrast change), they show that perceptual decision making in the human brain is related to a ramp-like evoked-potential, emerging from the centro-parietal areas of the brain, and peaking just before reaction-times (RT). The author researchers called it the centro-parietal positivity (CPP – **Figure 13b,c**).

This was a pioneer study in the investigation of electrophysiological build-up activity as described in the DDM in the human brain. Most of all, their study involved several experiments with clever designs, showing that the CPP was present for both auditory and visual decisions and when a response was required, or not. They further showed that the rise of the CPP depended on motion coherence (Kelly and O’Connell 2013). Altogether, this pinpoints the CPP as candidate for a multimodal representation of the decision-variable in human brain.



**Figure 13. Sensory evidence and decision signals observed in the human brain.** **a)** Target contrast reduction time course and grand-average reaction time (RT) distribution. **b)** Trials were sorted by reaction time and divided into three equal-sized bins. The centro-parietal positivity (CPP) is a neural signal undergoing gradual changes on the timescale of the physical contrast change, aligned with the stimulus onset (left) and the response (right). Vertical dashed lines denote mean reaction time. **c)** Left: Single-trial surface plots showing the temporal relationship between the CPP and target detection latency (curved black line). Single-trial signals were pooled across participants, sorted by reaction time and smoothed over bins of 50 trials. The latency of action execution was closely tied to that of the CPP. Right: CPP scalp topographies. Color bars represent amplitudes. Figure from (O’Connell, Dockree, and Kelly 2012).

## ***Part 2: Experiments***

## ***2.1. Audience experiment: Being under observation modifies the drift rate of the decision variable.***

The mere presence of other people is what makes our environment into a social one. When there is a potential observer (an audience) our behavior is modified. In charity donation tasks, the presence an audience enhances the size of donations made as compared to when donations are made in secret (Keise Izuma 2012; Keise Izuma and Adolphs 2013). However, behavior is not only modified during prosocial decisions with an audience. Instead, a wide variety of sensory-motor paradigms see performance being improved, or worsened, by the presence of an audience (reviews and meta-analyses in(Bond and Titus 1983; Uziel 2007). How the presence of an audience influences human behavior has been an important question in the field of psychology for at least one-hundred-and-thirty years (see(Stroebe 2012).

The leading theory was that an audience induces an increase of arousal (general brain activation, here assumed to be related to the stress). An increase in general arousal would in turn increase the frequency with the stronger habit, thereby producing correct responses in easy tasks and incorrect responses in difficult tasks (Zajonc 1965). Yet, a meta-analysis of 241 studies showed that, for 40% of the difficult tasks, performance was actually not worsened by the presence of others (Bond and Titus 1983). Moreover, physiological measures of arousal failed to be linked with the presence of an audience (Brennan and Enns 2015; Ukezone et al.

2015; Rousseau and Standing 1995; Laughlin and Wong-McCarthy 1975). The presence of a conspecific could even reduce stress (Davidson and Kelley 1973) and improve healing processes (Detillion et al. 2004). Thus, to date, there is no clear answer to the reasons why performance is improved or worsened in the presence of an audience.

To provide a mechanistic explanation of the audience effect on decision-making, we took advantage of the Drift Diffusion Models (DDM). In the last decades, the framework of sequential-sampling models, such as DDM, has proven to be a powerful approach to explain the process of decision making (Forstmann, Ratcliff, and Wagenmakers 2016; Leite and Ratcliff 2010; Ratcliff and McKoon 2008; Ratcliff et al. 2016; Smith and Ratcliff 2004; Summerfield and Tsetsos 2012; Vandekerckhove and Tuerlinckx 2007). DDM successfully capture the complex relationship between choice and reaction-times (RTs) by decomposing these behavioral data into internal cognitive components of decision processing. In this framework, a decision reflects a decision variable drifting with a given rate ( $v$ ), from an intermediate starting point ( $z$ ) towards one of the decision boundaries at hands. Each boundary is separated from the starting point ( $z$ ) of a given distance ( $a$ ) and acts as a decision threshold for an option; so that the response of a decision is initiated when the decision variable reaches one of the boundaries.

Sensory encoding of information basically relies on the quality of the available evidence (Ratcliff and McKoon 2008). Reliability of the decision depends on the distance between the starting point of the decision variable and the decision boundary; decision rules set by the read-out mechanisms (Forstmann, Ratcliff, and Wagenmakers 2016; Martijn J. Mulder and Maanen

2013; Oppenheimer and Kelso 2015; Summerfield and Tsetsos 2012). Reaching higher decision boundaries requires more evidence to be accumulated, thus leading to a better accuracy, but takes a longer time.

We asked participants to perform a perceptual dots-motion task, under observation (audience) and when not observed (secret). We used the DDM parameter to test if observation interacts with difficulty, thereby affecting the drift rate of the decision variable. This would suggest that the presence of an audience is integrated together with the evidence for the choice alternatives into a single source of evidence during the accumulation process. Alternatively the audience effect could be independent from difficulty, affecting the decision boundary or the non-decision time of the decision making process. Changes in the distance between the starting point and the decision boundary would suggest that individuals integrate the audience through the read-out mechanisms, setting and changing the decision rules, prior to starting the evidence integration and the decision process in itself.

Finally, inter-individual variability could be a crucial aspect, often disregarded, in this particular experimental field of psychology. Three personality traits, Self-esteem, Neuroticism and Extraversion, were suggested to explain that performances can either improve through 'positive assurance' (high Self-esteem and high Extraversion) or worsen because of a 'negative apprehension' (low Self-esteem and high Neuroticism) (meta-analysis in (Uziel 2007)). We thus measured participants' personality traits (Neuroticism and Extraversion, especially) and

assessed their correlation with the variations in performance between observed (audience) and non-observed (secret) task execution.

### ***2.1.1. Material and methods***

#### ***Subjects***

21 volunteers recruited by advertisement in the Lyon 1 Claude Bernard University students' mailing list participated in the study. All subjects gave written informed consent and received twenty euros for their participation and were screened using self-report to exclude any psychiatric or neurological history, current or previous substance abuse. The study was approved by the local ethics committee (Comité de Protection des Personnes Sud-Est III). One subject was excluded subsequently to a technical problem, leaving 20 subjects (age:  $21.2 \pm 2.5$ ; 9 women) for further analysis.

#### ***Stimuli***

The percentage of coherently moving dots was set at 8% for the difficult level and at 16% for the easy level. The participants were not told of the two difficulty levels. Random dots

kinematograms (RDKs) were programmed using the Matlab® Psychtoolbox (<http://psychtoolbox.org/>) (Brainard 1997; Pelli 1997). The mask stimulus was a drifting random dot display of 2000 ms duration. Dots were white on a black background, with each frame composed of 50 white Gaussian blobs with a diameter of 2.85 mm. The stationary dots began to move with a speed of  $2.7^\circ/s$  from their original locations and each dots had a life-duration of 500ms. The motion of the dots was made by replotting dots corresponding to the previous ones at a determined spatial offset in the same direction so that all the dots moved in their directions at the same speed. During the experiment, RDKs appeared in a square centered on the screen (Dell, 19", screen resolution set to 1280x1050, vertical refresh rate of 60 Hz.), taking 30.8% of the screen, with participants at a distance of 60 cm.

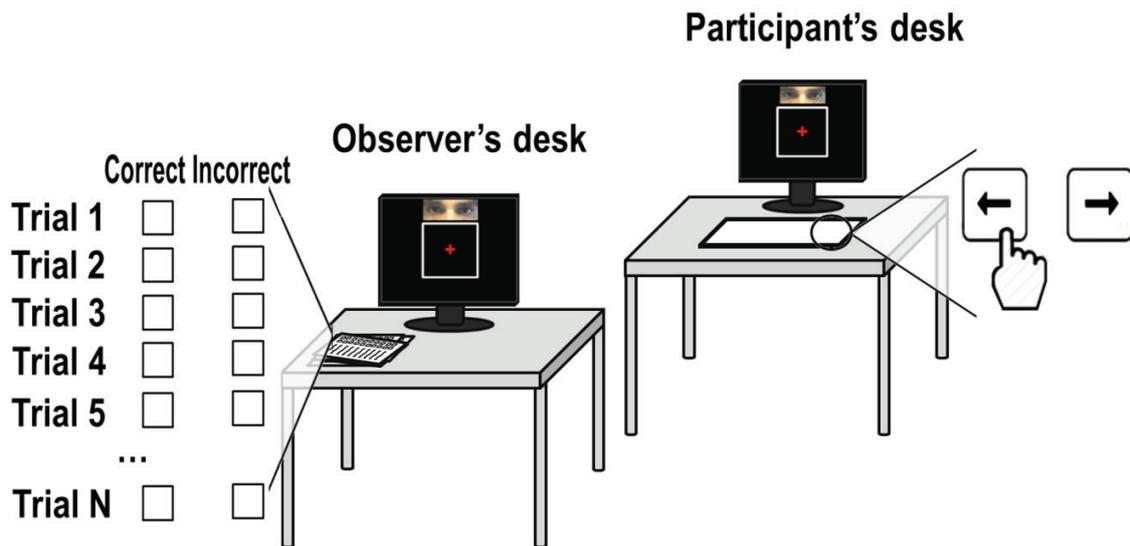
### ***Set-up***

In the experimental room, the desks were set up diagonally facing the same direction, with the observer's desk behind that of the participant's desk, allowing the observer too see the participant's computer screen (**Figure 14**). Once the participant had been welcomed and the consent form signed, the participant was asked to read the instructions, which were then explained again orally. Especially, participants were explained that both screens displayed the same images, so that the observer would see exactly the same thing as them; but an auditory feedback, which the observer could not hear, would also be given through headphones. The participant then performed the training, the Anticipated-Response Criterion (ARC) measure task and finally the task *per se* (four blocks of sixteen minutes each). At the end of the experiment

the ARC measure was taken a second time. Also, to control for possible confounding impact for filling in the personality inventories on task performances, forms were filled before the tasks for half of the participants and after for the other half.

### ***Conditions***

The cue on top of the square indicated the observation condition; it displayed either a picture of two eyes, during the audience condition, or two padlock drawings, during the secret condition. It remained on the screen during the entire trial, switching from eyes (audience) to padlocks (secret) every thirteen trials. The observation condition changed the information available to the observer. In the audience condition, the fixation cross became green for correct responses or red for errors, misses and when more than one response-button was pressed. In this way, the observer was aware of response accuracy. In addition, the experimenter acted as if he noted accuracy for each observed trials on a sheet of paper. However, in the secret condition, the fixation cross always became yellow during feedback and the observer could not know if the participant gave a correct response or not. For the participants to still have a feedback even during secret trials, an audio feedback was also given through headphones in both conditions (audience and secret). Conditions also depended on difficulty, (easy: 16% of dots coherence vs. difficult: 8% of coherence), leading to a two by two factorial design: Observation (audience vs secret) x Difficulty (Easy - 16% of dots coherence- vs. Difficult - 8% -).

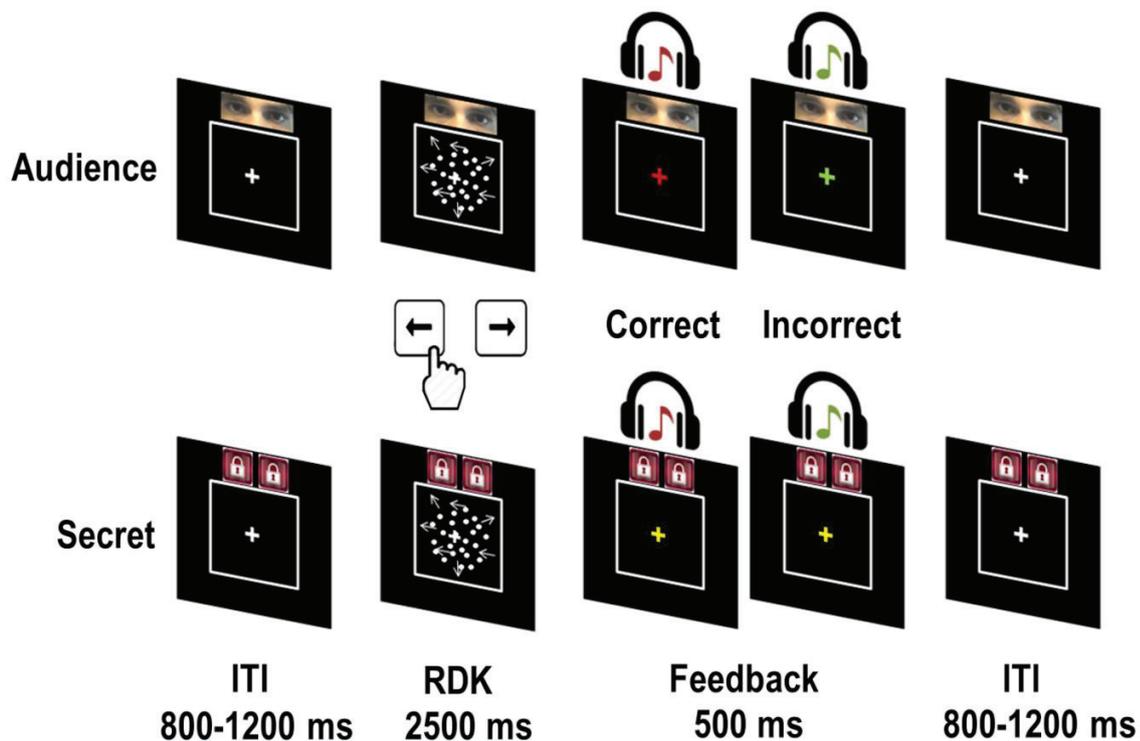


**Figure 14. Set up.** Two desks were installed, both with screens displaying the task. On the participant's desk, there was a keyboard for the participant to respond to the stimuli by pressing the left/right arrow. The observer sat at the other desk, behind the participant, (supposedly) recording participant accuracy during the audience trials.

### ***Trial design (Figure 15)***

A white square and a fixation cross, both centered on the screen, were displayed during the entire task. Each trial began with the cue for a jittered duration of 800-1200ms, used as Inter-trial-interval (ITI). The cue indicated the observation condition, using a picture of two eyes during the audience condition and a drawing of two padlocks during the secret condition. Then, the Random Dots Kinematogram (RDK) was played inside the square, and the participants had to answer about the direction of the coherently moving dots during its presentation (2500ms).

At the end of the RDK, the feedback was shown for 500 ms. The auditory feedback consisted in a positive noise for correct responses and a negative noise for incorrect responses. In addition, during the audience condition, the fixation cross became green for correct responses and red for incorrect responses. During the secret condition, the fixation cross always became yellow. After the feedback, the next trial started (ITI). The task was decomposed into 4 blocks of 144 trials each. 12 consecutive trials (mini-blocks) of the same observation condition (audience or secret) were alternatively presented. An equal number of 6 trials of easy and difficult task levels were presented within each mini-block of observation (audience vs. secret) condition in a randomized order.



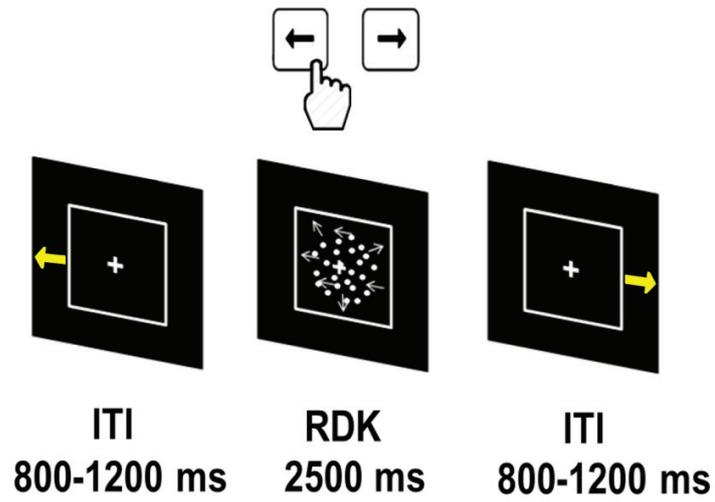
**Figure 15. Trial design.** Each trial began with the cue (used as Inter-trial-interval -ITI-), displaying the fixation cross, the square and the observation condition, for a jittered duration of 800-1200ms. The observation condition was indicated either with a picture of two eyes (audience), or two padlocks (secret). Then, the random dots kinematograms (RDK) were played inside the square for 2500 ms, and the participants had to indicate the dots' direction of motion during its presentation using the left/right arrows on the keyboard. At the end of the stimulus, the visual feedback was displayed for 500ms. In the audience condition, the fixation cross became green for correct responses, red for errors and for misses. In the secret condition, the fixation cross always became yellow. An audio feedback was also given through headphones in all conditions (audience and secret). Then, the next trial started.

## ***Training***

The training was composed of trials that were the same as those encountered in the task. 12 of such trials were performed (6 audience trials and 6 secret trials, within which there were 3 trials at 8% of dots coherence (difficult level) and 3 trials at 16% (easy level)). If the participant did not feel comfortable enough with the task, or if his accuracy was below 60%, a second training was performed.

## ***Anticipated Response Criterion (ARC) Measure***

The Anticipated Response Criterion (ARC) is the reaction-time (RT) needed by the participants to press a button as fast as possible. Any response shorter than this ARC during the task is an anticipated response. The trial design of the ARC measure was similar to the task, except that neither eyes nor padlocks were displayed (**Figure 16**). Also, additionally, an arrow indicated the button to press (left or the right) during the inter-trial interval (i.e. before the dots appeared). This arrow was displayed on the corresponding (left/right) side of the square. The instruction was to press the corresponding response button as soon as the moving dots appeared, without paying attention to the dots. The participants were firstly trained on 3 trials for this measure to understand its principle. 10 trials were then executed for each of the two ARC measures.



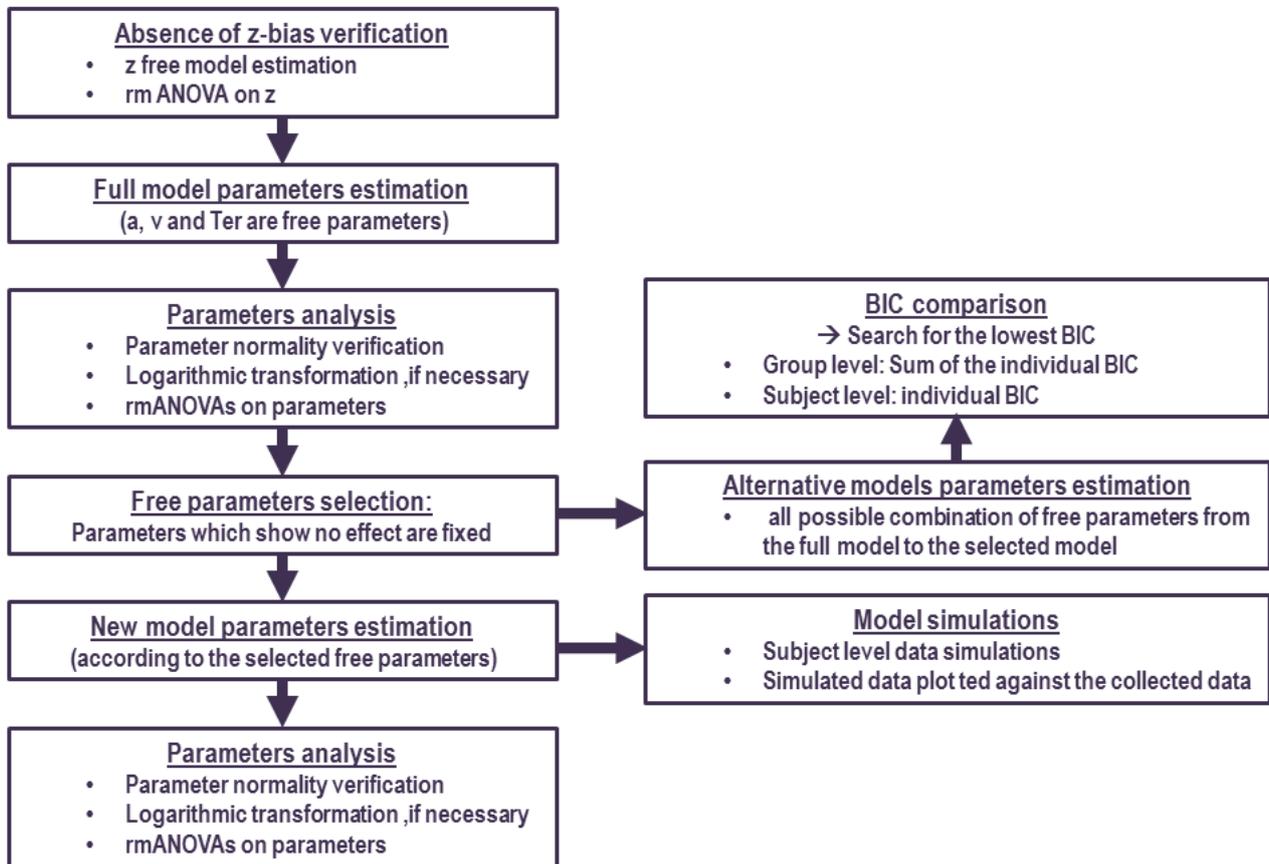
**Figure 16. Anticipated Response Criterion design.** During the Inter-Trial-Interval (ITI), a yellow arrow indicated the button to press (left or right). The subjects were instructed to press this button as fast as possible when the Random-Dots Kinematogram (RDK) appeared. Then, a new trial began by an ITI.

## *Drift diffusion models(cf Box 1)*

### ***Box 2. Fitting the drift diffusion models to the data***

For fitting the DDM, we used the MATLAB® DMAT: Diffusion Model Analysis Toolbox (Vandekerckhove and Tuerlinckx 2008). The DMAT extracts the components of the decision process and their variability from RT distribution and sensitivity data from all trials for each condition. RTs being the result of non-decision time added to the time it takes for accumulated evidence to reach one of the boundaries, and sensitivity coming from the reached boundary that determines which response is given, the model extracts the components of the decision process (values of drift rate, non-decision processes, and boundaries) from RTs distribution and sensitivity data simultaneously. All trials, corrects and errors were included in the DMAT parameter estimation. Parameters were estimated by maximizing a multinomial likelihood function. Each model was fitted to the data separately for each participant.

The same general procedure was followed for all DDM analysis (**Figure 17**). Left and right trials being equally distributed across the experiment (50% of trials for each direction, within each block), the underlying diffusion processes are supposed to be symmetric and no bias toward the left or right answer should arise. To ensure that no bias emerged toward either the left or the right response we ran a model where the starting point ( $z$ ) was estimated independently from the decision boundary for the left and the right button-presses separately. Then, the first model we ran allowed all three parameters to vary (the boundary –  $a$  -, the drift -  $v$  - and the non-decision time –  $T_{er}$  -). After statistical analysis, the parameters which did not show any effect of the tested factors were fixed in the next DDM fitting. In order to compare the goodness of fit of our models we also ran the intermediate models and compared the sum of the individual Bayesian Information Criterion (BIC) of the models. Once the best model was found, we analyzed the influence of the experimental factors on the remaining varying parameters.



**Figure 17. General pipeline for model selection and verification.** z: starting point of the decision variable; a: decision boundary; v: drift rate of the decision variable; Ter: non decision-time. rmANOVAs: repeated measures analysis of variance. BIC: Bayesian Information Criteria

### ***Statistical analysis***

Trials with Reaction-Times inferior to the ARC were excluded from behavior statistical analysis. Reaction-Times (RT) were log transformed for distribution normalization. Log RT for corrects and log RT for errors were analyzed separately using 2 way repeated-measures analysis of variances (rmANOVAs), the two factors being observation (secret vs. audience) and difficulty (easy vs. difficult). *Post-hoc* analyses were performed with LSD Fisher tests. Except for the normality tests, which were performed with Matlab; all statistical analyses were performed using Statistica (STATISTICA®, Dell Inc. 2015)

### ***Personality inventories and correlation tests***

We measured Extraversion and Neuroticism (Uziel 2007), to test their relationships with the audience effect, using the French version of Big-Five Inventory (BFI-FR; John et al. 1990; Plaisant, 2008), which measures five traits: (E) *Extraversion/ Energy/ Enthusiasm*, (A) *Agreeableness/ Altruism/ Affection*, (C) *Conscientiousness/ Constraint/ Control of impulse*, (N) *Neuroticism/ Negative affectivity/ Nervousness* and (O) *Openness/ Originality/ Open-mindedness*. We added the Interpersonal Reactivity Index (IRI), which relates to four social behaviors (Davis, 1980): Perspective Taking (tendency to spontaneously adopt the psychological point of view of others), Fantasy (tendency to transpose themselves imaginatively into the feelings and actions of fictitious characters in books movies and plays), Empathic Concern

(other-oriented feelings of sympathy and concern for unfortunate others) and Personal Distress (self-oriented feelings of personal anxiety and unease in tense interpersonal settings). We tested the relationship between personality scores and the difference induced by observation in sensitivity ( $d'_{\text{audience}} - d'_{\text{secret}}$ ) and in reaction-times ( $RT_{\text{Audience}} - RT_{\text{Secret}}$ ), using Pearson correlation tests.

### ***2.1.2. Results***

#### ***Reaction-times***

The analyses were performed on log-transformed reaction-times. For intelligibility, the mean values given are non-transformed RT expressed in milliseconds (ms). Reaction-times from errors (RTE) showed a main effect of observation, RTE being slower in audience than in secret ( $RTE_{\text{Audience}} = 1429$  ms;  $RTE_{\text{Secret}} = 1361$  ms;  $F_{1,19} = 6.29$ ;  $p = 0.0213$ ; Cohen's  $d = 0.34$ ). Difficulty had no effect on RTE ( $RTE_{\text{Difficult}} = 1411$  ms;  $RTE_{\text{Easy}} = 1378$  ms.;  $F_{1,20} = 1.36$ ;  $p = 0.258$ )

Concerning RT from correct trials (RTc), the analysis revealed a main effect of difficulty and a main effect of observation, RTs being slower during Difficult than during Easy trials

( $RT_{\text{Difficult}} = 1321$  ms;  $RT_{\text{Easy}} = 1132$  ms.;  $F_{1,20} = 135.3$ ;  $p < 0.000001$ ) and slower in Audience than in Secret ( $RT_{\text{Audience}} = 1238$  ms.;  $RT_{\text{Secret}} = 1216$  ms;  $F_{1,20} = 7.55$ ;  $p = 0.0124$ ; **Figure 18a**)

### ***Sensitivity***

There was a main effect of difficulty on sensitivity ( $d'$ ),  $d'$  being better during Easy than during Difficult trials ( $d'_{\text{Easy}} = 0.86$  a.u.;  $d'_{\text{Difficult}} = 0.70$  a.u.;  $F_{1,20} = 146.6$ ;  $p < 0.000001$ ). The observation\*difficulty interaction reached significance ( $F_{1,20} = 7.84$ ;  $p = 0.0110$ ). *Post-hoc* tests revealed that observation had no effect on sensitivity during easy trials ( $d'_{\text{Audience}} = 0.86$  a.u.;  $d'_{\text{Secret}} = 0.86$  a.u.;  $p = 0.91$ ). However, during difficult trials,  $d'$  was better in Audience than in Secret ( $d'_{\text{Audience}} = 0.72$  a.u.;  $d'_{\text{Secret}} = 0.68$  a.u.;  $p = 0.00101$ ; **Figure 18b**)

### ***Drift Diffusion Models***

We started with the selection of the best fitting model. We first checked that ( $z$ ) was not different between left and right responses using a one way rmANOVA with response direction as factor. The analyses showed no effect of response direction ( $F_{1,37} = 0.027$ ;  $p = 0.871$ ), ensuring that no bias emerged toward either the left or the right response. Consequently, we applied in

all our models a starting point equal to half the distance between the left and right decision criteria ( $z = \frac{1}{2} a$ ). Each model was fitted to the data separately for each participant.

The first model we ran allowed all three parameters (the boundary –  $a$  -, the drift -  $v$  - and the non-decision time –  $Ter$  -) to vary. The estimated parameter values did not follow a normal distribution, we thus used a decimal logarithmic transformation ( $\log(v)$ ) and ensured it normalized their distribution using Lilliefors tests before we applied the 2-ways rMANOVA. The 2 factors were Observation and Difficulty. In this model ('full model'), neither the boundary ( $a$ ) nor the non-decision time ( $Ter$ ) showed an effect of either of the two factors (Observation and Difficulty). We thus applied a model in which only the drift ( $v$ ) was free to vary across conditions (' $v$  free').

