Thèse   **2022**

Effects of emotions on social cognition

Qiao, Emilie

UNIVERSITÉ DE GENÈVE

FACULTÉ DE MÉDECINE

Professeur Patrik Vuilleumier, directeur de thèse
Professeur Corrado Corradi-Dell'Acqua, co-directeur de thèse

TITRE DE LA THESE

EFFECTS OF EMOTIONS ON SOCIAL COGNITION

THESE
Présentée à la
Faculté de Médecine

de l'Université de Genève

pour obtenir le grade de
Docteure en Neurosciences

par

Emilie QIAO-TASSERIT

de Chine

Thèse N° 314

Genève

DOCTORAT EN NEUROSCIENCES

des Universités de Genève et de Lausanne

Thèse de

Emilie QIAO-TASSERIT

originaire de Chine

Intitulée

EFFECTS OF EMOTIONS ON SOCIAL COGNITION

Soutenue le : 17 septembre2021

La Faculté de médecine, sur préavis du jury de thèse formé par :

Professeur Patrik Vuilleumier, Faculté de médecine, Université de Genève, directeur de thèse
Professeur Corrado Corradi-Dell'Acqua, Faculté de médecine, Université de Genève, co-directeur de thèse
Professeure Ulrike Rimmele, Faculté de médecine, Université de Genève, Présidente
Professeure Simone Shamay-Tsoory, Université de Haïfa, experte externe
Professeure Giorgia Silani, Université de Vienne, experte externe

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Genève, le 12 janvier 2022

Thèse n° 314

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N.B.   *La thèse imprimée doit porter la déclaration précédente * et remplir les conditions énumérées dans les « Informations aux étudiants relatives aux thèses de doctorat à l'Université de Genève ».*

To Christophe, Mélodie and Nathan,

"As water reflects the face,

so others reflect your heart back to you."

Proverbs 27:19

(New International Version, 2011)

« On trouve dans l'eau le reflet de son propre visage,

on trouve chez les autres le reflet de ses propres sentiments. »

Proverbes 27:19

(Nouvelle Français Courant, 2019)

Acknowledgements

Looking back at all the amazing people that I met during my PhD journey, I feel very moved and honored.

Patrik, you always come to my desk with a cup of coffee and brilliant ideas, making me wonder whether there is a secret smartness ingredient added in your coffee. I enjoy listening to your all your amazing stories shared like a storyteller during the lunch breaks. I am fascinated by your secret sense for feeling the results, your incredible knowledge about science as well as all sorts of arts and sports, your anti-conformism and above all your unique kindness. I felt guided and supported in my big projects as well as in my smaller projects. I was pleased to be entrusted with ABIM co-organization and other outreach projects. Seeing how much you supported me even when I had the impression that I was walking in the desert really warms my heart. I feel so privileged to have been able to work with you. With English words, I only manage to say thank you, but I mean much more.

Corrado, you have been my savior and hope in the middle of the PhD. You rescued me so many times with your incomparable technical skills and sharp-mindedness. I knew that you accompanied me in my journey, and it gave me the courage to go on even in challenging times. You have been so patient with me that I believe you deserve a medal. I like feeling your contagious passion, whenever we found an interesting result or solved a bug. I like how friendly you are and your hilarious way to tell stories, especially about your lovely kids. I remember that from the moment I listened to you at a lab meeting, I dreamt about working with you. Thank you for making my dream come true.

Simone and Giorgia, I thank you so much for being part of my jury committee. Your impressive work inspired me, and I am very pleased to discover how sympathetic you are while discussing with you about my thesis.

Ulrike, I am very proud to have you in my jury committee. I like having nice discussions with you about science and kids, listening to your soft tone of voice reflecting a gentle heart.

David, I am impressed by the way you managed to shape the CISA as such a great working environment. I learned a lot from meeting fabulous people and attending captivating lectures. Mélodie and I keep magnificent souvenirs from ISSAS. I really felt that you supported me, offering me such exceptional opportunities to combine motherhood and work in science and often having kind words of encouragements.

Bruno and Fred, you are the tamers of the electromagnetic waves, full of knowledge and willingness to share. I am happy to know that when I come to the BBL, I will find a great team, also with Emmanuel. Bruno, you made scanning sessions so fun thanks to your good temper and excellent jokes. I like looking at how interested young students listen to you every year during the brain awareness week visit. You must have inspired some new neuroscientists.

Sylvain, I have to AcqKnowledge that you have a gift for revealing physiological music out of the noise.

Christophe, I thank you for coding the library that allowed the thermode to function perfectly, and to have created a well-functioning database where to store my data.

Philippe, no computer problem resists to you. Thank you because you solved all my computer troubles with smiles and encouragements.

Thank you Marcello and Arthur for helping me in gathering the data of a fourth study (not described in this thesis).

I loved discussing with my fantastic colleagues and campus friends. I will mention only the people still around or who left more or less recently, although I still keep in my mind memorable moments with people who left longer time ago. From Patrik's lab: Roberta, Carole, Ilaria, Seb, Nahuel, Maël, Julian &

Gwladys, Edo, Rafal, Despina, Natalia, Vanessa, Raph, Judith, Heather, Lucas, Joana, Mixue, Michal, Birsu, Jie, Marion, Mitsouko, Zeynep, Monika. From Corrado's lab: Lia, Gil, Laura, Giada, Leyla. From the rest of the 3rd floor: Narly, Sophie, Alison, Virginie, Kinga, Guillaume, Anne-Lise, Delphine, Emilie, Timothée, Théophane, Julia, Pierre, Johanna, Itsaso, Christophe, Victor, Martin, Vincent. From the 3rd floor across the terrasse: Christian, Minerva, Mina, Hugues, Christophe, Cyrille, Joël, Nicolas, JP, Pascal, Jamil, Daniel, Julie, Estelle. From the 2nd floor: Daphné, Swann, Adrien, Arthur, Freya, Naïma, Kim, Ewa, Ben, Solange, Eva, Andrea, Danny, Alexandra, Lina, Florian, Céline, Angela, Constant, Steve, Emma, Eva, Donald, Tiffany, Alessio, Patricia, Didier, Garance, Cyrielle, Coralie, Simon, Asli, Liudmila, Nina, Teerawat, Tobia.

Cristina, the mamma of the CISA PhDs, you have been taking care of us so well with uplifting spirit, humor and encouragements. The many exciting lectures and workshops you organized helped my motivation to stay high.

Carole, I find extraordinary the way you manage to promote our work to the public. It was so rich to do outreach with you. I thank you for giving me amazing opportunities to share with other people what I have learned at the CISA and for pushing me out of my comfort zone with trust in me.

Marion, Sandrine, Daniela (CISA), Marie-Ange, Raquel, Sara, Françoise (NEUFO), Ulrike (LNDS), Marie-France (FacMed), you are the smiling face of the administration. Thanks to your efficiency, administrative work has been very smooth and even pleasant.

Anne-France, Silvia, Pierre, you turned the cafeteria into a super friendly place. I still remember the delicious desserts you gave me during my pregnancy and the lunch together. Mélodie and Nathan still like a lot your luminous teddy sheep.

François, thank you for sharing your immense teaching experience with me while I was teaching with you.

Frauke and Karl-Heinz, your precious advice gave me direction when I needed.

Laure, you gave me a wonderful opportunity to share my work with the public and to apply it into a beautiful real world situation. You managed to enhance magically a conversation into a pleasant program. I like discussing with you and observing the excitement in your eyes when you describe your new projects.

Dino, Ruben, Sam, your eloquence and creativity helped me express my work in a new light. Thank you for taking the time and energy to help me finding the right words, ideas, and ways to express them, in such a fun atmosphere.

I thank the CISA graduate school, the LNDS, the CUSO, the Regard, the Unige mentoring, MT180 and Famelab programs where I learned a lot and met awesome people.

I thank the FNS MD-PhD program, the fondation Boninchi, the fondation Vachoux, the fondation Henriette Meyer and the CISA for selecting me as deserving financial support.

I thank all the participants who took time to help me with my experiments.

To all my friends from Geneva, Paris and other places, I hope that you know that you count for me and that you can count on me.

Mummy and daddy, I did not know what it means to be a parent until I became one. Thank you for being mine.

Mélodie and Nathan, my treasures, I just want you to remember that mummy loves you, unconditionally.

Christophe, when we got married during my PhD, we had no idea about all the challenges that we had to face given the very special needs of our children. I think that I realized how hard it was for me too when you wrote to your family that you just spent the most difficult years of your life. Still, after all these countless sleepless nights, appointments and procedures, we continue to enjoy discussing, playing and laughing together. I am learning so much from you, from who you are. I love you, deeply.

Abstract

Can our own emotions alter our ability to infer others' thoughts and emotions or even feel others' pain, potentially leading to misunderstandings?

In a first experiment, we tested the effect of emotions on cognitive and affective theory of mind (ToM), which is our ability to infer thoughts and emotions in others. We induced emotions in participants with joyful, neutral, and fearful movie clips. Then participants read stories describing a protagonist in false-belief situations (cognitive ToM), and in joyful or fearful situations (affective ToM). Using functional MRI, we found no effect of emotions on the ability to infer false-beliefs. However, we found that when participants were induced with joy or fear, and had to infer incongruent emotions (respectively fear or joy) in the story protagonist, brain activity was reduced in the superior temporal gyrus, in the precuneus and in the frontoparietal operculum (including the posterior insula and sensorimotor cortices). These results support the embodied social cognition account, suggesting that the brain response to others emotions may be modulated by the congruence between our own and others' affect.

In a second experiment, we further tested the effect of emotions on pain and empathy for pain. After watching the same movie-clips, participants received a painful thermal stimulation (first-hand pain), and watched images of wounded hands (others' pain). Brain responses to first-hand pain were reduced after joyful movie clips, in the bilateral posterior insula, known for pain processing. In contrast, brain responses to others' pain were reduced after fearful movie-clips, in regions involved in empathy for pain, namely in the anterior insula and middle cingulate cortex. Interestingly, we found that highly empathetic participants presented a greater recruitment in the medial prefrontal cortex after fearful movie-clips, suggesting compensatory cognitive processes. Moreover, multivoxel pattern analyses confirmed that positive emotions favored similar neural representations for empathy for pain and first-hand pain in the

anterior insula. Our results support the Broaden-and-Build account, suggesting that positive emotions may allow access to pain in others, while fear may prevent it.

Overall, our results reveal that our own emotions may bias the way we process in the brain emotions and pain in others.

Résumé (Abstract in French)

Nos propres émotions peuvent-elles altérer notre capacité à inférer les pensées et les émotions des autres ou même encore à ressentir leur douleur, menant potentiellement à des incompréhensions?

Dans une première expérience, nous avons testé l'effet des émotions sur la théorie de l'esprit (TdE) cognitive et affective, qui est notre capacité à inférer des pensées et des émotions chez autrui. Nous avons induit des émotions chez les participants avec des extraits de films joyeux, neutres et effrayants. Puis les participants ont lu des histoires décrivant un protagoniste dans des situations de fausse croyance (tdE cognitive), et de joie ou de peur (TdE affective). En utilisant l'IRM fonctionnel, nous n'avons pas trouvé d'effet des émotions sur la capacité à inférer de fausses croyances. Cependant, nous avons trouvé que quand les participants avaient été induits avec de la joie ou de la peur, et ont eu à inférer des émotions incongruentes (de la peur ou de la joie respectivement) chez le protagoniste de l'histoire, l'activité cérébrale était réduite dans le gyrus temporal supérieur, le précuneus et l'operculum frontopariétal (incluant l'insula postérieur et les cortex sensorimoteurs). Ces résultats soutiennent la théorie de la cognition sociale incarnée, suggérant que la réponse cérébrale aux émotions d'autrui pourrait être modulée par la congruence entre notre propre état affectif et celle d'autrui.

Dans une deuxième expérience, nous avons testé plus loin l'effet des émotions sur la douleur et l'empathie pour la douleur. Après avoir regardé les mêmes extraits de films, les participants ont reçu une

stimulation thermique douloureuse (douleur sur soi), et ont regardé des images de mains blessées (douleur sur autrui). Les réponses cérébrales à la douleur sur soi étaient réduites après les extraits de films joyeux dans l'insula postérieur bilatéral, connu pour le traitement de la douleur. Par contre, les réponses cérébrales à la douleur sur autrui étaient réduites après des extraits de films de peur, dans des régions impliquées dans l'empathie pour la douleur, à savoir l'insula antérieur et le cortex cingulaire moyen. De manière intéressante, nous avons trouvé que les participants très empathiques présentaient un r2ecrutement plus important du cortex préfrontal médial après les extraits de films effrayants, suggérant des mécanismes cognitifs compensatoires. De plus, les analyses de pattern multivoxels ont confirmé que les émotions positives ont favorisé des représentations neuronales similaires pour l'empathie pour la douleur et la douleur sur soi dans l'insula antérieur. Nos résultats soutiennent la théorie de l'élargissement et de la construction, suggérant que les émotions positives pourraient permettre l'accès à la douleur d'autrui, alors que la peur pourrait l'empêcher.

Dans l'ensemble, nos résultats révèlent que nos propres émotions peuvent biaiser la manière dont nous traitons dans le cerveau les émotions et la douleur d'autrui.

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Chapter 1: General Introduction

"The warmth of relationships throughout life has the greatest positive impact on 'life satisfaction'". "Happiness is love. Full stop." These conclusions come from one of the main authors of the longest longitudinal study ever conducted, that started in 1938 at Harvard and is still running today, called the Grant study (Vaillant 2012). Thus, the study of the lives of hundreds of individuals followed during decades revealed that relationships are key for developing a happy and meaningful life. Relationships are based on our ability to understand and feel what others are thinking and feeling, namely on our empathy. However, perhaps contrary to intuition, empathy appears to be highly vulnerable and easily malleable by various external factors. Yet, it is still unclear whether our own emotions may affect our empathy, potentially leading to misunderstandings and isolation. This thesis contribute to elucidate whether and how emotions can affect cognitive and affective theory of mind (ToM) and empathy for pain.

In the first section of this introduction, I will highlight reasons to study empathy, define the umbrella term "empathy" and describe its neural substrates. In the second section, I will give examples of contextual factors influencing empathy in children and adults, decreasing and increasing it. In the third section, I will define the word "emotion", describe its neural substrates and present its potential effect on empathy, given two plausible theoretical accounts. In the fourth and last section, I will show the way this thesis contribute to understand the effects of emotions on empathy, state the research questions and the contrasting predictions derived from the two theoretical accounts.

1. Significance of Empathy

1.1 Importance of Empathy

Empathy helps forming and maintaining relationships that are at the core of a happy and meaningful life. Empathy may promote prosocial behaviors and generosity is associated with happiness (Lamm, Rütgen, and Wagner 2019). Indeed, spending money on others, as compared to on oneself, increases self-reported happiness and is related to increased activity in the striatal reward region (Lara B Aknin et al. 2013; Aknin, Dunn, and Norton 2011; Dunn, Aknin, and Norton 2008; Park et al. 2017a). Identifying and understanding emotions in others are also part of emotional competences, often called emotional intelligence, that is associated with positive relationships with others (Lopes et al. 2005).

From the perspective of evolution and species survival, empathy allows parents to care for their offspring, to favor help and cooperation and to reduced conflict within a community (Klimecki 2019). Nevertheless, empathy towards individuals from outside of the community and perceived as dissimilar promotes tolerance.

Indeed, empathy is related to morality. Representing mental states of others helps judging if an action is bad or not for others. Interestingly, the brain network associated with morality overlaps with the one activated when inferring thoughts and beliefs in others in a larger extent that with the one activated when inferring emotions in others (Bzdok et al. 2012). Moreover, temporarily impairing the functioning of a region associated with inferring thoughts in others, the namely the temporoparietal junction (TPJ), using transcranial magnetic stimulation, led to judge actions related to bad intentions as more permissible (Young et al. 2010).

Incarcerated males with high psychopathic traits reported less empathy for pain when imagining pain in others, as compared to those with low psychopathic traits. They also presented decreased brain activation in areas related to affective response. Yet, imagining first-hand pain elicited greater activation in regions

associated with empathy for pain (Decety et al. 2013). Similarly, our ability to represent intentions in others may be fundamental for our sense of justice as well as our ability to forgive (Decety and Yoder 2016; Patil et al. 2017). Noteworthy, empathy and forgiveness have been identified as factors that favor marriage satisfaction (Chung 2014; Paleari, Regalia, and Fincham 2005).

A lack of empathy may therefore lead to isolation, unhappiness or even immoral conduct. Not being able to infer someone's emotions based on their situation may lead to misunderstandings and conflicts, while not feeling someone's pain may prevent helping him. Conversely, empathy skills may lead to flourishing relationships, paving the way to health and happiness.

1.2 Definition of Empathy

The word "empathy" is derived from the Ancient Greek *empatheia* meaning "physical affection" or "passion". It binds the words *en* and *pathos*, in English "in, at" and "passion, suffering". The German philosopher Robert Vischer has probably invented this word in 1873 to refer to esthetic empathy, describing the relationship of a subject with a piece of art to get access to its meaning. Vischer's word in German *Einfühlung* means "in-feeling" or "feeling-into" and has later been used by other German authors such as Sigmund Freud to describe psychological processes.

Taken as an umbrella term (Cuff et al. 2014), the word empathy has received various definitions and models (Lamm et al. 2019; Schurz, Radua, et al. 2020; Shamay-Tsoory 2011a, 2015). I will focus on one particular recent data-driven model. This model emerged from a meta-analysis that uses clustering methods on brain data from 4207 participants performing various socio-cognitive tasks (Schurz, Radua, et al. 2020). It describes that understanding others' mental content may require processes that can be divided into two levels. The lower one is more specific to the context, the stimuli and tasks, whereas the

higher one is broader and more abstract. This higher level is further decomposed into cognitive and affective processes and a combination of these two types of processes in parallel.

Cognitive processes of empathy refers to reasoning about mental states such as goals, intentions or beliefs. It is studied by asking participants to infer a belief in others for instance from written statements or stories, attribute a personality trait to others or play strategic games with a partner. These tasks belong to a larger set of tasks associated to what is called cognitive Theory of Mind (ToM) or mentalizing, when we infer thoughts and beliefs in others. A combination of cognitive and affective processes of empathy is required in tasks where participants have to infer emotions in others for example from written stories, from drawn or animated situations, from stories told in videos or with pictures of people. These tasks can be associated to tasks associated to affective ToM, when we infer emotions in others. Affective processes of empathy refers to feeling and sharing in our own body an emotion or a pain witnessed in others, at the emotional, motor and somatosensory levels. It is elicited in tasks where participants have to observe or share an emotion or a pain in others, for instance from videos, written vignettes, pictures of eyes, faces or body parts.

In this thesis, I investigated in a first study the effects of emotions on cognitive and intermediate empathy, in a cognitive and affective ToM task where participants had to infer a belief or an emotion from written stories. I also studied in a second study the effects of emotions on affective empathy in a task where participants had to watch pictures of painful hands.

I will briefly mention other processes related to empathy that are not the focus of this thesis. The motivational processes of empathy drive us to feel concerned for someone and to act for his well-being. This form of empathy is related to compassion that has the specificity to elicit positive emotions (Singer and Klimecki 2014). The motor processes of empathy refers to a motor response, such as automatically mimicking others' emotions expressed on the faces, voices or gestures, or activating a muscle where we

observe pain in others (Van der Graaff et al. 2016; Mahayana et al. 2014). In addition, the term "empathy" sometimes refers to emotional contagion, which is the tendency to take the sensory, motor, physiological and affective states of others (Prochazkova and Kret 2017). Emotional contagion has been described as supporting emotional empathy (Shamay-Tsoory 2011a). However, a person "contaminated" by an emotion is not conscious that this emotion is not his own one.

The distinction between the different processes of empathy is important because they are thought to be supported by partially dissociable brain substrates.

1.3 Neural Substrates of Empathy
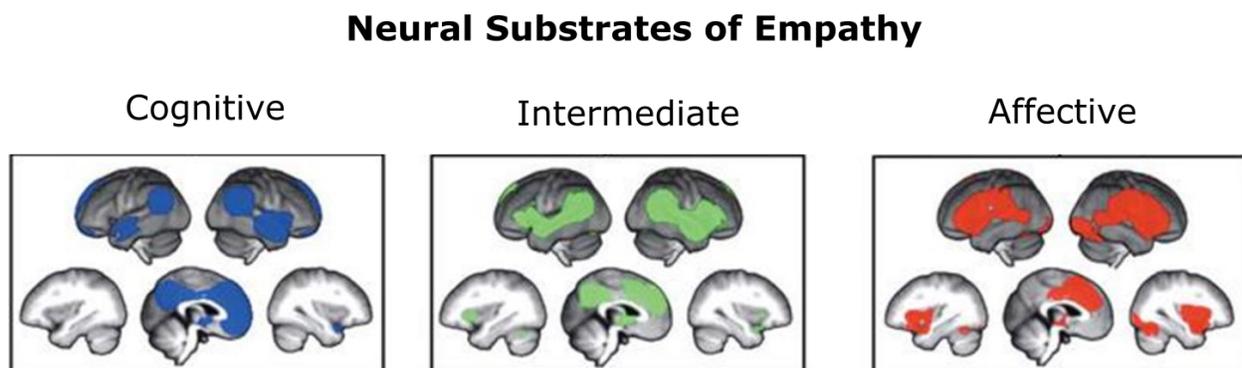
Figure 1. Brain activations associated with cognitive, intermediate and affective empathy (adapted from (Schurz, Radua, et al. 2020)).

1.2.1 Neural Substrates of Cognitive Empathy

The cognitive processes of empathy are related to activations in regions processing more abstract and transmodal information, and in regions distinguishing our thoughts from the reality, such as the

temporoparietal areas, the medial prefrontal cortex (PFC), the anterior and middle cingulate cortex and the precuneus (Schurz, Radua, et al. 2020).

The temporoparietal junction (TPJ) and the medial PFC were activated across various ToM related tasks (Molenberghs et al. 2016a; Schurz et al. 2014). Different theories have attributed to these regions different functions, as they are also involved in other cognitive processes, such as autobiographical memory (Spreng, Mar, and Alice S.N. Kim 2009) or attention (Mitchell 2008; Scholz et al. 2009). For instance, the TPJ may help to process beliefs and transient covert mental states, to predict external event, to distinguish oneself from the others, to relocate attention or to extract and synthetize social context, in order to guide attention and make decisions (Lamm et al. 2019; Schaafsma et al. 2015; Schurz and Perner 2015). The medial PFC may help to process socially relevant information and enduring mental states or traits. The ventral part may support more emotional (Shamay-Tsoory and Aharon-Peretz 2007; S. G. Shamay-Tsoory, Aharon-Peretz, and Perry 2009; Shamay-Tsoory, Tibi-Elhanany, and Aharon-Peretz 2006) and the dorsal part more cognitive ToM (Corradi-Dell'Acqua et al. 2020; Corradi-Dell'Acqua, Hofstetter, and Vuilleumier 2014; Kalbe et al. 2010).