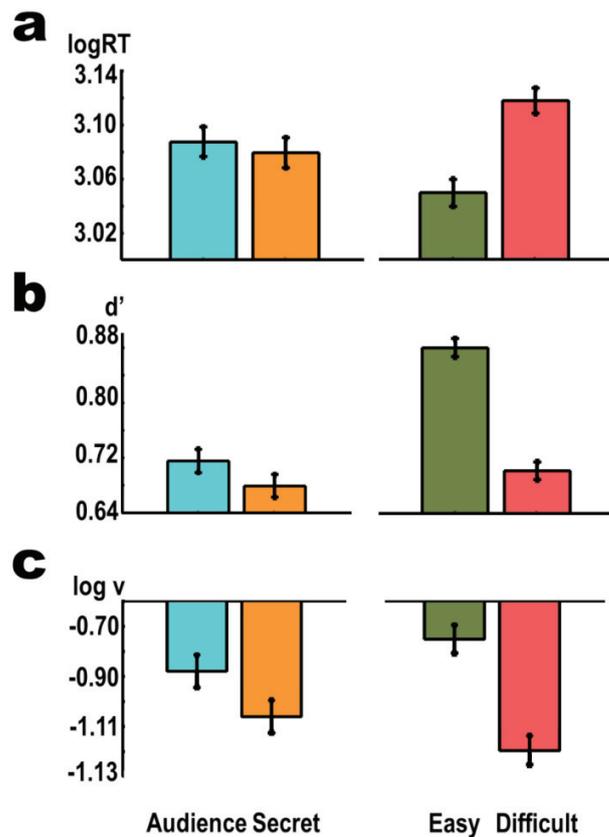
In order to compare the goodness of fit of our models we also ran the intermediate models (either the drift and the boundary, ' $v$  free -  $a$  free', or the drift and the non-decision time, ' $v$  free -  $Ter$  free', were allowed to vary) and compared the sums of the individual Bayesian Information Criterion (BIC) of the models. The model in which only the drift ( $v$ ) was allowed to vary showed a lower BIC than all other models (BIC sums: full model:  $1.44 \times 10^4$ ,  $v$  free:  $1.36 \times 10^4$ ;  $v$  free –  $a$  free:  $1.41 \times 10^4$ ;  $v$  free –  $Ter$  free:  $1.41 \times 10^4$ ). To ensure that this reflected individual fits, we also compared the BICs of the models within each individual. 20 over 21 subjects were best fitted with the model where only the drift is allowed to vary (' $v$  free'); the one subject left was best fitted with the addition of variations in the non-decision time (' $v$  free - $Ter$  free').

Furthermore, we ran the simulations of the data predicted by the model using the estimated parameter, for each subject (**Annex 1**).

Once again, for normality purpose, we analyzed  $\log(v)$  using the same 2 way rmANOVA. In order to compare the goodness of fit of our models we also ran the intermediate models (either the drift and the boundary or the drift and the non-decision time were allowed to vary) and compared the sum of the individual Bayesian Information Criterion (BIC) of the models. We subsequently applied a 2 way (Observation and Difficulty) rmANOVAs on the drift parameter ( $v$ ) from the 'v free' model. Note that  $\log(v)$  values are negatives, so that higher absolute values of  $\log(v)$  actually mean lower drift rates ( $v$ ) of the decision variables. Difficulty and Observation had a main effect on the drift rate ( $v$ ),  $v$  being higher during Easy than during Difficult trials ( $\log(v)_{\text{Easy}} = -0.75$ ;  $\log(v)_{\text{Difficult}} = -1.19$ ;  $F_{1,20} = 32.2$ ;  $p = 0.000015$ ) and higher in Audience than in Secret ( $\log(v)_{\text{Audience}} = -0.88$ ;  $\log(v)_{\text{Secret}} = -1.06$ ;  $F_{1,20} = 7.48$ ;  $p = 0.0128$ ; **Figure 18c**)

### ***Influence of personality***

The difference in RTs induced by observation ( $RT_{\text{Audience}} - RT_{\text{Secret}}$ ) was positively correlated to both Openness ( $p = 0.0387$ ;  $\rho = 0.4652$ ; **Figure 19a**) and Perspective Taking ( $p = 0.0188$ ;  $\rho = 0.5200$ ; **Figure 19b**). The difference in sensitivity induced by observation ( $d'_{\text{Audience}} - d'_{\text{Secret}}$ ) was negatively correlated with Extraversion ( $p = 0.0326$ ;  $\rho = -0.4790$ ; **Figure 19c**). No other correlation was found to be significant (**Table 1**).



**Figure 18. Behavior and DDM parameter estimates.**

Observation effects are on the left, difficulty effect on the right. **a)** Reaction-Times (RT): RT were slower in audience than in secret and slower during difficult than during easy trials. **b)** Sensitivity ( $d'$ ):  $d'$  was better in Audience than in Secret (during difficult trials) and better during easy trials than during difficult trials. **c)** DDM. The drift rate of the decision variable ( $v$ ) was higher in audience than in secret and higher during easy trials than during difficult trials. Log RT,  $d'$  and log  $v$  are expressed in arbitrary units. Bars represent the standard errors of the mean (s.e.m).

### ***2.1.3. Discussion***

The mere presence of an observer (audience) modifies behavior, in a wide variety of tasks. But the mechanisms underlying these effects remain unclear. Here, we took advantage of the Drift Diffusion Models (DDM) framework to compare observed and non-observed decisions, on two distinct difficulty levels within a unique task.

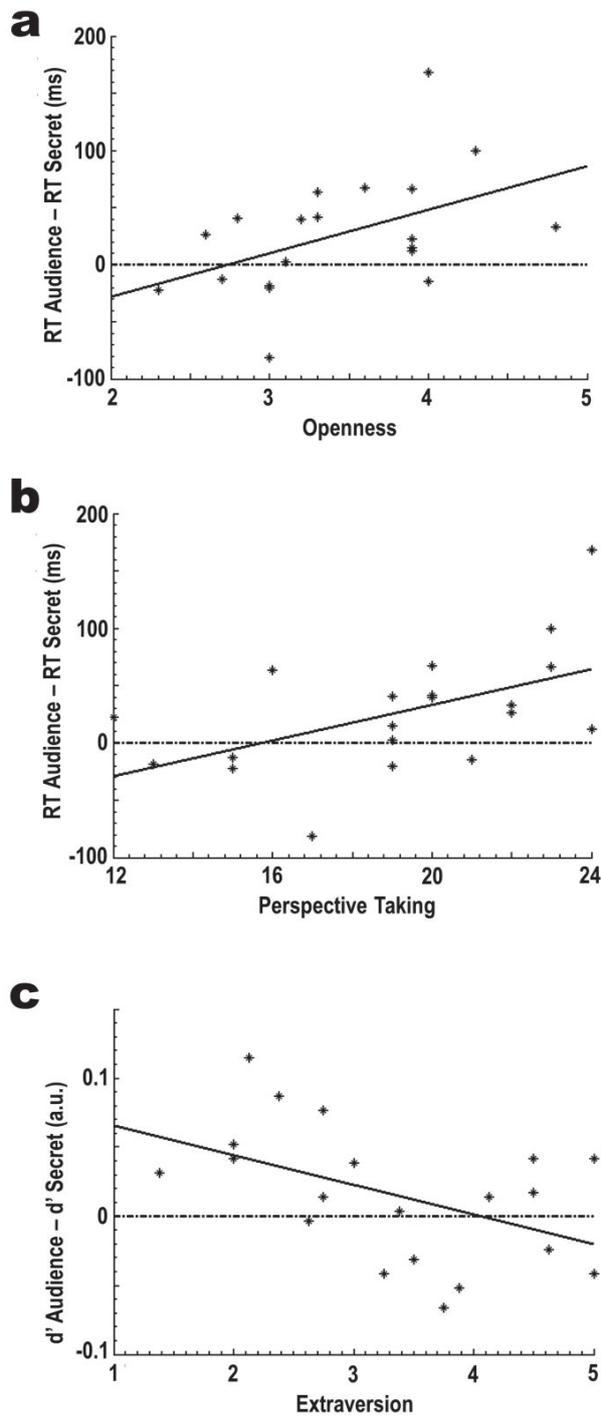
Reactions-times (RT) were longer and sensitivity was lower during difficult trials than during easy trials. DDM showed that this was related to a lower drift rate of the decision variable during difficult trials than during easy trials. More importantly, RT were longer and sensitivity was higher in audience than in secret. Crucially there was a higher drift rate of the decision variable in audience than in secret. This study provides a mechanistic explanation of the effect of an audience on performance in perceptual decision making.

Making a decision with an audience does not change the initial primary sensory processing or the motor output, reflected in the non-decision time, nor does it modify the decision boundary. Instead, audience affects the efficiency of sensory accumulation via the drift rate of a decision variable. In a study where participants perform a computer-based color discrimination task, judging if a scrambled square is depicted by mostly blue or orange pixels, the drift rate was also found to be changed by social conformity (Germar et al. 2016; 2013).

Furthermore, we tested the hypothesis that the effect of an audience on task performance was driven by personality traits in relation to social contexts. We measured personality traits related to social cognition, including those suggested by Uziel (Extraversion and Neurotism). Our results indicated a negative correlation between change in sensitivity under observation and Extraversion, whereas the literature predicted a positive one (Uziel 2007). Personality traits seem to play a role in how an audience influences behavior. Individual characteristics were also underlined in the effect of the presence of others on food consumption (Herman 2015). However, it appears that how personality traits impact the changes in behavior under observation is a more complicated picture than depicted by Uziel (2007). We showed two personality traits were also involved in the effect of the presence of others: Contextual adaptability and Openness. Both were positively related to the difference in reaction-time between decisions with an audience and decisions in secret.

Finally, given the main effects of audience, our results tend to confirm that the audience effect is independent from difficulty. Several studies already weakened the prevalent Drive theory proposed by Zajonc in 1965 (Bond and Titus 1983; Brennan and Enns 2015; Davidson and Kelley 1973; Detillion et al. 2004; Gagné and Zuckerman 1999; Laughlin and Wong-McCarthy 1975; Rousseau and Standing 1995; Uziel 2007) and our study agrees with the results of these earlier studies to strongly suggest that the Drive Theory is obsolete.

Difficulty is usually defined by two distinct tasks which are assumed to be more or less complex relative to each other. Though, different tasks are sustained by dissimilar cognitive processes and it is tedious to compare across their results. Audience has a different impact on the learning of a task and the mere execution of a simple, well-trained, task (Gagné and Zuckerman 1999). Here, we used a unique task with different levels of difficulty instead of comparing two different tasks assumed to be of different difficulties, as done before. In order to free the results from the confounding effects induced by comparing different tasks, further study should also allow a careful examination of the audience effect on each type of task (perceptual, attentional, learning, calculus, etc.) at different difficulty levels to help clarify the effect of an audience on behavior.



**Figure 19. Personality traits and behavior.** **a)** Openness ( $p = 0.039$ ;  $\rho = 0.47$ ) and **b)** Perspective Taking ( $p = 0.018$ ;  $\rho = 0.52$ ) are positively correlated with the difference in Reaction-Times (RT) between audience and secret. **c)** The difference in sensitivity ( $d'$ ) between audience and secret is negatively correlated with Extraversion ( $p = 0.032$ ;  $\rho = -0.48$ ). RT differences are expressed in milliseconds (ms),  $d'$  difference is expressed in arbitrary units (a.u.)

Trait	$RTs_{\text{Audience}} - RTs_{\text{Secret}}$		*	$d'_{\text{audience}} - d'_{\text{secret}}$	
	p-value	rho		p-value	rho
Extraversion	0.5781	-0.1323	*	0.0323	-0.4790
Agreeableness	0.9947	0.0016		0.6415	0.1109
Conscientiousness	0.2623	-0.2632		0.9519	0.0144
Neuroticism	0.7193	0.0857		0.1623	0.3248
Openness	* 0.0387	0.4652		0.1193	-0.3597
Perspective Taking	* 0.0188	0.5200		0.6175	-0.1189
Fantasy	0.1896	-0.3059		0.3657	-0.2137
Empathic Concern	0.4498	0.1791		0.9201	0.0240
Personal distress	0.6269	-0.1158		0.4939	0.1624

**Table 1. Correlation tests between the difference in behavior induced by observation and personality traits. Significant correlations are marked with a star.**

## ***2.2. Vicarious reward: Experiment 1***

The goal of the vicarious behavioral experiments was to find a paradigm enabling the use of DDM to investigate the influence of others on the person affected by a decision. We wanted to determine which decision parameters are modified when a decision only impact the well-being of others. The participants performed a random-dots task to win payoffs, for them or for another. We chose the random dot task paradigm because of the accumulated literature on the brain network involved in the decision making process related to them. We aimed to find a main effect of the beneficiary in behavior and, using DDM, to decipher which decision parameter is modified by prosociality for others. In the first version of the vicarious perceptual decision paradigm, the other was thought to be an anonymous other participant – supposedly randomly selected by a computer. In the second version, we asked the participants to choose a relative whom they would be willing to play for. The second version was also performed in MagnetoEncephaloGraphy.

Before launching the experiments, we performed pilot studies on colleagues and friends. The goal was to find the percentage of dot coherence required to produce an average of 70% correct responses in our pretest sample, This was because the Matlab® toolbox used to fit the drift diffusion model to the experimental data requires this level of performance. The pretests showed that in front of the generated kintematograms , the ‘pretesters’ dropped to chance level performance (<60%) under 13% of dots coherence level and reached a 90% maximum plateau from 17% of dots coherence.

### ***2.2.1. Material and methods***

#### ***Participants***

36 healthy subjects were recruited by advertisements in the Lyon 1 Claude Bernard University students' mailing list. Subjects were screened using self-reports to exclude any psychiatric or neurological history, current or previous substance abuse (except nicotine and festive alcohol consumption). All participants gave written informed consent and received twenty euros for their participation. The study was approved by the local research ethics committee (Comité de Protection des Personnes Sud-Est III); all methods were performed in accordance with the relevant guidelines and regulations. Two subjects were excluded for not doing the tasks for the other beneficiary of the decision. One subject had to be excluded for technical problems (log files corrupted). This left 33 subjects for further analysis (15 females; mean age =21.84, range 18-34).

#### ***Stimuli***

Random dot kinematograms (RDKs) were programmed using the Matlab® Psychtoolbox (Brainard 1997; Pelli 1997). The mask stimulus was a drifting random dot display of 3000 ms duration. Dots were white on a black background, with each frame composed of 50 white

Gaussian blobs with a diameter of 2.85 mm. The stationary dots began to move with a speed of  $2.7^\circ/s$  from their original locations and each dot had a life-duration of 500ms.

The motion of the dots was made by replotting dots corresponding to the previous ones at a determined spatial offset in the same direction so that all the dots moved in their directions at the same speed. 3 coherence levels were used: 13%; 15% and 17% of coherently moving dots. During the experiment, RDKs appeared in a square centered on the screen (Dell, 19", screen resolution set to 1280x1050, vertical refresh rate of 60 Hz.), taking 30.8% of the screen, with participants at a distance of 60 cm.

### ***Procedure***

Two participants of the same gender were asked to come at the same session. At their arrival, the participants were sat in the experimental room, were they were informed and signed the consent forms. Before the task, they were trained to familiarize with the design and timings of the task. The training was composed of 126 trials at 15, 17 or 19% of coherently moving dots. After they were trained, they completed the 4 blocks of the task, which each lasted 10 minutes approximately. Each participant performed a total of 300 trials. Difficulty levels, payoffs, beneficiary and dot directions were pseudo-randomized within each block and across participants.

### ***Instructions***

The experimenter told the participant that they would gain 10€ for performing the experiment, and that they could add to this payoff by giving correct responses. They were also told that half of the trials would be performed for another (anonymous, selected randomly,) participant, for whom they could win money too. The participants were asked to discriminate the (left/right) direction of coherently moving dots among randomly moving dots.

They were instructed to give one, and only one, response while the dots were moving: if they gave more than one response or did not respond (miss), they would have an error feedback (loss). For participants to treat all decisions as equally relevant, for both themselves and the other, they were told that one trial for each beneficiary (self and other) would be randomly selected by a computer program to determine both their individual final payoffs. If the response on the selected trial was correct, the associated payoff would be won and added to the final payoff. But if it was incorrect, the payoff would be lost.

### ***Trial design***

A square was always present in the middle of the screen. On top of this square appeared the cue, which indicated the beneficiary and payoff trial conditions. The dots were displayed inside the area defined by the square. The square and the cue were colored yellow or blue, according to the beneficiary of the payoff associated with the trial. The color was used to emphasize the beneficiary of the trial, and was counterbalanced between subjects

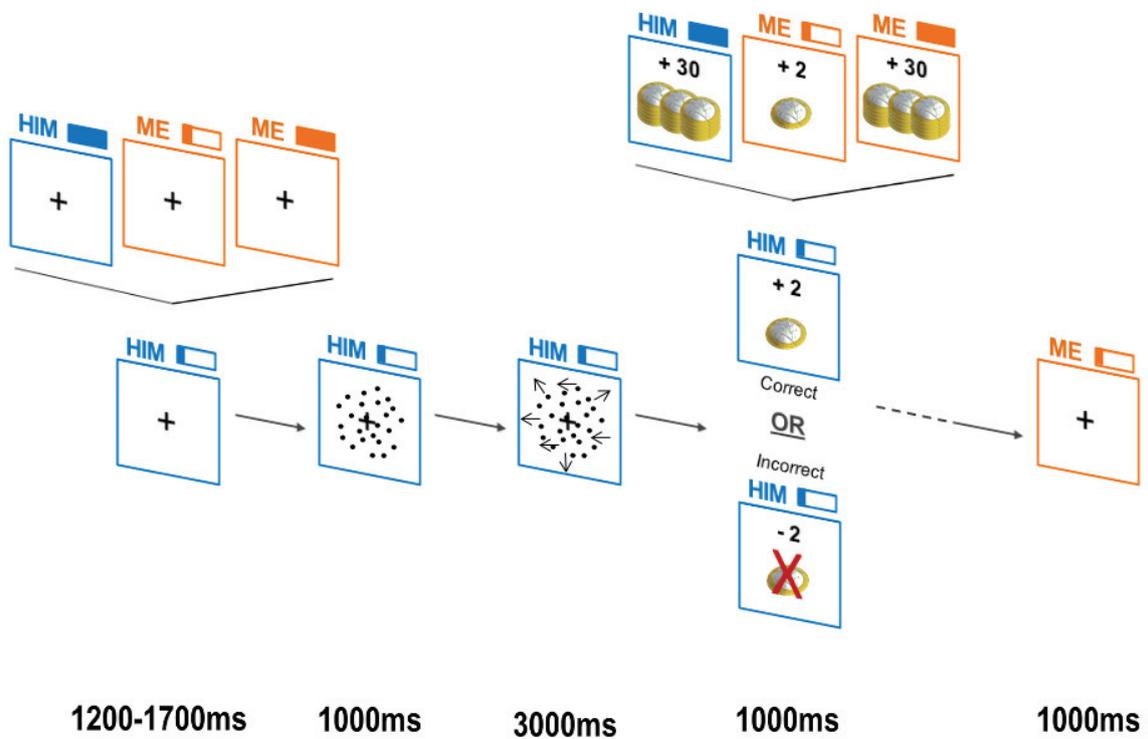
Each trial (**Figure 20**) began with the cue, which had a jittered duration from 1200 to 1700ms and was used as inter-trial-interval (ITI). The cue consisted in a word announcing the beneficiary of the decision ('him' for others-affecting decisions, 'me' for self-affecting decisions) to the left of a rectangle filled proportionally to the payoff/penalty associated with the decision (2, 4, 6, 8 or 10 euros for low payoff/penalty and 22, 24, 26, 28 or 30 euros for high payoff/penalty). This cue remained on the screen during the entire subsequent trial.

After the cue, the first frame of the RDK to come (a picture of stationary dots) was shown for 1000ms. Then, dot motion began and lasted for 3000ms, during which the subject had to respond. At the end of the 3000ms of dot motion, the feedback illustrated the payoff for 1000ms. If the response was correct, a pile of coins proportional to the payoff was shown together with the value of payoff itself ("+2", "+4", "+6", "+8", "+10", "+22", "+24", "+26", "+28" or "+30") above. For incorrect responses and misses, the pile of coin was covered with red-colored cross, displayed together with the penalty ("-2", "-4", "-6", "-8", "-10", "-22", "-24", "-26", "-28" or "-30") above it. At the end of the trial, a new ITI was displayed, showing the cue for the trial to come.

### ***Statistical analysis***

Reaction-Times (RT) were log transformed for distribution normalization. Log RT for corrects and log RT for errors were analyzed separately, using three way repeated measures

analyses of variances (rmANOVAs). The factors were Beneficiary (two levels: other vs. self), Payoff (two levels: high – 20; 22, 24, 26, 28, or 30€ - vs. low – 2, 4, 6, 8 or 10€) and the level of coherently moving dots, further called 'difficulty' (three levels: 13% vs. 15% vs. 17%). Sensitivity was analyzed with the same 3-way rmANOVA. Except for the normality tests, which were performed with Matlab, all statistical analyses were performed using Statistica (STATISTICA®, Dell Inc. 2015)



**Figure 20. Trial design.** Each trial began with the cue, which had a jittered duration from 1200 to 1700ms and consisted in a word announcing the beneficiary of the decision ('him' for others-affecting decisions, 'me' for self-affecting decisions) to the left of a rectangle filled proportionally to the payoff/penalty associated with the decision. Next, the first frame of the RDK to come was shown for 1000ms. Then, dot motion began and lasted for 3000ms, during which the subject had to respond. Then, the feedback illustrated the outcome for 1000ms. If the response was correct, a pile of coins proportional to the payoff was shown together with the value of payoff itself above. For incorrect responses and misses, the pile of coin was covered with a red-colored cross, displayed together with the penalty. At the end of the trial, a new ITI was displayed, showing the cue for the trial to come.

### *Fitting the drift diffusion model to the data*

For fitting the diffusion model to the data (Ratcliff and Tuerlinckx 2002; Vandekerckhove and Tuerlinckx 2007), we used DMAT (see **Box 2. Fitting the drift diffusion models to the data** ). We first checked that the starting point of the decision variable ( $z$ ) was not different between left and right responses using a one way rmANOVA with response direction as factor. The analyses showed no effect of response direction ( $F_{1,37} = 0.351$ ;  $p = 0.558$ ), ensuring that no bias emerged toward either the left or the right response. Consequently, we applied in all our models a starting point equal to half the distance between the left and right decision criteria ( $z = \frac{1}{2} a$ ). Each model was fitted to the data separately for each participant.

The first model we ran allowed all three parameters ( $a$ ,  $v$  and  $T_{er}$ ) to vary. We applied a 3-way rmANOVA. The 3 factors were Beneficiary of the decision, Payoff/Penalty associated with the decision and Difficulty (dots coherence). The boundary ( $a$ ) showed no effect of any factor. We thus ran a model in which only the drift ( $v$ ) and the non-decision time ( $T_{er}$ ) were free to vary across conditions. Once again, we analyzed  $v$  and  $T_{er}$  using the same 3 way rmANOVA. In order to compare the goodness of fit of our models we also compared the sums of the individual Bayesian Information Criterion (BIC) of the models.

## 2.2.2. Results

### *Reactions-times (RTs)*

The analyses presented in this section were performed on log-transformed reaction-times (logRT). For intelligibility, the mean values given are non-transformed RT expressed in milliseconds (ms). No effect of any of the three factors (Beneficiary, Payoff/Penalty and Difficulty) was found on logRT from errors. All the following results concern logRT for correct responses. Log RT for corrects showed a main effect of Difficulty ( $F_{2,64} = 34.7$ ;  $p < 0.0000001$ ), RT being faster as the coherence increases ( $RT_{Easy} = 1516$  ms;  $RT_{Medium} = 1601$  ms;  $RT_{Difficult} = 1635$  ms;  $RT_{Easy}$  vs.  $RT_{Medium}$ :  $p < 0.001$ ; Cohen's  $d = 0.239$ ;  $RT_{Medium}$  vs.  $RT_{Difficult}$ :  $p = 0.016$ ; Cohen's  $d = 0.102$ ; **Figure 21a**). The Beneficiary and the Payoff/Penalty both showed no main effect on logRT from correct responses. The Payoff/Penalty\*Difficulty and the triple Beneficiary\*Payoff/Penalty\*Difficulty interaction effects were significant ( $F_{2,64} = 7.26$ ;  $p = 0.00144$  and  $F_{2,64} = 4.01$ ;  $p = 0.0228$ , respectively). Given the main effect of difficulty, we ran separate rmANOVAs for each level keeping Beneficiary and Payoff/Penalty as factors. No effect was found at the Medium level.

At the Easy level, RT were faster for high than for low Payoff/Penalty ( $RT_{low} = 1538$  ms;  $RT_{High} = 1494$  ms;  $F_{1,32} = 5.33$ ;  $p = 0.0276$ ; Cohen's  $d = 0.140$ ). But, an interaction between Beneficiary and Payoff/Penalty was also found ( $F_{1,32} = 5.49$ ;  $p = 0.0255$ ) and the *post-hoc* tests

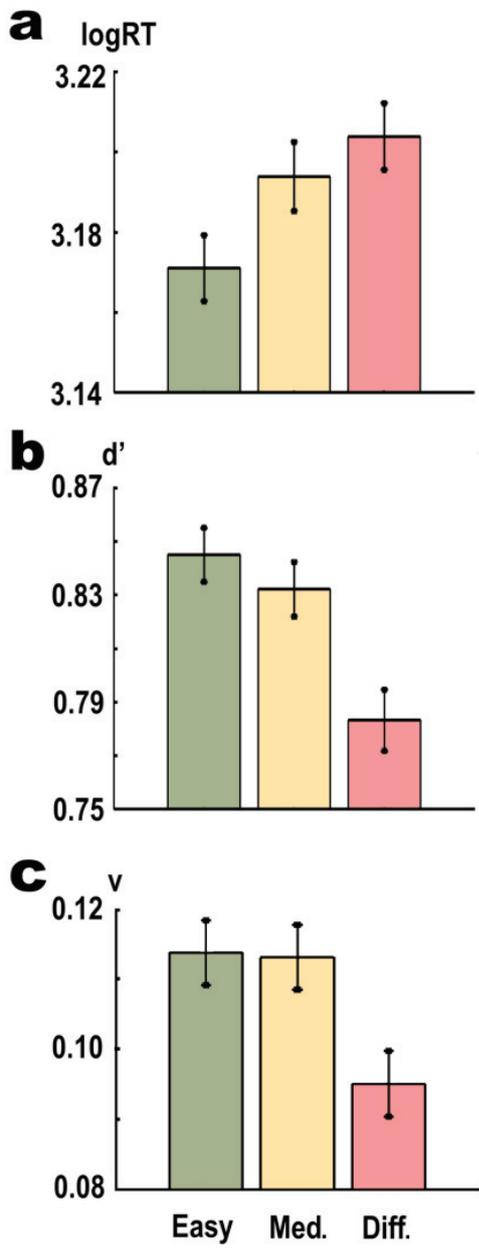
revealed that this Payoff/Penalty effect was only true during other-affecting decisions ( $RT_{low} = 1548$  ms;  $RT_{High} = 1468$  ms;  $p = 0.00125$ ; Cohen's  $d = 0.258$ ). At the Difficult level, RT were slower for high Payoff/Penalty than for low Payoff/Penalty ( $RT_{low} = 1603$  ms;  $RT_{High} = 1666$  ms;  $F_{1,32} = 5.95$ ;  $p = 0.0204$ ; Cohen's  $d = 0.164$ ; **Figure 22a**) and no effect of the beneficiary was found.

### ***Sensitivity***

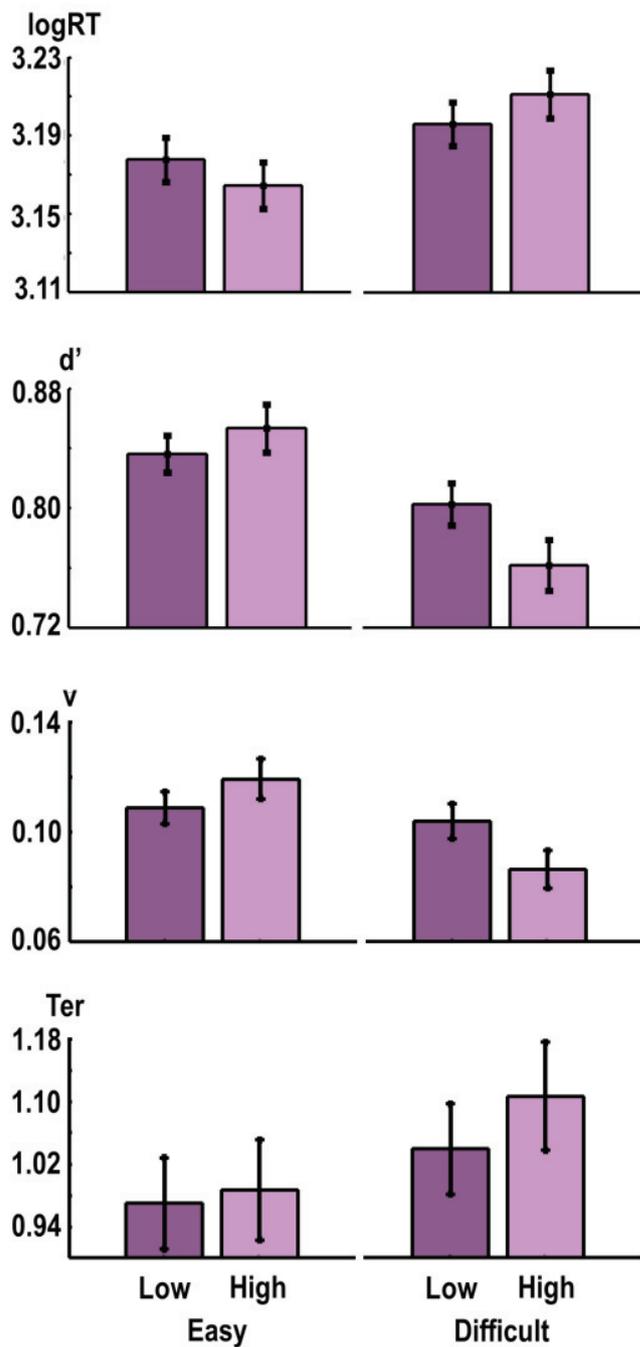
The analysis showed a main effect of difficulty on sensitivity ( $F_{2,64} = 25.1$ ;  $p < 0.0000001$ ). *Post hoc* tests showed that sensitivity ( $d'$ ) was higher during Medium difficulty trials than during Difficult trials ( $d'_{Medium} = .83$  a.u.;  $d'_{Difficult} = 0.78$  a.u.;  $p = 0.000001$ ; Cohen's  $d = 0.38$ ; **Figure 21b**) but did not differ between Medium difficulty trials and Easy trials. The Payoff/Penalty\* Difficulty interaction reached significance ( $F_{2,64} = 4.54$ ;  $p = 0.0143$ ). Given the main effect of Difficulty, we ran 2-way rmANOVA at each difficulty level, keeping Beneficiary and Payoff/Penalty as factors. No effect was found at the Medium level.

At the Easy level, there was a Beneficiary\*Payoff/Penalty interaction ( $F_{1,32} = 4.26$ ;  $p = 0.047$ ). *Post-hoc* analysis explained that  $d'$  was higher for high Payoff/Penalty than for low Payoff/Penalty during Self-affecting decisions only ( $d'_{High} = 0.87$  a.u.;  $d'_{Low} = 0.83$  a.u.;  $p = 0.0116$ ;

Cohen's  $d = 0.16$ ). At the Difficult level,  $d'$  was lower for high than for low Payoff/Penalty ( $d'_{\text{High}} = 0.80$  a.u.;  $d'_{\text{Low}} = 0.76$  a.u.;  $F_{1,32} = 7.32$ ;  $p = 0.0109$ ; Cohen's  $d = 0.31$ ; **Figure 22b**)



**Figure 21. Sanity Check.** **a) Reaction-Times** (RT) increases as difficulty increases. **b) Sensitivity** ( $d'$ ) decreases when difficulty increases, although there was a plateau of accuracy from the medium (Med.) to the easy level. **c) Drift rate** ( $v$ ) of the decision variable is lower during difficult (Diff.) trials than during easy trials and medium difficulty trials. Easy trials are on the left in green, medium difficulty trials are in the middle in yellow and difficult trials are on the right in red. Log RT and  $d'$  are expressed in arbitrary units. Bars represent the standard errors of the mean (s.e.m).



**Figure 22. Effect of payoff/penalty during easy and difficult trials.** **a)** Reaction-times (RT) analysis shows that during easy trials decisions are faster for high than for low payoff/penalty while decisions are longer for high than for low payoff/penalty during difficult trials. **b)** Sensitivity ( $d'$ ) is better for high than low payoff/penalty during easy trials, however  $d'$  is worse for high than low payoff/penalty during difficult trials. **c)** The drift rate ( $v$ ) of the decision variable follows the same pattern than  $d'$ . **d)** The non-decision time ( $Ter$ ) is higher for high than low payoff/penalty, whatever the difficulty of the task. Log RT,  $d'$ ,  $v$  and  $Ter$  are expressed in arbitrary units. Bars represent the standard errors of the mean (s.e.m).

## *Drift diffusion models*

We started with the selection of the best fitting model. The first model we ran allowed all three parameters - the boundary ( $a$ ), the drift ( $v$ ), and the non-decision time ( $Ter$ ) - to vary ('full model'). In this model, the boundary ( $a$ ) showed no effect of any of the three factors (Beneficiary, Payoff, Difficulty). We thus applied a model where only the drift ( $v$ ) and the non-decision time ( $Ter$ ) were free to vary across conditions (' $v$  free- $Ter$  free'). In order to compare the goodness of fit of our models we also compared the sums of the individual Bayesian Information Criterion (BIC) of the models. The ' $v$  free- $Ter$  free' model indeed had a lower BIC than the 'full model' ( $BIC_{full\ model} = 17795$ ;  $BIC_{v\ free-Ter\ free} = 15204$ ).

To ensure that this reflected individual fits, we also compared the BICs of the models within each individual. 32 over 33 subjects were best fitted with the ' $v$  free- $Ter$  free' model, the one subject left being better explained by the full model. Furthermore, we ran the simulations of the data predicted by the model using the estimated parameter, for each subject (**Annex 2**).

We subsequently applied a 3 way (Beneficiary, Payoff, and Difficulty) rmANOVAs on the drift ( $v$ ) and the non-decision time ( $Ter$ ) parameter estimates from the ' $v$  free- $Ter$  free' model. Payoff/Penalty had a main effect on the non-decision-time ( $Ter$ ),  $Ter$  being higher for high than for low Payoff/Penalty ( $Ter_{High} = 1.07$  a.u.;  $Ter_{Low} = 0.97$  a.u.;  $F_{1,32} = 6.85$ ;  $p = 0.0134$ ; Cohen's  $d =$

0.17). Difficulty had a main effect on the drift rate ( $v$ ) of the decision variable ( $F_{2,64} = 10.9$ ;  $p = 0.00008$ ).

The *post-hoc* analysis showed that the drift was higher during Medium difficulty trials than during Difficult trials ( $v_{\text{Medium}} = 0.113$  a.u.;  $v_{\text{Difficult}} = 0.095$  a.u.;  $p = 0.00018$ ; Cohen's  $d = 0.34$  - **Figure 21c**) but did not differ between Medium and Easy trials. The Payoff/Penalty\* Difficulty interaction effect on the drift ( $v$ ) also reached significance ( $F_{2,64} = 3.24$ ;  $p = 0.0457$ ). Given the main effect of Difficulty, we ran 2-ways rmANOVA at each difficulty level, keeping Beneficiary and Payoff/Penalty as factors. No effect was found for the Medium difficulty trials or for Easy trials. However, during Difficult trials, the drift ( $v$ ) was lower for high Payoff/Penalty than for low Payoff/Penalty ( $v_{\text{High}} = 0.104$  a.u. ;  $v_{\text{Low}} = 0.086$  a.u.;  $F_{1,32} = 5.34$ ;  $p = 0.0275$ ; Cohen's  $d = 0.32$ )

### **2.2.3. Discussion**

We asked the participants to perform a random dot task to win - and avoid losing - money, for themselves and for another anonymous participant. Reaction-Times (RT) and sensitivity showed a main effect of difficulty, with faster RT and higher sensitivity when difficulty decreased. It shows that participants understood the task and performed it correctly. Moreover, using DDM, these changes associated with task difficulty were explained by variations in the drift rate of the decision variable, as it was expected (Ratcliff and McKoon 2008).

We also found an effect of Payoff/Penalty at the easy and at the difficult task levels, both on sensitivity and RT. But the effect was reversed from one difficulty level to the other: the participants were faster and more accurate for high Payoff/Penalties than for low Payoff/Penalty at the easy level but slower and less accurate for high than for low Payoff/Penalties at the difficult level. Using DDM we found that the drift rate of the decision variable follows the same pattern: the drift rate is higher for high payoff/penalty than for low payoff/penalty during easy trials but lower for high than for low payoff/penalty during difficult trials.

Sequential-sampling models have previously been used to account for the effects of payoffs in a perceptual decision making. These studies have reported a bias in the starting point of the decision variable induced by asymmetrical payoffs associated with the possible response

alternatives (Simen et al. 2009; M. J. Mulder et al. 2012). The starting point of the decision variable shifted closer to the decision boundary associated with the alternative having the higher payoff.

In contrast, our experimental set-up was designed to avoid response probability manipulations toward one of the (left or right) alternatives, in terms of probability (through trials randomization) and in terms of payoff (by assigning the same payoff/penalty to both response alternatives). We aimed to compare identical decisions made by the participants, either for themselves or for another person. Our results suggest that when payoff/penalty is identical for both response alternatives then payoff/penalty is integrated together with the sensory evidence during the accumulation process of perceptual decision making. Further studies should decipher the effect of Payoff/Penalties at different difficulty levels and its effect on the drift rate of the decision variable.

In addition, non-decision time was higher for high payoff/penalty than for low payoff/penalty, suggesting interplay between the non-decision time and the drift rate of the decision variable in the effect of payoff/penalty observed in behavior. An effect on the non-decision-time indicates that payoff/penalty acts on cognitive mechanisms that are outside of the decision process. Non-decision time is usually referred to as reflecting the early encoding of the stimulus of interest and the execution of the motor response, both external to the visuo-motor decision process in itself (Ratcliff and McKoon 2008; Martijn J. Mulder and Maanen 2013; Ravenzwaaij, Dutilh, and Wagenmakers 2012; Zhang et al. 2016; Zhang and Rowe 2014).

However, the Drift diffusion Models cannot distinguish between different mechanisms within the non-decision time. Furthermore, the non-decision time is thought to be necessary to account for speed-accuracy trade-offs (Martijn J. Mulder and Maanen 2013) and it has been shown that speed-accuracy instructions also modulate the non-decision time (Zhang and Rowe 2014). Variation in the non-decision time can mean that different strategies are applied (Schuch 2016) and could include other components that influence the decision making processes. It could suggest that payoff/penalty induces a change in the strategy applied and modifies the speed-accuracy trade-offs when making perceptual decisions.

The present experiment was designed to study the effect of the beneficiary associated with the decision. However, the beneficiary associated with the decision had no main effect on RT or sensitivity. Since we found no main effect of the beneficiary on behavior, we did not achieve our goal (studying the influence of the beneficiary of a decision). Humans have an aversion for loss (Mauricio R Delgado et al. 2008), this loss aversion could have driven their decision process. We believe that the strength of loss aversion overcame the possible modulation of the decisional process by others. As a consequence, we removed the penalties in the vicarious behavioral experiment 2. The participants could then lose nothing and would perform the task only to win payoff for themselves and for the other.

We also chose to simplify payoffs and maintained only one value for high or low payoffs. Moreover, familiarity plays an important role in decision making when taking others into account (Mobbs et al. 2009), therefore we decided to ask the participants to perform the task

for a close relative instead of another anonymous participant. Finally, accuracy plateaued in between the medium (15% of dots coherence) and the easy level (17% of dots coherence). This suggests a plateau of performance, which cannot be modulated by our factors, at the 17% dots coherence level. We therefore excluded the 17% level and kept only the 13% and the 15% levels for the following experiment.

### ***2.3. Vicarious reward: Experiment 2<sup>6</sup>: Vicarious rewards modulate the drift rate of evidence accumulation from the drift diffusion model***

When playing at a shooting range in a fairground, we accumulate sensory evidence (about target movement) until we can shoot accurately, and win the prize. Now, if such decisions are made so that the prize goes to a close friend, will we process and use information in the exact same way? More precisely, how do motivational incentives for someone else influence the mechanisms engaged in making simple perceptual choices as compared to the same decisions associated with the same incentives, but for oneself?

In the last decades, the framework of sequential-sampling models, such as drift-diffusion models (DDM), has proven to be a powerful approach to explain the process of making a decision (Ratcliff and McKoon 2008; Forstmann, Ratcliff, and Wagenmakers 2016; Vandekerckhove and Tuerlinckx 2007; Leite and Ratcliff 2010; Ratcliff et al. 2016; Summerfield and Tsetsos 2012). DDM successfully capture the complex relationship between choice and reaction-times (RTs) by decomposing these behavioral data into internal cognitive components of decision processing.

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<sup>6</sup> The vicarious behavioral experiment 2 is published in *Frontiers in Behavioral Neuroscience* and can be found at the following doi: 10.3389/fnbeh.2019.00142.

In this framework, a decision reflects a decision variable drifting with a given rate ( $v$ ), from an intermediate starting point ( $z$ ) towards one of the decision boundaries at hands. Each boundary is separated from the starting point ( $z$ ) of a given distance ( $a$ ) and acts as a decision threshold for an option; so that the response of a decision is initiated when the decision variable reaches one of the boundaries. In the example of the shooting range, the decision variable would accumulate information about the position of the moving ducks over time and when (relative) certainty about their position is reached; the decision of pulling the trigger is made.

Sensory encoding of information basically relies on the quality of the available evidence (Ratcliff and McKoon 2008). Foggy weather would slow the rate at which the decision variable rises, as compared to clear climate conditions. Reliability of the decision depends on the distance between the starting point of the decision variable and the decision boundary; the decision rules set by the read-out mechanisms [2,6–8]. Reaching higher decision boundaries requires more evidence to be accumulated, thus leading to a better accuracy, but takes a longer time. Which of the evidence accumulation stage (drift of the decision variable) or the read-out mechanisms (distance between the starting point and the decision boundaries) would be adjusted differently based on vicarious information (the beneficiary of the decision)? How is the perceptual decision process modulated when the source of motivation concerns a close relative rather than oneself?

Here, we designed a new paradigm, enabling the use of drift diffusion models (DDM) to investigate the influence of the payoff associated with- and the person affected by- a perceptual

decision. The participants performed a random-dots task (left/right direction categorization) to win low or high payoffs, for themselves or for a close relative. We tested which of the DDM parameters are modified between other-affecting and self-affecting decisions: the drift rate of the decision variable (encoding) or the decision boundary (read-out)?

Changes in the distance between the starting point and the decision boundary (a) would mean that people integrate beneficiary-related motivation through the read-out mechanisms, setting the decision rules prior to starting the evidence integration itself. Alternatively, a direct influence of self/other motivation on the decisional process could affect the drift rate of the decision variable, which is an index of the quality of evidence used for the decision. This would suggest that sources of motivation (payoff for self/payoff for other) are integrated together with the evidence for the choice alternatives into a single source of evidence during the accumulation process. Finally, a variation in the non-decision time would indicate that the beneficiary-related motivation acts on cognitive mechanisms outside of the decision process itself, such as primary encoding of the stimuli and motor execution.

### ***2.3.1. Material and methods***

#### ***Participants***

40 healthy subjects were recruited by advertisements in the Lyon 1 Claude Bernard University students' mailing list. Subjects were screened using self-reports to exclude any psychiatric or neurological history, current or previous substance abuse (except nicotine and festive alcohol consumption). All participants gave written informed consent and received twenty euros for their participations. The study was approved by the local research ethics committee (Comité de Protection des Personnes Sud-Est III); all methods were performed in accordance with the relevant guidelines and regulations. 2 subjects were excluded, one for chance level performance and the other for technical problems, leaving 38 subjects for further analyses (15 females; mean age =21.84, range 18-34).

#### ***Stimuli***

Random dot kinematograms (RDKs) were programmed using the Matlab® Psychtoolbox (Brainard 1997; Pelli 1997). The mask stimulus was a drifting random dot display of 2000 ms duration. Dots were white on a black background, with each frame composed of 50 white Gaussian blobs with a diameter of 2.85 mm. The stationary dots began to move with a speed of

2.7°/s from their original locations and each dot had a life-duration of 500ms. The motion of the dots was made by replotting dots corresponding to the previous ones at a determined spatial offset in the same direction so that all the dots moved in their directions at the same speed. During the experiment, RDKs appeared in a square centered on the screen (Dell, 19", screen resolution set to 1280x1050, vertical refresh rate of 60 Hz.), taking 30.8% of the screen, with from participants at a distance of 60 cm.

### ***Procedure***

Previously to coming to the laboratory, the volunteers were asked to choose a close relative for who they would be willing to play for, on half of the experiment. At their arrival, the participants sat in the experimental room, were informed and gave their written consent. Their relationship with the chosen person was asked (7 participants chose one of their parents – mother or father -, 7 chose a sibling, 8 chose their lover, 3 chose a friend and 2 their roommate). A few demonstration trials were shown, for them to see how the condition cue (Payoff and Beneficiary) were displayed. Subjects were trained and then finally completed the task. It lasted 64 minutes approximately, in four blocks of 16 minutes each. All were debriefed when the task was over.

## ***Training***

Before the task, subjects were trained to be familiar with the design and timing. The training was composed of 10 trials of 15% coherently moving dots, which is the easy level of the task. To ensure that participants did not respond randomly, a sensitivity ( $d'$ ) criterion was set at  $d = 0.6$  (i.e. 60% correct, which is higher than chance level). If subjects were below this criterion in the training session, they performed a second identical training. All of the included subjects eventually reached the criterion and subsequently performed the task.

## ***Instructions***

Participants were explained that they would play a game in order to win money, either for themselves or for the close relative they had chosen. They were told that they would earn 10€ for doing the experiment and could win 2€ or 10€ more for themselves and also 2€ or 10€ for their relative. The participants were asked to discriminate the left/right direction of coherently moving dots.

They were instructed that they had to give one, and only one, response during the dot motion: if they gave more than one response or did not respond (miss), the program would consider it as incorrect. Money was not accumulated over trials, nor was such accumulation shown to the participants. They were told that one trial of each of the beneficiary conditions

(self and other) would be randomly selected (by a computer program) to determine their final payoffs.

The payoff associated with the trial would be won by the beneficiary, if it was a correct trial. Participants were told (and believed) that the payoff for the other (as well as for themselves) would be sent after completing the experiment. In reality, the close relative received nothing and all participants received 20€ (as if the selected trial was won for himself and associated with a high payoff). This procedure : i) ensured that participants treated all decisions as equally relevant, both for themselves and their close relative, ii) avoided any competition effects to arise between self and other interests. Also, accuracy was implicitly emphasized by telling the participants that, although they would have to adapt to the given 2s to answer, time should not be a problem since the duration of the stimuli was chosen based on previous experimental results (pilot study).

### ***Task design (Figure 23)***

A square was always present in the middle of the screen. On top of this square appeared the cue, which indicated the beneficiary and payoff conditions of the forthcoming trial. The dots were displayed inside the area defined by the square. The square and the cue were colored in yellow or blue, according to the beneficiary of the payoff associated with the trial. The color was used to emphasize the beneficiary of the trial, and was counterbalanced between subjects.

Each trial began with the cue, which had a jittered duration from 800 to 1200ms and was used as inter-trial-interval (ITI). The cue consisted of a word announcing the beneficiary of the decision ('him' for others-affecting decisions, 'me' for self-affecting decisions) to the left of a rectangle filled proportionally to the payoff associated with the decision (full filled rectangle for 10 €, one-fifth filled rectangle for 2€). This cue remained on the screen during the entire subsequent trial. After the cue, the first frame of the RDK to come (a picture of stationary dots) was shown for 1000ms. Then, dot motion began and lasted for 2000ms, during which the subject had to respond. Motion coherence was either 13% (difficult) or 15% (easy), for all participants. At the end of the 2000ms of dot motion, the feedback illustrated the payoff for 500ms. If the response was correct, a pile of coins proportional to the payoff (2 or 10€), was shown together with the value of the payoff itself ("+2", "+10"). For incorrect responses and misses, a red-colored cross was displayed together with "+ 0" above it. At the end of the trial, a new ITI was displayed, showing the cue for the trial to come.

A total of 104 trials per Beneficiary\*Payoff\*Difficulty condition were performed, leading to 832 trials per subject. The task was composed of 4 blocks, of 208 trials each. Each block included 26 trials of each of the 8 conditions. Difficulty levels, Payoffs, Beneficiaries and dot movement direction were pseudo-randomized within each block and across participants. Randomization of dot direction was designed to avoid a bias toward one of the two (left or right) alternatives, constraining it to no more than 3 consecutive trials of the same dot direction.

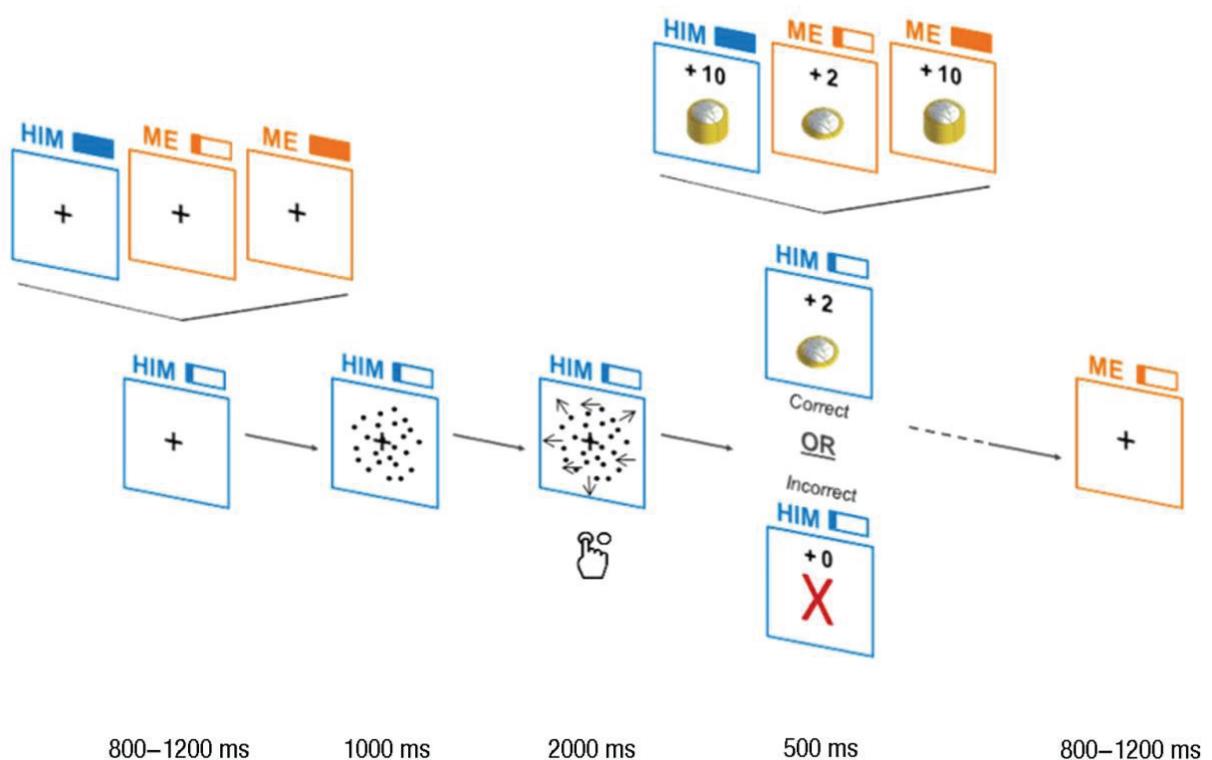
It is to be noted that we actually ran a first experiment using another anonymous, randomly selected, participant as ‘the other’. However, there was no main effect of the beneficiary on RT nor on  $d'$  (**Table 2**). Since we were aiming to characterize how others are taken into account in the perceptual decision making process, and based on the literature showing that familiarity increase vicarious effects (Mobbs et al. 2009; Kawamichi et al. 2013), we adapted our task with a close relative.

### ***Statistical analysis***

Reaction-Times (RT) for correct responses and RT for errors were analyzed separately and RT were logarithmically transformed. logRT and sensitivity ( $d'$ ) normality distribution was ensured using Lilliefors tests. logRT and  $d'$  were then analyzed using 3 way repeated measures analyses of variance (rmANOVAs). The factors were: ‘Beneficiary’ (two levels: other vs. self), ‘Payoff’ (two levels: high - 10€ - vs. low – 2€) and ‘Difficulty’ (two levels: 13% motion coherence - difficult - vs. 15% coherence- easy -). All *post-hoc* analyses were performed using LSD Fisher tests.

Beneficiary and Payoffs were overt factors, indicated by cues on each trial, but difficulty was not explicitly communicated to participants. During debriefing, we asked participants how many difficulty levels they perceived. Most of them perceived the two difficulty levels, only two of them thought there were more levels and one did not consciously perceive any.

There was no effect of gender on behavior (**Table 3**). Although there could be effects of sex hormone variations on decision making in young women, we did not record the phase of the menstrual cycle in our sample. All statistical analyses were performed using Statistica (STATISTICA®, Dell Inc. 2015), except for normality tests and drift diffusion model fitting, performed on MATLAB®.



**Figure 23. Vicarious experiment 2 trial design.** Each trial began with a cue, showing ‘me’ or ‘him’ (for self- and other-affecting decisions respectively) and a full filled rectangle (high payoff) or a one-fifth filled rectangle (low payoff) on the top of a square. The cue and the square were depicted in yellow or in blue, according to the beneficiary. Then, the first

frame of the RDK (stationary dots) appeared in the square for 1000ms. Following this the moving dots were presented for 2000ms and the subject had to respond while the dots were moving. At the end of the 2000ms of dot motion, the payoff was presented. If the response was correct, a pile of coins proportional to the payoff was shown together with the value of payoff itself (“+2”, “+10”) above it. For incorrect responses and misses, a red-colored cross was displayed together with “+ 0” on top of it. Then, a new trial began and the cue of the upcoming trial was shown.

### ***Fitting the drift diffusion model to the data***

The drift diffusion models (DDM) assumes that two-choice decisions are made by a noisy process that accumulates information over time from a starting point ( $z$ ) towards one of two choice criteria or boundaries (here, corresponding to left and right response decision, respectively; **Figure 24a**). When one of the boundaries is reached, a response is initiated. The starting point and the decision boundaries are separated by distance ( $a$ ).

The evidence that drives the accumulation process, the drift rate ( $v$ ), is derived from the representation of the stimulus. The better the quality of the evidence, the larger the drift rate toward the appropriate decision boundary, and the faster and more accurate the response (**Figure 24c**). The components of processing acting outside the decision process itself, such as encoding and response output, are combined in a single parameter: the non-decision time

parameter ( $T_{er}$ ). RT being the result of non-decision time added to the time it takes for accumulated evidence to reach one of the boundaries, and sensitivity coming from the reached boundary that determines which response is given, the model extracts the components of the decision process (values of drift rate, non-decision processes, and boundaries) from RT distribution and sensitivity data simultaneously.

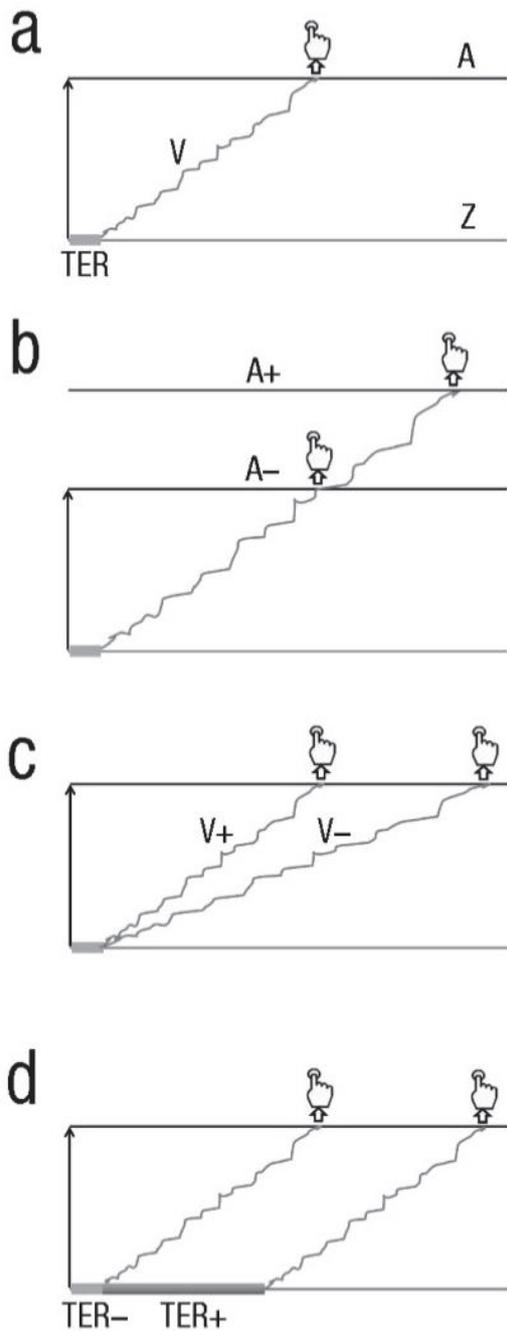
For fitting the diffusion model to the data (Ratcliff and Tuerlinckx 2002; Vandekerckhove and Tuerlinckx 2007), we used the MATLAB Diffusion Model Analysis Toolbox (DMAT (Vandekerckhove and Tuerlinckx 2008)). The DMAT extracts the components of the decision process and their variability from RT distribution and sensitivity data from all trials for each condition. All trials, correct responses and errors are thus included in the DMAT parameter estimation. Parameters are estimated by maximizing a multinomial likelihood function. Left and right trials being equally distributed across the experiment (50% of trials for each direction, within each block), the underlying diffusion processes are supposed to be symmetric and no bias toward the left or right answer should arise.