Depending on the task, other regions may be activated such as the precuneus, the temporal lobes (including the superior temporal cortex, medial temporal lobes and temporal poles), the amygdala, the cingulate cortices (anterior and posterior) and the inferior frontal gyri (Molenberghs et al. 2016a; Schaafsma et al. 2015; Schurz et al. 2014; Shamay-Tsoory 2015). The diversity of activations depending on the tasks demonstrates the heterogeneity of processes underlying what we call ToM. For instance, when judging cognitive ToM stories, participants infer where a protagonist believes an object is, although this object has been moved in his absence. Judging such outdated beliefs are found to activate not only the TPJ and medial PFC, but also the anterior and posterior cingulate cortices, the precuneus, the bilateral angular gyri and superior temporal sulci, the left temporal pole, amygdala and superior frontal gyrus (Mar 2011). A particular case often associated with ToM is when taking the visual perspective of others'. Studies

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showed that this process shares common regions with other ToM tasks but not with the core ToM regions

common across several tasks, as demonstrated in a meta-analysis, highlighting more specific processes

(Arora, Schurz, and Perner 2017; Schurz et al. 2013, 2015; Spunt and Adolphs 2014).

Neural Substrates of Cognitive and Intermediate Empathy in the case of ToM
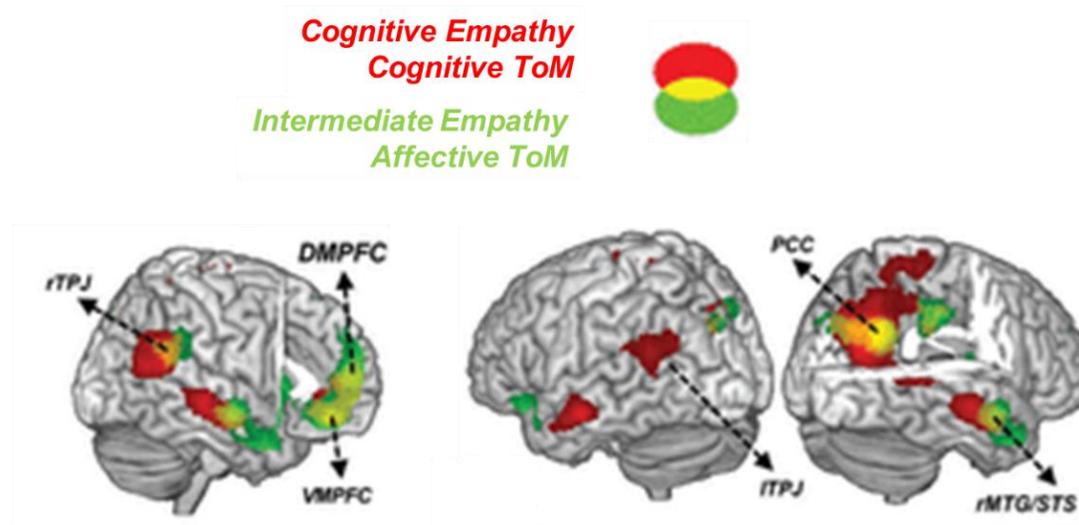
Figure 2. Brain activations associated with cognitive and intermediate empathy in the case of a cognitive

and affective ToM task. In this task, participants had to read stories and judge a protagonist's beliefs and

emotions given the situation described in the stories (adapted from (Corradi-Dell'Acqua et al. 2014)). rTPJ

and lTPJ: left and right temporoparietal junction. DMPFC and VMPFC: dorsal and ventral medial prefrontal

cortex. PCC: posterior cingulate cortex. rMTG/STS: right medial temporal gyrus/superior temporal sulcus.

1.2.2 Neural Substrates of Intermediate Empathy

Tasks that combine both cognitive and affective processes of empathy are related to large activations in

the bilateral temporal lobes. Activations also overlap with cognitive empathy related regions such as the

bilateral temporoparietal cortex and precuneus, and with the affective empathy related regions such as the left insula and inferior frontal gyrus (Schurz, Radua, et al. 2020). Moreover, in affective ToM stories, judging a protagonist's emotion activated the ToM network, especially in the TPJ and medial PFC. Indeed, the medial PFC has been found to also be involved in attributing and perceiving emotions (Skerry and Saxe 2014) and, along with the left superior temporal sulcus, in representing emotions perceived across different modalities (Peelen, Atkinson, and Vuilleumier 2010).

However, judging affective stories elicited greater activity in the medial PFC and ventral striatum than cognitive ToM stories. Judging cognitive ToM stories elicited greater activity in the precuneus and angular gyrus than affective ToM stories. Nevertheless, when judging cognitive and affective ToM stories, multivoxel pattern analyses showed shared neural substrates in the TPJ but not in the medial PFC. (Corradi-Dell'Acqua et al. 2014). This finding is consistent with brain lesions and Transcranial Magnetic Stimulation (TMS) studies in the medial and dorsal PFC that have showed a dissociation between cognitive and affective ToM (Kalbe et al. 2010; Shamay-Tsoory et al. 2005; S. G. Shamay-Tsoory et al. 2009; Shamay-Tsoory et al. 2006).

1.2.3 Neural Substrates of Affective Empathy

The affective processes of empathy are related to activations in regions processing more sensory and unimodal information, allowing to share emotional, motor and somatosensory representations with others. These regions are located in the bilateral anterior insula, the anterior and middle cingulate cortex, the right frontal cortex especially in its inferior portion, the inferior parietal lobule (in the supramarginal gyrus), the pre and post-central gyri, the supplementary motor area and temporal pole (Schurz, Maliske, and Kanske 2020; Shamay-Tsoory 2015).

Interestingly, the inferior frontal cortex, the parietal lobule and the ventral premotor cortex show mirroring properties. Indeed, mirror neurons are localized mainly in the inferior parietal lobe, the inferior frontal gyrus and the adjacent ventral premotor cortex but also in limbic, visual and cerebellar areas (Molenberghs, Cunnington, and Mattingley 2012). These neurons are activated when observing an action performed by others and when performing the same action ourselves, and also in various other tasks from imitating and understanding actions to social cognition (Mahayana et al. 2014; Molenberghs et al. 2012). Thus, the mirror neuron system has been associated not only with motor processes of empathy but also with emotional contagion, along with other brain regions related to specific types of stimuli. For instance, emotional contagion from fearful faces may be related to activation in the amygdala and from painful faces in the insula (Prochazkova and Kret 2017; Tamm et al. 2020; Zhou et al. 2020).

Furthermore, regions associated with affective empathy shared activations with both empathy for emotions in others and first-hand emotions in the left insula, the somatosensory pre and postcentral gyri and the supramarginal gyri (Schurz, Radua, et al. 2020). Interestingly, the right supramarginal gyrus may help overcome our tendency to project our own emotions onto other people, namely to overcome our emotional egocentricity bias (Bukowski et al. 2020; Riva et al. 2016; Silani et al. 2013).

Empathy for pain is associated with activation in the anterior insulae along with the anterior and middle cingulate cortices. These regions are notably involved in the affective component of pain and interoceptive awareness. Moreover, other regions are involved depending on the tasks. Imagining someone's pain from pictures of body parts in pain was related to stronger activities in regions involved in understanding actions (inferior parietal and ventral premotor cortices) and in somatosensory areas. Seeing a real person receiving an electrical shock was associated with greater activation in the ToM network (ventromedial PFC, TPJ and temporal cortex, precuneus) (Fan et al. 2011; Lamm, Decety, and Singer 2011).

These activation for empathy for pain were shared with first-hand pain activations in the bilateral anterior and middle insulae and in the middle cingulate cortex (Corradi-Dell'Acqua et al. 2016; Corradi-Dell'Acqua, Hofstetter, and Vuilleumier 2011). Indeed, first-hand pain elicited by heat was related to activations in the anterior and posterior insulae and in the anterior cingulate cortex, as well as in the thalamus, the secondary somatosensory cortex and periacqueducal gray (Wager et al. 2013).

Neural Substrates of Pain and Empathy for Pain
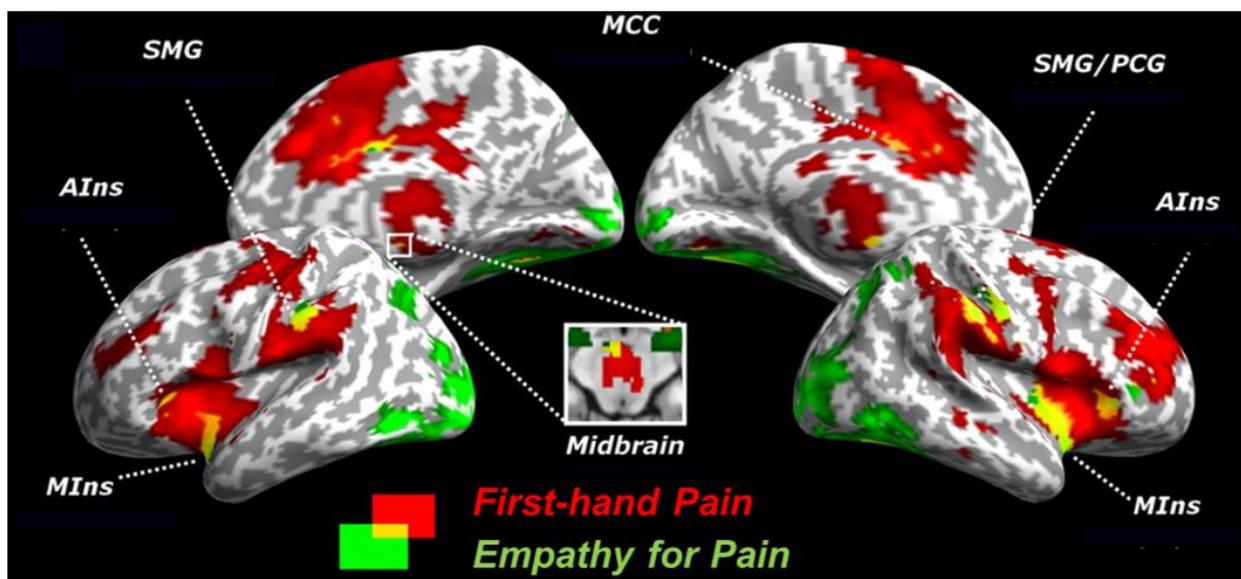
Figure 3. Brain activations associated with first-hand pain and empathy for pain. In this task, participants received painful thermal stimulations and watched pictures of painful hands (adapted from (Corradi-Dell'Acqua et al. 2011)). AIns and MIns: anterior and middle insula. SMG: supramarginal gyrus. MCC: middle cingulate cortex. PCG: postcentral gyrus.

Given the shared activities between empathy for pain and first-hand pain, the affective facet of empathy has been described as feeling *as* the other, as opposed to the motivational processes of empathy that is

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feeling *for* the other (Klimecki, Leiberg, Ricard, et al. 2013; Lamm et al. 2019; Singer and Klimecki 2014). The motivational processes of empathy, associated with empathic concern and compassion, elicits activations in a network associated with positive emotions in the striatum and orbitofrontal cortex (Singer and Klimecki 2014).

A common and intuitive thinking is that empathy is an innate ability that therefore cannot be undermined. However, in the next section, I will present studies contradicting this belief, although they were not always differentiating between the different facets of empathy. In sum, empathy appears to be highly flexible and depending on the context, it may be nurtured, altered and trained.

2. Factors Influencing Empathy

A meta-analysis including 13,737 American college students showed that empathic concern and perspective taking decreased between 1979 and 2009. This decrease was even more pronounced after 2000 (Konrath, O'Brien, and Hsing 2011) and paralleled with an increase in violence and bullying as well as in narcissism (Twenge et al. 2008; Twenge and Campbell 2008; Twenge and Foster 2008, 2010; Twenge and Im 2007). Indeed, narcissism is related with deficits in empathy, particularly in affective empathy, and in emotion processing (Baskin-Sommers, Krusemark, and Ronningstam 2014; George and Short 2018; Ritter et al. 2011; Ronningstam 2016; Scalabrini et al. 2017). The authors of this meta-analysis speculate that empathy decline might be related to increased media and technology consumption, to changes in parenting practices and decreased number of siblings, and to increased expectations of success. They suggest that interacting during a half hour with family and friends while taking their cognitive and emotional perspectives could be a start for training empathy, as attempts to train empathy especially in children have been reported as successful (Feshbach and Cohen 1988; Gordon 2003; Hatcher et al. 1994).

2.1 Development of Empathy During Childhood

The ability to develop an empathetic personality is the result of an interaction between genetic and environmental factors (Knafo and Plomin 2006). Genetic factors related to the oxytocin, vasopressin or dopamine receptors have been reported to be involved in the individual differences in empathy. Moreover, intranasal administration of oxytocin has the potential to enhance social cognition and prosocial behaviors, depending on the social and situational context. It may for instance improve affective empathy, emotion recognition, compassion towards women and generosity (Abu-Akel et al. 2015; Bartz et al. 2010, 2011; Domes et al. 2019; Hurlemann et al. 2010; Palgi, Klein, and Shamay-Tsoory 2013; Shahrestani, Kemp, and Guastella 2013; Zak, Stanton, and Ahmadi 2007). Twins studies reported mitigated results sorting apart the effects of genetics, but several showed that monozygotic twins have more similar degrees of empathy than heterozygous ones (Mcdonald and Messinger 2011; Uzefovsky and Knafo-noam 2017).

Among the environmental factors, we can cite the quality of the relationship between the child and the caregiver. This relationship fosters the feeling of security and the attachment bonds. Synchrony during playful moments between the child and the parent reflects the quality of their relationship. This synchrony requires shared affects and attunement, sensitizing infants to emotional resonance and empathy. It has therefore been associated with the development of empathy and to attachment (Feldman 2007, 2017; Leclère et al. 2014). The warmth personality of the parents, the presence or absence of trauma during childhood may also influence the development of empathy (Levy, Goldstein, and Feldman 2019; Mcdonald and Messinger 2011; Zhou et al. 2002). Parental values of justice and fairness was associated with infants and toddlers preference for prosocial behaviors (Cowell and Decety 2015). Although childhood adversity has been mostly associated with impaired empathy, it may also sensitize to suffering in others, help take their perspective and understand their mental and emotional states (Greenberg et al. 2018). Furthermore, individuals who faced high levels of lifetime adversity were able to resist to the decrease of compassion

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associated with numerous victims, especially if they believe that they can be efficient in helping them (Lim and DeSteno 2016).

Interestingly, Denmark, one of the countries consistently reported as the happiest (Martela et al. 2020) has also been reported as having one of the highest levels of empathy (Chopik, O'Brien, and Konrath 2017). It has integrated mandatory empathy classes one hour per week as part of the official curriculum since 1993 for 6 to 16 years old children, called *Klassens time* (Alexander and Sandahl 2016). In these classes, students are invited to speak about problems and the whole class works to find solutions. Other activities can for instance train to recognize and express emotions. At school, children with different strengths and weaknesses are mixed. They are encouraged to collaborate on common projects as well as during moments of plays, and they are discouraged to compete. Another program in Canada, named *Roots of Empathy*, aims at preparing parents to be empathetic, responsive, responsible and nurturing with their children and at fostering the development of empathy in children (Gordon 2003). This rich program favors communication between parents and children and between children. Children learn to take the perspective of others, to recognize emotions, to take care of others, to reach consensus, to challenge cruelty and injustice and to develop resilience.

As ToM skills are associated with better social and academic skills, trainings have been developed to improve ToM in children with success. In those trainings, children need to think about alternative perspectives or mental states, when facing situations presented in stories, pictures, videos or role-plays (Hofmann et al. 2016), although pretend-plays may not be very effective (Lillard et al. 2013). Adolescents also improved empathic concern and perspective taking after empathy training including listening without judging and self-observation (Hatcher et al. 1994). Moreover, inclusive schools containing children with disabilities were associated with greater ToM development (Smogorzewska, Szumski, and Grygiel 2020). Furthermore, encouraging children to talk about the thoughts and feelings of immigrants increased

prosocial behavior towards them (McLoughlin and Over 2019). Interestingly, prosocial behaviors such as giving may be more rewarding than receiving in toddlers (Aknin, Hamlin, and Dunn 2012).

Affective empathy can already be observed the first day of life. A baby cries differently if another baby is crying next to him, as compared to other loud noises. He can recognize very early if the environment is hostile or welcoming, relying especially on the amygdala and posterior insula (Decety and Michalska 2010; Tottenham 2015). Empathic concern has been documented at 6-8 months old. A toddler can offer help to someone suffering, for instance by comforting or distracting him. Cognitive empathy is more developed around 2 years old. Around 3 years old, he can express his concern and interest for someone suffering (Mcdonald and Messinger 2011). Around 4-5 years old, he can answer accurately to false belief tasks, where someone believes that an object is still at the same place while this object has been moved in his absence (Wiesmann et al. 2020). When growing, a child will analyze more finely the situation, predict the level of pain according to its cause, evaluate if the pain is accidental or intentional, and help in a more and more relevant fashion (Mcdonald and Messinger 2011; Uzefovsky and Knafo-noam 2017). He will develop his ability to regulate emotions with the development of the PFC (Decety 2010, 2015; Tottenham 2015) that may develop slowly, probably until around 30 years old (Somerville 2016).

2.2 Individual Differences During Adulthood

Our genes and history shape our individual ability to empathize with others until adulthood, as reflected by differences in functional connectivity at rest (Cox et al. 2012). Indeed, although we appear bad at assessing our own level of empathy (Devlin et al. 2014; Murphy and Lilienfeld 2019), individuals with high cognitive empathy showed stronger connectivity among regions involved in socio-cognitive processing, interoception and autonomic monitoring, namely in the superior temporal sulcus, the ventral anterior insula and the brainstem. Individuals with high affective empathy showed stronger connectivity among

socio-emotional regions, namely in the ventral anterior insula, the perigenual anterior cingulate, the amygdala and the orbitofrontal cortex.

Women have consistently reported higher empathy than males in tasks and questionnaires measuring empathy. They were especially better in affective empathy, emotions recognition, emotion contagion and altruistic prosocial behaviors and made less utilitarian answers to utilitarian personal dilemmas (Christov-Moore et al. 2014; Fumagalli et al. 2010). When attributing emotions to faces, females showed greater activation in a region with mirroring properties, the right inferior frontal gyrus, as compared to males, suggesting greater emotional contagion (Schulte-Rüther et al. 2008). Men more particularly than women presented less activation within the empathy network when facing an unfair person suffering, in fronto-insular and cingulate regions. Moreover, they also presented activations in reward regions, possibly reflecting a desire for revenge (Singer et al. 2006). Motivation related to monetary rewards increased the empathic accuracy when imagining the thoughts and feelings of another. This effect was especially strong in men (Ferguson, Cameron, and Inzlicht 2020; Klein and Hodges 2001).

Troubles in empathy can be observed in psychopathy and autism. On the one hand in psychopathy, patients have impaired affective empathy as manifested by difficulties feeling emotions in others (Cox et al. 2012; van Dongen 2020; Gillespie, McCleery, and Oberman 2014; Meffert et al. 2013; Zaki 2020b). However, although feeling pain in others may not be spontaneous, this ability could be activated on demand. When patients were explicitly asked to imagine pain in others, brain activations related to empathy for pain became quasi-similar to healthy subjects. Moreover, additional activation in the PFC were observed (Meffert et al. 2013). This finding suggest that cognitive empathy may be preserved and may help them to imagine themselves in others' shoes using more reasoning processes, potentially to manipulate others' or worsen their outcomes. On the other hand, in autism, despite deficits in sensory and interoceptive processing, patients seem to be better able at feel emotions in others than describing

their perspective, suggesting a greater deficit in cognitive empathy (Harmsen 2019; Mazza et al. 2014; Uzefovsky and Knafo-noam 2017).

On the other side, people who demonstrated extreme empathy abilities by donating their kidney anonymously, namely the extraordinary altruists, may present greater empathic distress and less distinction between oneself and other suffering (Brethel-Haurwitz et al. 2018; Crockett and Lockwood 2018; Marsh et al. 2014; O'Connell et al. 2019).

2.3 Factors Decreasing Empathy

2.3.1 Medical Expertise

Medical students may start to have a decrease of empathy especially when they start to see real patients (Bellini and Shea 2005; Chen et al. 2007, 2012; Hojat et al. 2009; Neumann et al. 2011; Smith, Norman, and Decety 2017). To be noted, stable (Cameron and Inzlicht 2019; Xie et al. 2018) or increased empathy have also been reported depending on the measures (Handford et al. 2013; Kataoka et al. 2009; Smith et al. 2017).

Physicians might get habituated to pain, their scale of pain might get stretched, they might be influenced by their peers evaluations, they might think that pain is over-rated to get more antalgics as they might be reluctant to prescribe antalgics that can potentially carry side effects (Dirupo et al. 2021). Moreover, physicians and medical students have reported that stress, time pressure and adverse working conditions may negatively influence the development of their empathy (Ahrweiler et al. 2014; Park et al. 2015).

Expert physicians in acupuncture, compared to non-experts, rated pictures of pain with needles as less painful or unpleasant and their brain activity were suppressed in regions associated with the affective dimension of pain such as the anterior insula, cingulate cortex, periacqueducal gray and somatosensory

cortex. However, their response was greater in regions associated with cognitive control and mentalizing such as the medial PFC and TPJ (Cheng et al. 2007).

Down-regulation of responses to pain in others may allow to free up cognitive resources to provide help (Decety, Yang, and Cheng 2010). Indeed, while watching pictures of pain, medical students presented wide prefrontal activations suggesting the influence of medical knowledge, as compared to non-medical students (Xie et al. 2018). Furthermore, nurses watching pain in a hospital context elicited greater activation in the right TPJ, as compared to in a home environment that elicited greater activation in the insula and anterior middle cingulate cortex. This finding suggests that medical caregivers might adopt a detached perspective in a hospital environment, which might be helpful for providing care without being overwhelmed by patients' pain (Cheng, Chen, and Decety 2017).

2.3.2 Perception of Others' Dissimilarities

Shaped by experience, we may feel greater empathy towards the individuals that we perceive as similar to ourselves, as compared to dissimilar. Moreover, we may like them better, help them more and harm them less (Aue 2014; Bruneau, Cikara, and Saxe 2017; Cikara and Van Bavel 2014; Mina Cikara, Bruneau, and Saxe 2011; Montoya, Horton, and Kirchner 2008). In a study, when participants had to infer thoughts in another person, a region related to self-reflection in the medial PFC was more engaged when this other person was described as similar (from the same college and political affiliation), as compared to dissimilar. This result suggest that we may rely on our own mental content as a reference to infer the mental content of other people, especially when we perceive them as being similar (Jenkins, Macrae, and Mitchell 2008; Mitchell, Banaji, and Macrae 2005). Cognitive control mechanisms may influence empathy for pain for individuals described as dissimilar in their feeling of pain. Indeed, observing a neutral reaction in someone receiving pain was associated with areas related to cognitive control (right inferior frontal cortex) and to self-other distinction (dorsomedial PFC), in addition to areas associated with affective components of pain

(anterior insula and dorsal anterior cingulate cortex) (Lamm, Meltzoff, and Decety 2010). Moreover, brain activities related to empathy for pain were increased for close romantic partners (López-Solà et al. 2020).

However, these activities may be decreased when seeing images of individuals from different ethnical group receiving pain, as compared to from the same ethnical group (e.g. Caucasian towards Asian, and vice versa) in insular and cingulate cortices (Avenanti, Sirigu, and Aglioti 2010; Cheon et al. 2011; Chiao and Mathur 2010; Han 2018; Mathur et al. 2010; Xu et al. 2009). Torture of a terrorist was considered as more morally acceptable if performed by members of one's own nation's security service as compared with another nation's one, and the victim was considered as more blamable (Tarrant et al. 2012). Empathy for pain may also be decreased for people that we perceive as being untrustworthy based on first-impression, as being unfair (Hein and Singer 2008; Sessa and Meconi 2015; Singer et al. 2006) or who belong to an opposite political party or sports' club.

For instance, soccer fans may be more likely to help a suffering person if they believe that this person belongs to the same soccer team, as compared to a rival one. Help towards a same team member was predicted by brain activation in a region related to empathy for pain, in the anterior insula, and by self-report of empathic concern. In contrast, the absence of help towards a rival team member was predicted by the activity in a region associated with the pleasure at others' pain (Schadenfreude), in the nucleus accumbens, and by negative evaluation of the other (Hein et al. 2010). Furthermore, Schadenfreude may be associated with reinforcement-learning activity in the ventral striatum. It may predict harm and decreased help toward rival out-group members (Cikara 2015).

In-group preference is useful in the perspective of evolution, favoring the survival of a group of individuals, but has the potential to help less or exclude individuals that we perceive as dissimilar. Judging dissimilar people may rely on the use of stereotypes, potentially leading in extreme cases to dehumanization (e.g. scantily-clad women, homeless people, people assigned with an economic value) and to violence (Bruneau

and Saxe 2018; Cikara 2015; Minam Cikara, Eberhardt, and Fiske 2011; Cogoni, Carnaghi, and Silani 2018, 2021; Contreras, Banaji, and Mitchell 2012; Harris et al. 2014; Harris and Fiske 2006; Mitchell et al. 2008).

2.3.3 Decrease of the Sense of Responsibility

Obeying to an order to inflict pain decreases empathy and the sense of agency, as revealed by the classical Stanley Milgram's obedience experiment. In this experiment, participants under coercive orders inflicted extreme levels of pain although they were able to hear their so-believed victim screaming out of pain (Caspar et al. 2016, 2020; Cheetham et al. 2009). In modern versions of this test, when inflicting electrical shock under coercion, as compared to when freely decided, participants reported the shock as less painful for the victim and felt less responsible. Moreover, activity were reduced in regions associated with empathy for pain, first-hand pain and guilt (Caspar et al. 2020). Not feeling fully responsible of a pain in others decreases activity in regions associated with empathy for pain, in the anterior insulae and anterior MCC, as compared to when feeling fully responsible (Lepron, Causse, and Farrer 2014; Yu et al. 2014). Indeed, the anterior insula may integrate information about pain in others and about our responsibility in causing this pain (Koban, Corradi-Dell'Acqua, and Vuilleumier 2013). Moreover, one may become more prone to inflict harm when he believes that he is serving a greater good, when he is obeying to orders and feeling less personally responsible or when he is in a context where his own moral standards become less salient for instance in a crowd (Cikara 2015).

2.4 Factors Enhancing Empathy

The evidence that empathy is not fixed has led to develop various training techniques. People who believed or were induced with the idea that we can change how empathetic we are, in other words that a growth mindset applies, tend to actually show higher empathy. They put efforts into feeling, listening, answering and helping even when it is challenging (Hughes and Zaki 2015; Schumann, Zaki, and Dweck

2014). Moreover, empathy has been described as being driven by motivation. This account opens ways to interventions aiming at increasing the motivation to empathize with others (Zaki 2014). For instance, interventions could highlight that in-group people value empathy (Fowler and Christakis 2010; Nook et al. 2016), could encourage to affirm personal values over group identity (Cohen et al. 2007) and reappraise negative emotions related to empathy such as suffering or anger towards out-group members (Halperin et al. 2013; Halperin and Gross 2011).

2.4.1 Adopting Empathetic Behaviors

Trainings in empathy have been developed in particular for health caregivers (Patel et al. 2019). Indeed, the relationship between physicians and patients was associated with better patients satisfaction and outcomes, increased report of symptoms and diagnostic accuracy, higher adherence to treatment and fewer malpractice claims (Burns and Nolen-Hoeksema 1992; Canale et al. 2012; Hojat et al. 2011; Neumann et al. 2011; Rakel et al. 2009, 2011). Moreover, physicians who were able to better distinguish themselves from others, regulate their emotion and tended to help others benefited from a greater sense of compassion associated with positive emotions. On the other side, physicians with high personal distress, difficulty regulating and identifying emotions were more prone to burnout symptoms (Gleichgerrcht and Decety 2013).

Patients gave higher empathy score to physicians who learned to detect non-verbal cues of emotion and to recognize and respond to opportunities for compassion (Patel et al. 2019). In addition, responding empathetically, for instance, by sitting down, looking at patients in the eyes, verbally acknowledge, validate and support patients also increases perceived empathy (Larson 2005; Patel et al. 2019). These behaviors may not be a given in a context where caregivers are often by limited by time and stress. Many other trainings have been developed with lower success, such as for instance commenting videotaped interactions, learning about active listening and communication skills, regulating patient-physician interactions or reading patients testimonies. For instance, reading good quality fictions that invite the

reader to take the perspective of the characters and simulate their mental and emotional lives can improve cognitive and affective ToM (Kidd and Castano 2013; Van Kuijk et al. 2018; Tamir et al. 2015). Attending live theater can increase empathy, influence opinions consistently with the presented socio-political issues, and increase donations to charities related and also unrelated to the show (Rathje, Hackel, and Zaki 2021). Seeing or imagining vivid details of a catastrophe scenery may increase the reported empathy for the victims (Vollberg, Gaesser, and Cikara 2021; Zaki 2020a). Moreover, empathy and help towards a single identifiable victim may be greater than towards numerous victims (Lee and Feeley 2016). In addition, pain caused by someone, as compared to by accident, elicited higher brain activity, in empathy for pain associated regions such as the insular and medial cingulate cortices and somatosensory regions (Akitsuki and Decety 2009).

Mindfulness practices in physicians does not seem to improve their perceived empathy by patients (Patel et al. 2019; Riess et al. 2012). Nevertheless, meditation techniques have been developed to train compassion. Indeed, compassion is protective from burn-out, as compared to empathic distress where pain in others is more internalized (Klimecki, Leiberg, Lamm, et al. 2013; Klimecki, Leiberg, Ricard, et al. 2013).

2.4.2 Contacts With Dissimilar Others

Various interventions have been developed to increase empathy towards out-group members. They aim at taking the perspective of others through for instance movies or texts, playing their role or having a positive contact with them (Bruneau and Saxe 2012; Christ et al. 2014; Mina Cikara et al. 2011; Dovidio et al. 2017; Gutsell, Simon, and Jiang 2020), or playing virtual games as an out-group avatar (Hasler, Spanlang, and Slater 2017). In-group preference and memory of others' out-group affiliation may be decreased by reading stories that describe an out-group member facing an event and his associated mental states (Bruneau, Cikara, and Saxe 2015). Indeed, empathy towards dissimilar individuals may be learned through experience.

In an experiment with Balkan and Swiss German individuals, participant received a costly help from an out-group member, refusing money to prevent participant's pain. After about 2 trials only, they showed increased activation in empathy for pain related regions for the suffering of out-group members, in the anterior insula, as well as decreased activity in reward regions, suggesting less Schadenfreude (Hein et al. 2016).

Along the same line, frequent contacts with people from another ethnical group can counter the associated ethnical bias in empathy for pain, in the activity of the anterior cingulate cortex (Cao et al. 2015). Moreover, playing in the same competitive team as people from another ethnical group may also eliminate the ethnical bias in empathy for pain (Sheng and Han 2012). Furthermore, positive direct contacts with people from stigmatized out-groups may buffer negative messages about them propagated by mass medias (Fuochi et al. 2020). Interestingly, the positive emotions elicited by being nice with strangers or acquaintances may be underestimated and repetitively engaging nice conversations with them may reduce the negative belief of being awkward and promote well-being (Boothby et al. 2018; Epley and Schroeder 2014; Sandstrom and Dunn 2014). However, the effects of emotions on empathy are still unclear even though we are affect by emotions every day.

3. Emotions Influence on Empathy

3.1 Definition of Emotion

Defining what an emotion is have been the subject of debates (Gendron 2010; Izard 2010; Mulligan and Scherer 2012; Widen and Russell 2010). Here, I will present the four main models explaining emotions (Brosch, Pourtois, and Sander 2010).

3.1.1 Discrete Theories of Emotion

According to discrete theories of emotion, emotions can be divided into a small number of discrete categories such as happiness, sadness, anger, disgust, fear and surprise. These categories are accompanied by specific bodily changes at the physiological, brain and facial expression levels and help to increase attention and perception (Brosch et al. 2010).

They have been labelled as basic since they are supposed to be predetermined by evolution and universal in humans and across species. Thus the predictions that emotions are mainly bottom-up processes triggered by specific stimuli and that they are at least partly hard-wired in the brain (Brosch et al. 2010; Gendron and Feldman Barrett 2009; Hamann 2012a; Tracy and Randles 2011). However, empirical evidence showed that emotional reactions are variable between people from different cultures, within the same culture or even within the same individual across time, giving rise to other theories of emotions (Barrett 2009).

3.1.2 Dimensional Theories of Emotion

Dimensional theories of emotions propose that emotions can be represented on a graph with a small number of dimensions, often valence and arousal, reflecting the pleasantness and the intensity of an experience. Such representations might guide approach or withdrawal behaviors, and has been used in constructivist theories (Brosch et al. 2010; Hamann 2012a).

3.1.3 Constructivist Theories of Emotion

According to constructivist theories, emotions are constructed from the interplay of basic psychological operations that are not specific to emotions, such as perception, attention and memory (Brosch et al. 2010; Hamann 2012a). The conceptual act model claim that emotions arise from the combination of bodily sensations, more or less pleasurable or arousing, called "core affects". These interoceptive sensations as well as exteroceptive sensations (tactile, visual, auditory, etc.) are transformed into meaningful discrete

emotion categories in a quick, automatic and implicit fashion. This transformation is influenced by the linguistic and social contexts as well as past and current experiences, explaining flexibility in emotional reactions. The emotion categories are learned mainly based on language and on statistical regularities in sensorimotor patterns captured by the brain from past experiences (i.e. knowledge, concepts, episodic memories) to form internal representations. This transformation of sensations into emotions, called conceptualization or categorization, may help to better communicate, predict and regulate emotions in oneself and in others (Barrett 2017; Barrett, Gendron, and Huang 2009; Gendron and Feldman Barrett 2009; Lindquist 2013). This model emphasis top-down mechanisms of emotions and the role of language and memory. It predicts that emotions rely on networks supporting other mental states (Brosch et al. 2010).

Constructionist and appraisal models both consider emotion as an act of making meaning. Nevertheless, the constructionist models derive meaning from bodily states and from the related situation, whereas appraisal models derive meaning from the situation and take bodily states as a result of the meaning analysis (Gendron and Feldman Barrett 2009).

3.1.4 Appraisal Theories of Emotion

According to appraisal theories, emotions are triggered by an event that elicits specific mechanisms based on the evaluation of the relevance of this event. This evaluation is subjective and based on criteria such as novelty, pleasantness, our goals, concerns and values, or our potential to cope with this event, explaining the differences in emotional reactions between individuals (Brosch et al. 2013; Moors 2014; Scherer 2009b). This evaluation determines the boundaries of the emotion category and drives an organismic instantaneous response.

Following the component process model, this response includes an autonomic response (e.g. tears, increase in heart or respiration rates, pupil dilation, sweating), a motor expression (through face, voice,

gestures and postures), a tendency to action (e.g., approach or move away) and finally a feeling (when

becoming aware of the emotions) (Brosch et al. 2013). Thus this model focus on evaluation processes and

on the flexible and dynamic interaction between the stimuli and the needs and goals of the observer

(Brosch et al. 2010).

3.2 Neural Substrates of Emotions

3.2.1 Discrete Theories of Emotion

Neuroimaging studies have identified brain areas consistently activated for basic emotions (Hamann

2012a). Fear has been associated with activation in the amygdala, disgust in the insula, anger in the

orbitofrontal cortex, sadness in the subgenual anterior cingulate cortex and happiness in the dorsal

anterior cingulate cortex. However, brain regions such as the amygdala, the anterior insula, the lateral

orbitofrontal cortex and posterior anterior cingulate cortex are activated for several categories of basic

emotions (Hamann 2012a; Lindquist et al. 2012; Vytal and Hamann 2010).

Recent decoding techniques showed that emotion categories are not contained within a region or a

system (Hamann 2012a; Horikawa et al. 2020; Kragel et al. 2016; Kragel and LaBar 2016a; Lindquist et al.

2012; Saarimäki et al. 2016, 2020; Wager et al. 2015). Instead, emotions are associated with simultaneous

activations of distributed cortico-subcortical networks that are overlapping but that might be unique to

each emotion category. These networks included regions associated with sensorimotor and self-relevant

information, as well as perceptual, language, memory and executive control processes. The midline

frontal and parietal regions might integrate these activations supporting self-awareness. Thus, emotion

categories activating similar brain networks might reflect close subjective feeling. Within these networks,

areas helping to differentiate emotion categories included cortical midline structures (medial PFC,

precuneus and posterior cingulate cortex) and sensorimotor regions (pre and postcentral gyrus, posterior

insula). Limbic regions helped discrimination in a lesser extent as they may share information common to all basic emotions. The networks extended to classical emotion areas such as the insula and the amygdala, and were consistent with lesion studies associated with emotion impairments (Nummenmaa and Saarimäki 2019; Saarimäki et al. 2016).

3.2.2 Dimensional Theories of Emotion

The representation of emotions along the two dimensions of valence and arousal have been associated with activations in the amygdala and in the orbitofrontal cortex respectively (Hamann 2012a). However, recent studies showed that a small number of dimensions might not be enough to accurately describe emotions (Horikawa et al. 2020; Kragel et al. 2016; Kragel and LaBar 2016a). Self-reported emotional experience may correspond to a rich array of emotional categories that rely on distributed neural representations with a high number of dimensions, such as safety, control, approach, etc. (Horikawa et al. 2020).

3.2.3 Constructivist Theories of Emotion

The constructivist theories posit that emotion categories are constructed from general cortico-subcortical networks related to perception, motivation, memories or anticipations. These networks are not specific to emotions and partially shared between emotion categories (Horikawa et al. 2020; Kragel et al. 2016; Kragel and LaBar 2016a; Lindquist et al. 2012; Saarimäki et al. 2016, 2020; Wager et al. 2015). For instance at the cortex level, anger and fear similarly activated the dorsal attention, frontoparietal and default mode networks. Happiness, sadness and disgust activated the somatomotor and salience networks. These networks interact differentially depending on the related emotion category with subcortical regions such as the thalamus, the amygdala, the basal ganglia or the hippocampus. Interestingly, these interactions are reduced in sadness, potentially hindering higher brain control mediation over affective responses and affective learning (Wager et al. 2015). The differences in the combinations between networks as well as

in the interactions between cortical and subcortical regions contain information allowing to distinguish between emotion categories.

A data-driven meta-analysis identified six distributed functional groups consistently activated in emotion processing. The construction process might start by the core affect in (i) the lateral paralimbic (insula, striatum, OFC) and (ii) the core limbic regions (PAG, hypothalamus, amygdala and thalamus). Then the conceptualization might occur in (iii) the medial posterior and (iv) the medial prefrontal, influenced by (v) language/executive functions in cognitive and motor areas. (vi) Occipital/visual might help visual and attentional processes of emotional stimuli (Hamann 2012b; Kober et al. 2008; Lindquist et al. 2012; Lindquist and Barrett 2012).

These networks have been associated with intrinsic networks (Lindquist and Barrett 2012). Intrinsic networks, known for being activated during rest periods, reflect the anatomical connectivity between brain regions and thus predict activity during tasks. For instance, the core affect have been associated with the limbic and salience networks and the exteroceptive sensations to sensorimotor and visual networks. The conceptualization has been associated with the default mode network, as well as language areas and the frontoparietal network supporting executive control, helped by the dorsal attention network.

Interestingly, this theory posits that experiencing emotions rely in part on the same neural substrates that support knowledge about emotions. Furthermore, this knowledge is related to prior experiences of emotions that are represented in sensorimotor cortices as reenactments of these emotions from specific situations. This model is thus tight with the embodied social cognition account (Lindquist 2013; Oosterwijk and Feldman Barrett 2014). This account proposes that observing actions, feelings and emotions in other people engages the same neural circuits as if experiencing or simulating them oneself (Gallese, Keysers, and Rizzolatti 2004).

3.2.4 Appraisal Theories of Emotion

The componential appraisal theories predict that five functional networks support emotions. These networks are activated in parallel and in a dynamic synchronization. Each network corresponds to each component: appraisal processes, motor expression, autonomic physiology, action tendency and subjective feeling (Sander, Grandjean, and Scherer 2018; Scherer 2009a).

A recent study revealed the networks associated with the 4 components that are non-experiential (Leitão et al. 2020). The appraisal component was associated with activations in limbic areas classically related to emotions, such as the amygdala, the anterior cingulate cortex and the anterior insula. The expression component was associated with a motor network including the primary motor cortex, the cerebellum and the striatum. The autonomic physiology component was associated with areas involved in the affective modulation of peripheral physiology, such as the thalamus, the basal ganglia, the amygdala, the posterior insula and the right PFC. The motivation component was associated with regions involved in tendencies to approach and avoid, such as the orbitofrontal cortex, the anterior and posterior cingulate cortex, the right dorsolateral PFC, the bilateral insula and parietal areas.

These large-scale cortico-subcortical networks engage dynamically in moments of synchronization in a bilateral sensorimotor networks centered on somatosensory/association areas in parietal cortices, posterior insula, basal ganglia, as well as dorsomedial PFC and posterior cingulate cortex (Leitão et al. 2020). Interestingly, the componential process model predicts that emotions and their associated feelings emerge from synchronized changes across components processes. Therefore, the synchronization between networks might reflect the emergence of emotions from the integration of sensorimotor and self-related processes. This finding supports an embodied mechanism and an action-oriented function of emotions, as felt representations of body states might be integrated with processes orienting actions, along with self-relevant information in memory, to direct adaptive behaviors to relevant events.

3.3 Influence of Emotions on Empathy

The way emotions may affect empathy is still unclear. Emotions may influence various cognitive processes (Brosch et al. 2013; Pourtois, Schettino, and Vuilleumier 2013), such as perception and attention (Ohman, Flykt, and Esteves 2001; Phelps, Ling, and Carrasco 2006; Vuilleumier 2005), memory (Phelps 2004; Sharot, Delgado, and Phelps 2004), financial decision-making (Sanfey et al. 2003) or moral reasoning (Greene et al. 2001).

Moreover, contextual factors that influence empathy may involve emotions. For instance, physicians have reported that stress may decrease their empathy (Ahrweiler et al. 2014; Neumann et al. 2011). Indeed, stress may dampen empathy for pain (Buruck et al. 2014). Obeying to orders to harm others was related to decreased empathy for pain and to personal distress (Cheetham et al. 2009). Empathic distress was related to negative emotions and to burnout. On the other side, compassion was related to positive emotions (Singer and Klimecki 2014). Maternal warmth and playful behaviors observed between the mother and the child were associated with greater empathy in children (Mcdonald and Messinger 2011). Positive encounters and help from an out-group member increased positive emotions towards out-group members, mediating the increase of empathy towards them (Hein et al. 2016). Furthermore, regulating emotion using cognitive reappraisal strategy may affect the evaluation of facial expression of pain (Naor et al. 2020). Therefore, emotions may also influence empathy. In addition, emotions may share social functions with empathy. Positive emotions may foster relationships, as they may help intimacy, reputation and influence other people (Sels et al. 2021). Expressing fear or reflecting the fear of others may both help signaling a threat to others (Adolphs 2013; De Gelder et al. 2004).

In clinical setting, psychiatry patients with disorders related to emotions are often suffering from isolation and high personal distress (Guhn et al. 2020a; Lenton-Brym et al. 2018; Shamay-Tsoory et al. 2009)

associated with impaired empathy. Depressed patients tend to have a negative mood and to feel less happy for a happy person but equally concerned for a negative one, as compared to healthy controls (Guhn et al. 2020a). They also showed poor cognitive empathy as reflected by lower perspective taking, ToM and empathic accuracy, potentially related to broader cognitive deficits (Schreiter, Pijnenborg, and Aan Het Rot 2013). Patients suffering from generalized anxiety disorder tend to fear and avoid social situations. They also tend to feel humiliated and embarrassed due to potential scrutiny and negative evaluation by others (Cui et al. 2017a). They were better at sharing negative than positive emotions in others (Morrison et al. 2016; Zainal and Newman 2018). They showed impaired ToM as they tended to attribute more intense emotions and greater meaning to thoughts, feelings and intentions in others, and especially negative ones (Cui et al. 2017a; Hezel and McNally 2014). Patients suffering from bipolar disorder alternate depressive and manic or hypomanic episodes, characterized by elevated or irritable mood. They showed decreased empathy for pain depending on the severity of the manic symptoms (Yang et al. 2017) and impaired cognitive ToM (Shamay-Tsoory et al. 2009). Patients suffering from borderline personality disorder show pervasive instability in behavior, self-image, affects and interpersonal relationships as well as intense emotional reactivity and impulsivity. They showed higher affective empathy as compared to healthy controls, potentially leading to greater personal and interpersonal distress, whereas cognitive empathy seemed preserved (Harari et al. 2010; Salgado, Pedrosa, and Bastos-Leite 2020). As negative emotions prevail in these disorders and as broader cognitive impairments may be associated, it is unclear whether positive and negative emotion may influence empathy in healthy people.

A study found that emotion induction with happy music or movie-clips, as compared to sad or neutral ones, hinders taking the perspective of others (Converse et al. 2008). The authors proposed that happy emotion may favor heuristic processing over more analytical ones that may be required to take the perspective of others. But another study found that induction of both anxiety and surprise favored self-

perspective when inferring beliefs in others, potentially related to uncertainty (Todd et al. 2015). Interestingly, individuals with higher positive emotion trait of personality self-reported greater empathetic tendencies However experimentally, they were less accurate at tracking in videos people's negative emotions and better at tracking positive ones, suggesting an effect of emotion congruence (Devlin et al. 2014). Moreover, the effects of emotion induction on ToM have been investigated during a Master's thesis work (Holmberg 2018). After watching a single movie-clip supposedly inducing sadness, happiness or anger, participants made affective and cognitive ToM judgements through vignettes describing interactions with or without Faux Pas. The author reporting the study found no effect of emotion induction and explained that this lack of effect may be related to the fact that emotion induction was not efficient for some participants.

Indeed, emotions can be induced in various ways such as using emotional pictures, music, situational procedures (e.g. speech in front of a jury), autobiographical memories, imagery (e.g. imagine your birthday party), odors, narratives, or movie-clips (Sharvit et al. 2015; Siedlecka and Denson 2019). Indeed, after a movie-clip, we may remain "infused" with the emotion from the movie-clips, which may modulate cognitive processes such as memory, attention or face perception. This effect has thus been labelled "affect infusion model", or "Kuleshov effect" in the film editing vocabulary (Calbi et al. 2017; Forgas 1995; Harlé et al. 2012; Mobbs et al. 2006; Qiao-Tasserit et al. 2017). This effect has also been associated to emotional "inertia" that favors the persistence of prior emotional state over change (Pichon et al. 2014a).