We ran a model in which the starting point ( $z$ ) was estimated independently from the decision boundary for the left and the right button-presses separately. We then checked that ( $z$ ) was not different between left and right responses using a one way rmANOVA with response direction as factor. The analyses showed no effect of response direction ( $F_{1,37} = 971$ ;  $p = 0.001$ ), ensuring that no bias emerged toward either the left or the right response. Consequently, we

applied in all our models a starting point equal to half the distance between the left and right decision criteria ( $z = \frac{1}{2} a$ ). Each model was fitted to the data separately for each participant.

The first model we ran allowed all three parameters to vary (the boundary –  $a$  -, the drift -  $v$  - and the non-decision time –  $T_{er}$  -). The estimated parameter values did not follow a normal distribution, we thus used a decimal logarithmic transformation and ensured it normalized their distribution using Lilliefors tests (**Table 1**) before we applied the 3-way repeated-measures Analysis of Variance (rmANOVA). The 3 factors were the Beneficiary of the decision, the Payoff associated with the decision and the Difficulty (dot coherence).

The boundary ( $a$ ) and the non-decision time ( $T_{er}$ ) showed no effect of any factor. We thus ran a model in which only the drift ( $v$ ) was free to vary across conditions. Once again, we analyzed  $\log(v)$  using the same 3 way rmANOVA. In order to compare the goodness of fit of our models we also ran the intermediate models (either the drift and the boundary or the drift and the non-decision time were allowed to vary) and compared the sum of the individual Bayesian Information Criterion (BIC) of the models.



**Figure 24. Drift Diffusion Models (DDM) and hypotheses.** a) DDM main parameters. DDM assumes that two-choice decisions are made by a noisy process that accumulates information, with a given drift rate ( $V$ ), over time. This process goes from the starting point ( $Z$ ) toward the decision boundary. When the boundary is reached, a response is initiated (with a button press, in usual experimental set-ups). The starting point and the boundary are separated by the distance ( $A$ ). **(b-d) Effects of boundary modulation, drift-rate changes and non-decision time variation on response initiation.** b) Boundary modulation. A boundary increase ( $A+$ ) leads to decisions that require more sensory evidence, and thus a longer time than when a lower boundary is set-up ( $A-$ ). c) Drift-rate change. A drift rate increase ( $V+$ ) produces faster sensory evidence accumulation than a lower one ( $V-$ ), producing faster reaction-times. d) Non-decision time variation. A longer non-decision time ( $TER+$ ) leads to slower decisions than a shorter one ( $TER-$ ).

### **2.3.2. Results**

Participants performed a RDK (left/right direction categorization) task to win low or high payoffs, for themselves or for a close relative. Reaction-Times (RT) and sensitivity ( $d'$ ) were collected and analyzed using 3 way repeated measures analyses of variances (rmANOVAs), with 'Beneficiary' (two levels: Other vs. Self), 'Payoff' (two levels: High vs. Low) and 'Difficulty' (two levels: Difficult - vs. Easy) as factors.

#### ***Sensitivity ( $d'$ )***

Participants missed only 1 trial in the experiment. A main effect of task Difficulty was found,  $d'$  was better during Easy trials than during Difficult trials ( $d'_{\text{Easy}} = 0.82$ ;  $d'_{\text{Difficult}} = 0.79$ ;  $F_{1,37} = 57.4$ ;  $p = 0.0000001$ ; Cohen's  $d = 0.362$  – **Figure 25a**). All interaction effect also reached significance, including the triple interaction effect ( $F_{1,37} = 16.8$ ;  $p = 0.000220$ ). We consequently ran 2 way rmANOVAs for each difficulty level, keeping Beneficiary and Payoff as factors.

During Easy trials,  $d'$  was better for Self than for Other ( $d'_{\text{Self}} = 0.83$ ;  $d'_{\text{Other}} = 0.80$ ;  $F_{1,37} = 16.2$ ;  $p = 0.000276$ ; Cohen's  $d = 0.305$  – **Figure 26a**) and better for Low than for High Payoffs ( $d'_{\text{Low}} = 0.83$ ;  $d'_{\text{High}} = 0.81$ ;  $F_{1,37} = 11.5$ ;  $p = 0.001683$ ; Cohen's  $d = 0.266$  – **Figure 26d**).

During Difficult trials, both Beneficiary ( $d'_{\text{Self}} = 0.77$ ;  $d'_{\text{Other}} = 0.80$ ;  $F_{1,37} = 24.7$ ;  $p = 0.000015$ ; Cohen's  $d = 0.375$ ) and Payoff ( $d'_{\text{Low}} = 0.77$ ;  $d'_{\text{High}} = 0.81$ ;  $F_{1,37} = 30.0$ ;  $p = 0.000003$ ; Cohen's  $d = 0.465$ ) were significant. The Beneficiary\*Payoff interaction also reached significance ( $F_{1,37} = 19.9$ ;  $p = 0.000072$ ). Sensitivity for Self-affecting decisions associated with a Low Payoff was lower than for Other-affecting ones ( $d'_{\text{Self}} = 0.74$ ;  $d'_{\text{Other}} = 0.80$ ;  $p < 0.000001$ ; Cohen's  $d = 0.780$ ) and lower than when associated with a High Payoff (Self:  $d'_{\text{High}} = 0.80$ ; Other:  $d'_{\text{High}} = 0.81$ ;  $p < 0.000001$ ; Cohen's  $d = 0.816$  – Figure 27a).

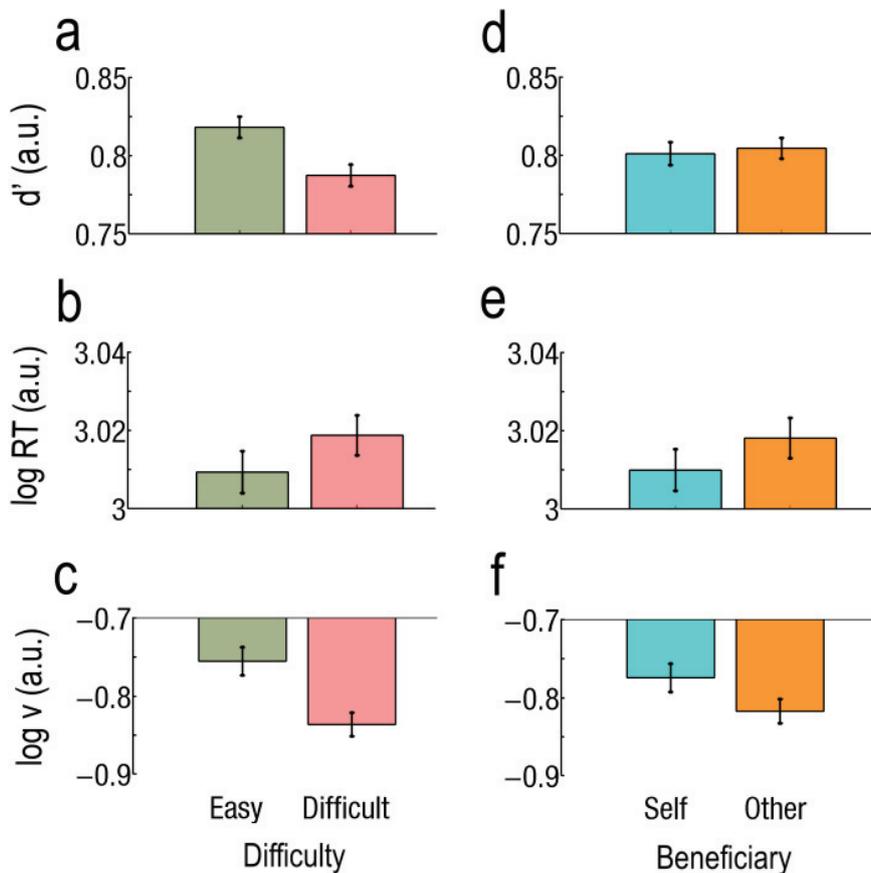
### ***Reaction-times***

The results presented here come from analyses performed on logarithmically transformed Reaction-Times (decimal logarithm), for correct and error trials separately. For intelligibility, the mean values in the following paragraph are given as non-transformed RT, in milliseconds (ms). Difficulty had an effect on log RT from errors, subjects being slower during Difficult than during Easy trials ( $RT_{\text{Difficult}} = 1146$  ms;  $RT_{\text{Easy}} = 1110$  ms;  $F_{1,37} = 6.6$ ;  $p = 0.0146$ ; Cohen's  $d = 0.209$ ). This was the only effect on RT from errors.

All the following results concern correct responses. We found a main effect of task Difficulty (**Figure 25b**) and a main effect of Beneficiary (**Figure 25e**) on log RT (for correct responses). That is, RT were slower during Difficult than during Easy trials ( $RT_{\text{Difficult}} = 1055$  ms;

$RT_{\text{Easy}} = 1033$  ms;  $F_{1,37} = 36.56$ ;  $p < 0.001$ ; Cohen's  $d = 0.144$ ) and slower for Other than for Self ( $RT_{\text{Other}} = 1054$  ms;  $RT_{\text{Self}} = 1035$ ms;  $F_{1,37} = 18.86$ ;  $p < 0.001$ ; Cohen's  $d = 0.125$ ). The triple interaction effect was not significant ( $F_{1,37} = 0.22$ ;  $p = 0.645$ ). However, both the Beneficiary\*Difficulty and the Payoff\*Difficulty interaction effects reached significance ( $F_{1,37} = 37.10$ ;  $p < 0.000001$  and  $F_{1,37} = 4.26$ ;  $p = 0.0461$  respectively). Given the main effect of Difficulty, we then ran separated 2-way rmANOVA at each Difficulty level, keeping Beneficiary and Payoff as factors.

RT were slower for Other than for Self, during easy trials only ( $RT_{\text{Other}} = 1047$  ms,  $RT_{\text{Self}} = 1020$  ms,  $F_{1,37} = 32.6$ ;  $p = 0.000002$ ; Cohen's  $d = 0.180$  – **Figure 26b**). Payoff had an effect at both Difficulty level, but with opposite direction. During easy trials, RT were slower for High than for Low Payoffs ( $RT_{\text{High}} = 1049$  ms,  $RT_{\text{Low}} = 1017$  ms,  $F_{1,37} = 23.5$ ;  $p = 0.000022$ ; Cohen's  $d = 0.203$  – **Figure 26e**)., while during difficult trials, they were faster for High than for Low Payoffs ( $RT_{\text{High}} = 1045$  ms,  $RT_{\text{Low}} = 1065$  ms,  $F_{1,37} = 21.53$ ;  $p = 0.000043$ ; Cohen's  $d = 0.142$ ; **Figure 27b**).



**Figure 25. (a, b, c) Main effect of difficulty.** Easy trials are green on the left, Difficult trials red and on the right. **a)** Sensitivity ( $d'$ ) is worse, **b)** Reaction-Times (RT) is longer, and **c)** drift rate ( $v$ ) is lower during Difficult trials than during Easy trials. **(d, e, f) Main effects of beneficiary.** Self-affecting trials are cyan on the left, Other-affecting trials are orange on the right **d)** Sensitivity did not differ but there was **e)** a faster RT and **f)** a higher drift-rate ( $v$ ) for Self than for Others. Log RT,  $d'$  and log  $v$  are expressed in arbitrary units (a.u.). Bars represent the standard errors of the mean (s.e.m).

### ***Drift diffusion model parameters***

We started with the selection of the best fitting model. The first model we ran allowed all three parameters (the boundary –  $a$  -, the drift -  $v$  - and the non-decision time –  $T_{er}$  -) to vary. In this model ('full model'), neither the boundary ( $a$ ) nor the non-decision time ( $T_{er}$ ) showed any significant effect of any of the three factors (Beneficiary, Payoff or Difficulty). We thus applied a model where only the drift ( $v$ ) was free to vary across conditions (' $v$  free'). In order to compare the goodness of fit of our models we also ran the intermediate models (either the drift and the boundary, ' $v$  free -  $a$  free', or the drift and the non-decision time, ' $v$  free -  $T_{er}$  free', were allowed to vary) and compared the sums of the individual Bayesian Information Criterion (BIC) of the models. The model in which only the drift ( $v$ ) was allowed to vary showed a lower BIC than all other models (BIC sums: full model:  $7.62 \times 10^4$ ;  $v$  free:  $7.30 \times 10^4$ ;  $v$  free –  $a$  free:  $7.46 \times 10^4$ ;  $v$  free –  $T_{er}$  free:  $7.45 \times 10^4$ ). To ensure that this reflected individual fits, we also compared the BICs of the models within each individual. 36 over 38 subjects were best fitted with the model in which only the drift is allowed to vary (' $v$  free'); the 2 other subjects were best fitted with the addition of modulations of the boundary  $a$  (' $v$  free -  $a$  free'). Furthermore, we ran the simulations of the data predicted by the model using the estimated parameter, for each subject (**Annex 3**).

We subsequently applied a 3 way (Beneficiary, Payoff, Difficulty) rmANOVAs on the drift parameter ( $v$ ) from the ' $v$  free' model. Note that  $\log(v)$  values are negatives, so that higher absolute values of  $\log(v)$  actually mean lower drift rates ( $v$ ) of the decision variables. Difficulty

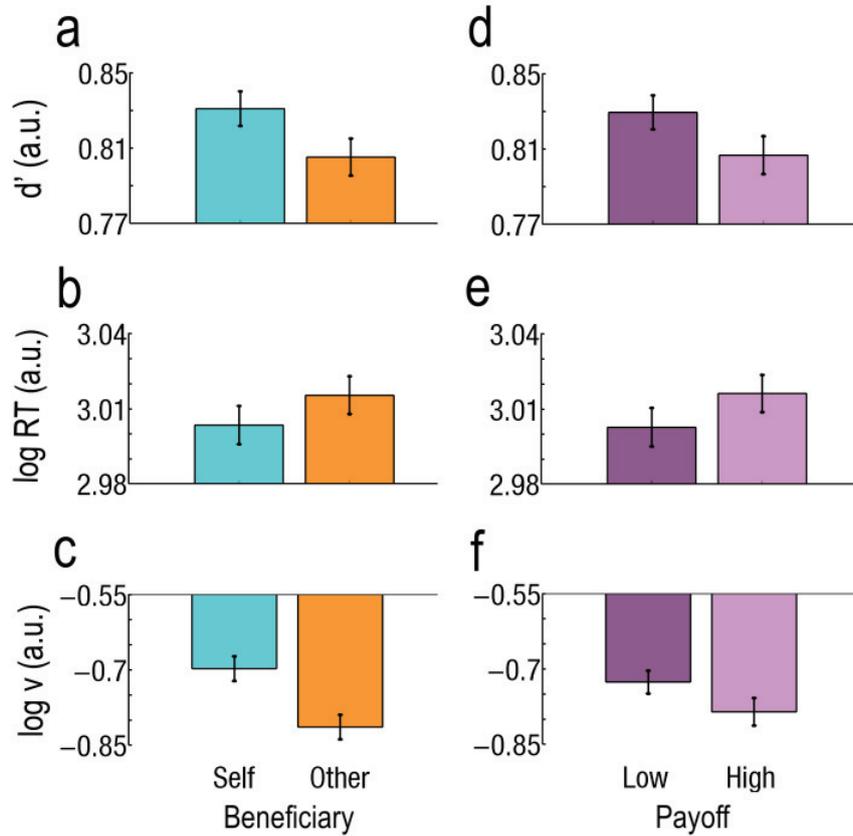
had a main effect on the drift rate ( $v$ ), which was higher during Easy than during Difficult trials ( $\log(v)_{\text{Easy}} = -0.76$ ;  $\log(v)_{\text{Difficult}} = -0.84$ ;  $F_{1,37} = 35.9$ ;  $p = 0.000001$ ; Cohen's  $d = .503$  - **Figure 25c**). Beneficiary also had a main effect, ( $v$ ) being higher during Self- than during Other-affecting decisions ( $\log(v)_{\text{Self}} = -0.78$ ;  $\log(v)_{\text{Other}} = -0.82$ ;  $F = 4.42$ ;  $p = 0.0423$ ; Cohen's  $d = 0.273$  - **Figure 25f**).

The Beneficiary\*Payoff interaction also reached significance ( $F_{1,37} = 6.28$ ;  $p = 0.01673$ ). For decision associated with a High Payoff, ( $v$ ) was higher for Self than for Other ( $\log(v)_{\text{Self}} = -0.76$ ;  $\log(v)_{\text{Other}} = -0.83$ ;  $p = 0.000078$ ; Cohen's  $d = 0.385$ ). The Beneficiary\*Difficulty and the Payoff\*Difficulty interactions were significant ( $F_{1,37} = 29.5$ ;  $p = 0.0000004$  and  $F_{1,37} = 13.3$ ;  $p = 0.000801$ , respectively). We consequently ran 2 way-rmANOVAs at each Difficulty level, keeping Beneficiary and Payoff as factors.

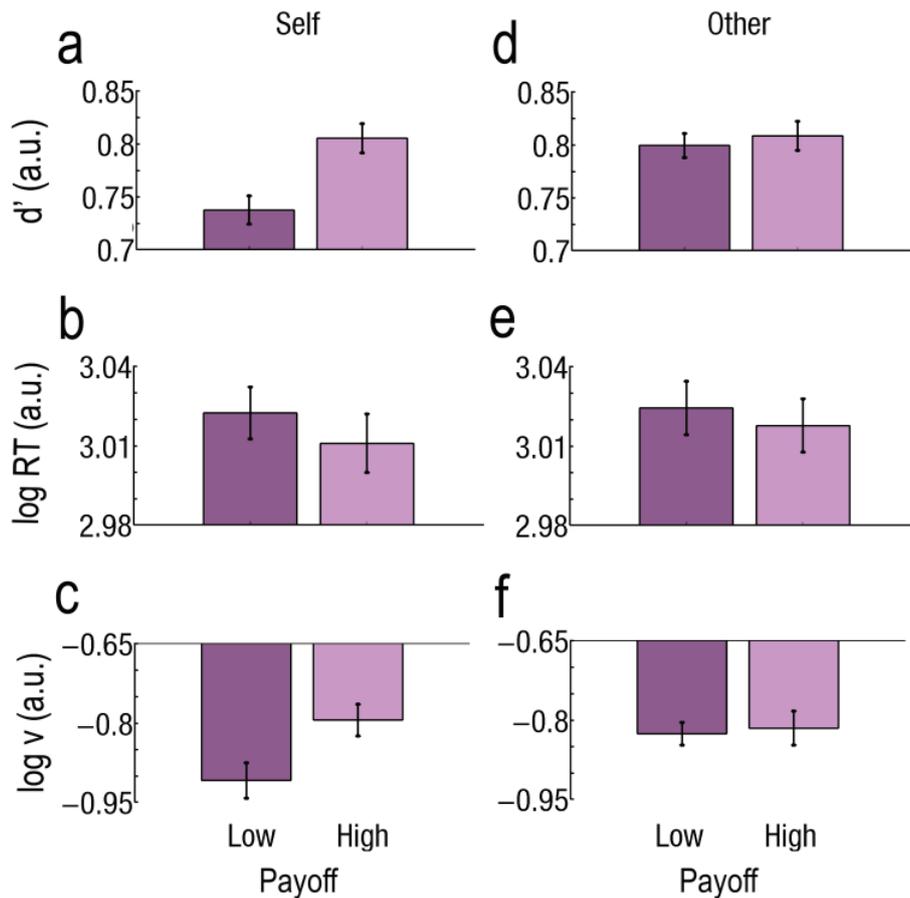
During Easy trials, both Beneficiary and Payoff had a main effect: the drift ( $v$ ) was higher for Self than for Other ( $\log(v)_{\text{Self}} = -0.70$ ;  $\log(v)_{\text{Other}} = -0.81$ ;  $F_{1,37} = 19.8$ ;  $p = 0.000076$ ; Cohen's  $d = 0.587$ ; **Figure 26c**) and higher for Low than for High Payoffs ( $\log(v)_{\text{High}} = -0.79$ ,  $\log(v)_{\text{Low}} = -0.73$ ,  $F_{1,37} = 6.18$ ;  $p = 0.017588$ ; Cohen's  $d = 0.179$ ; **Figure 26f**).

During Difficult trials, Payoff had a main effect ( $\log(v)_{\text{High}} = -0.81$ ,  $\log(v)_{\text{Low}} = -0.87$ ,  $F_{1,37} = 9.28$ ;  $p = 0.004265$ ; Cohen's  $d = 0.409$ ) but the Beneficiary\*Payoff interaction was also significant ( $F_{1,37} = 8.80$ ;  $p = 0.005251$ ). Payoff actually had an effect only for Self-affecting

decisions, with a higher drift ( $v$ ) for High than for Low Payoffs ( $\log(v)_{\text{High}} = -0.80$ ,  $\log(v)_{\text{Low}} = -0.91$ ;  $p = 0.000045$ ; Cohen's  $d = 0.592$ ; **Figure 27c**).



**Figure 26. Effect of beneficiary and payoff for easy trials only. (a, b, c) Beneficiary.** Self-affecting trials are cyan and on the left, Other-affecting trials are orange and on the right. During Easy trials, **a)** Sensitivity ( $d'$ ) is better, **b)** Reaction-Times (RT) is faster, and **c)** drift rate ( $v$ ) is higher for Self than for Other. **(d, e, f) Effect of payoff.** Low Payoffs are in deep purple on the left, High Payoff are in light purple on the right. **d)** Sensitivity ( $d'$ ) is better **e)** RT is faster **f)** and ( $v$ ) is higher for Low than for High Payoffs. Log RT,  $d'$  and  $\log v$  are expressed in arbitrary units (a.u.). Bars represent the standard errors of the mean (s.e.m).



**Figure 27. Effect of payoff for difficult trials for self and close relative (other). (a, b ,c) Effect of payoff for Self. a)** Sensitivity ( $d'$ ) is lower, **b)** Reaction-Times (RT) is slower, and **c)** drift rate ( $v$ ) is lower for Low Payoffs than for High Payoffs **(d, e, f) Effect of payoff for Other.** There is no difference in **d)** sensitivity ( $d'$ ), **e)** neither RT **f)** nor  $v$  between Low and High Payoffs. Log RT,  $d'$  and  $\log v$  are expressed in arbitrary units (a.u.). Bars represent the standard errors of the mean (s.e.m).

### **2.3.3. Discussion**

Taking advantage of the Drift Diffusion Model (DDM) and the perceptual decision-making framework, we provided a mechanistic explanation of how others are integrated into the decisional process. Our results indicate that the beneficiary of the incentive associated with a decision modifies how decisions are performed. Decisions were faster for self than for others. As explained by the DDM, this was related to a higher drift rate ( $v$ ) of the decision variable. In the present experiment, better sensitivity and faster RT were mirrored by higher drift rates. Higher drift rates have been found to explain shorter RT in tactile discrimination as well (Martijn J. Mulder and Maanen 2013).

A change in the drift rate of the decision variable indicates a modification of the integration process itself, as branding does for economic value-based choices (Philiastides and Ratcliff 2013). Our result indicates that sensory evidence is integrated faster for self than for others. In the example of the shooting range, if we aim to reach a target to win a prize for a close relative, the decision process would not differ in the amount of evidence we would accumulate before making the decision to shoot, but rather in the efficiency of accumulation of the sensory evidence.

It may be that participants tried to imagine their relative receiving the payoff, although not instructed to do so. This would have required a higher cognitive demands and redirect part of the attentional load and neuronal energy from the evidence accumulation process. Using the Game Theory and Public Good Games, studies show that taking into account another person into a decision engages the processes of *mentalizing* (or the Theory of Minds) (Stallen and Sanfey 2013; C. D. Frith and Singer 2008)

It could also be that, when performing a self-affecting decision, more attentional resources are spent on the task (because of a higher motivation, due to direct self-benefit), thereby increasing the efficiency of evidence accumulation. In a study on value-based decision making combined with DDM, it has been suggested that, when choosing on behalf of another, a dual-process takes place. Stimulus value integration, reflected in the drift rate ( $v$ ), would be firstly computed based on self-preferences and then adjusted to the other's inferred preferences (Harris, Clithero, and Hutcherson 2018). For others with similar preferences, RTs were longer and linked to a change in drift rate.

Analogous mechanisms could have occurred during our experiment as well. The importance accorded to the evidence, reflected in the drift rate ( $v$ ) of the decision variable, could have been initially lower during other-affecting decisions, or it could have been re-adjusted during the time of the decision. Alternatively, RTs for dissimilar others were also longer but associated with a higher decision boundary ( $a$ ), which could have been implemented to

overcompensate an increased uncertainty about their preferences (Harris, Clithero, and Hutcherson 2018).

Payoffs for others could have been integrated into the perceptual decision process through a change in the decision rules, outside of the mechanism of sensory evidence accumulation, and change the distance between the starting point of the decision variable and the decision boundary. Other researchers also suggested that payoff can modify both stages, evidence accumulation and decision boundary. It postulates two processes, one for payoffs and another for stimulus information and that on a given trial attention is directed toward one of these, never both (Diederich and Busemeyer 2006; Diederich 2008). Sequential-sampling models have previously been used to account for the effects of payoffs in a perceptual decision task with time constraints.

These studies have reported changes in the distance from the starting point to the decision boundaries, a bias in the starting point of the decision variable, induced either by prior probabilities of being correct (Leite and Ratcliff 2010; M. J. Mulder et al. 2012) or by asymmetrical payoffs associated with the possible response alternatives (Simen et al. 2009; M. J. Mulder et al. 2012). These changes were characterized by a shift of the starting point of the decision variable closer to the decision boundary associated with the alternative having the higher probability or associated with the higher payoff. The starting point is then further from the other boundary (for the other alternative at hand) and the decision variable is less likely to reach it, establishing a bias and a change in response proportion.

In contrast, our experimental set-up was designed to avoid response probability manipulations toward one of the (left or right) alternatives, in terms of probability (through trial randomization) and in terms of payoff (by assigning the same payoff to both response alternatives). We aimed to compare identical decisions made by the participants, either for themselves or for another person. It would be interesting to adapt our paradigm to asymmetrical alternatives, with the payoff going to one of the beneficiaries depending on the correct answer. Following our results, it could be expected that a bias toward the response associated with self-payoff would emerge.

Finally, a variation in the non-decision time ( $T_{er}$ ) would have indicated that the beneficiary-related motivation acts on cognitive mechanisms that are outside of the decision process itself, such as primary encoding of the stimuli and motor execution. Non-decision time is usually referred to as reflecting the early encoding of the stimulus of interest and the execution of the motor response, once the decision process is completed, both external to the visuo-motor decision process in itself (Ratcliff and McKoon 2008; Martijn J. Mulder and Maanen 2013; Ravenzwaaij, Dutilh, and Wagenmakers 2012; Zhang et al. 2016; Zhang and Rowe 2014). Moreover, the non-decision time is thought to be necessary to account for speed-accuracy trade-offs (Martijn J. Mulder and Maanen 2013) and it has been shown that speed-accuracy instructions also modulate the non-decision time (Zhang and Rowe 2014). Variation in the non-decision time can mean that different strategies are applied (Schuch 2016) and could include

other components that influence the decision making processes. However, the Drift diffusion Model cannot distinguish between different mechanisms within the non-decision time.