Overall, the emotions effects on empathy are not easily predictable, with available evidence leading to mixed outcomes. Importantly, however, two seminal theoretical accounts from affective and social psychology/neuroscience draw clear and contrasting predictions.

3.3.1 The Embodied Social Cognition Account

Models of embodied social cognition account posit that we may feel emotions in others by simulating them in our own body (Gallese 2007; Gallese et al. 2004; Keysers and Gazzola 2007). Therefore, being joyful may set an unfavorable ground for simulating and feeling fear or pain in others. Conversely, being fearful may prevent from feeling joy in others while favoring feeling their pain, as fear and pain are both negative experiences.

Evidence for this account show for instance that we tend to subtly mimic emotions in others in synchrony and respond to pain in others by contracting muscles in similar locations (Avenanti et al. 2005). Moreover, interoceptive abilities may influence the way we evaluate emotions in others (Dirupo et al. 2020). Furthermore, the perception of facial emotion expression in others may be enhanced when being in a congruent emotional state (Calbi et al. 2017; Mobbs et al. 2006; Qiao-Tasserit et al. 2017).

3.3.2 The Broaden-and-Build Account

The broaden-and-build account posits that we have a more broaden attention when we are feeling positive, allowing exploration and building up resources for a healthy, resilient and flourishing life (Fredrickson 2004, 2013; Fredrickson et al. 2013; Fredrickson and Branigan 2005; Fredrickson and Joiner 2002, 2018; Fredrickson and Levenson 1998). In the opposite, we tend to have narrowed attention when feeling negative (Fredrickson 1998). Therefore, being fearful may set an unfavorable ground for feeling emotions and pain in others, regardless of the emotions valence. Conversely, being joyful may open access to feel both positive and negative emotions as well as pain in others.

Evidence for this account show that positive emotions for instance broadened visual attentional selectivity (Rowe, Hirsh, and Anderson 2007; Vanlessen et al. 2016), broadened semantic associations (Isen et al. 1985; Phillips et al. 2002; Rowe et al. 2007) and helped solving problems creatively (Ashby, Isen, and

Turken 1999). Fear showed opposite effects increasing selective attention against distractors (Finucane 2011) and limiting semantic associations (Rossell and Nobre 2004). Interestingly, positive emotions reduced ethnical biases (Johnson and Fredrickson 2005), decreased egocentric perspective taking (Todd et al. 2015), came with prosocial behaviors (Lara B Aknin et al. 2013; Lara B. Aknin et al. 2013; Dunn et al. 2008) and compassion (Singer and Klimecki 2014).

4. Our Contribution

This thesis aims at revealing whether and how our emotions may bias the way we feel emotions and pain in others, at the behavioral, physiological and brain levels. We tested whether emotions could modulate empathy, hoping that emotion regulation or induction tools could be helpful for feeling empathy and enhancing the quality of relationships.

In two studies, we induced emotions in participants using movie-clips. We investigated their effects on cognitive and affective ToM (cognitive and intermediate empathy) in a first study, and on empathy for pain (affective empathy) in a second study.

Effects of Emotions on Empathy

Cognitive   Intermediate   Affective

Cognitive ToM   Affective ToM   Empathy for pain

Study 1   Study 2
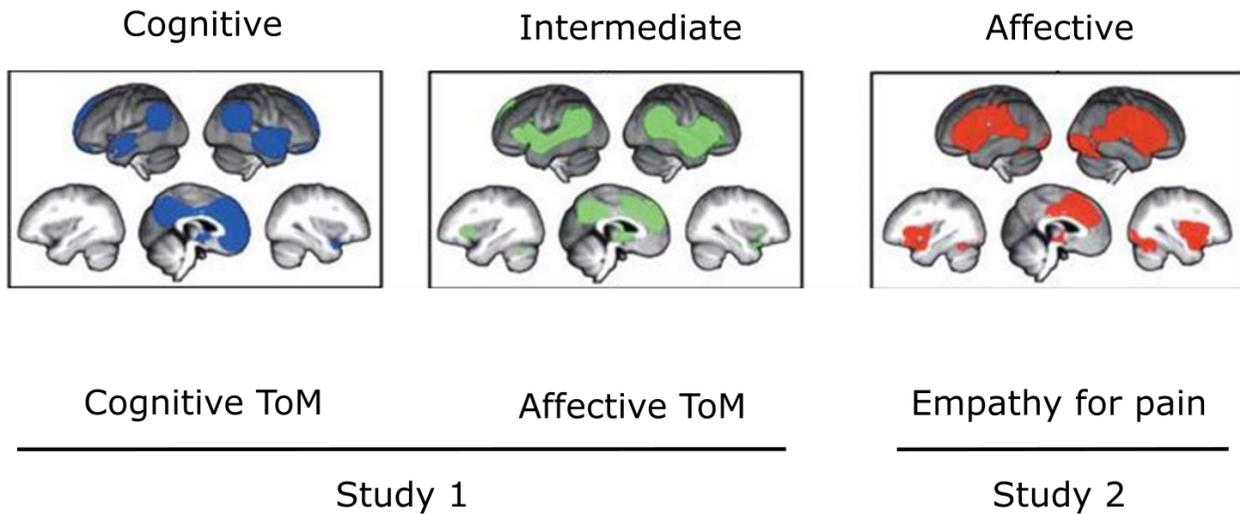
Figure 4. The aim of this thesis is to investigate the effects of emotions on empathy. The upper panel reveal the brain activations associated with cognitive, intermediate and affective empathy (adapted from (Schurz, Radua, et al. 2020)). The lower panel shows that we investigated the effects of emotions on cognitive and intermediate empathy using a cognitive and affective ToM task in study 1, and on affective empathy using an empathy for pain task in study 2.

We tested the predictions from the embodied social cognition and broaden-and-build accounts. In the first study, the embodied social cognition account applied to affective ToM predicts that induced joy may favor inferring joy and hinder inferring fear in others, while induced fear may favor inferring fear and hinder inferring joy. However, the broaden-and-build account predicts that induced joy may favor inferring both joy and fear, contrary to induced fear that may hinder both. In the second study, the embodied social cognition account predicts that induced joy may hinder empathy for pain while fear may favor it. In the opposite, the broaden-and-build account predicts that induced joy may favor empathy for pain while fear may decrease it.

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These studies evolved from a previous experiment where we investigated the effects of emotions on the perception of ambiguous faces, presented in the Annex section. There, we induced emotions in healthy participants using joyful, neutral and fearful movie-clips. We then presented to participants morphs of faces ranging from a continuum of fearful to happy expressions. Participants classified ambiguous faces as more fearful after fearful movie-clips and as more joyful after absorbing joyful movie-clips. Moreover, participants who scored high on depression and anxiety questionnaires tended to classify ambiguous faces as more fearful. This study showed that emotions induced by movie-clips could modulate the perception of facial expressions.

In the two present studies, we used the same validated movie-clips than previously for inducing emotions in participants. Indeed, movie-clips produced changes in brain activity and connectivity patterns during subsequent resting-state. For instance, the bilateral insula, the anterior and posterior cingulate cortex and the inferior parietal lobule were more activated after emotional movies than while watching them (Eryilmaz et al. 2011b; Richiardi et al. 2011).

4.1 Effects of Emotions on Cognitive and Affective ToM

It is unclear how emotions might influence the way we feel and understand emotions and beliefs in others based on the knowledge of their situation, both at the behavioral and brain level. In a first study, we studied the effects of emotional movie-clips on cognitive and affective ToM.

We induced emotions in participants by showing them one minute of joyful, neutral, or fearful movie-clips. After each movie-clip, to assess their effect on affective ToM, participants read stories describing protagonists evolving in various situations that changed from being fearful to joyful, or from being joyful to fearful. Participants had to indicate whether the protagonists were feeling positive or negative after the situation change. Participants also read cognitive ToM stories where protagonists evolved in situations

that changed, this time in a way that outdate protagonists' beliefs. Participants had to indicate the outdated false belief or the actual current situation, depending on the trials. As controls, participants also read stories without protagonist where a situation changed and previous recordings became outdated. Participants had to indicate what the recordings show or what the current situation is, depending on the trials. 15 participants performed the first experiment that was behavioral, while 33 participants performed the second one that was similar but performed inside of an MRI scanner.

4.1.1 Embodied Social Cognition Account and ToM

This account predicts that we may simulate emotions in our own body to infer emotions in others while such simulation may not be required to infer beliefs in others. Therefore, this account predicts no effect of emotions on cognitive ToM but effects on affective ToM. Indeed, it predicts that feeling joyful oneself may favor feeling joy and hinder feeling fear in others. Vice-versa, feeling fearful oneself may favor feeling fear and hinder feeling joy in others. We could then expect greater behavioral accuracy and brain activations in affective ToM tasks when the induced and inferred emotions are congruent, as compared to incongruent. Alike, we could also expect dampened responses when incongruent, preserving homeostasis.

In the brain, we predict that incongruent emotions may suppress the activity in regions involved in ToM such as the temporo-parietal and medial prefrontal regions and the precuneus. We also expect this suppression of activity in motor and sensory regions associated with emotions such as the pre and post-central areas, the somatosensory and insular cortices, as embodied social cognition predicts bodily simulation to understand others (Keysers, Kaas, and Gazzola 2010; Soylu 2016; Spunt and Adolphs 2019).

Indeed, greater motor simulation involved greater activity in the inferior parietal lobe (central operculum and secondary somatosensory cortex) and in insular cortices, known for linking perception and sensory experience (Kragel and LaBar 2016b; Lorey et al. 2009). Moreover, impairments in the precentral gyrus,

key to motor control, were associated with ToM deficits in Parkinson's disease, along with impairments in the postcentral and middle and inferior frontal gyri (Díez-Cirarda et al. 2015). Impairments in somatosensory and insular cortices were associated with impaired recognition of emotions in others, as conveyed by faces and voices (Adolphs et al. 2000; Borg et al. 2013). Furthermore, the right somatosensory cortex helped to discriminate between emotions in others and, along with the insula, it may link perception to subjective feelings (Chang et al. 2013; Kragel and LaBar 2016b; Sel et al. 2020).

4.1.2 Broaden-and-Build Account and ToM

This account predicts that feeling joyful oneself may broaden attention towards others and towards their emotions regardless of the category. Thus, feeling joyful may favor inferring beliefs and feeling both joy and fear in others, while feeling fearful may hinder it. We could then expect greater behavioral accuracy and brain activations in affective ToM tasks when induced with joy, regardless of whether induced and inferred emotions are congruent or not. Alike, we could also expect dampened responses when induced with fear. We expect to measure this modulation by emotion in regions related to ToM, in particular in the TPJ and medial PFC.

4.2 Effects of Emotions on Pain and on Empathy for Pain

The way our own emotions might influence the way we feel pain in others is unclear, both at the behavioral and brain levels. Here, we conducted two experiments to study the effects of emotional movie-clips on pain and empathy for pain using behavioral, physiological and fMRI measures.

We induced emotions in participants by showing them the same joyful, neutral, or fearful movie-clips as in the previous experiments. After each movie-clip, participants received a painful thermal stimulation to elicit first-hand pain, or watched pictures of wounded hands to elicit empathy for pain. They also received painless stimulations and watched painless pictures as controls. After the experiment, participants had to

fill questionnaires that reflected how empathetic they perceive themselves to be. 17 participants performed the first experiment. They had to rate the intensity of first-hand pain and of pain in others while we recorded galvanic responses. 24 participants performed the second experiment inside of an MRI scanner. The empathy for pain task was this time implicit, as participants had to judge the laterality of the hand on the picture.

4.2.1 Embodied Social Cognition Account and Empathy for Pain

This account predicts that, as we can consider both fear and pain as negative experiences, feeling joy may dampen first-hand pain and empathy for pain, while feeling fear may increase them. We would then expect greater galvanic and brain responses to first-hand pain and empathy for pain when induced with fear, as compared to neutral or joyful induction. Alike, we could also expect dampened responses when induced with joy.

Indeed, first-hand pain and empathy for pain shared similar neural representations (Corradi-Dell'Acqua et al. 2016, 2011) as reflected by the findings that first-hand pain analgesia induced by placebo (Rütgen, Seidel, Riečanský, et al. 2015; Rütgen, Seidel, Silani, et al. 2015), acetaminophen (Mischkowski, Crocker, and Way 2016) or hypnosis (Braboszcz, Brandao-Farinelli, and Vuilleumier 2017) reduce empathy for pain. We could then expect that alike first-hand pain (Berna et al. 2010; Lyby et al. 2012; Wiech and Tracey 2009), negative contexts may increase empathy for pain.

4.2.2 Broaden-and-Build Account and Empathy for Pain

As fear and pain are not of the same category of emotion although they are both negative, it may be less relevant to embody others' pain while being fearful ourselves. In the case of pain and empathy for pain, this account predicts that joy may broaden attention beyond oneself, potentially alleviating first-hand pain and allowing the access to pain in others. Conversely, fear may narrow attention down to first-hand pain and exclude pain in others.

We would then expect greater galvanic and brain responses to first-hand pain when induced with fear and to empathy for pain when induced joy, as compared to neutral induction. Alike, we could expect dampened responses to first-hand pain when induced with joy (as compared to neutral and fear) and to empathy for pain when induced with fear (as compared to neutral and joy).

We expect to measure this dampening in rated pain intensity, galvanic recordings and brain activities, in regions related to pain such as the posterior insula, and to empathy for pain such as the anterior insula and middle cingulate cortex. We also expect that high empathy traits as measured by questionnaires may counteract this dampening. Furthermore, we predict that multivoxel patterns analyses may show increased neural similarity between first-hand pain and empathy for pain after positive movie-clips, in regions involved in both first-hand pain and empathy for pain such as the insula. This finding would suggest that when we feel positive, we might represent pain in others as more similar as our own one, confirming the predictions related to the broaden-and-build account.

Chapter 2: Summary of the Results

I contributed in all the steps of these two studies: designing of the experiments, preparing the stimuli, coding the experiments, recruiting participants, collecting and analyzing data, preparing articles for publication.

1. Effects of Emotions on Cognitive and Affective ToM

We investigated the effects of emotions on cognitive and affective ToM. 33 participants watched joyful, neutral and fearful movie clips, and read stories where they had to infer beliefs (cognitive ToM), joy or fear (affective ToM) in the protagonist. We found no effect of emotions on cognitive ToM. However, we found in the affective ToM task, that when participants had to infer an emotion (joy or fear) that was incongruent with their induced emotional state (fear or joy respectively), brain activity was reduced in the superior temporal gyrus, the precuneus and the frontoparietal operculum. These results support the embodied social cognition account, suggesting that the brain response to others emotions is modulated by the congruence between our own and others' affect.

2. Effects of Emotions on Pain and Empathy for Pain

We investigated the effects of emotions on pain and empathy for pain. 24 participants watched joyful, neutral and fearful movie-clips, and received thermal pain or watched pictures of wounded hands. We found that for pain, joyful induction was associated with reduced galvanic and brain response in the bilateral posterior insula. However, for empathy for pain, fearful induction was associated with reduced galvanic and brain response in the bilateral anterior insula and middle cingulate cortex. Moreover, participants with higher empathetic abilities responded more slowly and showed greater medial PFC activation to others' pain after fearful movie-clips, suggesting compensatory cognitive processes.

Furthermore, multivariate pattern analyses confirmed that pain and empathy for pain shared greater neural similarity after positive emotion induction in the anterior insula. These findings supports the Broaden-and-Build theory that posits that positive emotions broadens attention, helping to empathize with other people.

Chapter 3: General Discussion

How can our emotions affect the way we understand others? This thesis aims at revealing the effects of emotions on social cognition. Social cognition tasks have been divided into three categories depending on whether they involved more cognitive, affective or combined processes in between the two (Schurz, Radua, et al. 2020). Here, we investigated the effects of emotions on the cognitive and intermediate pathways in the case of cognitive and affective ToM in a first study, and on the affective pathway in the case of empathy for pain in a second study. In both studies, we induced emotions in participants by inviting them to watch joyful, neutral and fearful movie-clips. Then in the study 1, they read stories where they had to infer the protagonists' beliefs (cognitive ToM task), joy or fear (affective ToM task). In the study 2, they received thermal pain (first-hand pain task) or watched pictures of wounded hands (empathy for pain task).

We particularly focused on testing two theoretical accounts. On the one hand, the embodied social cognition account posits that we activate our own body representation of emotions for simulating emotions in others (Keysers et al. 2010; Soylu 2016; Spunt and Adolphs 2019). This account predicts that our emotions might clash with emotions in others that are incongruent. Thus, induced joy might prevent embodying fear and pain in others, while induced fear might prevent embodying joy in others. However, this account does not hold predictions on potential effects of emotions on cognitive processes. On the other hand, the Broaden-and-Build account posits that positive emotions broadens attention, allowing access to others, while fear narrows attention, reducing attention to other people around (Fredrickson 1998, 2004). Hence, induced joy might allow access to others mental contents and feelings, such as beliefs, joy, fear and pain, while induced fear might prevent such access.

1. Key Findings

1.1 Effects of Emotions on Affective and Cognitive ToM

We found that when participants were induced with joy and had to infer fear in others, or when they were induced with fear and had to infer joy in others based on reading about their situation, brain activations were reduced in the superior temporal gyrus, precuneus and frontoparietal operculum. Hence, we discovered altered brain processing when inferring emotions in others (affective ToM), especially when the emotions-to-be-inferred were incongruent with previously induced emotions in the observer. Moreover, we found no effect of emotion induction when inferring beliefs in others (cognitive ToM). These findings support the embodied social cognition theory, by suggesting that our emotions alter brain responses to emotions in others, based on the congruence between our own and others' affect (Keysers et al. 2010; Soylu 2016; Spunt and Adolphs 2019).

1.2 Effects of Emotions on Pain and Empathy for Pain

We found that on the one hand induced joy suppressed galvanic response and brain activity related to first-hand pain in the bilateral posterior insula. On the other hand, induced fear suppressed galvanic response and brain activity related to empathy for pain in the bilateral anterior insula and middle cingulate cortex. Moreover, participants with high empathetic abilities were slower at responding and showed greater medial PFC activations when watching pain in others after fearful induction, reflecting compensatory cognitive mechanisms. Furthermore, multivariate pattern analyses showed that joy induction was associated to greater pattern similarity between first-hand pain and empathy for pain in the anterior insula. These results support the Broaden-and-Build theory that posits that positive emotions broaden attention (Fredrickson 2004), allowing access to other people, while negative emotion reduce this access to other people and to their pain.

2. Theoretical Contributions

Many models have described social cognition. Some models have described an affective and a cognitive pathway for understanding others (Shamay-Tsoory 2011b; Stietz et al. 2019). However, a recent data-driven model described a cognitive, an affective and an additional intermediate pathway in between the two (Schurz, Radua, et al. 2020). This thesis aimed at revealing the effects of emotions on these three pathways, in the case of cognitive and affective Theory of Mind for the cognitive and intermediate pathways, and in the case of empathy for pain for the affective pathway.

2.1 Effects of Emotions on Cognitive and Affective Theory of Mind

Cognitive ToM refers to the cognitive representations of others mental states such as beliefs and thoughts. A classical case is the case of false-belief, where someone has the false-belief that an object is still where he left it while someone else moved it in his absence. Affective ToM, also labeled cognitive empathy and emotional perspective-taking, refers to tasks where we have to reason about others' affective states, for example from reading about their situation (Corradi-Dell'Acqua et al. 2014). Affective ToM has been categorized as belonging to the cognitive pathway (Shamay-Tsoory 2011b), since inferring an emotion from a situation may require cognitive processes. For instance, if we read that someone has a disease and receives a new treatment, we need to analyze the situation and take this person's perspective to infer his belief about the treatment. If we infer that this person believes that the new treatment is efficient, we might infer that this person is feeling hopeful or happy. If we infer that this person believes that the new treatment is inefficient, we might infer that this person is feeling hopeless or sad.

It has been shown that cognitive and affective ToM share overlapping activations, especially in the right TPJ, right MTG/STS, posterior cingulate cortex and in the medial PFC. Furthermore, cognitive and affective

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ToM share similar neural representation as shown with pattern analysis in the TPJ and MTG/STS but not in the medial prefrontal cortex (Corradi-Dell'Acqua et al. 2014). Indeed, affective ToM has been associated with the ventromedial PFC (Shamay-Tsoory and Aharon-Peretz 2007; S. G. Shamay-Tsoory et al. 2009; Shamay-Tsoory et al. 2006) and cognitive ToM with the dorsal PFC (Corradi-dell'Acqua et al. 2020; Kalbe et al. 2010), suggesting that cognitive and affective ToM have common and dissociated processes.

Affective ToM might rely not only on cognitive mentalizing processes but also on additional affective processes. Indeed, tasks related to empathy and to ToM have been meta-analyzed and resulting data have been entered in a hierarchical clustering analysis (Schurz, Radua, et al. 2020). This data-driven approach revealed that data were better explained not by two categories, a cognitive and an affective one, but by three categories, adding an intermediate category in between the two. Classical cognitive mentalizing tasks such as false-belief fell into the cognitive category and classical affective empathy tasks such as empathy for pain fell into the affective category. Tasks that seem to require both cognitive and affective processes such as affective ToM fell into a standalone intermediate category. Neural substrates showed that this intermediate category gather both activations typically associated to the cognitive pathway such as temporal, precuneus and medial PFC areas as well as to the affective pathway such as anterior insula and inferior frontal gyrus. Therefore, processes related to the affective pathway such as embodied simulation might apply to this intermediate category, at least on the affective processes and related brain areas. The embodied simulation theory posits that observing others' feelings and actions activates the observers' own past experiences of these feelings and actions in the body, helping to feel and understand others' feelings and actions (Gallese 2007; Gallese et al. 2004; Morelli and Lieberman 2013; Wicker et al. 2003). However, previously induced emotions might hinder such reenactment when incongruent.

Our results support this theory. We found that emotion induction was followed by reduced brain activations in the superior temporal gyrus, precuneus and frontoparietal operculum (including sensorimotor cortices and posterior insula) when participants had to infer an emotion in others that was

incongruent with their induced one. Our result is consistent with previous findings showing an congruence

effect, for instance between induced emotions and facial expression (Calbi et al. 2017; Mobbs et al. 2006;

Qiao-Tasserit et al. 2017) or the fact that individuals with high positive emotion trait were less accurate

at tracking others' negative than positive emotions (Devlin et al. 2014). This incongruence effect found in

our result support the embodied social cognition account that has previously been predominantly

associated to the affective pathway. Thus, our results also support the three-way model of social

cognition, suggesting that affective ToM relies on embodied processes described mostly for the affective

pathway and not only on processes related to the cognitive pathway where we found no effect of

emotions. As emotions seem to affect embodiment processes, we could hypothesize that emotions might

modulate other processes associated to the embodied social cognition account such as empathy for pain,

a classical task of the affective pathway.

2.2 Effects of Emotions on Empathy for pain

The affective pathway is the affective route for understanding others and has been labeled empathy or

emotional empathy. It is the capacity to experience affective reactions to the observed experiences of

others. In others words, it is the sharing of others' feelings. A classical case for studying the affective

pathway is empathy for pain. Previous studies have demonstrated that empathy for pain relies on self-

pain processes. Indeed, self-pain and empathy for pain shared overlapping activations in bilateral anterior

insula and middle cingulate cortex. Furthermore, they shared similar neural representations in bilateral

anterior insula as revealed by pattern analysis (Corradi-Dell'Acqua et al. 2011). As evidences, self-pain

analgesia, for instance using placebo (Rütgen, Seidel, Riečanský, et al. 2015; Rütgen, Seidel, Silani, et al.

2015), paracetamol (Mischkowski et al. 2016) or hypnosis (Braboszcz et al. 2017), was accompanied by

decreased empathy for pain. Therefore, empathy for pain seems grounded in self-pain neural response.

Alike others processes related to the affective pathway such as emotional contagion and facial emotion recognition, empathy for pain has been associated to embodied simulation (Shamay-Tsoory 2011b). This process might be facilitated by shared neural activations between self and others' representations. Given that empathy for pain is sharing neural representations with self-pain and is associated to the embodied simulation theory, we expected that we would find the same effects of emotions for self-pain and for empathy for pain. Previous literature have shown that negative emotions such as sadness (Berna et al. 2010; Boettger, Schwier, and Bär 2011; Tang et al. 2008; De Wied and Verbaten 2001; Zelman et al. 1991), fear and disgust (Meagher, Arnau, and Rhudy 2001) increase sensitivity to self-pain, while positive emotions decrease it (Berna et al. 2010; Boettger et al. 2011; Roy, Peretz, and Rainville 2008; Tang et al. 2008; Villemure, Slotnick, and Bushnell 2003; Weisenberg, Tepper, and Schwartzwald 1995; Whipple and Glynn 1992; de Wied and Verbaten 2001; Zelman et al. 1991). In consequence, we expected that negative emotions would increase empathy for pain while positive emotions would decrease it.

However, we found that although joy was associated with decreased self-pain as measured by galvanic response and brain activity in bilateral posterior insula consistently with previous literature, joy was not associated to decreased empathy for pain. On the contrary, fear was associated to decreased empathy for pain as measured by galvanic response and brain activity in bilateral anterior insula and middle cingulate cortex. These results are in line with the Broaden-and-Build theory that posits that positive emotions broadens attention allowing access to others' information (Fredrickson 2004), while negative ones would narrow attention (Fredrickson 1998) preventing to pay attention to others' pain.

Emotions might modulate attention, allowing greater embodiment of others' pain in positive and neutral states more than in fearful states. Indeed, pattern similarity analysis revealed higher similarity between self-pain and others' pain in joyful and neutral state than in fearful one. We may model the effects of emotions on empathy for pain as a two steps process. Emotion would modulate the breadth of attention to others' pain in a first step, allowing or not to proceed to embodiment in a second one. This model

reminds of appraisal theories or emotion. They posit that we first evaluate if an incoming stimuli is relevant according to personal criteria such as goals, coping potential and values. If we evaluate the stimulus as relevant, it leads in a second step to physiological, motivational, expression, and subjective feeling (Leitão et al. 2020; Scherer 2009b). Alternatively, we could also hypothesize that in a first step, we would embody others' pain. In a second step, attention would amplify or hinder this embodied representation, under positive emotions or negative emotions respectively. These steps could happen sequentially or in parallel. We need further experiments to explore how this effect might relate to attention or appraisal modulation, as we did not directly find an effect of emotions directly on the attentional or appraisal brain network.

We cannot disentangle the effects of the valence from the effects of specific emotion category. Self-pain might help feel pain in others but not fear, while self-fear might help feel fear in others but not pain. We might need to be induced with the same emotion category as the emotion in others (fear/fear) to facilitate embodiment, and not only with same valence experiences (fear/pain). Moreover, pain may be a particular experience, as it seems more evolutionary advantageous to be sensitive to pain in others when we have the resources to help, thus when we feel positive. Prosocial behaviors and compassion are indeed associated with positive emotions (Park et al. 2017b; Singer and Klimecki 2014). Hence, positive emotions might increase the motivation to empathize while negative emotions might decrease such motivation, given that empathy has been described as a motivated account (Zaki 2014). It might be detrimental to be sensitive to pain in others while being ourselves in a fearful state. Our fear might signal a danger and narrow attention to detect potential cues of threat (Finucane 2011), thus keeping attentional resources for our own survival and maybe decreasing the perceived salience of pain in others. Given the different effects of emotions on ToM and on empathy for pain, it is challenging to provide a general effect of emotions on social cognition.

2.3 Effects of Emotions on Social Cognition

We found in the first study that when self-emotions conflict with emotions in others, brain activity decreased in areas that are key for social cognition, supporting the embodied account. However, we found in the second study that self-fear decreased empathy for pain related brain activity, supporting the Broaden-and-Build account. Our findings suggest that understanding others is a complex phenomenon not easily explained by a single existing account.

A first hypothesize explaining why we found results supporting different accounts is that we used different types of stimuli. We might present a Broaden-and-Build effect when we watch images like in the second study, and an embodied effect when we read texts like in the first study. This explanation is unlikely because we found results compatible with an embodied effect with face images in the study attached in the annex section (Qiao-Tasserit et al. 2017). A second hypothesize is that we present a Broaden-and-Build effect when we have to perform a rating or an implicit task like in the second study, but not when we have to perform a classification task like in the first study. This explanation is again unlikely because previous literature have found an embodied effect with rating task in placebo and egocentric bias studies (Rütgen, Seidel, Riečanský, et al. 2015; Silani et al. 2013). A third hypothesis is that the Broaden-and-Build effect is specific to pain, that was present only in the second study. However, this hypothesis contradicts previous studies reporting an embodied effect with pain in placebo and induction of self-pain studies (Antico, Cataldo, and Corradi-Dell'Acqua 2019; Silani et al. 2013).

A last more plausible hypothesis is that on the one hand, we might present a Broaden-and-Build effect when we have different affective experiences in ourselves as compared to in others (self-joy or self-fear and others' pain). On the other hand, we might present an embodied effect when we can expect the same specific (isomorphic) emotions in oneself and in others (self-joy and others' joy, self-fear and others' fear in our study; self-pain and others' pain in a previous study (Antico et al. 2019)). To test this isomorphism

hypothesis, a future study could replicate the first study without using the same specific emotions in oneself and in others but different affective experiences (self-joy and others' tenderness, self-fear and others' anger). According to this hypothesis, we predict a Broaden-and-Build effect, self-joy allowing brain sensitivity to others' tenderness and anger, and self-fear decreasing it.

Building on this hypothesis, we can speculate that when we receive information about someone else, we check whether we may expect a potential match between our own and others' specific affective experience given the context. (i) If we can expect a potential match of specific affect, we might follow an embodied effect, and confirm or infirm whether our own and others' affect are congruent. Congruence would allow brain sensitivity to others' affect while incongruence would decrease it. As a real life example, we can imagine that we are Swiss and watching a soccer game opposing Switzerland and France, in the company of a friend who is both Swiss and French. We can expect a potential match of affective experience given that we might both feel joy if Switzerland is leading the game, although the friend might feel fear because France is losing. When Switzerland is leading, if the friend is actually feeling joy (congruent self-joy and others' joy), we might be sensitive to our friend's joy but less sensitive to his fear (incongruent self-joy and others' fear). (ii) If we cannot expect a potential match of specific affect (e.g. self-fear and others' pain), we might follow a Broaden-and-Build effect, depending only on our own positivity or negativity. Our positivity would allow brain sensitivity to others' affect while negativity would decrease it.

3. Limitations and Future Directions

We studied the effects of joyful, neutral and fearful emotional states on others' joy, fear and pain. We cannot disentangle the effects of valence (fear/pain) from the effects of specific emotions. For instance, within the negative emotions, fear is associated with narrowed attention towards threat (Fredrickson

1998; Ohman et al. 2001) and can cause avoidance behaviors, while sadness is associated with higher self-focus (Wood, Saltzberg, and Goldsamt 1990). Further experiments could explore the effects of other emotion categories and other combinations of induced and inferred emotions, such as the effects of self-sadness on others' sadness (same emotion category) and fear (same valence).

Positive emotions have been associated to broadened attention (Fredrickson 2004). It might be interesting to test whether we can find the same effects we found in the empathy for pain task by modulating attention independently of emotional state, for instance, by manipulating salience, distractors, or cognitive load to see whether the effects attributed to positive emotions actually rely on attention modulation. Indeed, it was reported that it is easier to select sad emoticons after sadness induction than after neutral or positive induction, suggesting that attention selection could be biased towards mood-congruent stimuli (Becker and Leinenger 2011). Emotions might play on other mechanisms such as the motivation to approach others. Joy has been described as a low and fear as a high motivational emotion (Adolphs 2013; Gable and Harmon-jones 2014). Therefore, it might be interesting to compare induction with high versus low approach positive feelings (e.g., desire for food versus amusement with cat videos), and negative feelings (e.g., disgust versus sadness) (Gable and Harmon-jones 2014; Gable and Harmon-Jones 2010).

We used the same emotion induction paradigm, using joyful, neutral and fearful movie-clips. Previous literature showed that films (or audio-visual stimuli) were among the most effective procedures inducing both positive and negative states (Siedlecka and Denson 2019; Westermann et al. 1996; Zhang, Yu, and Barrett 2014). We know from previous studies that the movie-clips we used affected brain activity and connectivity pattern during the following resting-state period, especially in areas related to social cognition and emotions, such as the anterior insula, anterior cingulate cortex, precuneus, medial PFC or the amygdala (Eryilmaz et al. 2011a; Pichon et al. 2014a). Moreover, these videos involved human characters, which might bias how we perceive emotions of others after the movies. Therefore, the effects

of the videos that we find on social cognition might be related more to the specific features of movie-clips and less to the effects of emotional states. It would be interesting to replicate our findings using other induction techniques, such as music, odors, remembering emotional souvenirs that might engage greater personal emotional processes. Moreover, negative subliminal primes, for instance pictures of sad eyes, have been found to increase response to others' pain (Meng et al. 2012; Song, Wei, and Ke 2019). It might be interesting to test the effect of subliminal emotional primes on the social cognition tasks we used to investigate to which extent the effects of emotions we found are involving top-down conscious processes.

To draw general conclusions, we would also need to investigate the effects of emotions on other tasks related to the affective, intermediate and cognitive pathways, such as sharing the emotion seen on facial expressions, indicating feelings in social animations, or inferring intentions in a strategic game (Schurz, Radua, et al. 2020). For instance, the empathic accuracy task that has been associated to the intermediate pathway, similarly to our affective ToM task, was also affected by the congruence-incongruence effect. Participants with high trait positive emotion were less accurate at tracking others' negative emotions and better in some aspects at tracking others' positive emotions (Devlin et al. 2014).

The stimuli might be more relevant if the participants knew the persons described in the stories or seen on the pictures. We could explore whether similarity and familiarity to others might increase embodiment and relevance, as empathy for in-group members might be higher than for out-group members (Brown, Bradley, and Lang 2006). A question relevant in psychiatric setting is to investigate the effects of emotions on how we infer what other people believe about ourselves. Indeed, in social anxiety for instance, negative emotions are associated with the concern that other people think negatively about oneself and with poor ability to share others' positive emotions (Cui et al. 2017a; Kashdan and Roberts 2004; Morrison et al. 2016). Only healthy participants participated in our studies, and we believe that including patients with emotion disorders might help exploring how emotion induction might be helpful in a clinical setting.

4. Conclusions

This thesis aimed at determining whether and how our own emotions could modulate cognitive and affective ToM in a first study, and empathy for pain in a second study. We found that emotion induction did not affect cognitive ToM related brain activations. However, in the affective ToM task, brain activity when inferring incongruent emotions in others was reduced in the superior temporal gyrus, the precuneus and the frontoparietal operculum. This finding supports the embodied social cognition account, as brain response in regions related to social cognition seem modulated by the congruence between our emotions and emotions in others. Yet, we found a different effect of emotions on empathy for pain. Induced fear was associated to suppressed brain activity related to empathy for pain, while self and others pain shared greater pattern similarity after joy induction. This effect was in line with the Broaden-and-Build theory that posits that positive emotions broadens attention allowing to share others' feelings, while negative emotions narrow attention, suppressing feeling others' affective experience. Therefore, understanding others appears to be a complex phenomenon that, to our knowledge, cannot be explained by a single existing model. Nevertheless, our results indicate that our emotions affect the way we process emotions in others, although we need more studies to better understand the underlying mechanisms. The way we understand others might not depend only on incoming stimuli, but also on internal, individual and environmental factors that we can at least partially manipulate. I hope that being aware that emotions can affect the way we understand each other could help better communicate and leave happier together.

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Chapter 4: Articles

4.1 Influence of Emotions on Cognitive and Affective ToM

Qiao-Tasserit, Emilie, Corrado Corradi-Dell'Acqua, and Patrik Vuilleumier. In prep. "Influence of Transient Emotional Episodes on Affective and Cognitive Theory of Mind."

Title: Influence of Transient Emotional Episodes on Affective and Cognitive Theory of Mind

Abstract

Our emotions may influence how we interact with others in different ways. Previous studies have shown an important role of emotion induction in generating empathic reactions to emotions experienced in others. However, it remains unclear whether our own emotions can influence our ability to infer people's mental states, a process associated with Theory of Mind (ToM) and implicated in the representation of both cognitive (e.g., beliefs, intentions) and affective states in others. We examined this question by presenting joyful, neutral, and fearful movie-clips to induce emotions in 33 healthy participants who subsequently had to evaluate states of joy or fear (affective ToM) or beliefs (cognitive ToM) in protagonists of various verbal scenarios. Using functional magnetic resonance imaging, we found that brain activity in the superior temporal gyrus, the precuneus, and sensorimotor cortices were modulated by the preceding emotional induction, with lower response when the to-be-inferred emotion was incongruent with that elicited in the observer (affective TOM). Instead, we found no effect of emotion induction on the appraisal of people's beliefs (cognitive ToM). Our findings support embodied accounts of mentalizing, by suggesting that our own emotions alter the engagement of key brain regions for social cognition, depending on the compatibility between one's own and others' affect.

1 Introduction

As social creatures, we need to figure out what others are feeling and thinking in order to build relationships, collaborate, help each other, and live happily. To do so, we possess the ability to infer emotions and thoughts in other people by piecing together a wide range of behavioral and contextual information. This ability, named Theory of Mind (ToM), is especially useful when social context (e.g., health-related restrictions) constrains how we interact with other people, e.g., by prioritizing indirect (distal) relations at the expense of more proximal contacts. Even within such limited setting, we can effectively understand whether someone is in a joyful or anxious situation, and consequently we might react with joy or anxiety ourselves. What happens however if someone's emotion clashes with our own pre-existing emotional state? Can we still understand and react adequately to another person's joy if we are afraid?

Prevailing theoretical accounts may lead to contrasting hypothesis, yet to our knowledge, only few studies investigated the role played by our emotions on high-level inferential abilities related to ToM, with mixed findings. For instance, Holmberg (2018) found that manipulating individuals' emotions with movie-clips had no effect on their ability at appraising others' cognitive and affective states from brief narratives. Instead, Converse et al. (2008) found that participants had more difficulties taking the perspective of others after a happy music or happy movie-clip, as compared to neutral or sad ones. Finally, Todd et al. (2015) found that anxiety (but not other negative states) may decrease the ability to inhibit self-perspective when inferring others' belief. This divergent set of results most likely reflects the heterogeneity among different studies, which induced different emotional states (sadness, anxiety, fear, happiness), with different methods (clips, music, autobiographical memory), some of which were poorly effective on participants (Holmberg 2018). Furthermore, previous studies employed also different measures of ToM (vignettes, visual/conceptual perspective taking, etc.), with little distinction between cognitive and affective subcomponents, and no further differentiation according to specific emotional

states. This begs for a more systematic investigation on the role of emotion on people's ToM abilities, grounded on a solid theoretical framework for both emotion induction and appraisal domains at work during inferences about others' states.

ToM abilities have been extensively investigated through neuroimaging techniques. In particular, a wealth of studies mapped brain structures underlying the appraisal of others' thoughts or beliefs (Cognitive ToM), and pinpointed a network comprising the temporo-parietal junction (TPJ), middle/superior temporal gyrus, precuneus (PC), as well as lateral and medial prefrontal cortices (PFC), commonly engaged in various ToM tasks (see Bzdok et al. 2012; Krall et al. 2015; Molenberghs et al. 2016; Van Overwalle and Baetens 2009; Schurz et al. 2017, 2020; Veluw and Chance 2014, for meta-analyses). Importantly, parts of this network also activate when individuals appraise other people's emotions (Affective ToM) which, in addition, recruits the temporal pole, amygdala, the insula, and parts of medial PFC that are not modulated by Cognitive ToM processes (Corradi-Dell'Acqua et al. 2014; Hynes, Baird, and Grafton 2006; Schlaffke et al. 2015; Sebastian et al. 2012; Völlm et al. 2006). The differential role of insula and PFC in Cognitive and Affective ToM has been also confirmed in studies employing neurostimulation techniques (Kalbe et al. 2010) or testing brain damaged patients (Corradi-Dell'Acqua et al. 2020; Shamay-Tsoory et al. 2010; Shamay-Tsoory and Aharon-Peretz 2007; Shamay-Tsoory et al. 2006). However, the most comprehensive representation of the ToM network to day is provided by Schurz et al. (2020), who performed Representation Similarity Analysis on meta-analytic brain maps from 188 neuroimaging studies testing ToM (both Cognitive and Affective) and Empathy. Following a data-driven approach, they identified three relevant networks for social cognition: a predominantly cognitive network, characterized by TPJ, middle temporal gyrus, PC, and PFC; a predominantly affective network, characterized by temporal pole, amygdala, insula, inferior frontal gyrus, and middle cingulate cortex; and a third network combining cognitive and affective components of social cognition. The latter network is often observed in Affective ToM paradigms, but partially overlaps with that observed during Cognitive

ToM. To our knowledge, no study so far examine whether the responsiveness of these networks is differentially influenced by emotions in the viewer.

One hypothesis is that emotion induction might affect ToM abilities similarly to what was reported for emotional facial processing and empathy. Indeed, despite their differences, these two lines of research converge in arguing that we might understand (and empathize with) the emotions of others by mapping them on our own body representations, triggering covertly similar neural and muscular responses (Gallese 2007; Gallese et al. 2004; Keysers and Gazzola 2007). Some evidence shows, for instance, that we react to others' affect by simulating similar muscle contractions in our own body, as observed for both facial expressions (Hess and Blairy 2001; Prochazkova and Kret 2017; Wood et al. 2016) and limb movements (Avenanti et al. 2005, 2006, 2010). Accordingly, pre-existing emotions in oneself might facilitate our ability to simulate or embody someone else's state when congruent, and/or hinder the same process when incongruent. This hypothesis is consistent with studies employing ambiguous facial expressions, showing that when people are in one emotional state (e.g., fear), they are more sensitive to face features diagnostic of the same state, and less sensitive to features associated with an incongruent state (e.g., joy) (Calbi et al. 2017; Mobbs et al. 2006; Qiao-Tasserit et al. 2017). Furthermore, receiving pleasant/unpleasant tactile stimulation can bias the way in which individuals assess similar somatic events in others, with more neutral ratings when the to-be-assessed state is inconsistent with one's own (Riva et al. 2016; Silani et al. 2013). Finally, conditions like depression and social anxiety have been associated with lower affective responses towards others' positive emotions (Guhn et al. 2020b) but stronger ability to infer negative thoughts (Zainal and Newman 2018), potentially related to difficulties inhibiting congruent self-related processes in relation to others' information (Cui et al. 2017b). Based on these studies, we would predict that people's proficiency in affective ToM (and corresponding neural responses) might be altered by their own emotions depending on the consistency between one's and other's states, in line

with the predictions of *embodied* accounts. This account, however, makes no prediction about the effect of emotions on the ability to infer non-emotional mental states, such as thoughts or beliefs.

An alternative, but equally plausible, hypothesis derives from the *Broaden-and-build* theory that highlights a differential impact of emotional state on various cognitive processes. According to this account, positive emotions like joy may enhance attention towards other people, and therefore affect our response to both their feelings and beliefs, while negative emotions like fear may narrow down our attention to more personally relevant information and factual details (Fredrickson 1998, 2004). This account is supported by evidence that positive emotions can broaden visual attention (Rowe et al. 2007; Vanlessen et al. 2016), semantic associations (Isen et al. 1985; Phillips et al. 2002; Rowe et al. 2007), and creativity in problem solving (Ashby et al. 1999). Interestingly, they may also reduce egocentric perspective-taking (Todd et al. 2015) and increase prosocial behaviors (Aknin et al. 2013; Aknin et al. 2013; Dunn, Aknin, and Norton 2008) or compassion (Singer and Klimecki 2014). Instead, negative emotions can restrict attention (Finucane 2011), limit semantic associations (Rossell and Nobre 2004), and suppress pain empathy responses to the sight of injured hands (Li et al. 2017; Qiao-Tasserit, Corradi-Dell'Acqua, and Vuilleumier 2018). Based on this framework, we would therefore expect that positive emotions in oneself might improve proficiency in both Cognitive and Affective ToM (and associated neural responses), regardless of the state being appraised in others. Instead, while negative emotions should exert an opposite effect.

The current study aims at testing directly these two opposing hypotheses emerging from previous literature on emotion processing and ToM. For this purpose, we took a well-established method for emotion induction, where individuals watched either joyful, neutral, or fearful movie-clips previously validated in both their emotional effects on viewers and their lingering effects on brain activity, including in insula, amygdala, PC, and PFC (Eryilmaz et al. 2011a; Pichon et al. 2014a; Qiao-Tasserit et al. 2017, 2018). These regions are implicated in both affective and social processes, and key components of ToM

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networks defined by previous studies (Schurz, Radua, et al. 2020). Following the emotion-inducing video clips, participants performed a Cognitive and Affective Theory of Mind task adapted from previous studies (Corradi-Dell'Acqua et al. 2020, 2014), where they had to read short narratives and subsequently judge the cognitive/affective state of the story's protagonist. The stories described a protagonist in a joyful or fearful situation (affective ToM), or in a false-belief situation (cognitive ToM), or in a control condition without any human protagonist (physical object description). Across two experiments, we collected behavioral, physiological, and neural responses through fMRI with the purpose of determining whether emotion induction in participants could modulate their affective and cognitive ToM abilities, and how this influenced corresponding brain network activity. Our key question, however, was whether these modulations would confirm predictions of *embodied* social cognition or those of the *Broaden-and-Build* account.

2   Materials and Methods

2.1   Participants

59 neurotypical volunteers took part in the present study. 26 participated in experiment 1 (15 females, mean age: 27.23, std: 7.79, range: 20-48) and 33 in experiment 2 (17 females, mean age: 25.33, std: 5.31, range: 18-38). Participants had no history of psychiatric or neurological disease. They all gave written informed consent. This study was approved by the local ethics committee and conducted according to the declaration of Helsinki.