The present study is a first step towards a better comprehension of how others influence decision making processes. Altogether, our results suggest the beneficiary affected by the decision is integrated together with the sensory evidence into the decision variable and affects the efficiency of the accumulation process during perceptual decision making. The present work provides further evidence of the strength of sequential sampling models in a unified theory of choices (Summerfield and Tsetsos 2012; Polanía et al. 2014; 2015), with outcomes that are self-interested or vicarious. However, while the main effect of beneficiary was significant on RT and drift rate ( $v$ ), when analyzing difficulty levels separately, the effect was not present during difficult trials. This may be attributed to the fact that sensory evidence was too low for the drift to be modulated. Although the study of payoff *per se* was not our main goal, it is puzzling to observe that its effect was reversed between the easy and difficult levels. Further studies are needed to confirm both results. A future direction would also be to specify how social distance to others changes perceptual decisions, as previously investigated using economic games in which participants chose between selfish and generous alternatives (Strombach et al. 2015).

Statistics Factor	logRTc		d'	
	BEN	F <sub>1,32</sub> =2.09	p=0.158	F <sub>1,32</sub> =1.69
PAY	F <sub>1,32</sub> =0.67	p=0.418	F <sub>1,32</sub> =2.61	p=0.116
DIF	F <sub>2,64</sub> =34.7	p< 0.000001	F <sub>2,64</sub> =25.1	p< 0.000001
BEN * PAY	F <sub>2,64</sub> =0.66	p=0.423	F <sub>2,64</sub> =0.09	p=0.766
BEN * DIF	F <sub>2,64</sub> =0.03	p=0.971	F <sub>2,64</sub> =0.95	p=0.392
PAY * DIF	F <sub>2,64</sub> =7.26	p=0.0014	F <sub>2,64</sub> =4.54	p=0.014
BEN * PAY * DIF	F <sub>2,64</sub> =4.01	p=0.023	F <sub>2,64</sub> =1.99	p=0.144

**Table 2. When the other is anonymous, the main effect of beneficiary is not significant on Reaction-Times and on sensitivity (d').** There were three difficulty levels (13%, 15%, 17% of dots coherence) in this version. Otherwise, factors were identical. The analysis was performed on logarithmically transformed reaction-times from correct trials (logRTc) on 33 participants. BEN: Beneficiary; PAY: Payoff; DIF: Difficulty.

Factor	logRTc		d'	
	F <sub>1,37</sub>	p	F <sub>1,37</sub>	p
Gender	1.10	0.302	0.075	0.785
BEN * Gender	2.26	0.141	0.378	0.543
PAY * Gender	1.23	0.274	0.235	0.631
DIF * Gender	1.14	0.294	0.253	0.618
BEN * PAY * Gender	0.00	0.992	0.636	0.430
BEN * DIF * Gender	0.16	0.689	0.515	0.478
PAY * DIF * Gender	1.24	0.273	1.35	0.253
BEN * PAY * DIF * Gender	1.75	0.194	0.261	0.612

**Table 3.** There was no effect of gender on Reaction-Times (RT) nor on sensitivity (d'), nor on interaction with any of our three factors (BEN: Beneficiary; PAY: Payoff; DIF: Difficulty). The analysis was performed on logarithmically transformed reaction-times from correct trials (logRTc).

	<i>Condition</i>							
	<i>Self</i>				<i>Other</i>			
	<i>Low</i>		<i>High</i>		<i>Low</i>		<i>High</i>	
	<i>Easy</i>	<i>Difficult</i>	<i>Easy</i>	<i>Difficult</i>	<i>Easy</i>	<i>Difficult</i>	<i>Easy</i>	<i>Difficult</i>
<b>v</b>	.049	.061	.233	> .5	.232	.001	.001	.017
<b>a</b>	.284	>.5	.035	.405	.368	.001	>.5	.005
<b>Ter</b>	.003	.193	.007	.084	.289	.004	.088	.003
<b>Log(v)</b>	.273	>.5	>.5	.301	>.5	.210	.459	.004
<b>Log(a)</b>	>.5	.298	>.5	.195	.063	.485	.052	.151
<b>Log(Ter)</b>	.140	>.5	>.5	.001	>.5	.389	>.5	.194

**Table 4. Log transformation effectively normalized parameter distributions.** P-values of the (Lilliefors) normality tests performed on the drift diffusion model estimated parameters and their logarithmic transformation. v: drift rate; a: boundary; Ter: non-decision time. Log() :decimal logarithmic transformation.

## ***2.4. MEG experiment: neural dynamics of perceptual decision for self and other rewards***

Before crossing the street, we accumulate sensory evidence (the movements of cars) until we make the decision to cross. If such perceptual decisions are made on behalf of one's child, will the brain process information in the exact same way or will the mechanisms at play differ when making this decision? More generally, how do motivational incentives for oneself and for someone close influence the neural mechanisms engaged in making simple perceptual choices? In recent years, social decision neuroscience has investigated how human and non-human primates decide to allocate resources between oneself and another group member, and which neural systems are engaged when making such decisions (Van Lange 1999; Mobbs et al. 2009; Haruno and Frith 2010; S. W. C. Chang, Gariépy, and Platt 2013; Báez-Mendoza and Schultz 2013; Strombach et al. 2015; Apps, Rushworth, and Chang 2016).

Taking other's interests into account allows animals to maintain relationships in social groups. Behavior observed in economic games that mimic real-life situations show individual differences in the division of resources (Van Lange 1999). Such social decisions, made when sharing resources with others, engage 'social brain' regions such as the temporo-parietal junction (TPJ) (Mobbs et al. 2009; Haruno and Frith 2010; S. W. C. Chang, Gariépy, and Platt 2013; Báez-Mendoza and Schultz 2013; Strombach et al. 2015; Apps, Rushworth, and Chang 2016). These economic decisions concern a person's preference about how to allocate

resources when *arbitrating* between one's own payoff and another person's. As a consequence, taking other's interest into account in the decision process is intrinsically associated with direct payoff for oneself. However, deciding how much resource to allocate to others is very different from making perceptual decisions, since the latter constitute a fundamental ability to adaptively transform sensory inputs into a correct behavioral response.

One important question, which remains to be addressed, is to understand the neural dynamics of perceptual decision making processes using a combination of precise temporal techniques (MEG) and of computational modeling to characterize the neuro-computational mechanisms underlying the influence of payoff for oneself and for others on perceptual decision making. The framework of sequential-sampling models, such as drift-diffusion models (DDM), has proven to be a powerful approach to explain the processes underlying perceptual decision-making (Smith and Ratcliff 2004; Gold and Shadlen 2007b; Ratcliff and McKoon 2008; Hauke R. Heekeren, Marrett, and Ungerleider 2008; Summerfield and Tsetsos 2012).

In this framework, the decision-making process is represented by an abstract variable drifting with evidence accumulation, from a given starting point towards one of several decision boundaries. Each boundary acts as a decision threshold for an option, so that the outcome of a decision is made when the decision variable reaches one of the boundaries. Such perceptual decisions engage a fronto-parietal network (Hauke R. Heekeren, Marrett, and Ungerleider 2008; Summerfield and Tsetsos 2012; Keuken et al. 2014; 2017; M. J. Mulder, van Maanen, and

Forstmann 2014; Boehm et al. 2015; Kelly and O’Connell 2015; Hanks and Summerfield 2017; Siegel, Engel, and Donner 2011).

When investigating the neural dynamics of such choices in humans, a positive ramp-like evoked EEG signal has been shown to emerge after target onset and to peak at the time of the motor response over Centro-Parietal areas (O’Connell, Dockree, and Kelly 2012). This Centro-Parietal Positivity (CPP) is a perfect candidate for a DDM decision variable correlate in the human brain because its time course builds as a cumulative function of sensory evidence and determines behavior via a boundary-crossing criterion. The Motor Readiness activity, related to movement preparation, also displays aspects of DDM, with evidence accumulation towards a decision boundary (Kelly and O’Connell 2013; Twomey et al. 2015) (Gluth, Rieskamp, and Büchel 2012; Smyrnis et al. 2012; Marieke K. van Vugt et al. 2014).

Here, using MEG and the DDM framework, we investigated how the beneficiaries of the rewards (oneself vs another) modify the dynamics of perceptual decision-making processes. Participants performed a random-dot task of varying difficulty level (level of moving dots coherency), level of Payoffs (low vs high), and beneficiaries (oneself or close relative). We tested whether vicarious information modifies the encoding stage, the accumulation process and/or the read-out mechanism. At the level of the MEG signal, we expected to find accumulation of evidence decision-related differences over the centro-parietal cortex, on an MEG equivalent of the CPP, and over pre-motor/motor cortices, on an MEG equivalent of the EEG Readiness Potential, both reflecting the decision variable. We hypothesized that neural signals undergoing

gradual changes after stimulus onset should show steeper slopes for faster response times (RTs), reflecting higher drift rates. Moreover, we expected that the amplitude of the MEG signals aligned to the motor response would show a threshold effect at the time of commitment, an essential characteristic of a decision variable.

### ***2.4.1. Material and methods***

#### ***Subjects***

##### ***Behavioral experiment***

40 healthy subjects were recruited by advertisements in the Lyon 1 Claude Bernard University students' mailing list. Two were excluded, because of chance level performances for one and one because technical problems, leaving 37 subjects for further analyses (15 females; mean age = 22, range 18-34). Subjects were screened using self-reports to exclude any psychiatric or neurological history and current or previous substance abuse (except nicotine and festive alcohol consumptions). All participants gave written informed consent and the study was approved by the local research ethics committee (Comité de Protection des Personnes Sud-Est III), all methods were performed in accordance with the relevant guidelines and regulations.

### ***Magneto-Encephalo-Graphy (MEG) experiment***

21 healthy subjects were recruited by advertisement in the Lyon 1 Claude Bernard University students' mailing list. Two subjects were excluded from further analysis, subsequently because of chance level performances for one and technical problems for the other, leaving 19 subjects (7 females, range 18-35; mean age 24). Subjects were screened using self-report to exclude any psychiatric or neurological history and current or previous substance abuse. The study was approved by the local research ethics committee and all subjects gave written informed.

### ***Procedure***

The volunteers came a first time to check that they met the inclusion criteria. Participants were explained that half of the task would be performed to win money for a close relative – whom they had to choose before coming to the experiment. The (behavioral or MEG) experiment was then scheduled. At their arrival the day of the experiment, participants signed the informed consents. After, they were invited to read the task instructions, which were then orally explained to them again. Finally, the participants were installed in the experimental environment, as comfortably as possible and trained until the task was understood.

## ***Training***

The training was composed of 10 trials at 15% of coherently moving dots, which corresponds to the Easy level. To ensure that participants did not respond randomly, a sensitivity ( $d'$ ) criterion was set at  $d = 0.6$  (i.e. 60% correct, which is higher than chance level). They performed a second training, if subjects were below this criterion during training or if they asked for it.

For the MEG part, the participant was familiarized with the task first outside and then the training itself took place inside the MEG shielded room. They could then get used to the MEG apparatus and the timings during which when they could blink (after feedback and until the stationary dots appeared) without loss of the data of interest for us. After training, we launched the task once ensured again that the participant were ready and comfortable.

The task was composed of 4 blocks, of 208 trials each. A break of the duration of their choice was allowed between each of the blocks. At the end of the experiment, participants were debriefed orally and through a questionnaire.

## ***Target Stimuli***

Random dot kinematograms (RDKs) were programmed using the Matlab® Psychtoolbox (Brainard 1997; Pelli 1997). The mask stimulus was a drifting random dot display of 2000 ms duration. Dots were white, on a black background, each frame being composed of 50 white Gaussian blobs with a diameter of 2.85 mm. The dots were moving with a speed of  $2.7^\circ/\text{s}$  from their locations through their (random or coherent) trajectories and each dot had a life-duration of 500ms.

The motion of the dots was made by replotting dots corresponding to the previous ones at a determined spatial offset in the same direction so that all the dots moved in their directions at the same speed. During the experiment, RDKs appeared in a square centered on the screen and taking up 30.8% of it, with participants at a distance of 60 cm from the screen (Dell, 19'', screen resolution set to 1280x1050, vertical refresh rate of 60 Hertz), for participants taking the behavioral experiment outside the MEG and at 135 cm for participants taking the MEG experiment. Inside the MEG, the task was displayed on a 25x19 cm screen with a resolution of 1024x768 pixels *at a refreshing rate of 60 Hz*.

### ***Instructions***

The participants were asked to discriminate the left/right direction of coherently moving dots in order to win Low Payoffs or High Payoffs for themselves, or for the beneficiary they

previously chose. Low and High Payoffs were respectively 2 € and 10€ outside the MEG and 10€ and 30€ inside. They were instructed to give one, and only one, response while the dots were moving: if they gave more than one response or did not respond, it would be considered as incorrect (although misses and errors were collected separately).

Moreover, for them to think every decision was equally important, they were told that one trial of each beneficiary condition (Self/Other) would be randomly selected by a computer program to determine their respective final payoffs: the payoff would be actually won if the selected trial was correct, but nothing would be added if it was an error.

### ***Conditions***

There was a square, centered on the fixation cross, all along the task (except for breaks). The inter-trial-interval announced the condition of the upcoming trial (**Figure 28**). This consisted of a word, displaying the beneficiary of the decision to come ('him' for others-affecting decisions, 'me' for self-affecting decisions) and a rectangle on the right of this inscription, filled proportionally to the payoff associated with the decision (full filled rectangle for 30€, one-third filled rectangle for 10€).

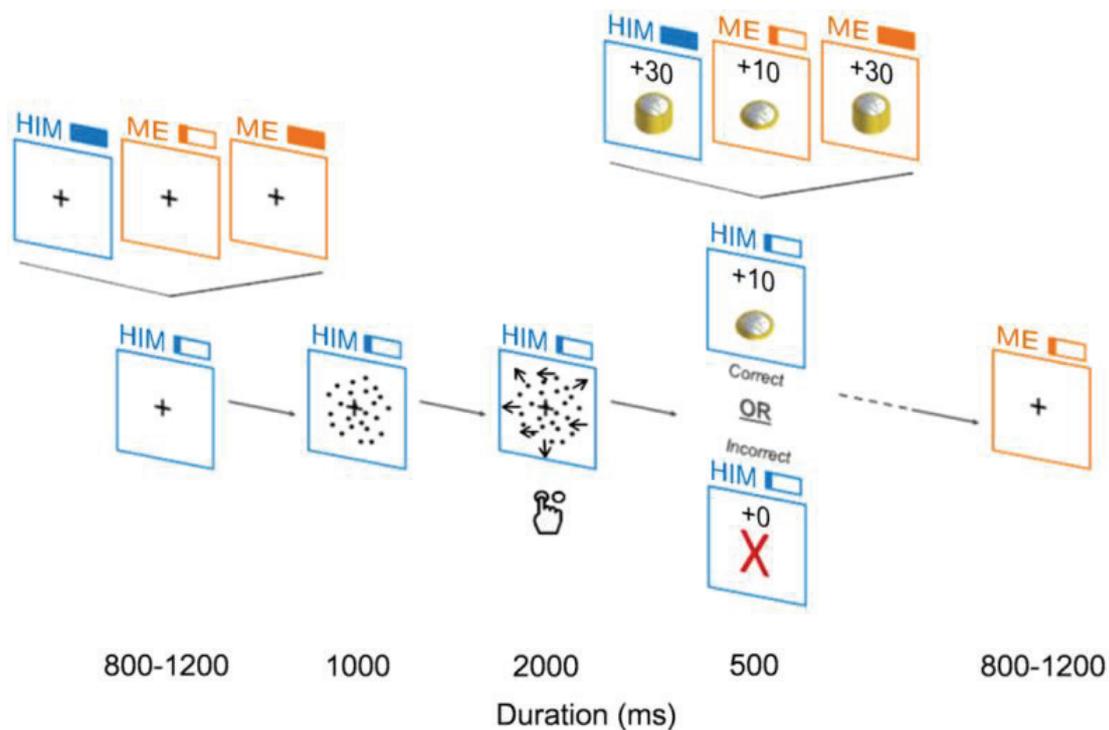
This (beneficiary-payoff) double-cue remained during the entire trial. It was displayed above a square where the dots would subsequently appear and this square and the cues were

depicted in a specific color (yellow or blue), according to the beneficiary of the trial. This color was used to emphasize the beneficiary of the decision, and was counterbalanced between subjects. In addition, trials were either easy (15% of dots coherence) or difficulty (13%), but participants were not informed of difficulty levels.

### ***Trial design***

Each trial began with the jittered (800-1200ms) inter-trial-interval (ITI). Then the first frame of the RDK to come (stationary dots) was displayed for 1000ms in the square below the (beneficiary-payoff) double-cue. Then, the RDK dot motion began and lasted 2000ms, during which the subject had to respond. Next, the feedback illustrated the outcome for 500ms. If the response was correct, a pile of coins proportional to the payoff was shown together with the payoff itself (“+10”, “+30”) above the pile of coins. For incorrect responses and misses, a red-colored cross was displayed together with “+0”.

The task outside and inside the MEG were identical except for one parameter: Payoff magnitude. Low Payoffs outside the MEG were 2€ and High Payoffs were 10€. Of course, instead of being in a MEG, with the helmet on the head, and instructions to blink only at specific times, participants were simply in a chair in front of a screen.



**Figure 28. Trials design:** Each trial began with a cue on the top of a square of a jittered duration of 800 to 1200 milliseconds (ms), saying ‘me’ or ‘him’ -for self- and other-affecting decisions respectively. A rectangle indicated the payoff associated with the decision, this rectangle was fully filled for high payoffs (30 €-) and one-fifth filled for low payoffs (10 €). The cue and the square were depicted in a specific color for each beneficiary (yellow for oneself and blue for other, and vice versa for counterbalance). Then, the first frame of the moving dots cinematic appeared in the square for 1000ms. Following which the target cinematic was presented for 2000 ms and the subject had to respond during this time. At the end of the 2000ms dot motion, the feedback was presented in term of payoff. If the response was correct, a pile of coins proportional to the payoff was shown together with the value of payoff itself (“+10”, “+30”) above it. For incorrect responses and misses, a red-colored cross was displayed together with “+ 0” on top of it.

### ***MEG data Recording***

Electrophysiological data were recorded in an electromagnetically shielded room using the Presentation software (Neurobehavioral Systems Inc.) and a CTF 275-channel whole-head MEG system (CTF Inc. Vancouver, Canada). Visual stimulation was projected from outside the magnetically shielded room, via mirrors onto a screen in front of the subject. Participants sat at approximately 1 m from the display screen. They responded to the target stimuli using a keypad, with their right hand. Ongoing neuromagnetic brain activity was acquired at a sampling rate of 600 Hz.

To allow continuous monitoring of subjects' head positions, three energized electrical coils were attached to the head fiducials (left and right pre-auricular, nasion). These coils emit small magnetic fields that are measured by the MEG sensors and can be used to locate each coil to correct for field movements of the subject's head every 200 ms. Vertical and horizontal bipolar electro-oculograms (EOG) were recorded for continuous eye movement monitoring and for offline artifact rejection. The subjects were asked to fixate the fixation cross during the entire trial and to blink only during the ITI.

### ***MEG Pre-processing and artifacts rejection***

Continuously recorded data were re-referenced to the average of the two mastoid references. A blink template has been characterized on each recorded block, for each subject. This template has been used for semi-automatic blink marking on the block of data. The marking has then been visually verified and perfected when needed. Blink markers were used to compute the average blink for each subject. The pre and post blink durations were used for blink rejection during data epoching. Trials containing an eye artifact within the time window of interest or in the baseline time-window were discarded during data epoching. The MEG raw data were also visually inspected for muscle artifacts, alpha bursts and SQUID jumps rejection. These were marked as bad data segments for automatic rejection during further data epoching. Data segments where the head position moved over 5mm from its recorded location were rejected as well.

The remaining MEG data were further analyzed using custom-made Matlab (The Mathworks, Natick, MA, USA) scripts, with the Matlab-based open source toolbox FieldTrip (<http://fieldtrip.fcdonders.nl>). We also computed the planar gradiometer of the sensor data. The data thus further showed the combined measurements of orthogonal planar gradiometers, reflecting the absolute strength of stimulus-evoked neural activity with a spatial peak in sensors closely overlying its cortical source (Wenzlaff et al. 2011)

### ***MEG Epoching and averaging***

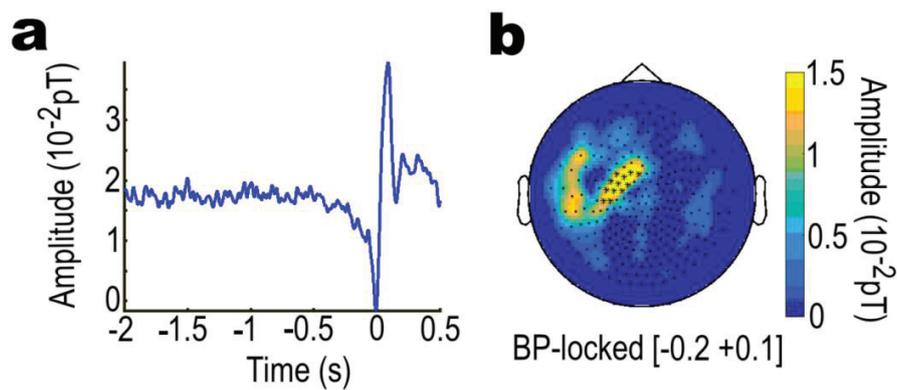
Target-Related-Fields (Target-RF) epoching and averaging was performed from –500ms to +2000ms locked on Target onset. Response-Related Fields were computed from -1000ms to +500ms relative to the timing of the button press. Before Target and Response Evoked-Fields averaging, we low-passed the data filtered at 40Hz. Baseline correction was done, for both Target Related-Field (Target-RF) and Response Related-Field (Response-RF), using the -500ms to 0 ms pre-Target baseline activity.

### ***Decision-related signals***

In order to identify decision related signals, Target-RF were divided into three bin categories: fast RT (800 ms < RT < 1000), medium RT (1000 ms < RT < 1200ms) and slow RT (1200 ms < RT < 1400ms). We first selected *a priori* sensors of interest: the Motor Readiness Field sensors and the Centro-Parietal Positivity (CPP) sensors.

The Centro-Parietal Positivity (CPP) should be located in the center of the scalp and extending to parietal areas, according to O’Connell & Kelly’s and sensors were selected as such (O’Connell, Dockree, and Kelly 2012; 2012; Kelly and O’Connell 2013; Twomey et al. 2015; Kelly and O’Connell 2015). Motor Readiness Field sensors were selected by comparing left and right

button-presses (see for example van Vugt et al., 2014) and restricted to the ones that significantly differed between the two (see MEG statistics; **Figure 29**). Target Related single-trial activity was computed using the mean over the selected sensors and organized by increasing Reaction-Times (RT).



**Figure 29. LRP sensors selection.** a) ERFs for the difference left-right button. b) **Topography.** The sensors which differ significantly between left and right response are highlighted with stars. The scale represents activity amplitude in pico-tesla (pT). BP: button-press.

### *Hypothesis regarding DDM*

Since the level of difficulty determines the amount of sensory evidence, it should affect the drift of the decision variable (see: **Box 1. Drift Diffusion Models** and **Box 2. Fitting the drift diffusion models to the data**). The effects of payoff and beneficiary could play either on the drift or on the distance between the starting point of the decision variable and the decision boundary.

A direct influence of our factors on the decisional process could affect the drift rate of the decision variable, which is an index of the quality of evidence used for the decision. This would suggest that these decisional factors (payoff/beneficiary) are integrated together with the evidence for the choice alternatives into a single source of evidence during the accumulation process.

Alternatively, changes in the distance between the starting point and the decision boundary would suggest that individuals integrate the beneficiary-related motivation through the read-out mechanisms, setting the decision rules, prior to starting the evidence integration and the decision process in itself.

## ***Statistics***

### ***Behavioral analysis***

Reaction-Times (RT) and sensitivity ( $d'$ ) from the behavioral and the MEG experiments were collapsed together, leading to a total of 57 subjects for the behavioral analysis. Sensitivity, being a binary variable, was analyzed using non-parametric Wilcoxon tests for paired samples. Reaction-Times (RT) faster than 300ms were considered as fast guesses and were removed from further analysis. RT for correct trials and RT for error trials were assessed separately. They were log-transformed for normalization. The three factors were: i) Beneficiary (two levels: other vs. self), ii) Payoff (two levels: high - 30€ - vs. low – 10€) and iii) Difficulty (two levels: 13% of dots motion coherence - difficult - vs. - easy -15% of dots motion coherence). *Post-hoc* analyses were performed using LSD Fisher tests. Statistical analyses were performed using Statistica (STATISTICA®, Dell Inc. 2015).

### ***MEG statistics***

Statistical analyses on MEG data were performed at the group-level and over subject grand-average across trials for each condition. Contrasts between conditions were tested for statistical significance using student T-tests, Bonferroni corrected. Elements that passed a

threshold value corresponding to a p-value of 0.005 were marked. Groups of significant sensors were selected as neighbors passing the significance threshold conjunctively for at least 68 ms ( $4 \times 17\text{ms}$ , 17 ms being the time period between 2 data samplings). Elements were considered neighbors if they were directly adjacent, either cardinally or diagonally.

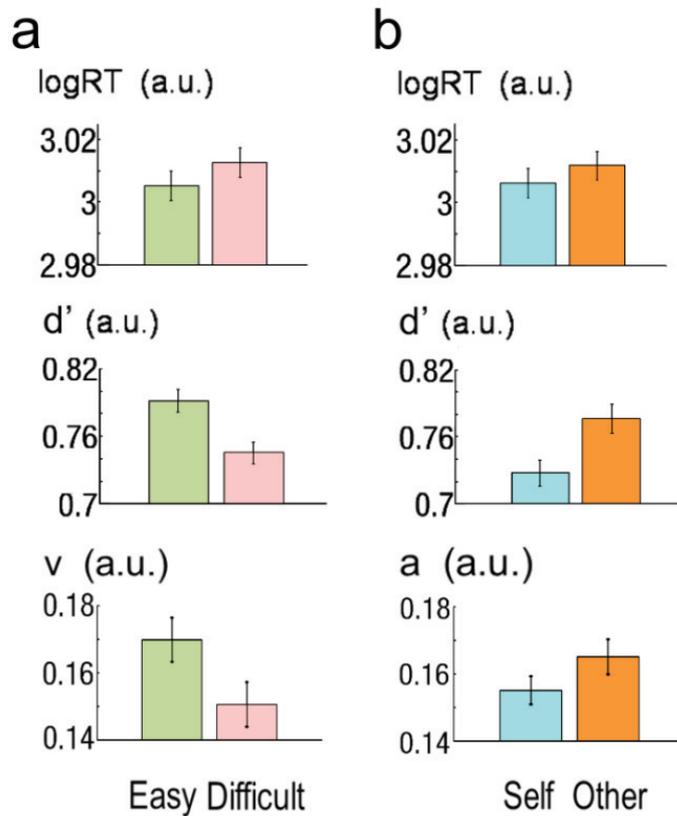
## 2.4.2. Results

### *Reaction-times*

Reaction-Times (RTs) analyses were performed on the log-transformed data, for correct and error trials separately. For intelligibility, in the following paragraph, the values are given as non-transformed RT - in milliseconds (ms). RTs from errors showed a main effect of difficulty, with longer RTs during difficult as compared to easy trials ( $RT_{\text{Difficult}} = 1142$  ms;  $RT_{\text{Easy}} = 1114$  ms; Cohen's  $d = 0.166$ ;  $F_{(1,56)} = 8.22$ .  $p = 0.00582$ ). This was the only effect on RTs from incorrect trials (i.e. showing errors).

Concerning RTs from correct (RTc) trials, there was a main effect of each of the three factors (*Difficulty*:  $F_{(1,56)} = 29.5$ .  $p = 0.000001$ ; Cohen's  $d = 0.138$ ; *Payoff*:  $F_{(1,56)} = 6.4$ ;  $p = 0.01402$ . Cohen's  $d = 0.0397$ ; *Beneficiary*:  $F_{(1,56)} = 11.0$ .  $p = 0.001619$ ; Cohen's  $d = 0.0435$ ). RTs were longer during Difficult than during Easy trials ( $RT_{\text{Difficult}} = 1043$  ms;  $RT_{\text{Easy}} = 1026$  ms; **Figure 30a**), longer for High Payoffs than for Low Payoffs ( $RT_{\text{High}} = 1038$  ms;  $RT_{\text{Low}} = 1030$  ms) and also slower for Other than for Self ( $RT_{\text{Other}} = 1041$  ms;  $RT_{\text{Self}} = 1028$  ms; **Figure 30b**).