2.2   Stimuli

2.2.1   Movie-Clips

We induced emotional states by presenting different movie-clips (each about 1 minute): 6 were joyful (e.g., extract from "When Harry met Sally"), 6 neutral (science documentary), and 6 fearful (e.g., extract from "The Shining" movie). Movies were taken from previous studies that implemented similar emotion-induction paradigms, and reported reliable changes in the first two minutes following the clips both in behavioral (Qiao-Tasserit et al. 2017) and neural responses (Eryilmaz et al. 2011b; Pichon et al. 2014; Qiao-Tasserit et al. 2018). See Eryilmaz et al. (2011) for full information about this database. This manipulation of the participant's own emotion based on movie type was labelled as the "self-emotion" conditions, orthogonal to our manipulation of the "others' emotion" conditions based on the content of stories in the TOM task, as described below.

2.2.2   Stories

Participants read 72 short stories in French, divided into 4 categories (*Others' Joy, Others' Fear, Others' Belief, Photo*) with 18 scenarios each. *Others' Joy, Others' Fear* and *Others' Belief* stories described a person engaged in various situations, and were followed by questions probing for this protagonist's emotion (joy/fear) or belief in specific parts of the stories. As high-level control, we also included a fourth category of stories with no human protagonist (*Photo*), which required to infer a change in visual elements of the story (e.g. outdated map or photograph). *Others' Belief* and *Photo* stories were based on previous studies (Corradi-Dell'Acqua et al. 2020; Corradi-Dell'Acqua, Hofstetter, and Vuilleumier 2014). *Others' Joy* and *Others' Fear* stories were designed in French language for this study but adapted from previous research (Corradi-Dell'Acqua et al. 2020, 2014; Hynes et al. 2006; Saxe and Kanwisher 2003; Saxe and Powell 2006). All narratives are listed in Supplementary Information, and were matched for number of words across the four categories.

2.3 Experimental Set-Up

2.3.1 Affective and Cognitive Theory of Mind Task

Fig 1. *Experimental Set-up.*
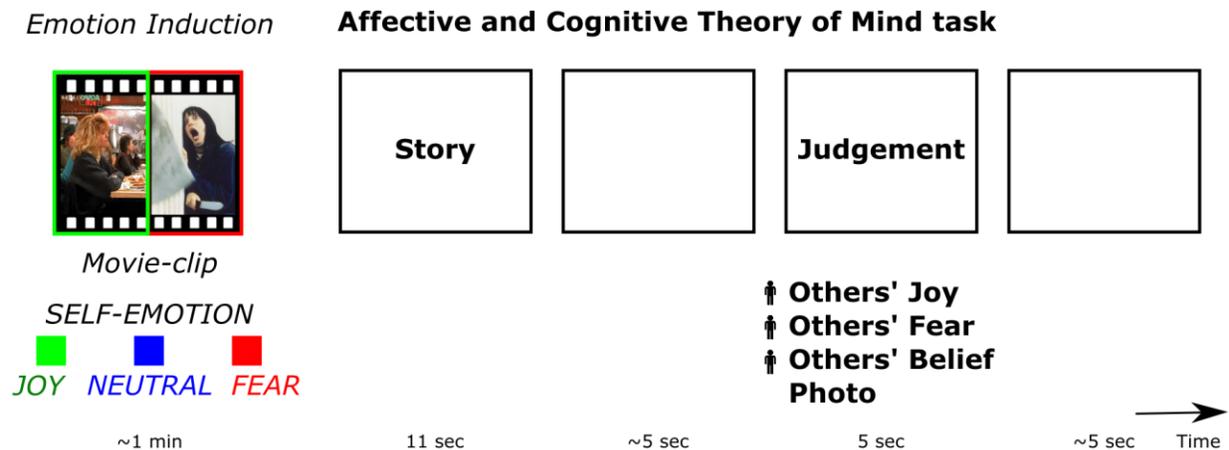
At the beginning of each trial, participants watched a joyful, neutral, or fearful movie-clip (induction of self-emotion). They then read a short story and gave a forced-choice judgement on whether the protagonist experienced joy, fear (Affective ToM), or a particular belief (Cognitive ToM). We used Photo stories, without protagonist, as controls.

Our paradigm was similar to Corradi-Dell'Acqua et al. (2020, 2014), as described in Figure 1. Participants read a short story during 11 seconds and then had 5 seconds to answer a judgement question probing their awareness for the previously-read narrative (the protagonist's joy/fear/belief or visual change in settings). To isolate the judgement epoch from the story-reading epoch, we displayed an empty jitter screen ranging of 2.5-9.5 seconds (mean 5) before and after every question. We presented a total of 72 stories in 18 blocks, divided in 3 sessions with short breaks in between. Each block was introduced by a movie-clip (about 1 minute) to modulate the participants' emotional state, and followed by four different stories (one per category). To potentiate emotion-induction, we semi-randomized the order of the blocks

within each session with movies of the same valence presented consecutively, and self-joy and self-fear blocks never followed directly each other (e.g., one possible sequence could be 2 joyful, 2 neutral, and 2 fearful blocks). Each participant underwent 3 main experimental sessions for about 45 minutes in total. Experiment 2 followed the same procedure as experiment 1 but was performed inside an MRI scanner.

2.3.2   Post-Experimental Ratings

After the experiment, we verified how participants perceived the different types of movie-clips and stories (outside of the scanner). To assess the effect of the movies, participants watched the beginning of every movie clip and recalled their subjective experience evoked by each clip during its first presentation. For each clip, they rated on a visual analog scale the degree of emotional arousal, valence ("afraid" to "amused"), and how much they felt absorbed during the movie (Eryilmaz et al. 2011b; Pichon et al. 2014b; Qiao-Tasserit et al. 2017). To assess the effect of stories, participants also rated each text after the experiment on a 9-point Likert-scale (pointer on 5 at the beginning). For stories with a human protagonist, they reported the extent to which they reflected about the protagonist's joy, fear and belief while reading the story, similarly to Corradi-Dell'Acqua et al. (2014). They also rated the plausibility and understandability of every text, including *Photo* stories. Finally, participants answered questionnaires assessing individual levels of empathy, using the Interpersonal Reactivity Index (Davis 1980) and the Empathy Quotient (Baron-cohen and Wheelwright 2004).

In Experiment 1, which was carried out to validate the paradigm behaviorally, only 12 (out of 26) participants carried out the post-experimental procedure. These data were then combined to those from the 33 participants from Experiment 2, leading to an overall population of N = 45.

2.3.3   Apparatus

We presented the stimuli with Matlab and Psychophysics Toolbox extensions (http://psychtoolbox.org/, Brainard 1997; Kleiner et al. 2007; Pelli 1997). In Experiment 1, participants sat in front of Dell PC screen

(1024 × 768 resolution) where stimuli were projected. Key-presses were recorded on Dell keyboard. In Experiment 2, participants performed the task while undergoing MRI scanning of brain activity. We projected the stimuli on a LCD projector (CP-SX1350; Hitachi –1024 × 768 resolution). Participants saw the stimuli through a mirror fixed on the head coil and answered with key presses on an MRI-compatible bimanual response button box (HH- 2 x 4-C; Current Designs). During this time, we acquired gradient-echo T2*-weighted transverse echo-planar images (EPIs) with blood oxygenation level-dependent (BOLD) contrast. We also acquired a high-resolution T1-weighted anatomical image, all with a 3T Magnetom TIM Trio scanner (Siemens, Erlangen, Germany). Each volume contained 36 slices of 3.2mm thickness with a gap of 0.6mm between slices. We used a repetition time of 2100ms, an echo time of 30ms, descending acquisition mode, a flip angle of 80° and an in-plane resolution of 64x64 voxels (isometric voxel size of 3.2mm).

2.3.4 Physiological Measures

In Experiment 2, we recorded electrodermal activity and pupil size. We tracked electrodermal activity with an MP36R system and SS57L sensors coupled with pre-gelled EL507 electrodes (Biopac Inc, Santa Barbara, CA). We pasted the electrodes on participants' second and third fingers of the non-dominant hand, on the middle phalanges, palmar side. We sampled the data at 200 Hz with AcqKnowledge software. We monitored pupil size using an eye-tracker ASL EyeTrac 6 (Applied Science Laboratories, USA) running with a sampling rate of 60 Hz. Due to technical problems, we were able to keep the electrodermal data of 22 participants and the pupil data of 23 subjects out of 33.

2.4 Data Processing

2.4.1 Behavioral Data

We first looked at participants' performance during our Affective and Cognitive TOM task. For each story category and each movie-clip conditions, we computed individual accuracy scores and median reaction times of correct responses, and then fed them to repeated-measures Analyses of Variance (ANOVAs) with Story Category (*Others' Joy, Others' Fear, Others' Belief, Photo*) and Self-Emotion (*Self-Joy*, *Self-Neutral*, *Self-Fear*) as within-subject factors. In a few specific conditions/participants without correct responses (only 3 conditions across all 33 participants in experiment 2), we replaced the missing value for the reaction times with the average response for all other conditions in the same subject. The same results were obtained when excluding these 3 participants. ANOVAs results were complemented with *post-hoc* paired t-tests.

For post-experimental ratings, we analyzed the different scores ascribed to Movies through repeated measures ANOVA testing the effect of Self-Emotion (*Self-Joy*, *Self-Neutral*, *Self-Fear*) and scores ascribed to Stories by an ANOVA testing the effect of Story Category. In the latter case, conditions could be modeled either as a 4-level factor (*Others' Joy, Others' Fear, Others' Belief, Photo*) for dimensions of plausibility and understandability, or as a 3-level factor (*Others' Joy, Others' Fear, Others' Belief*) for dimensions of joy/fear/belief that concerned stories of experimental interest with a human protagonist.

We also explored whether performance on the Affective and Cognitive Theory of Mind task was influenced by any individual differences reflected in post-experimental measures. This was achieved by repeating the same ANOVA on accuracy/reaction time with individual scores from questionnaires of interest included as covariate. We used the free software environment R version 4.0.0 (https://www.r-project.org/) along with R Studio (https://rstudio.com/) to carry out statistical analyses.

2.4.2 Physiological Data

We analyzed the electrodermal activity with Ledalab software version 3.4.9 (http://www.ledalab.de/, Benedek and Kaernbach 2010a, 2010b)). Each individual time-course data was down-sampled to 10 Hz, pre-processed through adaptive Gaussian smoothing, and visually inspected for potential movement artefacts, which were corrected through spline interpolation. The resulting signal was deconvolved using Continuous Decomposition Analysis to separate the data into tonic and phasic traces of electrodermal activity. For the purpose of the present study, we considered an electrodermal response as reliable if exceeding 0.01 μS. Hence, single-trial event-related responses were calculated as the sum amplitude of all supra-threshold phasic responses occurring within a time-window of interest. For movie epochs, this window was between 1 and 60 seconds from the movie onset (corresponding approximately to the duration of each clip); for the stories epochs, the time window was between 1 and 11 seconds from the story onset (corresponding to the duration of the presentation of the stories); for the judgment made following stories, the time window was between 1 and 5 seconds (corresponding to the duration given for the judgement). The cumulative electrodermal response (EDR) associated with each trial was then log-transformed [$EDR_l = \log(1 + EDR)$], to improve compliance with the normal distribution.

To analyze movies-evoked activity, we averaged individual EDRs for each subject and condition, and fed it to a repeated-measures ANOVA with Self-Emotion (*Self-Joy*, *Self-Neutral*, *Self-Fear*) as within-subject factor. In a similar fashion, judgment-related activity was analysed by averaging EDRs from each subject/condition and running a repeated-measures ANOVA with Story Category (*Others' Joy, Others' Fear, Others' Belief, Photo*) and Self-Emotion (*Self-Joy*, *Self-Neutral*, *Self-Fear*) as within-subject factors. For story-related activity, we followed the same methodology as Corradi-Dell'Acqua et al. (2014), considering that each single text could elicit in participants spontaneous mental attributions concerning the protagonist's emotion and belief to different degrees. Assuming the strength of such attributions in each text would correspond to rating given for the same scenario in the post-experimental debrief, single

trial electrodermal responses were modelled as function of the ratings of joy, fear and belief attribute to the protagonist in each story using a multi-level regression (in the predictors, we artificially assigned a zero rating to control *Photo* stories that did not contain any protagonist).As additional predictor of no-interest associated with reading demands, we also modelled the number of letters in each text.

We analyzed pupil size with the toolbox Ilab (Gitelman 2002). We detected blinks by pupil size and replaced them and 5 pre/post blinks samples with invalid values. We filtered out trials with more than 30% invalid values. For every participant/condition, we averaged pupil size values within a time window of 60 sec for movies epochs, of 11 sec for stories epochs and 5 sec for judgements epochs. We used those averages to perform similar statistical models than those used for the EDR.

2.4.3   Imaging Data

Preprocessing: We analyzed MRI images with SPM12 (Wellcome Department of Cognitive Neurology, London, UK). For each participant, we realigned functional images to the first volume of each session. We then coregistered the images with the T1 anatomical image, which was in turn used to estimate the deformation field necessary for the normalization to the standard Montreal Neurological Institute (MNI) through the unified segmentation approach (Ashburner and Friston 2005). We applied the deformation field to the functional images, which were then resampled to an isotropic voxel size of 2mm, and spatially smoothed with an isotropic full-width at half-maximum Gaussian kernel of 8mm.

First level analyses: We fed preprocessed data into a first-level analysis using the General Linear Model (GLM) framework as implemented in SPM. We modeled for each one of the 3 sessions (i) the movie epochs, (ii) the story epochs, and (iii) the judgement epochs. Movie epochs were modelled for each of the 3 Self-Emotions (*Self-Joy*, *Self-Neutral*, *Self-Fear*) by a boxcar function describing blocks with duration of the corresponding movies. Story epochs following each emotional movie were modelled as events of 11 seconds. As in Corradi-Dell'Acqua et al. (2014), stories from each category were combined in a unique

vector, associated with 4 parametric modulators: 3 post-experimental ratings describing the extent to which participants thought about the story protagonist's joy, fear, or belief (*Photo* stories were associated with the value 0), plus the number of words in each text. To avoid biases related to the order of the parametrical predictors, and to ensure that each effect associated was uniquely interpretable, story epochs were modelled by removing the serial orthogonalization option from SPM default settings. Finally, we modelled 12 judgment epochs (4 Story Categories * 3 Self-Emotions) as events of 5 seconds. This led overall to 30 predictors (3 movie + 3 story + 12 story parametric modulations + 12 judgments), each of which was convolved with the canonical hemodynamic response function (HRF) and associated with its first-order time-derivative. We also included six movement parameters as covariates of no interest (x, y, z translations, pitch, roll and yaw rotations). Therefore, we ended with 66 regressors for each of the 3 functional runs of the Theory of Mind task. We filtered the low-frequency signal drifts with a cutoff period of 128s.

Second-level analyses: The first-level parameter estimates associated with movie epochs were fed into a second-level factorial design with Self-Emotion (*Self-Joy*, *Self-Neutral*, *Self-Fear*) as within-subject factor, and ''subjects'' as random factor, using a random effects analysis. In similar fashion, the story epochs parameter estimates for each continuous regressor of interest (joy, fear, and belief ratings) were modeled through a flexible factorial design with Self-Emotion (*Self-Joy*, *Self-Neutral*, *Self-Fear*) as within-subject factor. Finally, the parameter estimates associated with judgment events were modeled through a factorial design using one within-subject factor with 12 levels (corresponding to 3 Self-Emotions * 4 Story Categories), and subjects as random factor. We allowed the within-subjects factor to have unequal variance between their levels, whereas equal variance was assumed for the ''subject'' factor. In all analyses, we identified voxels as significant only if they passed an extent threshold corresponding to $p<0.05$ corrected for multiple comparison (Friston et al. 1993), with an underlying height threshold of $p<0.001$ (uncorrected).

2   Results

3.1 Movies

Appendix A reports all the data and statistical comparisons associated with the processing of movie-clips.

In both experiments, when debriefed, participants rated joyful and fearful movies as more arousing and absorbing than neutral movies (Table S1). As expected, joyful movies elicited more positive feelings than neutral movies, whereas fearful movies elicited more negative feelings. At the physiological level (from Experiment 2 only), emotionally-valenced movies were associated with larger electrodermal response (EDR) and pupil size as compared with neutral movies. At the neural level (Experiment 2), emotionally-valenced movies engaged (relative to the neutral movies) a widespread network including bilateral occipito-temporal cortex extending to supramarginal gyrus, precuneus, and dorsal prefrontal cortex (Eryilmaz et al. 2011b), but decreased activity in posterior cingulate cortex, bilateral temporoparietal junction and right frontoparietal operculum extending to the posterior insula. We found no significant effects in the amygdala here (as in Qiao-Tasserit et al. 2018, but contrary to Eryilmaz et al. 2011b; Pichon et al. 2014b who used the same movies). Finally, joyful movies produced selective increases in right supplementary motor cortex and inferior frontal gyrus extending to superior temporal gyrus, compared to both neutral and fearful movies (see Table S2 for more details). No brain region showed selective increases for fearful movie-clips.

3.2 Stories

Table S3 shows all post-experimental ratings associated with the stories. As expected, *Others' Joy* stories induced the highest ratings of joy, whereas *Others' Fear* stories induced the highest ratings of fear. These stories did not differ in ratings about beliefs and plausibility. Participants rated all stories as equally understandable in Experiment 1, but in Experiment 2 the *Joy* stories were more understandable than the

others, whereas the *Photo* stories were considered slightly less understandable (see Appendix B for details).

At the physiological level, in line with evidence that processing emotional movies led to increases in both EDR and pupil size (when compared to neutral movies, see Table S1), the analysis of pupil size associated with the story epochs was associated with a significant main effect of Self-Emotion ($F_{(2.44)}$=4.84, p=0.01). *Post-hoc* t-tests showed that this effect reflected larger pupil size for those narratives following a fearful movies, relative to neutral movies ($t_{(22)}$=2.40, p=0.03). This effect was not significant while looking at EDR ($F_{(2.42)}$=0.27, *n.s.*). Moreover, we did not find a significant modulation by ratings of joy, fear and belief attributed to the protagonist in each story, neither as a main effect (EDR: $F_{(3.63)}$=1.02, *n.s.*, pupil size: $F_{(3.66)}$=2.25, *n.s.*) nor in interaction with the self-emotion conditions elicited by the preceding movie-clips (EDR: $F_{(6.126)}$=1.56, *n.s.*, pupil size: $F_{(6.132)}$=1.50, *n.s.*).

All brain activity results are listed in Table S4. Considerations about others' joy modulated the right temporoparietal junction. Considerations about others' fear were not associated to any suprathreshold modulation. Instead, considerations about others' beliefs led to increased activity in the precuneus and dorsal prefrontal cortex. Finally, none of the neural modulations related to considerations about others' joy/fear/belief were modulated by the self-emotion elicited by the preceding movie-clips.

3.3 TOM Judgements

3.3.1 Behavioral and Physiological Results

We next turned to the main phase of our paradigm concerning emotional influences on the Affective and Cognitive Theory of Mind task. Behavioral performance on this task (mean accuracy and median reaction times of correct answers) was compared across the different emotional contexts (see Table S3). Overall, accuracy was high in both experiments (Experiment 1: 84.48%, std 9.88%; Experiment 2: 84.67%, std

15.49%). Two-way repeated measures ANOVAs (4 Story Categories x 3 Self-Emotions) showed no significant main effect or interaction associated with Self-Emotion, for neither accuracy nor reaction times ($F \le 2.10$, *n.s.*). However there was a main effect of Story Category, for accuracy (Experiment 1: $F_{(3,75)} = 20.97$, $p < 0.001$, Experiment 2: $F_{(3,96)} = 3.80$, $p = 0.01$) and reaction times (Experiment 1: $F_{(3,75)} = 11.43$, $p < 0.001$, Experiment 2: $F_{(3,96)} = 11.82$, $p < 0.001$). *Post*-hoc paired-sample t-tests revealed that answers for *Others' Joy* stories overall were as accurate as (Experiment 1), or slightly more accurate than (Experiment 2), those for *Others' Fear*, and more accurate than for *Others' Belief*. *Others' Fear* answers were also more accurate than (Experiment 1), or as accurate as (Experiment 2), *Others' Belief* answers. The least accurate were the *Photo* answers. In terms of reaction times, participants answered the slowest to *Photo* stories and equally faster to the other story categories. Post-experimental questionnaire scores, when added as ANOVAs covariate, did not play a significant role on accuracy or reaction times ($F_{(6,258)} \le 1.39$, *n.s.*).

On the other hand, we found no significant modulation of physiological data during the judgment epochs when tested with a similar 4 Story Categories x 3 Self-Emotions ANOVAs (main effects or interaction for EDR: $F \le 1.53$, *n.s.*; pupil size: $F \le 2.45$, *n.s.*).

3.3.2   Imaging Results

Brain activations during the TOM judgement epochs are shown in Figures 2 to 4 and in Table 1. We first identified regions displaying enhanced activity when assessing others' emotional states (affective TOM), regardless of the emotion induction condition. Specifically, the judgment of both fear (*Others' Fear – Photo*) and joy (*Others' Joy – Photo*) in the scenario's protagonist, relative to judgement of *Photo* condition, significantly increases in activity in the medial prefrontal cortex (Figure 2.A, Table 1). Differential activation was also found in the bilateral TPJ when we lowered the threshold to p<0.001 uncorrected. In addition, judgments about others' joy also activated the precuneus and the posterior cingulate cortex, although a contrast between conditions (*Others' Joy – Others' Fear*) did not show suprathreshold effects.

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We then tested for interaction effects to determine whether judgment of others' joy or fear (relative to photo control) changed as function of the induced self-emotions. This revealed higher activity associated with fear judgements following congruent (fearful) as opposed to incongruent (joyful movies) (*[Others' Fear > Photo]$_{SELF-FEAR}$ − [Others' Fear > Photo]$_{SELF-JOY}$*), with main peaks in the bilateral temporal cortex (extending to posterior insula in the right hemisphere), as well as the caudate nucleus and occipital cortex. Figure 2B displays the regions implicated in this interaction, together with activity parameters extracted from the right temporo-insular cluster's local maxima. Critically, in this region, fear-related TOM judgements evoked lower activity following incongruent (self-joy) movies, as opposed to congruent (fearful) movies ($t_{(32)}$=2.53, p=0.017).