Moreover, there were *Beneficiary\*Difficulty* and *Payoff\*Difficulty* interaction effects ( $F_{(1,56)} = 4.130$ ;  $p = 0.0469$  and  $F_{(1,56)} = 24.456$ ;  $p = 0.000008$ , respectively). *Post-hoc* tests showed that Beneficiary and Payoff had an effect during Easy trials but not during Difficult trials. Easy trials were associated with longer RT for High Payoff than for Low Payoff ( $RT_{\text{High}} = 1039$  ms;  $RT_{\text{Low}} = 1013$  ms;  $p = 0.000008$ ; Cohen's  $d = 0.136$ ) and longer RT for Other than for Self ( $RT_{\text{Other}} = 1036$  ms;  $RT_{\text{Self}} = 1016$  ms;  $p = 0.000237$ ; Cohen's  $d = 0.1050$ ). The triple *Beneficiary\*Payoff\*Difficulty* interaction did not reach significance ( $F_{(1,56)} = 2.834$ ;  $p = 0.0979$ ), nor did the *Beneficiary\*Payoff* interaction ( $F_{(1,56)} = 0.021$ ;  $p = 0.886$ ).



**Figure 30. Behavior and DDM parameter** (n = 57). RTs from correct trials were logarithmically transformed (logRT) before analysis. **a) Sanity Check.** Easy trials are green on the left, difficult trials are red on the right. RT were longer, sensitivity (d') was better - for self-affecting decisions only - and the drift rate (v) was higher during Easy trials than during Difficult trials. **b) Effect of beneficiary.** RT were longer, d' was better - during Difficult trials for a High Payoff - and the decision boundary (a) was higher for Other-affecting decisions than for Self-affecting decisions. LogRT, d', v and a are expressed in arbitrary units (a.u.). Vertical bars represent the standard errors of the means (sem).

## *Sensitivity*

Payoff and Difficulty had a main effect on sensitivity ( $d'$ ),  $d'$  being better during Easy trials than during Difficult trials ( $d'_{\text{Easy}} = 0.78$  a.u.;  $d'_{\text{Difficult}} = 0.76$  a.u.;  $F_{(1,56)} = 63.9$ ;  $p < 0.000001$ ; Cohen's  $d = 0.274$ ; **Figure 30a**) and better for High Payoff than for Low Payoff ( $d'_{\text{High}} = 0.78$  a.u.;  $d'_{\text{Low}} = 0.77$  a.u.;  $F_{(1,56)} = 5.31$ ;  $p = 0.0249$ ; Cohen's  $d = 0.088$ ).

The *Beneficiary\*Payoff* interaction effect reached significance ( $F_{(1,56)} = 4.16$ ;  $p = 0.0459$ ), Payoff having an effect for self-affecting decisions only ( $d'_{\text{High}} = 0.78$  a.u.;  $d'_{\text{Low}} = 0.76$  a.u.;  $p = 0.0034$ ; Cohen's  $d = 0.162$ ). The *Beneficiary\*Difficulty* and the *Payoff\*Difficulty* interaction effects reached significance as well ( $F_{(1,56)} = 21.2$ ;  $p = 0.000024$  and  $F_{(1,56)} = 8.44$ ;  $p = 0.00525$ , respectively). To better understand these two interactions and given the main effect of difficulty, we ran 2-way rMANOVA for each Difficulty level, keeping Beneficiary and Payoff as factors.

Beneficiary had a main effect at both Difficulty levels,  $d'$  was better for Self than for Other during easy trials ( $d'_{\text{Self}} = 0.79$  a.u.;  $d'_{\text{Other}} = 0.77$  a.u.;  $F_{(1,56)} = 7.57$ ;  $p = 0.00798$ ; Cohen's  $d = 0.145$ ; **Figure 30b**) but better for Other than for Self during difficult trials ( $d'_{\text{Other}} = 0.77$  a.u.;  $d'_{\text{Self}} = 0.75$  a.u.;  $F_{(1,56)} = 17.3$ ;  $p = 0.000111$ ; Cohen's  $d = 0.260$ ). Payoff only had an effect during difficult trials,  $d'$  being better for High than for Low ( $d'_{\text{High}} = 0.77$  a.u.;  $d'_{\text{Low}} = 0.75$  a.u.;  $F_{(1,56)} = 15.3$ ;  $p = 0.000253$ ; Cohen's  $d = 0.258$ ).

### ***Drift diffusion parameters***

We fitted the Drift Diffusion Model to the behavioral data and tested the effect of Beneficiary, Payoff and Difficulty on the estimated drift rate ( $v$ ) and decision boundary ( $a$ ).

#### ***Decision boundary ( $a$ )***

Beneficiary had a main effect of on the decision boundary ( $F_{(1,56)} = 5.58$   $p = 0.0216$ ; Cohen's  $d = 0.172$ ),  $a$  being higher for Other than for Self ( $a_{\text{Other}} = 0.165$  a.u.;  $a_{\text{Self}} = 0.156$  a.u.; **Figure 30b**). This was the only effect on the decision boundary.

#### ***Drift rate of the decision variable***

There was a main effect of Difficulty on  $v$ , which was higher during Easy than during Difficult trials ( $v_{\text{Easy}} = 0.166$  a.u.;  $v_{\text{Difficult}} = 0.144$  a.u.;  $F_{(1,56)} = 11.6$   $p = 0.00125$ ; Cohen's  $d = 0.075$ ; **Figure 30a**). The *Beneficiary\*Difficulty* and *Payoff\*Difficulty* interaction effects also reached significance ( $F_{(1,56)} = 7.33$   $p = 0.00896$  and  $F_{(1,56)} = 6.21$   $p = 0.0156$ , respectively).

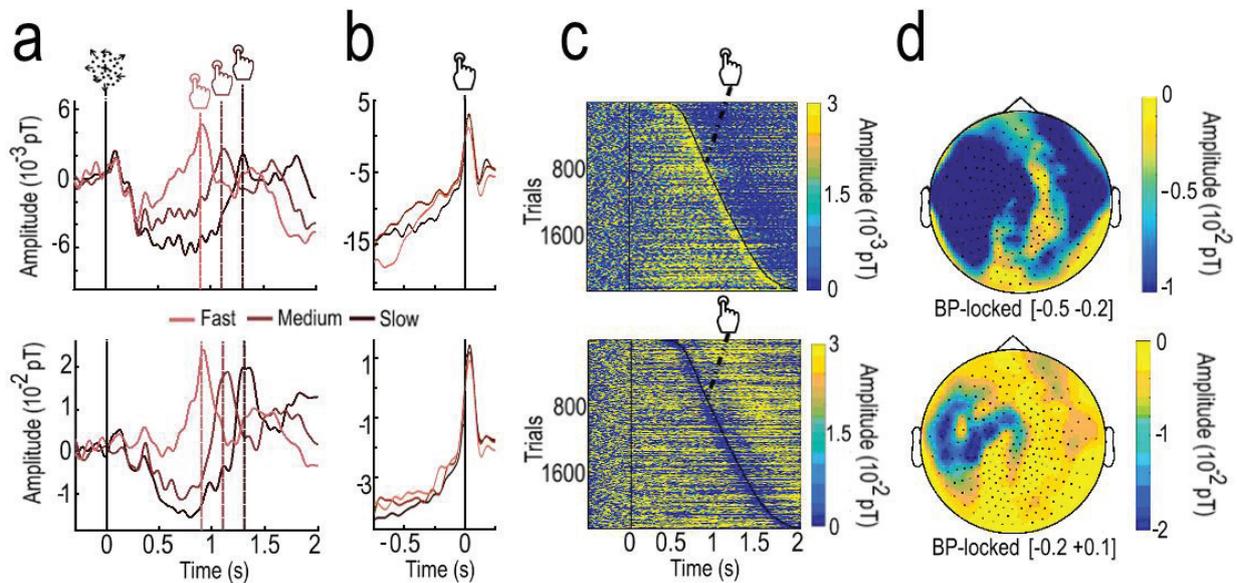
*Post-hoc* tests showed that Beneficiary or Payoff had no effect during difficult trials. However, there was a main effect of Beneficiary during easy trials, associated with a higher  $v$  for

Self than for Other ( $v_{\text{Self}} = 0.176$  a.u.;  $v_{\text{Other}} = 0.157$  a.u.;  $p = 0.000237$ ; Cohen's  $d = 0.128$ ; **Figure 30b**).

Taken by difficulty, Payoff had no effect. If taken by payoff, the Payoff\*Difficulty interaction effect is explained by the fact that the drift rate ( $v$ ) for High Payoffs was not affected by Difficulty, while decisions associated with a Low Payoff had a lower  $v$  during Difficult trials than during Easy trials ( $v_{\text{Easy}} = 0.174$  a.u.;  $v_{\text{Difficult}} = 0.135$  a.u.;  $p = 0.000237$ ; Cohen's  $d = 0.117$ ).

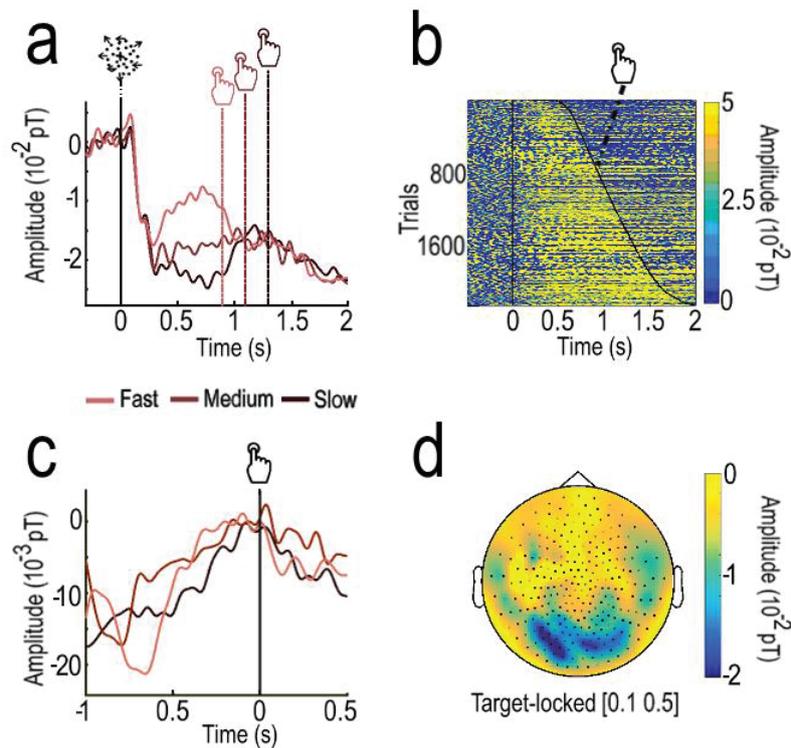
### ***Decision related signals.***

We divided Target-Related-Fields (Target-RF) and Response-RF from corrects trials into three reaction-times (RT) bin: Fast RT (800 ms < RT < 1000), Medium RT (1000 ms < RT < 1200 ms) and Slow RT (1200 ms < RT < 1400 ms). To better understand the link between MEG signals and perceptual decision making, we computed the single-trial mean activity over the sensors showing ERPs related to decision. To do so, we computed the activity related to target onset, taking only the correct trials and organizing them by increasing RT.

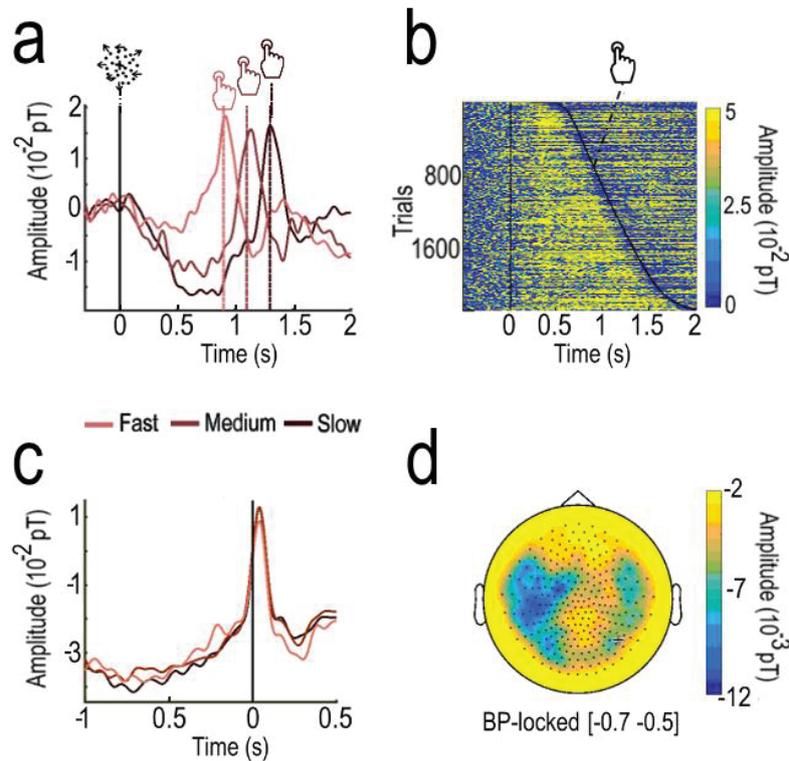


**Figure 31. Centro-Parietal (top) and left Fronto-Temporal (bottom) activity is linked to decision making. a) Target-RFs for slow (black), medium (brown) and fast (pink) RT.** The vertical dotted lines represent the fast, medium and slow mean RT. A ramping activity peaks at the moment of the button-press. **b) Response-RFs for slow, medium and fast RT.** For both Target- and Response- RFs, abscises represent time in seconds (s) after target onset and ordinates represent the amplitude of the brain magnetic activity, in pico-Tesla (pT). **c) Target related single-trial surface plots.** The vertical black line represents target onset. Activity of the centro parietal activity and left fronto temporal activity was closely tied to target detection latency (curved black line). Target-RFs, Response-RFs and single-trials were computed from correct trials. Single-trial activity was pooled across participants (normalized relative to each individual's baseline average), sorted by RT and smoothed over bins of five consecutive trials. Ordinates represent trials. Abscises represent time after target onset, in seconds (s). Scales on the right represent activity amplitude in pico-Tesla (pT). **d) Scalp topographies.** The triangle on the top of the schematically round head represents the nose and the two ears are represented on each the side. The scales on the right represent mean amplitudes in pT.

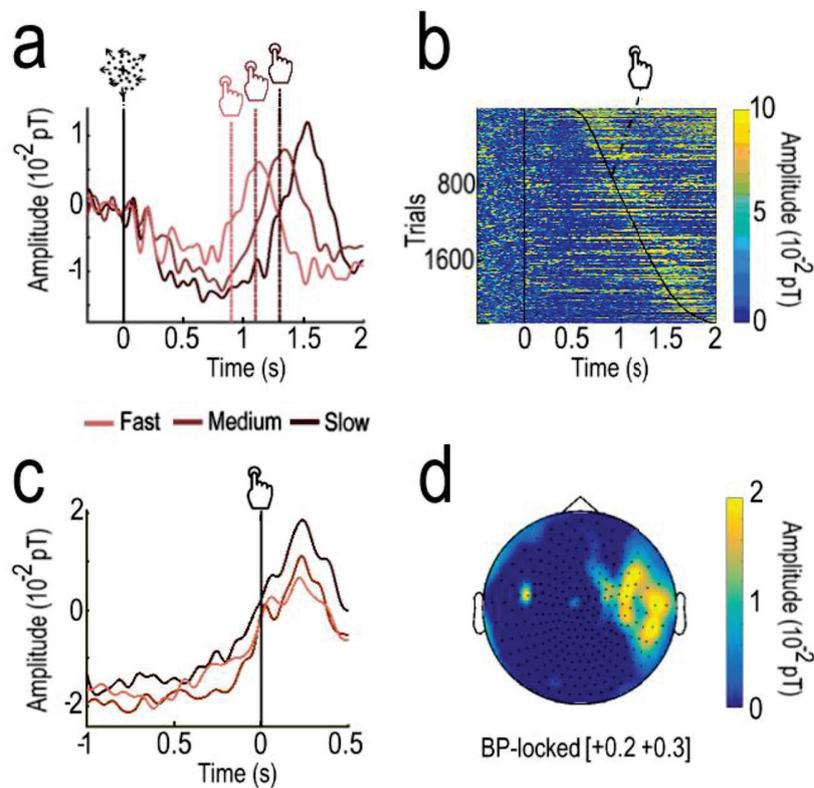
In keeping with previous reports (O'Connell, Dockree, and Kelly 2012; Kelly and O'Connell 2013; Twomey, Kelly, and O'Connell 2016), we could distinguish different ramping signals for slow, medium and fast RT following target onset and peaking at the moment of the button-press (**Figure 31 a,b**). Moreover single-trials display that the Centro-Parietal activity and the left-Fronto-Temporal activity was related to RT (**Figure 31c**). We also noticed distinct RFs for slow, medium and fast RT over left occipital (**Figure 32**), left temporal (**Figure 33**) and right fronto-temporal (**Figure 34**) sensors. Target- and Response-RFs did not show any statistical difference between easy and difficult trials.



**Figure 32. Left Occipital activity.** **a)** Target- and **c)** response-RFs for slow (black), medium (brown) and fast (pink) RT. The vertical dotted lines represent mean RT. Target-RFs are aligned on target-onset, response-RFs are aligned on button press. **b)** Target-related single-trial surface plots. The vertical black line represents target onset. The curved black line represents target detection latency (RT). Single-trial activity was pooled across participants (normalized relative to each individual's baseline average), sorted by RT and smoothed over bins of five consecutive trials. Ordinates represent trials. Abscises represent time after target onset, in seconds (s). Scales on the right represent activity amplitude in pico-Tesla (pT). **d)** Scalp topography. The triangle on the top of the schematically round head represents the nose and the two ears are represented on each the side. The scale on the right represents mean amplitudes in pico-tesla (pT).



**Figure 33 Left-temporal. a) Target- and c) response-RFs** for slow (black), medium (brown) and fast (pink) RT. The vertical dotted lines represent mean RT. Target-RFs are aligned on target-onset, response-RFs are aligned on button press. **b) Target-related single-trial surface plots.** The vertical black line represents target onset. The curved black line represents target detection latency (RT). Single-trial activity was pooled across participants (normalized relative to each individual's baseline average), sorted by RT and smoothed over bins of five consecutive trials. Ordinates represent trials. Abscises represent time after target onset, in seconds (s). Scales on the right represent activity amplitude in pico-Tesla (pT). **d) Scalp topography.** The triangle on the top of the schematically round head represents the nose and the two ears are represented on each the side. The scale on the right represents mean amplitudes in pico-tesla (pT).



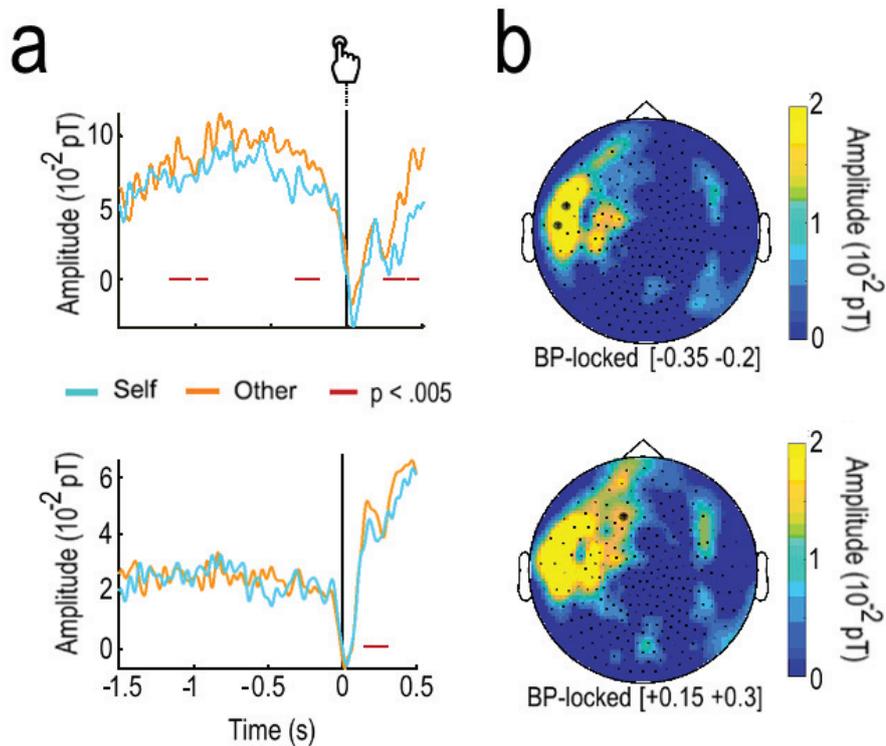
**Figure 34. Right Fronto-temporal. a) Target- and c) response-RFs** for slow (black), medium (brown) and fast (pink) RT. The vertical dotted lines represent mean RT. Target-RFs are aligned on target-onset, response-RFs are aligned on button press. **b) Target-related single-trial surface plots.** The vertical black line represents target onset. The curved black line represents target detection latency (RT). Single-trial activity was pooled across participants (normalized relative to each individual's baseline average), sorted by RT and smoothed over bins of five consecutive trials. Ordinates represent trials. Abscises represent time after target onset, in seconds (s). Scales on the right represent activity amplitude in pico-Tesla (pT). **d) Scalp topography.** The triangle on the top of the schematically round head represents the nose and the two ears are represented on each the side. The scale on the right represents mean amplitudes in pico-tesla (pT).

### ***Influence of the beneficiary on MEG activity during decision making***

During difficult trials, for High Payoffs, we found differences between Self- and Other-affecting decisions. During the time of the decision making process, a difference was found over the temporal cortex region, which exhibited a slow rising field. Other-related MEG activity was of higher amplitude than Self-related activity ( $p < 0.005$ ; **Figure 35**).

The difference was significant over three time periods before response initiation over the temporal sensors (MLT32 and MLT42): from -1170ms to -1023ms, from -993 to -915 ms and from -343 to -188ms. These sensors also showed significant differences at two time periods after response execution: from 228 ms to 376 ms and from 385 ms to 465 ms. In addition, the MEG signal over a frontal sensor (MLF52) differed between Self and Other as well, from 153 ms to 303 ms after response execution.

To further assess the difference between Self and Other, we computed the mean amplitude over each period of time with a significant effect for the temporal and frontal sensors respectively. The comparison confirmed that other-related MEG activity amplitude was higher for other than for self during each period of time and for both brain regions (**Table 5**).



**Figure 35. Differences in ERFs between Self and Other during and after decision-making. a) Response-RFs.** Self-related activity is represented in cyan, Other-related activity in orange. Red lines indicate significant timings for a threshold at  $p > 0.005$ . The brain activity, for High Payoffs during difficult trials, is time-locked to the response (button-press) and baseline corrected to the pre-target activity. Ordinates display the brain activity in  $10^{-2}$  pico-Tesla (pT). Abscise axes represent time in seconds (s). **b) Scalp topographies.** The significant sensors - MTL32, MLT42 (top) and MLF52 (bottom) - are depicted with black circles. The triangle on the top of the schematically round head represents the nose and the two ears are represented on each the side. The scales on the right represent mean amplitudes in pT.

	<b>Timing (ms)</b>	<b>df</b>	<b>T statistic</b>	<b>p-value</b>
Temporal	[-1170 -1023]	18	-4.44	$3.10^{-4}$
	[-993 -915]	18	-5.52	$3.10^{-5}$
	[-343 -188]	18	-3.88	$1.10^{-3}$
	[+228 +376]	18	-5.02	$8.10^{-5}$
	[+385 +465]	18	-4.24	$5.10^{-4}$
Frontal	[+153 +303]	18	-4.61	$2.10^{-4}$

**Table 5. Statistics Results over Self-Other difference.** Mean amplitude during significant timings for self/other response-RF were computed and compared, using two-tailed paired T-test statistics. Sensors: temporal: MLT32-MLT42, Frontal: MLF52; df: degrees of freedom.

### **2.4.3. Discussion**

We studied the neural dynamics of perceptual decision processes in humans and tested their modulation by payoffs for oneself *versus* a payoff for a close relative. At the behavioral level, higher perceptual difficulty (lower dot coherence) worsens performance (lower accuracy and slower RTs). Using Drift Diffusion Models (DDM), we found that difficult trials were linked to a lower drift rate of the decision variable than easy trials. Indeed, evidence availability determines the amount of sensory evidence accumulated into the decision variable. More importantly, other-affecting decisions were linked to an increased RT and a higher distance between the starting point of the decision variable and the decision boundary ( $a$ ), as compared to self-affecting decisions. At the brain system level, self- and other-affecting decisions exhibited differences over the left temporo-frontal area during, and after, perceptual decision making (the motor response being made with the right hand). Self and Other also differed over the frontal area after response execution.

In both the temporo-frontal and the frontal area, higher amplitudes were observed during other- than during self-affecting decisions. This may be linked to the higher decision boundary we found for other- than for self-affecting decisions. Consistently, a recent study linked longer RTs for similar others to higher decision threshold in a food choice task (A. Harris, Clithero, and Hutcherson 2018). In this case, higher decision boundary would have been

implemented to overcome increased uncertainty experienced when deciding for similar others. Such a change in the distance to the decision boundary (a) for self- and other-affecting decisions suggests that individuals integrate the beneficiary-related motivation through read-out mechanisms, setting the decision rules prior to starting the evidence integration and the decision process in itself.

After response execution there was also a difference between self and other over the medial frontal regions of the brain. MEG activity exhibited higher magnetic field amplitude for other- than for self-affecting decisions in pre-motor and frontal regions, during and after the decision making process. Being ulterior to the response, this should not result from the decision making process *per se*. It could be expectation of rewards for other and for self that differ. As shown in monkey studies, the Anterior Cingulate Cortex (ACC) encodes differently self- and other rewards (S. W. C. Chang, Gariépy, and Platt 2013).

Alternatively, since the stimuli were displayed even after the participants made their motor response, this late activity could possibly correspond to a verification of the decision just made. The Supplementary Motor Area (SMA) and the dorsolateral Prefrontal Cortex (dlPFC) have been shown to be implicated in Speed-Accuracy Tradeoff (SAT) modulation (Wenzlaff et al. 2011). This activity occurring post-response may thus relate to an internal 'checking' process aiming to judge the accuracy of the decision just made, before the external feedback is

displayed. It may also reflect an update of the speed-accuracy trade-off for future decisions (Padrón et al. 2016).

Concerning the electrophysiological markers of perceptual decision making in humans we observed two MEG signals, the centro-parietal positivity (CPP) and the fronto-temporal preparatory signal. They both fulfill defining features of a decision variable, *i.e.* their time course built as a cumulative function of sensory evidence and a decision was made when a boundary was reached. The CPP MEG signal closely resembles, in terms of its timing relative to RTs, topography and polarity, the one revealed by recent EEG studies (Kelly and O’Connell 2013; O’Connell, Dockree, and Kelly 2012; Twomey, Kelly, and O’Connell 2016). The CPP is a slow rising ramp-like activity peaking just before the response. It appears to be a major correlate of perceptual decision making in human electrophysiology (G. Chand and Dhamala 2015; G. B. Chand and Dhamala 2017; Guggisberg et al. 2008; Kaiser, Lennert, and Lutzenberger 2007; Mostert, Kok, and de Lange 2015; Siegel, Engel, and Donner 2011; Wenzlaff et al. 2011).

There is also growing evidence that the motor and pre-motor areas receive information about the processed sensory evidence and participate in the accumulation process up to the decision boundary (Wenzlaff et al. 2011; Smyrnis et al. 2012; Kelly and O’Connell 2013; 2015; Gluth, Rieskamp, and Büchel 2013; Noorbaloochi, Sharon, and McClelland 2015; Marieke K. van Vugt et al. 2014; Guggisberg et al. 2008). If a motor output is required when a decision is made, motor areas receive information about the decision variable. This information is transformed

into a behavioral response when the decision boundary is reached. However when the need for an overt response is removed, the motor related activity ceases to encode a decision variable, indicating that this effector-specific signal does not have a general role in decision formation. In contrast, the CPP signal was completely domain general: it exhibited the same decision-predictive dynamics regardless of sensory modality and stimulus features and tracked cumulative evidence even in the absence of overt action (O'Connell, Dockree, and Kelly 2012). The current study favors a continuous transformation of sensory evidence into a decision variable in centro-parietal region, steadily transmitted to the centro-frontal pre-motor and motor regions up to its conversion into a behavioral motor response.

Early occipital activity after target-onset is assumed to reflect visual primary encoding of the target stimuli, as previously detected with decoding techniques (Mostert, Kok, and de Lange 2015), pattern analysis (Myers et al., 2015) and by studying gamma band power (Castelhano et al. 2014; 2017; Guggisberg et al. 2008; Siegel, Engel, and Donner 2011; Wyart and Tallon-Baudry 2009). Differences in the amount of evidence available (here dot coherence) should induce a modification in the occipital response to the target stimuli between difficulty levels. However, target-Related Fields did not show any difference between easy and difficult trials over the occipital regions of the brain. In this task, coherence levels differed by two percent from each other, which might have been too subtle a change to catch any statistical difference in the MEG signal.