Fig 2. *Neural Response When Judging Others' Joy and Fear Stories.*

A. Brain Activations When Judging Others' Emotion

Others' Joy > Photo   Others' Fear > Photo

B. Congruence Effect When Judging Others' Fear

SELF-EMOTION
JOY   NEUTRAL   FEAR

Interaction:
[Others' Fear > Photo]$_{SELF-FEAR}$ - [Others' Fear > Photo]$_{SELF-JOY}$

Parameter Estimate in STG/PI Cluster Peak [48,-20,0]
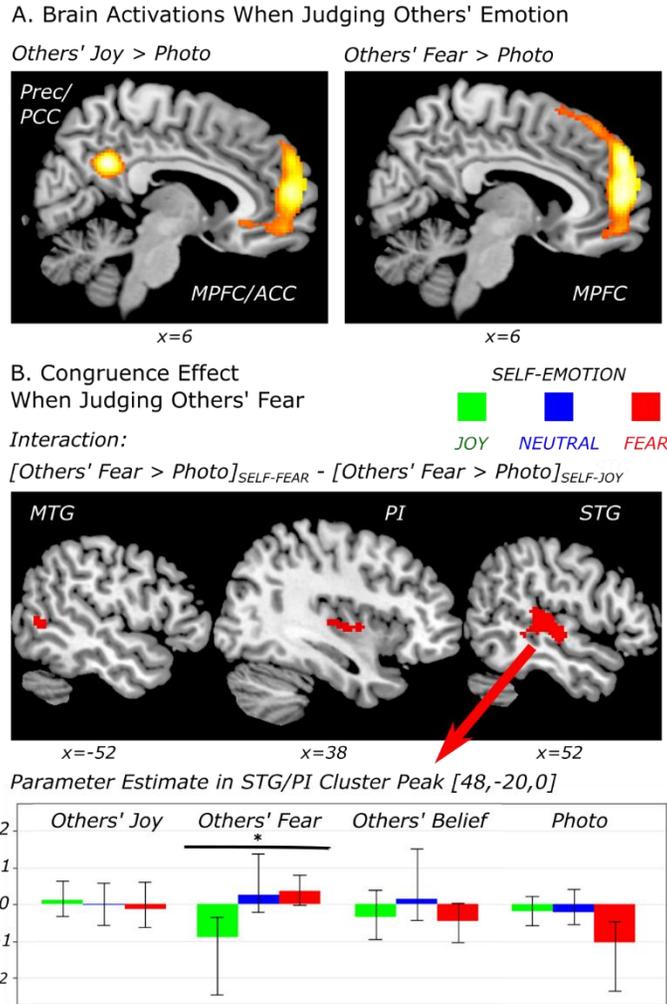
(A) The whole-brain map highlights higher activity evoked when judging Others' Joy and Others' Fear relative to control Photo stories. (B) Upper panel: Activation evoked when judging Others' Fear relative to Photo stories, while being in a congruent post-fearful induction condition, as compared to an incongruent post-joyful condition. Lower panel: Beta parameters of activity extracted from the right STG cluster peak showing a reduced activation when judging Others' Fear, while being in an incongruent post-joyful induction condition. Green, blue and red bars refer to responses observed after the joyful, neutral or fearful movie-clips, respectively, displayed with bootstrap based 95% confidence intervals. "": one-sample t-test at p < 0.05. Prec: Precuneus. PCC: Posterior Cingulate Cortex. MPFC: Medial Prefrontal Cortex. ACC: Anterior Cingulate Cortex. MTG: Middle Temporal Gyrus. PI: Posterior Insula. STG: Superior Temporal Gyrus.*

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This interaction analysis suggests that, at least for the case of others' fear judgement, neural response is reduced in parts of the TOM networks when the participants' own emotional state is incongruent with the one to be inferred. This effect accords with the embodiment model. We therefore also formally tested for a global congruency effect, through a specific two-way interaction contrast (*[Others' Joy$_{SELF-JOY}$ + Others' Fear$_{SELF-FEAR}$] > [Others' Joy$_{SELF-FEAR}$ + Others' Fear$_{SELF-JOY}$]*), in order to identify regions possibly holding "isomorphic" representations of self and other's emotions. This revealed significant modulations in the bilateral superior temporal gyrus (extending to frontoparietal operculum on both sides and to posterior insula on the right), as well as in the precuneus and calcarine cortex. Figure 3 displays these regions together with activity parameters extracted from their local maxima. In all cases, judgments of others' joy produced lower activity after exposure to an incongruent fearful movie ($t_{(32)} \geq 2.35$, $p \leq 0.03$), relative to a congruent or neutral clip. Along the same lines, judgments of others' fear elicited lower activations after an incongruent joyful (relative to fearful) movies ($t_{(32)} \geq 2.02$, $p \leq 0.05$; for the precuneus this effect was only marginally significant, $t_{(32)}=1.79$, $p=0.08$).

Fig 3. *Neural Response to the Congruence Effect Between Self and Others' Emotions.*
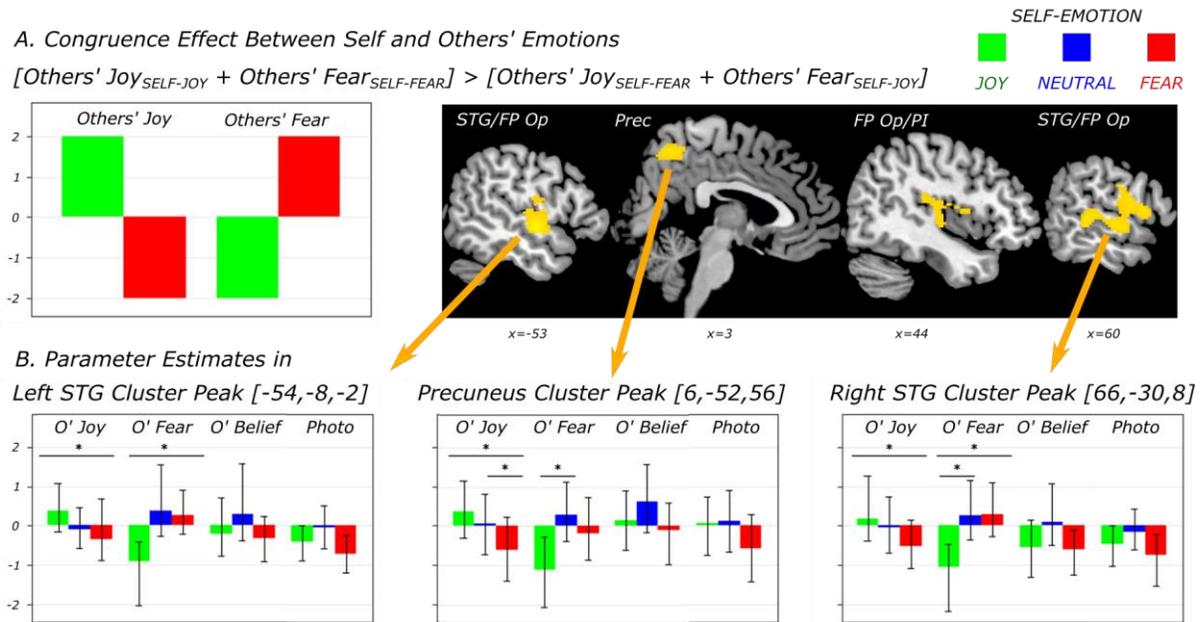
(A) Left panel: Idealized parameter estimates predicted by a congruence effect in line with the embodiment hypothesis, corresponding to suppressed activity when judging others' emotions (joy/fear) after exposure to an incongruent emotion (respectively, fear/joy) as compared to a congruent one (respectively, joy/fear). The colored bars depict responses while being in a joyful (green), fearful (red), or neutral (blue) self-emotion states, respectively. Right panel: Whole-brain map of brain regions responding to the incongruence effect. (B) Parameters extracted from the maximum cluster peak showing an incongruence effect as predicted in A. Graph bars are displayed with bootstrap based 95% confidence intervals. "*": one-sample t-test at $p < 0.05$. STG: Superior Temporal Gyrus. FP Op: Frontoparietal Operculum. Prec: Precuneus. PI: Posterior Insula.

Interestingly, in some conditions and regions, incongruent self-emotional state elicited lesser activity than self-neutral one: specifically, *Others' Fear$_{SELF-NEUTRAL}$ > Others' Fear$_{SELF-JOY}$* in right superior temporal sulcus ($t_{(32)}$=2.15, p=0.04) and precuneus ($t_{(32)}$=2.91, p=0.006), and *Others' Joy$_{SELF-NEUTRAL}$ > Others' Joy$_{SELF-FEAR}$* in precuneus ($t_{(32)}$=2.10, p=0.04). It thus suggests that modulations revealed by this interaction might be better explained in terms of incongruence-deactivation, rather than congruence-enhancement.

We tested the incongruence effect (*[Others' Joy$_{SELF-FEAR}$ + Others' Fear$_{SELF-JOY}$] > [Others' Joy$_{SELF-JOY}$ + Others' Fear$_{SELF-FEAR}$]*) and found no suprathreshold activation.

For completeness sake, we also tested the broaden-and-build alternative hypothesis (i.e., enhanced responses after positive emotions but reduced after negative emotions) using a dedicated contrast (*[Others' Joy$_{SELF-JOY}$ + Others' Fear$_{SELF-JOY}$] > [Others' Joy$_{SELF-FEAR}$ + Others' Fear$_{SELF-FEAR}$]*). However, this revealed no suprathreshold brain activation.

Finally, we compared the assessment of protagonists' beliefs (cognitive TOM) against the control condition (*Photo* stories), which highlighted widespread activity in a network involving the precuneus, the bilateral temporoparietal junction, the middle temporal gyrus, and the medial prefrontal cortex, consistent with previous studies employing the same kind of paradigm (Corradi-Dell'Acqua et al. 2020, 2014; Mar 2011; Saxe and Kanwisher 2003; Saxe and Powell 2006). These activations were observed when testing for the main effect of Beliefs, i.e., when combining activity following the three self-emotion conditions together. Subsequent interaction analysis were performed to assess whether the differential activity to *Others' Belief vs Photo* was modulated by self-emotions, but found no suprathreshold effect.

Fig 4. *Neural Response When Judging Others' Belief Stories.*

Brain Activations When Judging Others' Belief
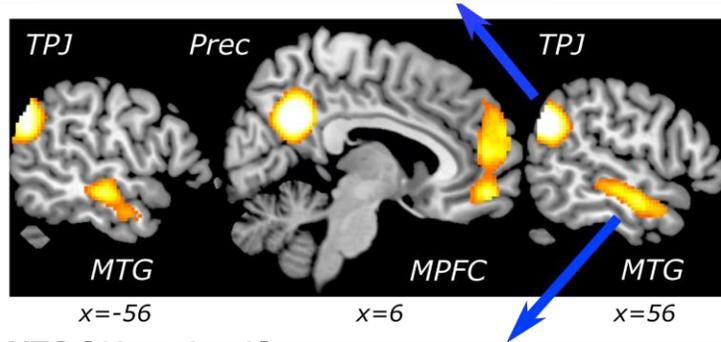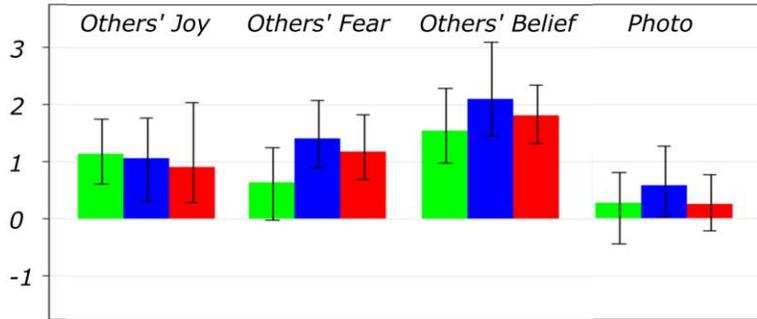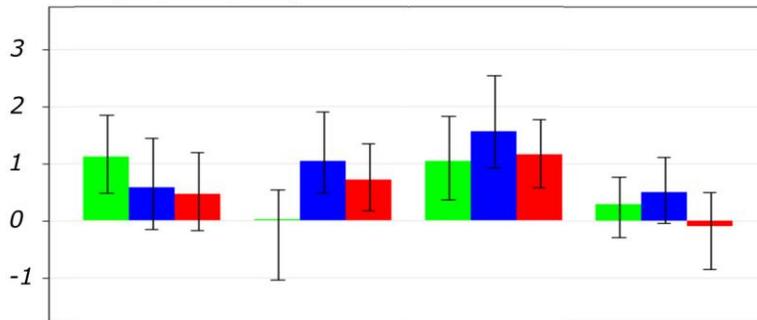
Middle panel: The whole-brain map highlights the main activity evoked when judging Others' Belief relative to control Photo stories (without protagonist). Upper and lower panels: The parameters extracted from the right TPJ and MTG cluster maximum showed no significant effect of emotion induction. Green, blue and red bars refer to responses provided after a joyful, neutral or fearful movie-clip respectively, and are displayed with bootstrap based 95% confidence intervals. TPJ: Temporoparietal Junction. Prec: Precuneus. MTG: Middle Temporal Gyrus. MPFC: Medial Prefrontal Cortex.

Table 1. *Neural Response When Judging Others' Mental Content.*

	SIDE	Coordinates			T	Cluster size
		x	*y*	*z*		
Others' Joy > Photos						
Precuneus/Post. Cingul. Cortex	M	4	-50	30	6.23	645***
Medial Prefrontal Cortex/Ant. Cingul. Cortex	M	8	56	12	5.79	2514***
Others' Fear > Photos						
Medial Prefrontal Cortex/Ant. Cingul. Cortex	M	8	54	10	6.69	3609***
Interaction:						
[Others' Fear$_{SELF-FEAR}$ > Photo$_{SELF-JOY}$] – [Others' Fear$_{SELF-FEAR}$ > Photo$_{SELF-JOY}$]						
Sup. Temporal Gyrus/Post. Insula	R	48	20	0	4.27	646**
Sup. Occipital/Fusiform Gyrus	L	-20	-78	18	4.27	610**
Middle Temporal Gyrus	L	-50	-60	4	4.33	
Prefrontal Cortex/Caudate	R	48	42	-6	3.85	363*
Congruence effect:						
[Others' Joy$_{SELF-JOY}$ + Others' Fear$_{SELF-FEAR}$] – [Others' Fear$_{SELF-JOY}$ + Others' Joy$_{SELF-FEAR}$]						
Sup. Temporal Gyrus/Prec. Gyrus/Post. Insula	R	66	-30	8	4.86	1296***
Sup. Temporal Gyrus/Planum Polare	L	-54	-8	-2	4.74	436*
Frontoparietal Operculum	L	-50	-12	8	3.85	
Precuneus	M	6	-52	56	3.86	309*
Calcarine Cortex	R	28	-66	8	3.98	635**
Others' Belief > Photos						
Temporoparietal Junction	R	54	-58	30	8.25	1081***
Temporoparietal Junction	L	-52	-60	30	6.82	1179***
Middle Temporal Gyrus	R	62	-16	-10	5.52	658**
Middle Temporal Gyrus	L	-62	-16	-12	5.86	481**
Precuneus/Post. Cingul. Cortex	M	4	-56	32	9.78	1959***
Medial Prefrontal Cortex/Ant. Cingul. Cortex	M	4	52	-10	5.31	2280***

Main activity evoked when judging Others' Joy, Fear and Belief, relative to control Photo stories (without protagonist). Interaction: brain activation evoked when judging Others' Fear relative to Photo stories, while being oneself in a congruent fearful as compared to an incongruent joyful induced-emotion. Incongruence effect: suppressed brain activity when judging others' emotions (joy/fear), while being

oneself in an incongruent (fear/joy) as compared to a congruent induced-emotion (joy/fear). All clusters survive correction for multiple comparisons at the cluster level (with an underlying height threshold corresponding to p < 0.001, uncorrected). Coordinates in standard MNI space refer to maximally activated foci: x= distance (mm) to the right (+) or the left (-) of the midsagittal line; y=distance anterior (+) or posterior (-) to the vertical plane through the anterior commissure (AC); z= distance above (+) or below (-) the inter-commissural (AC-PC) line. L and R refer to the left and right hemisphere, respectively. M refers to medial activations. Ant.: Anterior. Post.: Posterior. Cingul.: Cingulate. Sup.: Superior. Family-wise significance corrected for multiple comparisons at the cluster level is noted "" at p < 0.05, "**" at p < 0.01 and "***" at p < 0.001.*

4 Discussion

We found that emotion induction in participants modulated their brain activity when inferring emotions in others (affective ToM) in line with the predictions of the *embodied* social cognition account. More specifically, neural response evoked when appraising fear from stories was larger when individuals were in a fearful state themselves, as opposed to a joyful state (*[Others' Fear > Photo]$_{SELF-FEAR}$ - [Others' Fear > Photo]$_{SELF-JOY}$*), with predominant impact on the right STG extending to the PI, as well as on the left MTG and right caudate. This effect was also observed when formally testing for congruence effects between one's own and others' emotions (*[Others' Joy$_{SELF-JOY}$ + Others' Fear$_{SELF-FEAR}$] > [Others' Joy$_{SELF-FEAR}$ + Others' Fear$_{SELF-JOY}$]*), which confirmed modulations of STG, PI and frontoparietal operculum, as well as precuneus, when participants appraised either joy or fear while being in a compatible (vs. incompatible) emotional state. Importantly, however, these modulations were better explainable in terms of a suppression by incongruence, rather than -enhancement by congruence, given that activity observed after neutral movies was generally similar to that observed in congruent emotional conditions. On the other hand, when testing for affective modulations predicted by the *Broaden and Build* account, no significant changes in brain activity were found. Likewise, we found no effect of self- emotions on cognitive ToM responses, suggesting a selective impact on mentalizing about affective states rather than any mental states more globally.

Overall, our results provide novel evidence in favor of *embodied* processes associated with TOM abilities, by revealing that our emotions may attenuate our brain response to others' affective states when these are incongruent with our own. Albeit limited to the neural activations, with no reliable impact on behavioral performance in the TOM task (possibly due to ceiling effects), our results suggest that when inferring affect in others, self-emotions can alter the degree with which we embody others' state, by modulating the responses in specific parts of TOM networks, including the superior temporal cortex, posterior insula/frontoparietal operculum, and precuneus.

4.1 Embodied Effects When Inferring Emotions in Others

We started by examining the brain activations associated with the judgements of affective states (joy or fear) in others, and found large activations extending from the ventral to the dorsal medial PFC (Fig 2.A), especially for joy judgements in the precuneus. Under rigorous correction for multiple comparisons across the whole brain, no effect was observed in TPJ, but this region was visible under a less stringent threshold (see Results). These data dovetail with previous studies on Affective ToM, which identified a widespread network involving TPJ, STG/MTG, PC, insula, and medial PFC, partially overlapping with networks engaged by Cognitive ToM (Corradi-Dell'Acqua et al. 2020, 2014; Hynes et al. 2006; Schlaffke et al. 2015; Sebastian et al. 2012; Shamay-Tsoory and Aharon-Peretz 2007; S. G. Shamay-Tsoory et al. 2009; Shamay-Tsoory et al. 2006; Völlm et al. 2006). Remarkably, our new findings reveal that parts of this network are influenced by our self-emotion induction manipulation, suggesting that brain systems engaged by emotional experiences may also contribute to affective TOM to infer emotions in other people.

Albeit highlighted within the same contrast, brain regions displayed in Figure 3 are not traditionally considered as parts of the same network. On the one side, STG and precuneus have been associated with both Cognitive and Affective ToM (Bzdok et al. 2012; Krall et al. 2015; Molenberghs et al. 2016b; Van Overwalle and Baetens 2009; Schurz et al. 2017; Schurz, Radua, et al. 2020; Veluw and Chance

2014), suggesting that they might constitute core ToM regions involved in representing any kind of mental state in others. Interestingly, STG has been associated with the perception of socially relevant information (Adolphs 2001; Pourtois et al. 2004) and attribution of intentions and goals (Adolphs 2003; Schultz et al. 2004), potentially playing a role in action simulation. Furthermore, this region has also been implicated in the processing of facial features of both emotional and non-emotional nature, with different subportions underlying specific facial features (Schobert et al. 2018). Most interesting is the case of the precuneus, whose functional properties are not limited to ToM, but also extend to self-processing and episodic memory (Cavanna and Trimble 2006; Spreng, Mar, and Alice S. N. Kim 2009), possibly providing a hub for the integration of both external and internal information, via its widespread connectivity with higher associative regions (Utevsky, Smith, and Huettel 2014). Recently, Sharvit et al. (2020) implicated a similar network comprising precuneus, TPJ, STG and medial PFC in a task where individuals assessed the appropriateness of people's conducts, and precuneus activity in this task exhibited higher connectivity with a portion of the insular cortex sensitive to olfactory disgust. Our data do not only agree with, but also extend, these previous findings, by showing how this region bridges representations of self-related affective experiences with abstract evaluation of people's mental states.

On the other side, the frontoparietal operculum and insula are knowingly involved in body representation, somatosensory processing, somatic affect, and sensorimotor integration (Corradi-Dell'Acqua, Tomasino, and Fink 2009; Craig et al. 2000; Farrell, Laird, and Egan 2005; Kropf et al. 2019; Mengotti, Corradi-Dell'Acqua, and Rumiati 2012; Salimi-Khorshidi et al. 2009; Sharvit et al. 2020; Tsakiris et al. 2007). Interestingly, it has been argued that these regions could also contribute to the understanding of others' emotions through face or voice (Kragel and LaBar 2016b), as revealed for instance by evidence that transient opercular disruption with TMS impairs the recognition of facial expressions (Adolphs et al. 2000; Pourtois et al. 2004). Furthermore, like the precuneus, the operculum also seems to integrate external and internal information, as it was reported to support attention towards our own emotions such

as fear (Straube and Miltner 2011) or pain (Orenius et al. 2017). In a similar vein, the posterior insula also processes sensorimotor information at the interface between external (e.g., touch, temperature, pain, sounds) and internal (e.g., somatovisceral, vestibular) sensory information (Chang et al. 2013). Finally, the ventral precentral/premotor area may provide an interface between others' perception and self-performed actions as it is supposed to carry mirror properties. It is indeed activated both when observing and when performing goal-directed (Chouinard and Paus 2006; Kantak et al. 2012; Morin and Grèzes 2008) or defensive actions (Cooke and Graziano 2004; De Gelder et al. 2004). Moreover, its dysfunction has been associated with social deficits including those related to ToM abilities (Díez-Cirarda et al. 2015; Nebel et al. 2014).

Overall, all these regions represent plausible neuronal output for embodied effects in Affective ToM tasks. Indeed, a wealthy literature has hypothesized that we represent others' emotions through a process of simulation, whereby we re-map the movement/state observed in others in ourselves (Adolphs 2003; Keysers and Gazzola 2009; Kragel and LaBar 2016a; Molenberghs et al. 2016b; Ross and Atkinson 2020; De Waal and Preston 2017). Such simulation processes may trigger physiological and neuronal activity "as if" we would have experienced the observed emotion ourselves (Goldman and Sripada 2005; Spunt and Adolphs 2019). As a consequence, we could interpret our effects as consistent with the « somatic marker hypothesis », which suggests that emotions are expressed through changes in the representation of somatic/interoceptive states and represented in the activity patterns in insular/opercular structures (Craig 2009; Damasio et al. 1996). This marker could plausibly be expressed in our task when appraising the emotions of others, to subserve accurate emotion recognition, but be implemented or more efficient only when this state is not inconsistent with our own current affective state.