In conclusion, our results indicate that it is possible to use MEG to monitor the dynamics of sensory evidence, decision variable and motor preparation signals in humans. Our study paves the way for a complementary approach to EEG and electrophysiological recordings for a more mechanistically principled understanding of sensorimotor transformations and how they are influenced by social cognition.

## ***Part 3: General Discussion***

This work aimed to clarify how others influence the decision making process. Social interactions are fundamental to our functioning, as individuals but also as families, groups and as a society. Social cognition is a key to many aspects of our existence, if not all. Even the primitive behavior of food intake is modified by particular social features. Food intake is far from being the only behavior influenced by the presence of others. Rather, many behaviors are affected by social cognition. It is indeed when taking into account the social aspects of decision making that behavioral economists, and then neuro-economists, came to an understanding of the deviation of consumers behavior from the expected 'homo economicus'. The human decision-maker is not a pure utility/reward maximizer, but fairness, trust, altruism, morality, conformity, shame, guilt.... and many human traits influence decision making.

Social cognition is a wide domain, involving multiple processes that rely on various brain areas. It is composite and can induce a variety of effects, depending on the concerned activity (e.g. eating vs. sharing money vs. performing an accuracy task), the special features of the social context (audience vs. coaction, for example, or a friend vs. a colleague vs a hierarchical decider, ...) and individual personality traits. These modifications are also modulated by the image we want others to have of us. This takes hold of the challenges faced when studying social cognition. The larger part of the existing work in social cognitive neurosciences is based on paradigms inspired by the Game Theory, where participants have to allocate and share monetary rewards. These are elegant, enabling us to capture subtle interplays between matrix

outcomes and social cognition in the equilibrium between self and other rewards. The decisions are made with taking the other participant(s) into account in the decision-making process, but they also involve self-interest regarding outcome.

The goal of this doctoral (PhD) thesis was to study “Others” as a unique, single factor. We wanted to understand their bare influence on the human brain when making decisions. We studied which decision-making processes were influenced when having to take others into the decision making processes, either as simple observers, or as the recipient-beneficiary of the decision. We took advantage of the framework of perceptual decision making, which is well documented in animal neuroscience, human psychology and human neuroscience, as a solid theoretical background within which we could identify the effect of others on decision parameters. We took advantage of the Drift Diffusion Models to go further from behavioral variable and into the cognitive processes. DDM have proven to be a powerful approach to explain the process of making a perceptual decision.

Our behavioral results confirmed our first assumption: social cognition is complex. The results are sparse and depend on every single factor: coherence level, payoff associated with the decision, beneficiary of the decision, but also social discounting. We showed that the beneficiary of a decision or an observer during the decision both induce changes in behavior and in the related DDM parameter estimates. This means that perceptual decisions, e.g. basic sensory integration terminated by a motor execution, can be modified by a single factor relating

to others. We found that the beneficiary of a decision and audience induce modifications in the drift rate of the decision variable, suggesting a faster and more efficient uptake of the available evidence in the decision making process.

In MEG, we were able to identify temporal, centro-parietal (the Centro-Parietal Positivity found by Kelly and O'Connell in EEG), and centro-frontal (premotor and motor areas) activity involved in perceptual decision making. We discerned a slow, ramp-like, signal related to reaction-times resembling the CPP. Single trials analysis showed activity related to the response output. More importantly, magnetoencephalography (MEG) gave us insights on the comparison between self-affecting and other-affection decisions. Self-other comparison on the MEG data showed differences during and after the response output, over the (left) temporal and the centro-frontal areas during the decision-making process and frontal differences after the response-output.

### ***3.1. Overall behavior***

#### ***3.1.1. Humans actually do things for others***

In our first experiment (vicarious behavior 1), we found only effects of payoff and dot coherence but no main effect of the beneficiary on behavior. But the fact that people performed for the task for another participant in the same manner as for themselves is, in itself, interesting.

Among all the people that passed one of our vicarious reward experiments<sup>7</sup>, only two took the decisions not to perform the task and let it run by itself during other-affecting decisions (and were further excluded for analysis). Actually, after debriefing of these two participants we learned that one did it first. Then, the other saw it and copied this behavior. This occurred during the experiment when the other affected by the decisions was an unknown fellow participant (vicarious behavior 1).

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<sup>7</sup> Where decisions were made to win a payoff for others: vicarious experiments – behavior 1 and 2 and MEG.

Everyone could have chosen not to do anything during the 'other'-affecting trials of the task. But even during other-affecting decisions, most people took the trouble of trying to see the direction of the dots and make a decision about it. Furthermore, people could have left the decisions to 'chance' and decide randomly, without caring about the actual direction of the dots, for others. But accuracy did not drop to 50%.

People perform a task, and this task is performed for others to obtain a potential rewards. This behavior indicates humans' proneness for altruism. This is in line with the hypothesis that there is a spontaneous inclination toward cooperation in humans, e.g. as indicated by testing cognitive demands of cooperation and defection using mouse movement response dynamics (Kieslich and Hilbig 2014).

### ***3.1.2. The relationship with the other has to exist to affect decision-making***

In the vicarious behavior 1, 'the other' (beneficiary affected by the decision) was another (unknown) participant and no significant effect of the beneficiary was found. However, in vicarious behavior 2 (the second experiment) we changed who 'the other' was: we asked the participants to indicate a close relative they would be willing to play for during the experiment. Then, we obtained a main effect of the person affected by the decision on reaction-times (RT). It

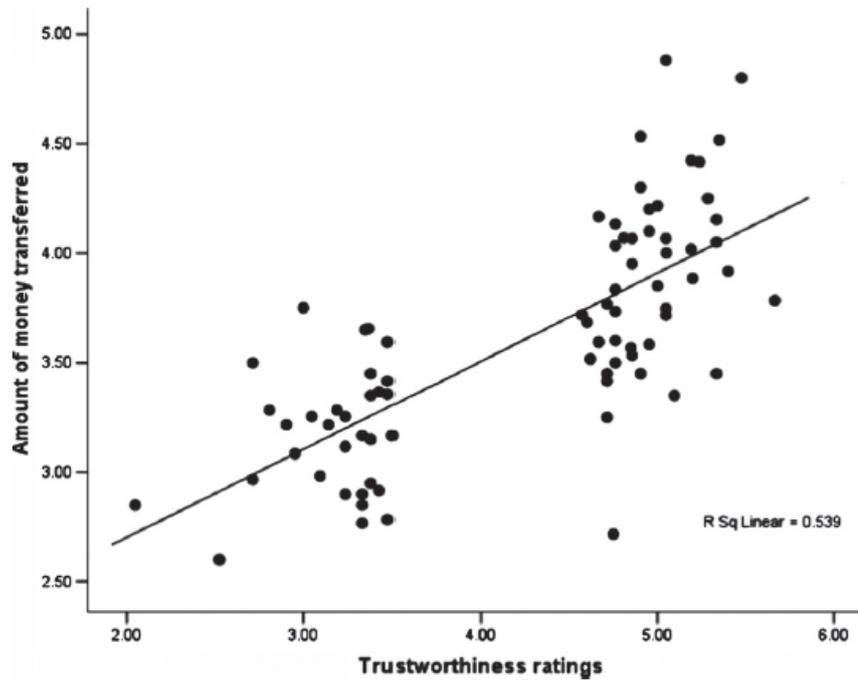
suggests that, for the decision process to actually change between self- and other- to affect perceptual decisions, the other has to be a close relative of the decider.

This is further evidence that the identity of the person affected by the decision is a key in its influence on decision making. Indeed, the social distance between two persons is key in the behavior of one toward another (Mobbs et al. 2009). Sharing rewards with a friend induce higher activation of the striatum than with a confederate or a computer (Fareri et al. 2012). We act, and even think, in different ways when we are all alone and in the presence of at least one other person. Who this other person is matters: we react differently when facing a moody friend or a rude stranger for example We distinctively execute a request if it is coming from a close relative or from a colleague, or doing the same thing for ourselves.

Sympathy and empathy is as crucial to social interaction and person perception as sight is to visual perception (Sally 1995). People with higher empathy traits cooperate more (Batson and Moran 1999). Even in cooperation, there is actually an in-group bias: we cooperate more with individuals of our group than with individuals out of the identified group (Stallen and Sanfey 2013; Rilling et al. 2008; Brewer 1979). Trust about other's likelihood to cooperate is enhanced when it is affect-based trust as compared to cognitive-based trust (Ng and Chua 2006). Altogether, this supposes that the relationship between the participant and the other has importance in the effect of this other on the decision to be made. It may seem straightforward, but it reinforces closeness as a factor for cooperation and altruism. Also, our results suggest that participating in the same experiment is not seen as an in-group clustering factor.

In the audience experiment, effects of others were also found. In that case, the other was the experimenter observing the performance of the decision. The experimenter-observer and the participant met before the experimental session, for the inclusion. The other was thus not an unknown person. In addition, the participants may well have wanted to please or impress the observing experimenter.

Social reputation influences decision making. Trustworthiness inferred from implicit facial cues (van 't Wout and Sanfey 2008) (**Figure 36**) and social information regarding the likelihood of mutual cooperation (Boone, Declerck, and Suetens 2008) make people cooperate more. Maybe we could have obtained a change in the decision process in our first experiment if we had told a story involving the unknown other participant before the subjects performed the task. It would be interesting to test how 'good' versus 'bad' character description about the other influence perceptual decision making for others. It is possible that nice history would give results similar to what we found for close relatives and bad history would influence participants to expend less effort in the task for the other.



**Figure 36. Relationship between trustworthiness and offer amount.** Scatter plot for normed trustworthiness ratings (horizontal axis) and the average offer amount send to that partner (vertical axis). Figure from (van 't Wout and Sanfey 2008).

## ***3.2. Drift diffusion models***

### ***3.2.1. Others***

In our second experiment (vicarious behavior 2), where the other was a close relative chosen by the subjects, the beneficiary of the decision had a main effect on reaction times (RT). Using Drift diffusion models, we found that this effect on RT was linked to a modulation of the drift rate of the decision variable. This indicates that the beneficiary of the decision is integrated into sensory evidence accumulation, and that sensory evidence is integrated faster for self than for others.

It may be that participants tried to imagine their relative receiving the payoff, although not instructed to do so. Indeed, Public Good Games studies show that taking into account another person into a decision engages the processes of the Theory of Minds (Stallen and Sanfey 2013; C. D. Frith and Singer 2008). Engaging the Theory of Minds network would have required higher cognitive demands and redirected part of the attentional load and neuronal energy from the evidence accumulation process during other-affecting decisions. It can also be that ToM was engaged in sustaining reputational concerns. The participants could have

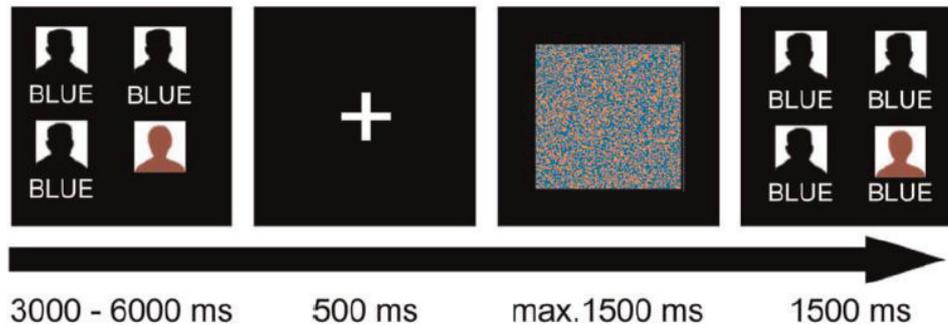
simulated the image of themselves they would project to their relative if they won money for them, making them grateful, or not, making them disappointed.

In a study on value-based decision making combined with DDM, it has been suggested that, when choosing on behalf of another, the brain network involved in ToM may communicate with valuation to adjust the drift rate during value integration (A. Harris, Clithero, and Hutcherson 2018). Participants had to choose food items that were either healthy (e.g. green salad) or not healthy (e.g. French fries). These choices were taken for two partners: one with similar preference and one with dissimilar preferences, the preferences being about choosing food based on healthiness *versus* choosing food based on tastiness.

For both similar and dissimilar others, RTs were longer and linked to a change in drift rate. Stimulus value integration, reflected in the drift rate ( $v$ ), would be firstly computed based on self-preferences and then adjusted to the other's inferred preferences. Event-related potentials (ERP) in the temporo-parietal junction (TPJ) were found to modulate the activity reflected by the ERP in the ventro-medial prefrontal cortex (VMPFC). Analogous mechanisms could have occurred during our experiment as well. The importance accorded to the evidence, reflected in the drift rate ( $v$ ) of the decision variable, could have been initially lower during other-affecting decisions, or it could have been re-adjusted based during the time of the decision.

It could also be that, when performing a self-affecting decision, more attentional resources are focused on the task (because of a higher motivation, due to direct self-benefit), thereby increasing the efficiency of evidence accumulation. In a functional Magnetic Resonance Imagery (fMRI) study of generous and selfish choices during a modified dictator game, the participants made more selfish than generous choices (Hutcherson, Bushong, and Rangel 2015). Moreover, selfish choices were related to longer reaction-times (RT) than generous choices; which is in line with our results. This suggests that people are more highly motivated for self-rewards.

We found that audience induces a higher drift rate of the decision variable than in secret. The drift has also been found to be changed by social conformity (Germar et al. 2016; 2013). The researchers asked the participants to perform a computer-based color discrimination task, judging if a scrambled square depicted mostly blue or orange pixels (**Figure 37**). The participants were told that others were doing the same task and that they were all connected to a server. Moreover, they were told that a random order of response was assigned between them. Actually, the participants performed the task individually and were always told that they would be the last to answer. They would then see what the (alleged) other participants answered on each trial before they gave their response.



**Figure 37. Trial sequence in the social conformity experiment (Germar et al. 2016).** First, participants see the responses given by (alleged) others. Then a fixation-cross is presented, followed by the stimulus of orange and blue pixels. The participants had to decide what the most present color was. Finally, they gave their answer

They showed that incongruence between other's response and the actual correct response about the stimulus induced a decrease in the drift rate of the decision variable. In contrast, congruency between other's response and stimulus induced an increase in the drift-rate of the decision variable. To sum up, social conformity induced a biased uptake of stimulus information, by preferentially accumulating sensory evidence which are in line with majority response (Germar et al. 2016; 2013). This can be linked to the bias in drift-rate induced by branding on economical clothing items choices (Philiastides and Ratcliff 2013). It suggests that social conformity acts as a preference, favoring the choice of agreement with others.

They also showed that social conformity was linked to a higher distance between the starting point of the decision variable and the decision threshold as compared to the non-social control condition, suggesting that stimuli were analyzed more carefully by participants under social influence (Germar et al. 2016; 2013). In the same line, Harris and colleagues found that the distance between the starting point of the decision variables and the decision threshold was higher for other than for self (A. Harris, Clithero, and Hutcherson 2018). This suggests that participants were more careful when making decision under observation, incrementing a higher decision criterion. Similarly, when collapsing the behavioral data from the vicarious experiment 2 and the MEG experiment we found that other-affecting decisions were associated with a higher decision boundary (and a lower drift rate of the decision variable, but only during easy trials).

### ***3.2.2. Payoff***

Concerning the influence of payoff, we were not surprised to find that it modified the decision process. Humans seek rewards. It has been established by several studies that sensitivity is improved and reaction-times are shortened (giving an overall better speed-accuracy trade-off) when higher rewards or punishments are associated with good performance (Engelmann, Herrmann, and Tomasello 2016; Blank et al. 2013; Green, Biele, and Heekeren 2012; Martijn J. Mulder et al. 2012).

Using Sequential-sampling models to account for the effects of payoffs in a perceptual decision, studies reported changes in the distance from the starting point to the decision boundaries. The prior probability of a response to be the correct one (Leite and Ratcliff 2010; M. J. Mulder et al. 2012) and asymmetrical payoffs associated with the possible response alternatives (Simen et al. 2009; M. J. Mulder et al. 2012) induce a shift of the starting point of the decision variable, closer to the decision boundary associated with the alternative having the higher probability or associated with the higher payoff.

The starting point is then further from the other boundary (for the other alternative at hand) and the decision variable is less likely to reach it, establishing a bias and a change in response proportion. In contrast, our experimental set-ups were designed to avoid response probability manipulations toward one of the (left or right) alternatives, in terms of probability (through trials randomization) and in terms of payoff (by assigning the same payoff to both response alternatives). We aimed to compare identical decisions made by the participants, either for themselves or for another person.

Our results were less straightforward than those of the existing literature. In both vicarious experiment 1 and vicarious experiment 2, there was an effect of payoff on behavior and DDM parameter estimates. But, there were interactions with the other factors: the direction of the effect varied as a function of coherence (and beneficiary in experiment 2). However, payoff had no influence for other. As if the decisions was taken as a sort of gift for the (unknown) other participant, and that this gift represented the same value whether a high or a

low payoff was associated with it. Moreover, for self-affecting decisions, the direction of the payoff effect changed as a function of dots coherence. But this hypothesis a priori contradicts results showing a common valuation for both self and other monetary rewards in the ventromedial prefrontal cortex (VMPFC) (A. Harris, Clithero, and Hutcherson 2018; Hutcherson, Bushong, and Rangel 2015; Chib et al. 2009). Nonetheless, both self- and other-payoffs could be evaluated by the same brain process in the VMPFC even if other-payoff were valued higher. Further studies should address this question.

### ***3.2.3. Sensory evidence***

Coherence levels were included for two main sanity checks: to ensure good performance of the task by the participants (gradual performance with gradual percentage of dot coherence) and a differential response in the visual cortex to the different dot coherence levels. While the vicarious behavioral experiments 1 and 2 confirmed the first sanity check – with a higher sensitivity and a shorter reaction-time for higher coherence levels - the MEG data did not allow us to see any statistical difference in the visual cortex response to the different coherence levels as expected given the existing literature.

Early occipital activity after target-onset is assumed to reflect primary encoding of the target stimuli. The occipital cortex sustains visual primary and secondary cortices. It should reflect visual sensory encoding, as previously shown with decoding techniques (Mostert, Kok, and de Lange 2015), pattern analysis (Myers et al. 2015), and in studying the amplitude of the gamma band power (Castelhano et al. 2014; 2017; Guggisberg et al. 2008; Siegel, Engel, and Donner 2011; Wyart and Tallon-Baudry 2009). Differences in the amount of evidence available (here, dot coherence) should induce a modification in the brain response to the target stimuli between difficulty levels. However, target-Related Fields did not show any difference between easy and difficult trials over the occipital regions of the brain. In this task, coherence levels differed by two percent from each other, which might have been too little for us to catch any statistical difference in our MEG signal. Moreover, difficulty did not affect behavior of the participants who took part in the MEG; this could also be a reason for why we did not find a brain difference.

We used dot coherence levels that only differed by 2%, where the existing papers used coherence levels differing by at least 15%. Although we found behavioral effects of our coherence percentage difference in the behavioral experiments, this effect disappeared in the MEG experiment. The experiment would have been better designed with only one coherence level; or with a staircase procedure keeping the performance around 70% (for the drift diffusion model fitting). The differences in participants behavior between behavioral and MEG experiments are puzzling. Indeed, we used exactly the same paradigm as the vicarious behavioral experiment 2. But at least part of the difference can be explained because fewer

subjects performed the task. This could induce a drop in the power of the drift diffusion estimation. Also, during MEG experiment, subjects are constrained in the MEG chair and cap, asked not to move and avoid blinking; this might impact behavior and, consequently, model fitting as well.

### ***3.3. Magnetoencephalographic insights***

We used Magnetoencephalographic (MEG) recordings of participant's brain activity during the vicarious perceptual decision task. We found a signal closely resembling the centro-parietal positivity (CPP), in terms of timing relative to reaction-times, to those revealed in EEG in previous studies (Kelly and O'Connell 2013; O'Connell, Dockree, and Kelly 2012; Twomey, Kelly, and O'Connell 2016). The centro-parietal activity is a slow rising ramp-like activity peaking just before the response. It appears to be a major correlate of perceptual decision making in human electrophysiology (G. Chand and Dhamala 2015; G. B. Chand and Dhamala 2017; Guggisberg et al. 2008; Kaiser, Lennert, and Lutzenberger 2007; Mostert, Kok, and de Lange 2015; Siegel, Engel, and Donner 2011; Wenzlaff et al. 2011)

More importantly, we found difference between self- and other-affecting decisions over left temporal and the left fronto-central sensors. The two clusters of sensors exhibited a ramping activity peaking at the moment of response output, suggesting that they are related to the decision process. In both regions, MEG brain activity was of higher amplitude during other- than for self-affecting decisions. The difference over the temporal area of the brain occurred during the decision making process (i.e. between target onset and motor response). The temporal cortex has been previously linked to evidence accumulation during perceptual decision making. This supposes that the beneficiary of a perceptual decision modulates the accumulation process. However, the MEG signal was of higher amplitude for other- than for self-affecting decisions, while the drift rate was lower for other than for self. This is a contradictory result that demands further investigations.

The left centro-frontal activity is closely related to the motor output. There is growing evidence that the motor and pre-motor areas of the brain receive information about the processed sensory evidence and participate in the accumulation process (Wenzlaff et al. 2011; Smyrnis et al. 2012; Kelly and O'Connell 2013; 2015; Gluth, Rieskamp, and Büchel 2013; Noorbaloochi, Sharon, and McClelland 2015; Marieke K. van Vugt et al. 2014; Guggisberg et al. 2008). If a motor output is required when the decision is made, the motor areas receive the information from, or about, the decision variable. This information is transformed in turn into a behavioral response when the decision boundary is reached. The motor output being the termination of the decision process, we can assume that the peak of activity over the motor cortex reflects the decision boundary. Higher MEG activity amplitude for other than for self

would then reflect a higher decision boundary. An increase of the decision boundary for other-affecting decisions as compared to self-affecting decisions is indeed what the drift diffusion model parameter estimation suggested. It is however to be noticed that the parameter estimation using the drift diffusion model did not give any significant results on the MEG participants alone. This result must then be taken carefully and should be further tested in future studies.

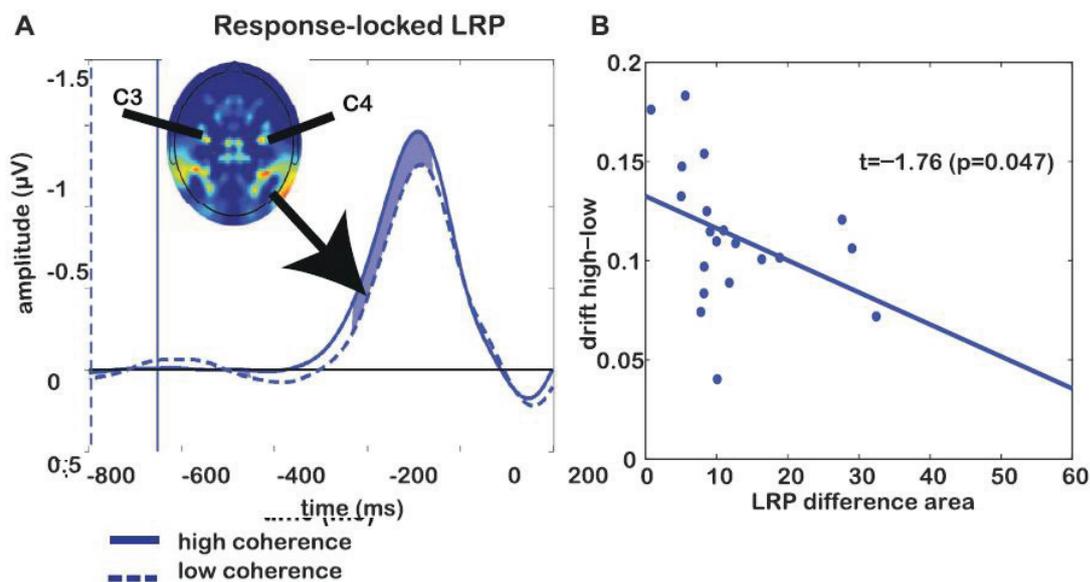
### ***3.3.1. Rethinking classical event-related potentials: the LRP and the P300***

Using electroencephalography, Germar and colleagues showed that social influence was related to a higher early visual event-related potential (Germar et al. 2016). This indicates that social influence would increase early attentional resources for stimulus discrimination. But this effect was not directly linked with the drift rate of the decision variable and thus did not explain social conformity in the response. Early sensory processing is believed to be represented by the non-decision time ( $T_{er}$ ), but they did not find any effect on this parameter – which is puzzling. Nonetheless, the onset latency of the Lateralized Readiness Potential (LRP) was correlated to the changes observed in the drift rate of the decision variable. The LRP had an earlier onset during social conformity, suggesting that participants processed the stimuli faster when they conformed than when they did not conform to the majority.

The Lateralized Readiness Potential (LRP), by definition, is the difference in activity of contra-lateral minus ipsilateral motor implicated sensors (i.e. the sensors over the hand motor brain area (Kelly and O'Connell 2013; Marieke K. van Vugt et al. 2014) (**Figure 38**). However, the Lateralized Readiness Potential (LRP) depends on motion coherence as well (Kelly and O'Connell 2013). Both the CPP (Centro-Parietal Positivity) and the LRP reflected aspects of evidence accumulation toward a decision boundary. But the CPP reached its half-maximal amplitude prior to the LRP. Keeping in mind that the CPP was present even when a motor response was not required for the decision, this suggests that the CPP and the LRP are closely linked in perceptual decisions involving a motor response, the CPP preceding the LRP in the decisional process. It seems that the CPP reflects the rise of a decision variable, accumulating information over-time, and transmits it to the motor areas - if a motor response is needed -, which in turn exhibits similar ramp-like activity in the LRP.

It is worth noticing that, using neural network models combined with EEG, researchers have also suggested the LRP as reflecting the crossing of the decision boundary (Marieke K. van Vugt et al. 2014). Other researchers noticed a close link between stock market buying decisions and motor brain activity (Gluth, Rieskamp, and Büchel 2012) and further investigated the Readiness Potential (RP) in relation to economic decisions in a EEG study (Gluth, Rieskamp, and Büchel 2013). They asked their subjects to look at series of ratings informing them about a stock but access to these ratings had a cost. The Readiness Potential was elicited by each rating

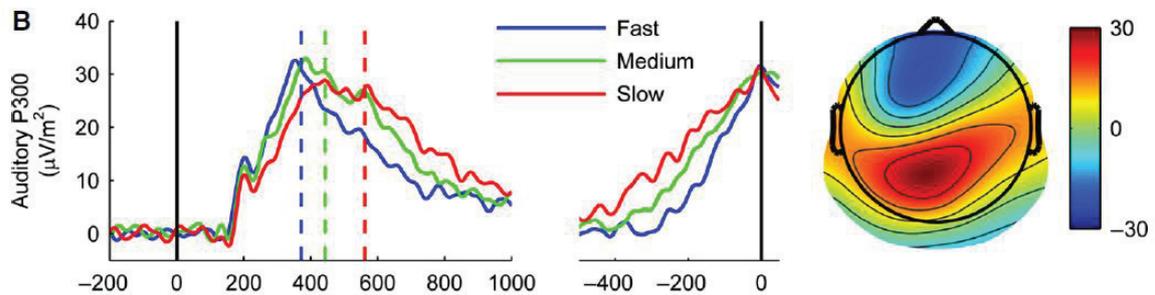
presentation, even when the subject did not actually respond. And the RP was stronger before a response, suggesting that the decision boundary was then crossed.



**Figure 38. Grand average response-locked LRP, demonstrating the difference between low and high coherence conditions.** Vertical lines indicate stimulus onsets for the respective conditions. Shaded area indicates the time window where low and high-coherence differ significantly (t-test with  $p < 0.05$ ). Inset shows a topographical map (nose up) of lateralized EEG activity, demonstrating that electrodes C3 and C4 are maxima of this measure (Marieke K. van Vugt et al. 2014).

It empowers the view that motor and premotor activity also exhibit the decisional process as described by the DDM (Drift Diffusion Model). The RP may be one of the correlates of the decision variable or a receiver of the information given by the decision variable on whether to decide or not. There is a possibility that the Readiness Potential (RP) and the CPP actually reflect the same decisional process. This process would be the one modeled by the decision variable of the Drift Diffusion Model (DDM), accumulating the sensory evidence toward a decision boundary.

Further compelling results came from a recent study led by R. O'Connell. The researchers showed that the very well-known and documented P300 could also be interpreted as an accumulation to bound signal that leads to decision (Twomey et al. 2015) (**Figure 39**). The P300 is a *“parieto-central positivity that occurs when a subject consciously detects an informative task-relevant stimulus”* (Huang, Chen, and Zhang 2015). This slow wave was first described by Sutton et al. in 1965. It is composed of two distinct components: the frontally distributed P3a and the parietal P3b, typically viewed as an index of novelty detection and stimulus categorization respectively (Sutton et al. 1965). It makes sense to think of novelty detection target categorization as some kind of decision. Perceptual decisions, as studied in laboratories, are in fact stimulus categorization tasks. Even detection tasks are decisions about the presence, or the absence, of a stimulus.



**Figure 39.** The P300 exhibits the critical dynamic properties of a neural decision variable. P300 waveforms aligned to stimulus onset (left column), response execution (middle column) and signal scalp topographies across a time window of  $-25$  to  $+25$  ms centered on response execution (right column). The colored vertical lines denote mean RT for each condition. The response aligned P300 for three equal-sized RT bins exhibiting a gradual build-up rate that **scaled with RT and reached a stereotyped zenith at response execution.** Figure from (Twomey et al. 2015)

All these results pinpoint that motor preparation, as well as the P300 waves need a reinterpretation in term of their decision making contributions. By giving a new look to experimental results on LRPs and its features in relation with decision making, we could learn about the subtleties of decision making and the emergence of a motor act. The P300, the RP and the CPP could reflect the same multimodal process of a build-up decision variable, until the reaching of a decision (Kelly and O'Connell 2015). This process would be gradually transmitted

to the motor area of the brain until a decision to act is reached, as mirrored in the LRP component. These signals seem to hold both for economic and perceptual decision making and the clarification of the link between them would be of great significance in the comprehension of decision making signals in the human brain.

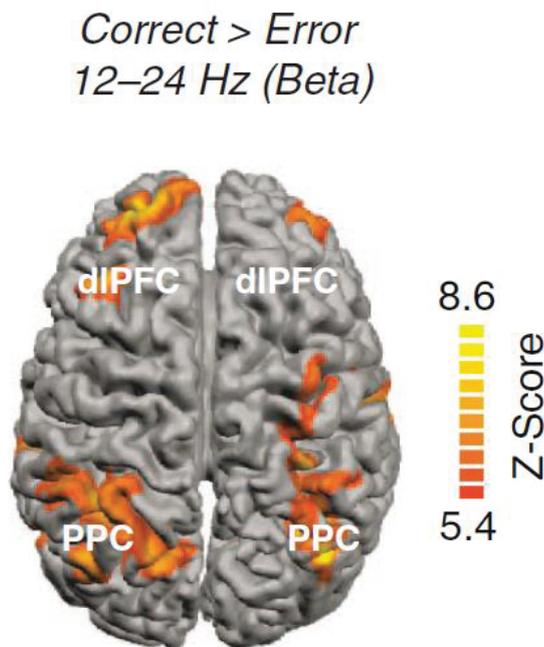
We also found difference between self- and other-affecting decisions after the response output over the centro-frontal sensors. Since it is a post response output activity, it should not result from the decision making process per se. It is here to be noted that the stimuli were displayed even after the participants answered. This late activity possibly corresponds to a verification of the decision just made. The Supplementary Motor Area (SMA) and the dorso-lateral prefrontal cortex (DLPFC) have been shown to be implicated in Speed-Accuracy Tradeoff (SAT) modulation (Wenzlaff et al. 2011). The activity post response-output would then relate to a secondary accumulation process in the fronto-parietal decision network aiming to 're-decide' (re-evaluate), in order to judge the accuracy of the decision just made before the display of the feedback. It could reflect an update of the speed-accuracy trade-off for further decisions (Padrón et al. 2016). The ongoing source analysis should shed light on the brain structures and underlying processes involved.

### ***3.3.2. Future directions***

Further analysis could also be done in the frequency domain, to better understand the difference between self- and other- affecting decision making. Brain oscillations also were found to have a relationship with the decision making process (Bode et al. 2012; Philiastides and Sajda 2006; Philiastides, Ratcliff, and Sajda 2006). Time-frequency analysis showed a proportional relationship between the power in the gamma frequency-band in visual cortices and the available sensory evidence. The increase in the visual gamma activity in response to stimuli predicts the gradual increase in the same frequency-band in pre-motor and primary motor cortices, occurring upstream to the response execution. It means that gradual accumulation of sensory evidence and response planning is reflected in the power of the gamma frequency-band (Siegel, Engel, and Donner 2011; Donner et al. 2009; Guggisberg et al. 2008).

Furthermore, Decision accuracy was found to be reflected in the power of the beta frequency-band (Siegel, Engel, and Donner 2011). This relationship between beta-band amplitude and accuracy was true for both the posterior parietal areas and the dorsolateral prefrontal cortex (DLFPC; **Figure 40**). This result suggests that the decision rule is coded through these beta frequency band activities in the frontal areas, which in turn transmit the rules to the parietal areas that accumulate the relevant sensory information through the gamma frequency. Briefly exploring time-frequency activity in our MEG study we found differences in the very high

gamma frequency band (120-150 Hz), bilaterally, over the temporal anterior sensors (**Annex 4**). Further investigation in the time-frequency domain and the coupling between frequency bands, could help construct a comprehensive picture of the influence of others in decision making. Indeed, the coupling between gamma oscillations and low frequency activity is believed to be determining in the decisional process (M. K. van Vugt et al. 2012; Wyart et al. 2012).



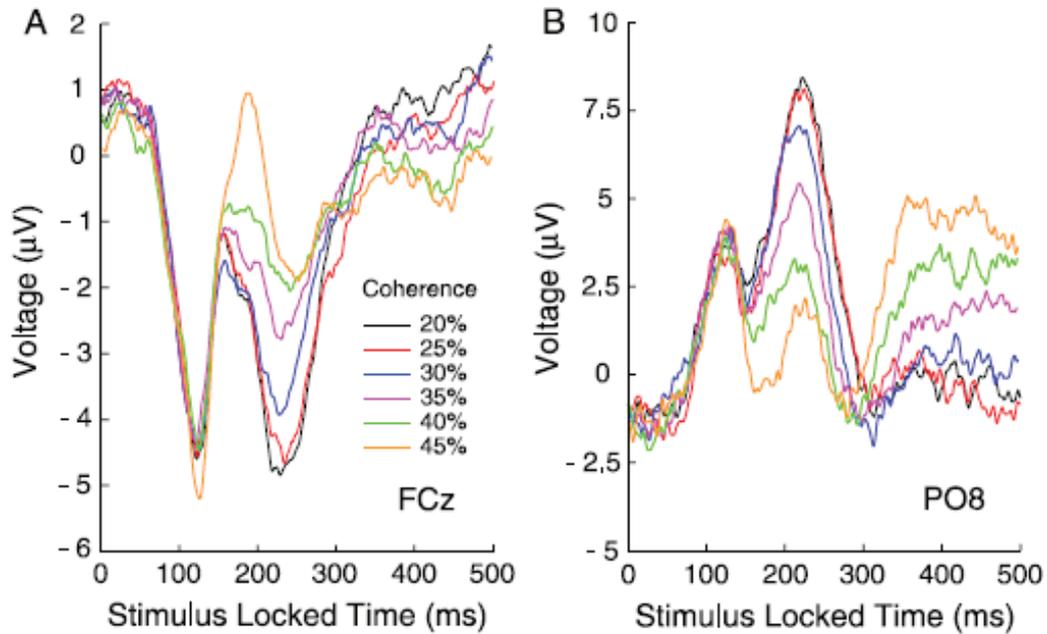
**Figure 40. Cortical distribution of the performance-predictive beta-band activity.** dlPFC, dorsolateral prefrontal cortex; PPC, posterior parietal cortex. Figure from (Siegel, Engel, and Donner 2011).

Other neural correlates of perceptual decision making have been found in human electrophysiology. Taking advantage of the temporal precision and new approaches to the analysis of Electro-Encephalo-Graphy (EEG), great work was done by Mario Philiastides and his colleagues, in decoding trial-per-trial brain activity (single-trial decoding) in face/car discrimination tasks with picture stimuli of varying blurriness levels (Philiastides and Sajda 2006; Philiastides, Ratcliff, and Sajda 2006; Ratcliff, Philiastides, and Sajda 2009; Blank et al. 2013; Philiastides, Heekeren, and Sajda 2014; Gherman and Philiastides 2015) but also in an auditory oddball paradigm (Goldman et al. 2009). Single-trial decoding consists in training a decoder over a pool of trials to discriminate between conditions and testing its decoding accuracy over all remaining trials. A good decoder, a decoder with detection accuracy higher than 60%, can then be used to identify the brain activity differing between the tested conditions across time, but also across space through sensor projection.

Using such single trial decoding techniques, M. Philiastides and colleagues detected an early component - the face-selective N170 - and further a late component (Philiastides and Sajda 2006). Between these two, they also revealed a third component - peaking at 220 ms post-stimulus onset -(Philiastides, Ratcliff, and Sajda 2006). The amplitude of this third component was correlated to the difficulty of the task. This, further called, difficulty component - D220 - influences the onset of the late component, which was itself correlated to the drift of the decision variable of the DDM (**Figure 41**). Following this line, further work showed that

separating trials as a function of the late component leads to different parameter decision estimate (Ratcliff, Philiastides, and Sajda 2009).

Decision neural correlates related to DDM can be found by decoding single-trial brain activity predicting decisions. One way to further confirm the MEG results of the present work could be to apply such decoding techniques to discriminate self- and other-affecting decisions. Given the temporality and the results of self-other difference in response related fields, we would expect a self/other classification occurring over the temporal anterior and premotor sensors possible from one second before motor response execution and correlated to the drift of the decision variable associated with each beneficiary. Other timing and topographies might well emerge, for example if the use of ToM is essential a TPJ involvement could be revealed. It is also possible that we identify a D220-like component (i.e. classifying easy and difficult trials) and that it differs between self- and other-affecting decisions, which would mean that the beneficiary of a decision influences the perceived difficulty of a stimulus.



**Figure 41. Average ERP analysis of the face-versus-car categorization task. A)** Average ERPs at each phase coherence level, across all subjects and across both face and car trials, for an electrode at a centrofrontal site (FCz). A high negativity, 220 ms after the onset of visual stimulation, can be seen for hard trials (i.e., low phase coherence trials). The amplitude of this negativity is reduced as the task becomes progressively easier. **B)** Average ERPs for an occipito-parietal electrode location (PO8). Although the effect at 220 ms remains unchanged, its orientation has changed sign (positive activation). Figure from (Philiastides, Ratcliff, and Sajda 2006).

### ***3.4. Conclusion***

The work presented in this thesis is further evidence that social cognition is a crucial part of decision making, influencing even the sensory-motor transformation involved in perceptual decision making. We also confirmed that humans have a tendency to cooperate, accurately performing the task for others, and that closeness of the relationship is a crucial factor impacting decision making and behavior in social context. Moreover, our work attests the utility of using computational modeling such as drift diffusion models in the understanding of brain and behavior. Such models can be used to decipher perceptual decision making but also economical decision making and their interplay with socio-cognitive processes as well.

The study of the brain magnetic fields related to decision making and their comparison between self- and other-affecting decisions indicated that evidence accumulation during decision making and speed-accuracy tradeoff modulation after decision were modified when deciding for others. Source analysis should shed light on the precise brain area involved. Further work would also be to apply time-frequency analysis in order to investigate the oscillatory correlates of other-affecting decision making. A comprehensive understanding of the socio-cognitive aspects of decision making is crucial, not only for treating the numerous pathologies involving social cognition, but also for developing optimized politic and management policies.

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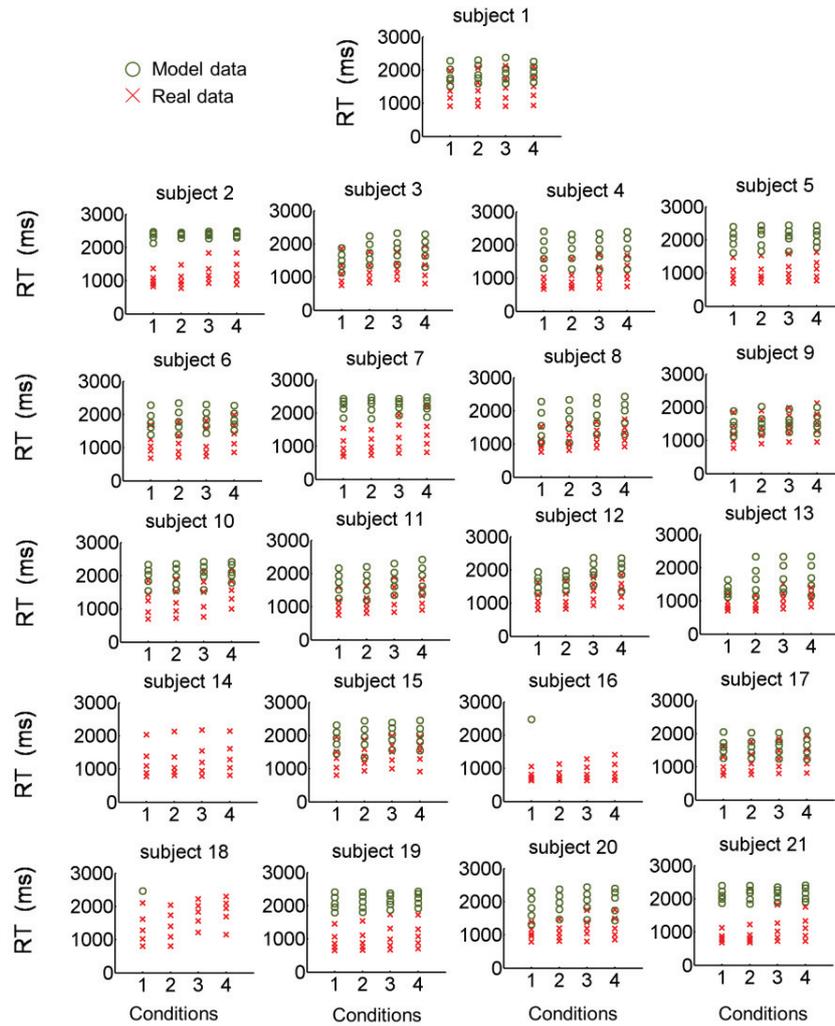
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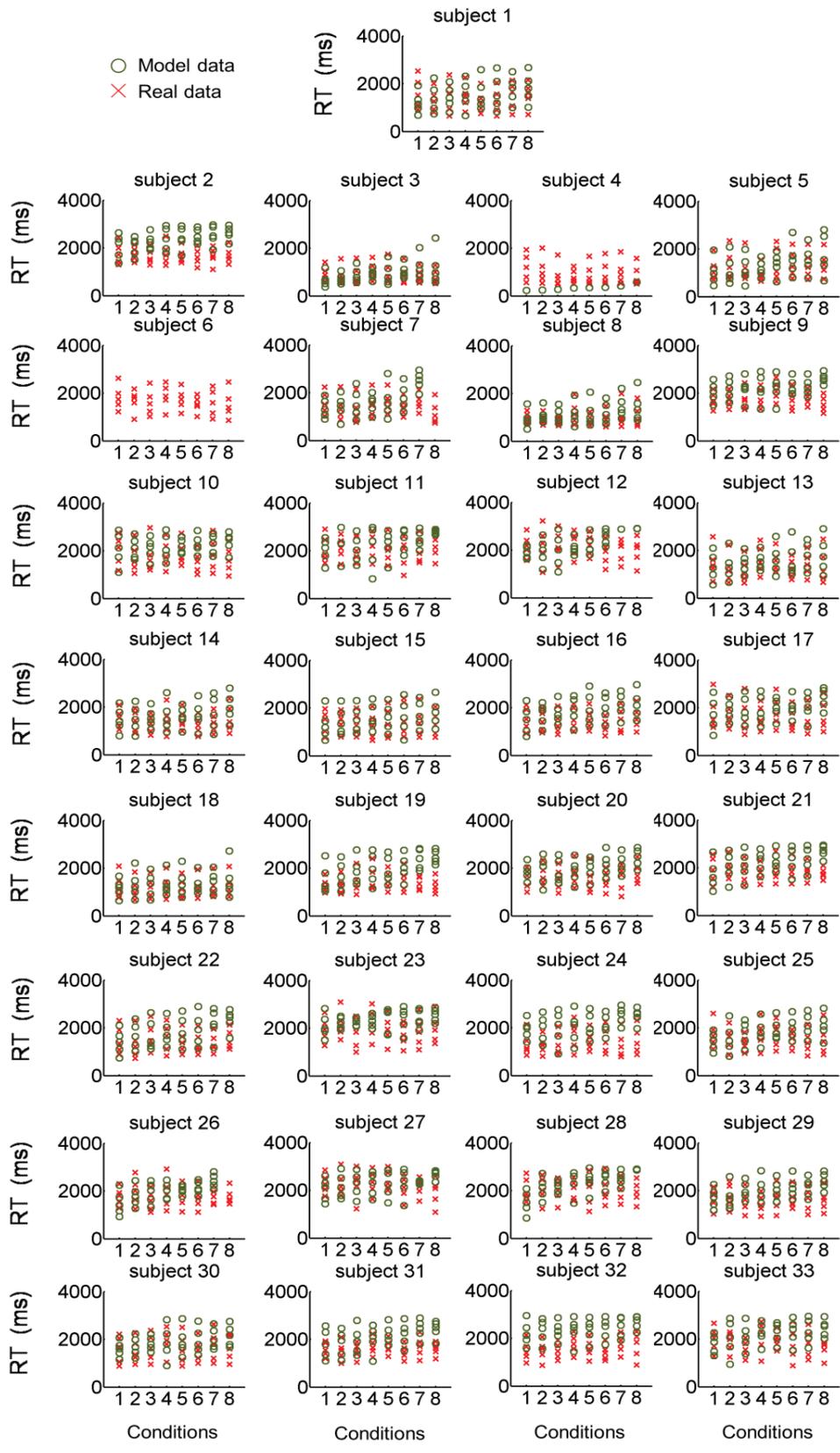
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## *Annexes*



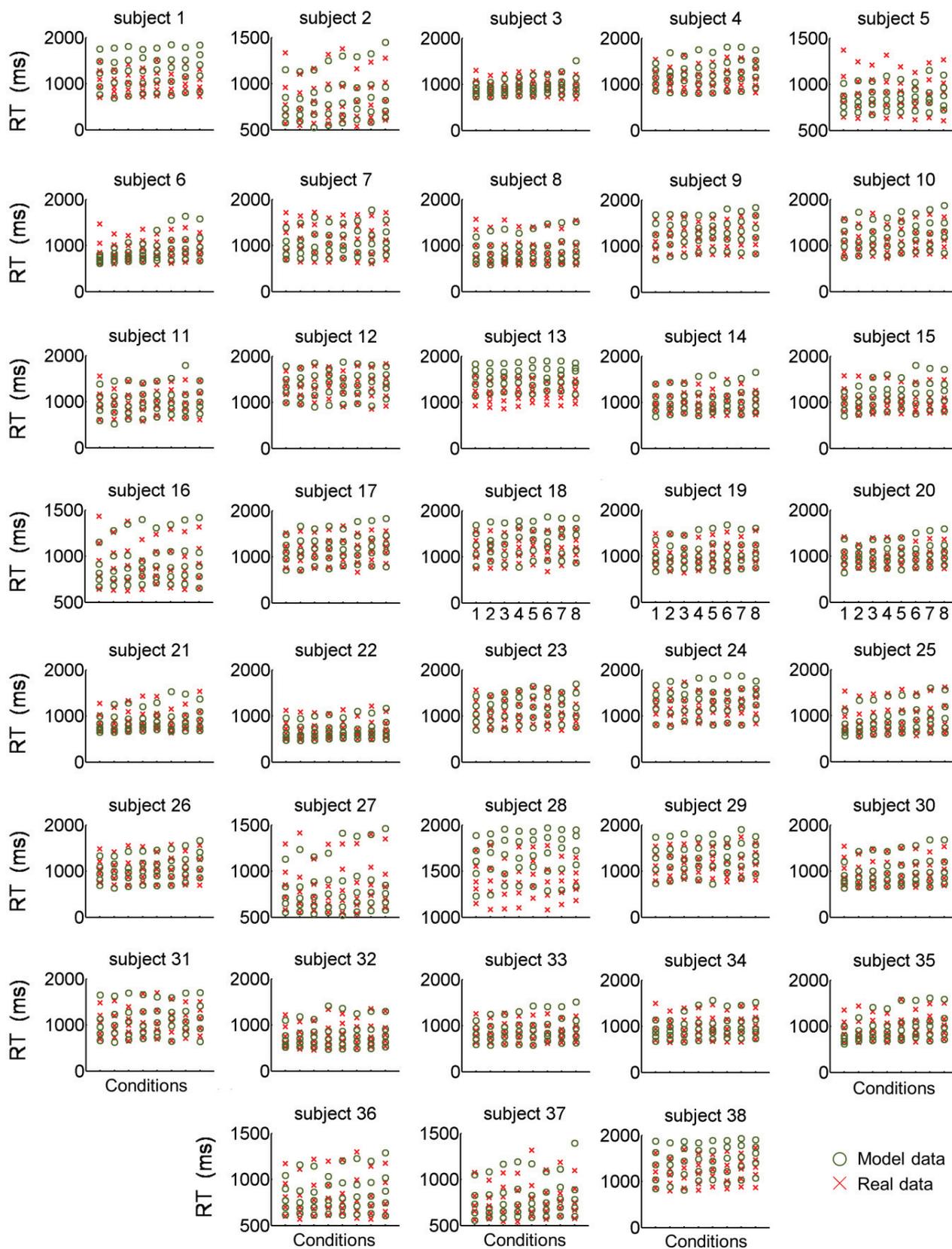
**Annex 1. Audience experiment - Single subject quantile probability plots.**

Quantile Reaction-Times (RT) for the .1, .3, .5, .7 and .9 quantiles (stacked vertically) are plotted for each experimental condition and for each subject. Predicted RT (model data) are represented by the green circles, collected RT (real data) are the red crosses. RT are expressed in milliseconds (ms).



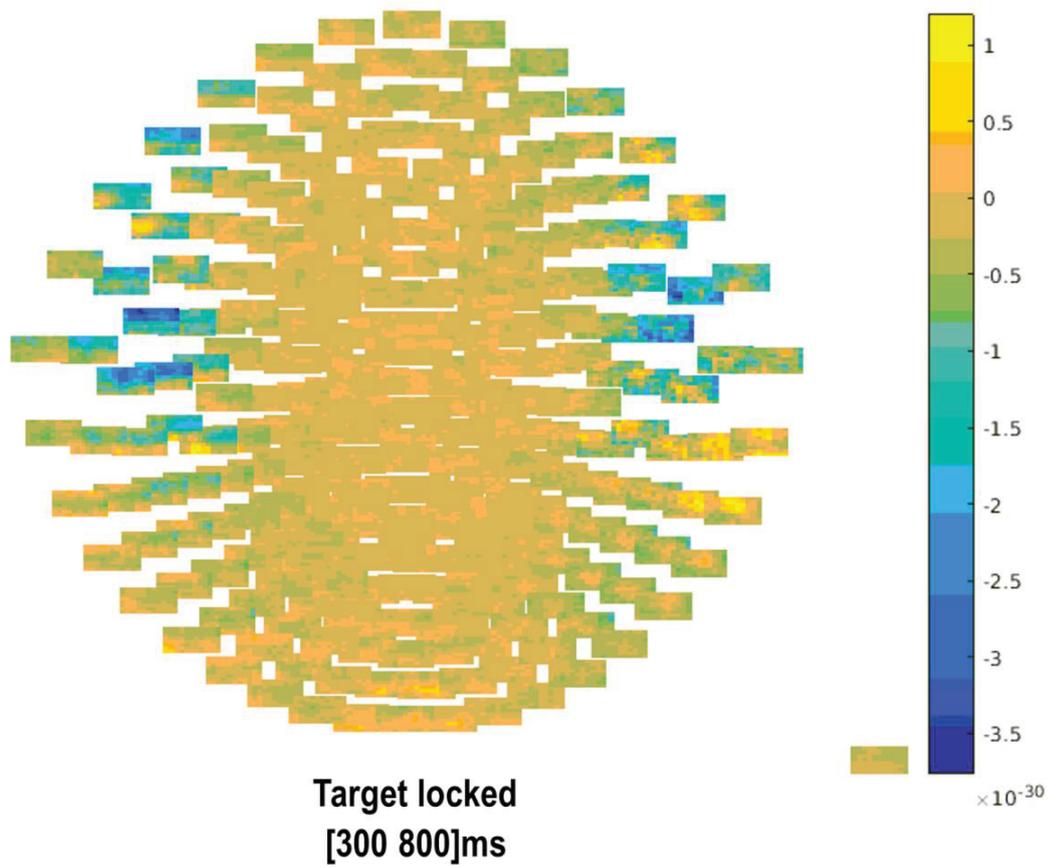
## **Annex 2. Vicarious rewards experiment 1 - Single subject quantile probability plots.**

Quantile Reaction-Times (RT) for the .1, .3, .5, .7 and .9 quantiles (stacked vertically) are plotted for each experimental condition and for each subject. Predicted RT (model data) are represented by the green circles, collected RT (real data) are the red crosses. RT are expressed in milliseconds (ms).



### **Annex 3. Vicarious rewards experiment 2 - Single subject quantile probability plots.**

Quantile Reaction-Times (RT) for the .1, .3, .5, .7 and .9 quantiles (stacked vertically) are plotted for each experimental condition and for each subject. Predicted RT (model data) are represented by the green circles, collected RT (real data) are the red crosses. RT are expressed in milliseconds (ms).



**Annex 4. Time-frequency map of the difference between other- and self-affecting decisions in the high gamma frequency band (120-150 Hz). We observe a bilateral temporal anterior difference**



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- **Communication et Vulgarisation Scientifique**  
(rédaction d'articles et enseignement)
- **Didactique** (exposition, présentation, pédagogie)
- **Langage informatique**  
(codes Matlab® et Presentation®, bash Linux)
- **Maîtrise des logiciels informatiques courants** (Word, Powerpoint, Excell, Google docs, GIMP)
- **Expériences comportementales et de neuro-imagerie chez l'Homme**
- **Gestion de projet**  
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- 2012 : **Master Physiologie et Neurosciences** (LYON 1)
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- 2018 à aujourd'hui : **Consultante en entreprise** : Conférences, formations et ateliers (fonction de la problématique)
- 2013 à aujourd'hui : **Enseignement supérieur**.  
**Explorations Électrophysiologiques** pour les **Hospices Civils de Lyon** (HCL), à l'Institut de Formation aux Métiers de l'Electro-imagerie Médicales (IFMEM): cours, Travaux dirigés et examens.
- Mai 2015 : **Organisation et animation de Pint of Science** à Lyon
- 2014-2016 : **Membre du Comité Editorial de Cortex Magazine**
- 2014-2016 : **Soutien Scolaire : Sciences et Mathématiques niveau lycée pour Etude Plus**  
(association à but non-lucratif)

## Articles et Publications

- **Bottemanne L.** and Dreher J-C. (2019) Vicarious Rewards Modulate the Drift Rate of Evidence Accumulation From the Drift Diffusion Model. *Front. Behav. Neurosci.* @
- **Bottemanne, L.**, Daligault, S., Dreher, J-C. MEG Correlates of Others in Perceptual Decision. *In preparation*
- **Bottemanne, L.**, Dreher, J-C. The Audience Effect Modulates the Uptake of Evidence Accumulation. *In preparation*
- **Bottemanne L.**, Prévions : et si nous faisons davantage confiance à notre intuition ? (2014) *Cortex Magazine* @
- **Bidet-Caulet A, Bottemanne L, Fonteneau C, Giard MH, Bertrand O.** (2014). *Brain Dynamics of Distractibility: Interaction Between Top-Down and Bottom-Up Mechanisms of Auditory Attention.* **Brain Topography** @

## Communications en meetings internationaux:

- **Bottemanne, L.**, Wydoodt, P., and Dreher, J-C. *Vicarious rewards modulate the decision threshold of the drift diffusion model.* Symposium for Biology of Decision Making, 2015, Paris.
- **Bottemanne, L.**, Wydoodt, P., and Dreher, J-C. *Social and motivational contexts modulate distinct perceptual decision making mechanisms.* Organization for Human Brain Mapping, 2014, Hambourg.

## Blog :

- **Analysis coding** ([lien](#)) a pour but d'aider d'autres à utiliser Matlab et la boîte à outils Fieldtrip.