To the best of our knowledge, although embodied effects have previously been described for emotional facial processing and pain empathy, this is the first study extending such effects to ToM abilities

for mental state inferences. Indeed, seminal accounts have posited that at least two neural pathways might subserve the processing of others' affect: an "affective" pathway, mediated by regions such as the insula and grounded in a representation of one's own affect; and a "cognitive" pathway, mediated by a network containing mPFC, TPJ, precuneus, and STG, underlying abstract propositional knowledge about others' mental states, such as beliefs, intentions, etc., associated with ToM abilities (Shamay-Tsoory 2011b; Stietz et al. 2019). However, this dichtotomous subdivision has been challenged by a recent meta-analysis, who argued that Affective ToM might indeed recruit a hybrid network, combining aspects of both "cognitive" and "affective" pathways (Schurz, Radua, et al. 2020). Our data fit well this claim, as they show how appraisal about others' emotions (1) is influenced by one's own affect consistently with the predictions of embodied accounts; (2) encompasses regions part of both "cognitive" (precuneus, STG) and "affective" (insula, operculum, ventral premotor cortex) networks. In this view, the brain appears sufficiently flexible to cross the predefined boundaries of each pathway, and combine them for a more comprehensive representation of others' affect.

4.2 Inconsistency Suppression vs. Consistency Enhancement

Our results could be best described in terms of an inconsistency-related suppression, as we observed lower neural responses to others' affect after being exposed to an opposite emotional state. This may appear counterintuitive as embodied accounts are generally conceived to manifest themselves also in terms of consistency-related enhancement. One possible explanation might reflect that the inconsistent condition stands out from all the others, because it takes the brain to hold at the same time two affective representations of opposite valence, potentially competing in regions that may bridge representations of self and others' related affective experiences. Such conflict does not arise in the consistent or neutral conditions, where the brain represents only one emotionally-valenced state at the time. In this perspective, the neural modulations observed in Figure 3 might not reflect an active simulation of other emotions on oneself, but rather the absence of conflicting signals between what participants experience

and what they observe in others. Hence, Affective ToM abilities may be only partially influenced by embodied processes, and our own affective state could simply put the brain in an unfavorable setting for responding to others' inconsistent emotions.

It could be also argued that the inconsistency-related suppression is the result of an inhibitory signal from other brain structures. Indeed, it has been often suggested that embodied processes require a counterweight mechanism at maintaining a differentiation between one's and others' affect, and prevent inappropriate use of the self as proxy for interpreting others' states (Silani et al. 2013). Within this framework, a previous study examined brain activity in individuals who underwent pleasant/unpleasant tactile stimulations whilst seeing others exposed to a consistent or inconsistent experience. The right supramarginal gyrus was more active during inconsistent (as opposed to consistent) events, and this suppression increased with the degree to which individuals were influenced by their own affect in assessing others (Silani et al. 2013). It is possible that in our study too, inconsistent conditions triggered neural mechanisms for maintaining self-other distinction which, in turn, inhibited the neural response in STG, precuneus, operculum, insula, etc. Unfortunately, when testing for any enhanced activity associated with inconsistent conditions ($[Others'\ Joy_{SELF-FEAR} + Others'\ Fear_{SELF-JOY}] > [Others'\ Joy_{SELF-JOY} + Others'\ Fear_{SELF-FEAR}]$), we found no suprathreshold activity, neither at the level of the supramarginal gyrus nor elsewhere. Hence, if such effect was present, it went undetected in our analysis.

4.3 Broaden and Build vs. Embodiment

We found no support for the Broaden-and-Build hypothesis, neither for cognitive nor affective ToM. This account predicted a broadening of attention under positive emotions (Fredrickson 2004; Rowe et al. 2007), potentially boosting the ability to infer others' feelings, emotions, and beliefs. On the other side, negative emotions such as fear might narrow down attention, and suppress attention towards other people. In this view, our data might (at least at first sight) appear at odds with earlier research, where the

same emotion induction manipulation used here influenced the sensitivity to others' pain consistently with the predictions of the Broaden and Build theory, and not of embodied accounts (Qiao-Tasserit et al. 2018). However, our present research differs substantially from our previous (Qiao-Tasserit et al. 2018) because here the emotions evoked by video-clips (fear vs joy) were closely matched with the to-be-inferred mental state, whereas in Qiao-Tasserit et al. (2018), these induced emotions were qualitatively distinct from the affective state observed in others (pain), with only a broad compatibility in terms of valence. In light of these considerations, we can conclude that embodied effects might be observable only if one's and others' state tap the same shared representation. If, however, self and others' state tap into distinct representations or share only core affective dimensions such as valence (as in Qiao-Tasserit et al. 2018), then emotion induction might operate more consistently with the predictions of the Broaden and Build theory.

An alternative interpretation could instead relate to the nature of the task, as Qiao-Tasserit et al. (2018) employed a paradigm where others' affect was not inferred explicitly, but rather influenced participants in a bottom-up fashion through visual stimuli. Hence it could be argued that the Broaden and Build effects might not apply to tasks requiring high-level inferential processes. We believe this explanation is unlikely. Indeed, in an earlier study, we employed the same emotion induction paradigm to a face recognition task with ambiguous emotional expressions (Qiao-Tasserit et al. 2017) and found that participants were more sensitive to visual facial features that were compatible with the induced emotions (see also Calbi, Heimann, et al. 2017; Mobbs et al. 2006). Although the latter study was not conceived to compare the predictions of embodied vs. Broaden and Build accounts, it nevertheless shows a consistency effect similar to the one described here, but with a picture-based paradigm (Qiao-Tasserit et al. 2017). We therefore surmise that it is not the task, but rather the close compatibility between one's and others' states, that may determine the way in which one's own emotions influence social proficiency.

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4.4 Limitations of the study and conclusive remarks

Although our emotion induction paradigm proved effective in influencing brain activity, it had no effect on overt behavioural ratings. Hence, neural modulations observed here might reflect a brain mechanism too subtle to impact the way individuals make explicit TOM inferences about others. It should be acknowledged, however, that accuracy was overall high, with a potential ceiling effect that could hinder the sensitivity of our paradigm. A second limitation pertains the absence of other emotional control conditions that would allow us to disentangle whether our effects are due to valence or specific emotion category. By relating critically the present results to our previous research (Qiao-Tasserit et al. 2017, 2018), we considered that our effects depend on a close match between one's and others' states (see above). However, the only way to fully disambiguate this issue would be to include a large range of different emotional states (e.g., sadness, disgust, etc.) in either the self or the other condition. Finally, the employed TOM narratives are not immune to critiques. Although post-scanning ratings confirmed the validity of our database, they also indicate that happy stories also often contained fear elements (Table S3). This might explain why, in our study, effects associated with the appraisal of joyful states were less pronounced than those associated with the appraisal of fear.

Keeping these limitations aside, we provide conclusive evidence that our own emotions influence how our brain activates to assess those of other people. We found that when inferring emotions in others that are incongruent with our own current affective state, activity is reduced in a widespread network comprehending precuneus, STG, insula, and operculum. These results help to disentangle between opposing theoretical accounts, suggesting that our own emotional state can affect the way we embody and simulate the emotions of other people. To conclude, we speculate that being more aware of the way our environment and feelings shape how we respond to others might foster social processes contributing to more peaceful and gratifying relationships.

5 Acknowledgements

6 References

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7 Appendixes

A. Movie Responses

The post-experimental ratings (from Experiments 1 & 2) and physiological data (Experiment 2) associated with movie-clips are reported in Table S1. Overall brain responses to the movies- (Experiment 2) are reported in Table S2. For both experiments, for each question of interest, we analyzed post-experimental ratings with a repeated-measures ANOVA, testing the effect of self-emotion (self-joy, self-neutral, self-fear). In both experiments, and all questions of interests, we found a main effect of emotion (Experiment 1: $F_{(2,50)}$=140.3, p<0.001; Experiment 2: $F_{(2,64)}$=118.1, p<0.001). *Post-hoc* paired t-test revealed that participants rated joyful movies as more positive, more arousing, and more absorbing than neutral movies (Experiment 1: $t_{(25)}$≥2.56, p<0.01; Experiment 2: $t_{(32)}$≥4.03, p≤0.001). Similarly, they rated fearful movies as more negative, more arousing, and more absorbing than neutral movies (Experiment 1: $t_{(25)}$≥4.74, p<0.001; Experiment 2: $t_{(32)}$≥5.82, p<0.001). Compared to joyful movies, fearful movies were rated as more fearful ($t_{(25)}$=13.96, p<0.001; Experiment 2: $t_{(32)}$=12.17, p<0.001) and intense (Experiment 1: $t_{(25)}$=2.96, p=0.007, Experiment 2: $t_{(32)}$=-2.78, p=0.009) in both experiments, and more absorbing in Experiment 1 (Experiment 1: $t_{(25)}$=2.58, p=0.02, Experiment 2: $t_{(32)}$=1.48, *n.s.*).

We carried out a similar analysis tfor physiological responses during movie epochs. For both electrodermal response (EDR) and pupil size, a one-way ANOVA showed a main effect of emotions (EDR: $F_{(2.42)=}$5.42, p=0.008, pupil size: $F_{(2.44)}$=37.07, p<0.001). *Post-hoc* t-test revealed that both joyful and fearful movies evoked larger EDR ($t_{(21)}$≥2.38, p<0.05) and pupil size ($t_{(22)}$≥4.61, p<0.001), than neutral movies (see Table S1). Overall, these data are in line with those from previous studies using the same movie database (Eryilmaz et al. 2011b; Pichon et al. 2014b; Qiao-Tasserit et al. 2017, 2018), and confirm a reliable affective engagement of participants during movie watching.

S1. Table. Post-Experimental Ratings and Physiological Response Associated With Movie-Clips.

	Experiment 1			Experiment 2		
	JOYFUL	*NEUTRAL*	*FEARFUL*	*JOYFUL*	*NEUTRAL*	*FEARFUL*
Valence	3.73(1.13)	1.15(0.51)	-1.87(1.49)	3.27(1.21)	1.14(0.49)	-1.15(1.58)
Arousal	7.12(1.60)	5.38(1.78)	8.37(1.74)	6.39(1.65)	4.70(1.75)	7.52(1.50)
Absorption	7.56(1.72)	6.33(2.07)	8.56(1.63)	7.20(2.12)	5.41(1.86)	7.88(1.53)
EDR	-	-	-	0.29(0.32)	0.19(0.22)	0.28(0.36)
Pupil Size	-	-	-	3.84(0.66)	3.73(0.67)	4.00(0.65)

Mean ratings are averages from individual median values, obtained on an 11-points Likert scale (range from 1 to 11, except for valence from -5 to +5). Standard deviations are noted in brackets. Electrodermal activity is given in µS and pupil size in mm.

S2. Table. Neural Response When Watching Movie-Clips.

	SIDE	Coordinates			T	Cluster size
		x	y	z		
Emotional vs. Neutral movie-clips: *(Joyful – Neutral) ∩ (Fearful – Neutral)*						
Middle Occipo-Temporal Cortex	L	-46	-64	12	9.70	5819***
Supramarginal Gyrus	L	-60	-48	26	7.30	
Fusiform Gyrus	L	-40	-56	-16	8.28	
Middle Occipo-Temporal Cortex	R	52	-54	10	10.10	4144***
Supramarginal Gyrus	R	62	-40	22	11.56	
Fusiform Gyrus	R	42	-60	-16	7.06	
Sup. Occipital Gyrus	R	18	-92	22	4.47	408*
Precuneus/Bilat. Sup. Par. Lob.	M	-4	-50	50	10.41	2419***
Precen. Gyrus/Inf. Front. Gyrus	R	46	2	54	7.32	1953***
Dorsolateral Prefrontal Cortex	R	16	4	68	6.03	
Dorsomedial Prefrontal Cortex	R	4	50	36	4.31	300*
Neutral vs. Emotional movie-clips: *(Neutral – Joyful) ∩ (Neutral – Fearful)*						
Posterior Cingulate Cortex	M	-2	-34	36	10.10	3544***
Medial Cingulate Cortex	M	6	-14	30	6.45	
Temporoparietal Junction	L	-44	-62	52	5.65	719***
Temporoparietal Junction	R	46	-54	48	3.38	346*
Central Operculum/Post. Insula	R	42	-12	18	5.35	442**
Joyful vs. Non-Joyful movie-clips: *(Joyful – Neutral) ∩ (Joyful – Fearful)*						
Inf. Frontal Gyrus	R	48	38	2	5.36	550**
Sup. Temporal Gyrus	R	52	4	-6	5.05	
Supplementary Motor Cortex	R	8	20	60	5.27	352*

All activation peaks survive correction for multiple comparisons at the cluster level (at an underlying height threshold corresponding to p < 0.001, uncorrected). L and R refer to the left and right hemisphere, respectively. M refers to medial activations. Sup.: Superior. Bilat. Par. Lob.: Bilateral Parietal Lobule. Inf.: Inferior. Post.: Posterior. Precen.: Precentral. Front.: Frontal. Family-wise significance corrected for multiple comparisons at the cluster level is noted "" at p < 0.05, "**" at p < 0.01 and "***" at p < 0.001.*

B. Story Ratings

The post-experimental ratings associated with the stories ratings are reported in Table S3. For both experiments, participants assessed their level of reasoning about protagonist's joy, fear, and belief (except for *Photo* stories), as well as plausibility and understandability. We performed a one-way repeated-measures ANOVA with Story Category as factor for each rating instruction separately. As predicted, participants' thoughts about protagonist's joy and fear were stronger in those stories specifically tailored at eliciting considerations about this specific emotions. (Experiment 1: others' joy: $F_{(2,50)}$=25.85, $p<0.001$, others' fear: $F_{(2,50)}$=85.74, $p<0.001$, Experiment 2: others' joy: $F_{(2, 64)}$=45.82, $p<0.001$, others' fear: $F_{(2, 64)}$=129.7, $p<0.001$). Please note that *Others' Joy* stories also elicited some considerations about fear (albeit in much less extent than joy, reflecting that scenarios eliciting emotions may imply multiple simultaneous appraisals based on both negative and positive elements (e.g., joy can be the outcome of a negative event becoming suddenly positive) (Scherer 2009b). We found no significant difference in the extent to which participants thought about protagonist's belief across the different scenarios (Experiment 1: $F_{(2.50)}$=0.46, *n.s.*; Experiment 2: $F_{(2.64)}$=2.77, *n.s.*). Participants rated all 4 story categories as equally plausible (Experiment 1: $F_{(3,75)}$=1.50, *n.s.*; Experiment 2: $F_{(3.96)}$=1.63, *n.s.*) and understandable, except in experiment 2 (Experiment 1: $F_{(3,75)}$=2.36, $p=0.08$; Experiment 2: $F_{(3,96)}$=11.1, $p<0.001$) where *Others' Joy* stories were easier to understand, and *Photo* stories less so, compared to others' stories.

S3. Table. *Accuracy, Reaction Times and Post-Experimental Ratings Associated With Stories.*

	Experiment 1				t-Test			
	Others' Joy stories [OJ]	Others' Fear stories [OF]	Others' Belief stories [OB]	Photo stories	OJ vs. OF stories	OJ vs. OB stories	OF vs. OB stories	Photo vs. 3 other stories
Accuracy (%)	89.89(9.91)	93.01(8.58)	81.91(13.75)	72.78(18.62)	1.91	3.42**	4.79***	≥3.07**
Reaction times (sec)	2.91(0.51)	2.90(0.49)	3.01(0.47)	3.21(0.38)	0.26	1.32	1.41	≥2.64*
Joy ratings	6.67(1.75)	3.35(2.34)	3.75(1.95)	N.A.	5.44***	7.38***	0.83	N.A.
Fear ratings	6.04(1.26)	7.15(1.26)	2.44(1.63)	N.A.	4.30***	8.15***	11.69***	N.A.
Belief ratings	5.48(2.06)	5.06(2.41)	5.29(2.35)	N.A.	1.34	0.41	0.44	N.A.
Plausibility	6.90(1.51)	6.87(1.51)	6.27(1.69)	6.75(1.58)	0.18	2.02	1.71	≤1.33
Understandability	8.00(1.26)	7.69(1.26)	7.17(1.99)	7.13(2.04)	0.94	2.07*	1.58	≤1.26, *vs. OJ* 2.77*
	Experiment 2							
Accuracy (%)	90.34(20.04)	85.23(25.82)	83.63(16.55)	78.88(13.68)	2.33*	2.17*	0.38	≥2.58*, *vs. OF* 1.36
Reaction times (sec)	2.83(0.51)	2.90(0.55)	2.93(0.41)	3.11(0.39)	1.16	1.55	0.36	≥2.77**
Joy ratings	6.83(1.48)	3.80(1.11)	3.27(1.67)	N.A.	6.15***	10.87***	1.45	N.A.
Fear ratings	6.26(1.33)	6.76(1.13)	2.48(1.63)	N.A.	2.75**	11.08***	13.30***	N.A.
Belief ratings	5.38(2.15)	4.85(2.34)	5.83(1.99)	N.A.	2.32*	0.97	1.95	N.A.
Plausibility	6.47(1.18)	6.21(1.52)	6.44(1.34)	6.73(1.25)	0.89	0.14	1.00	≤1.77, *vs. OF* 2.12*
Understandability	7.48(1.05)	7.11(1.32)	6.73(1.50)	6.53(1.58)	2.82**	3.87***	1.98	≥2.83**, *vs. OB* 1.47

Averages of individual (i) accuracy, (ii) medians of reaction times, and (iii) medians of ratings. After the experiment, participants were asked to answer for each story the 5 following questions on a 9-point Likert scale ranging from 1 to 9: 'When reading the story, to which extent did you think (i) about the protagonist's joy/ (ii) fear / (iii) belief/? That the story was (iv) plausible / (v) understandable?'. Standard deviations are noted in brackets. N.A.: Not applicable. Two samples paired t-tests have a degree of freedom of 25 in experiment 1 and of 32 in experiment 2. Significance is noted "*" at $p < 0.05$, "**" at $p < 0.01$ and "***" at $p < 0.001$.

S4. Table. *Neural Response When Reading Stories.*

	SIDE	Coordinates			T	Cluster size
		x	y	z		
Others' Joy						
Temporoparietal Junction	R	54	-54	38	4.36	472*
Others' Belief						
Precuneus	M	4	-62	38	3.92	505**
Dorsolat. Prefrontal Cortex	R	26	34	48	4.23	836***
Dorsomed. Prefrontal Cortex	R	8	56	34	3.66	

Main activity evoked when reading stories, that changed linearly with the likelihood of attributions of belief and joy (no suprathreshold effect of fear), as measured by post-experimental ratings of the same participants. All activations survive correction for multiple comparisons at the cluster level (with an underlying height threshold corresponding to $p < 0.001$, uncorrected). *R* refers to the right hemisphere. *M* refers to medial clusters. *Dorsolat.:* Dorsolateral. *Dorsomed.:* Dorsomedial. ***p < 0.001; **p < 0.01; *p < 0.05 family-wise corrected for multiple comparisons at the cluster level.

S5. Stories in Original French and Translated in English.

Others' Joy stories

Others' Joy stories started with a protagonist in a fearful situation (e.g. wait for a doctor's call to know the severity of a disease). A joyful event happened (e.g. the doctor announces healing) so that the protagonist's initial fearful emotion changed radically into a joyful emotion after the event. During the judgement epoch, participants had to select the protagonist's emotion (joyful or fearful) after the event (joyful).

Others' Fear stories

Others' Fear stories started with a protagonist in a joyful situation (e.g. lead a horse race). A fearful event happened (e.g. the horse slips and projects the protagonist behind) so that the protagonist's initial joyful emotion changed radically into a fearful emotion after the event. During the judgement epoch, participants had to select the protagonist's emotion (joyful or fearful) after the event (fearful).

Others' Belief stories

Others' Belief stories started with a protagonist with a specific knowledge about a situation (e.g., cookies are in the cupboard). An event happened (e.g., someone moved the cookies from the cupboard into the fridge) so that the protagonist's belief became inconsistent with the real current situation after the event. During the judgement epoch, participants had to select the protagonist's false-belief (cupboard) for half of the trials and the true state after the event (fridge) for the other half.

Photo stories

Photo stories had no protagonist and started with a situation represented in a photo (e.g. apple on a tree), a drawing or a description. An event happened (e.g. the wind blew the apple to the ground), so that the representation became outdated after the event. During the judgement epoch, participants had to select the real current situation (ground) for half of the trials and the outdated one (tree) for the other half.

Others' Joy stories

1) Clara attend un appel de son médecin pour connaître la gravité de sa maladie. Au téléphone, le médecin lui annonce qu'elle est guérie.

   Après cet appel, Clara est... 1) joyeuse 2) angoissée

   Clara is waiting for her doctor's call to know the severity of her disease. On the phone, the doctor announces her that she is healed.

   After this call, Clara is… 1) joyful 2) anxious

2) Louise a l'impression d'avoir raté son permis de conduire. Elle reçoit une lettre de réussite du permis.

   Quand Louise lit la lettre, elle est... 1) joviale 2) épouvantée

   Louise had the impression to have failed her driving license exam. She receives a letter of license success.

   When Louise reads the letter, she is… 1) jovial 2) scared

3) Mélanie s'est commandée une très belle robe pour le jour de son mariage. L'entreprise de livraison est en grève. La veille du mariage, la robe est livrée au domicile de Mélanie.

   Quand Mélanie ouvre le carton et découvre la robe, elle est... 1) comblée 2) terrifiée

   Mélanie ordered a very beautiful dress for the day of her wedding. The delivery company is on strike. The day before the wedding, the dress is delivered to Mélanie's house.

   When Mélanie opens the cardboard and discovers the dress, she is… 1) fulfilled 2) terrified

4) Juste avant un entretien d'embauche important, Justine a une envie pressante d'aller aux toilettes et ne les trouve pas. En allant vers l'ascenseur, elle voit écrit « WC » sur une porte.

   Quand Justine voit « WC », elle est... 1) ravie 2) mécontente

   Just before an important job interview, Justine has a pressing need to go to the toilets but does not find them. When going to the elevator, she sees "WC" written on a door.

   When Justine sees "WC", she is… 1) delighted 2) dissatisfied

5) En partant du travail, Alexandra a oublié son parapluie et voit qu'il pleut alors qu'elle a mis ses nouvelles chaussures payées chères. Un collègue lui propose de la déposer chez elle en voiture.

Quand le collègue lui fait cette proposition, Alexandra est... 1) enchantée 2) apeurée

When going to work, Alexandra forgot her umbrella and sees that it is raining while she is wearing her expensive new shoes. A colleague offers her to drop her off at her place.

When the colleague offers this proposition, Alexandra is… 1) delighted 2) frightened

6) Au cours d'un dîner romantique, Dorothée a l'impression de s'être cassé une dent. En sortant le solide de la bouche, elle découvre une bague de fiançailles cachée par son compagnon.

Quand Dorothée découvre la bague, elle est... 1) heureuse 2) craintive

During a romantic dinner, Dorothy has the impression to have broken one tooth. When taking the solid out of her mouth, she discovers an engagement ring hidden by her partner.

When Dorothy discovers the ring, she is… 1) happy 2) fearful

7) Marie fait du feu en forêt. Le vent l'attise et Marie ne parvient pas à le contrôler. Il se met à pleuvoir.

Quand Marie voit que la pluie tombe, elle est... 1) contente 2) inquiète

Marie is making a fire in the forest. The wind is fanning it and Marie does not manage to control it. It starts too rain.

When Marie sees that it is raining, she is… 1) glad 2) worried

8) Un serpent venimeux s'approche de Céline. Après un coup de bâton, il s'éloigne.

Quand le serpent s'éloigne de Céline, elle est... 1) apaisée 2) paniquée

A venomous snake is getting close to Céline. After a stroke of stick, he goes away.

When the snake is going away from Céline, she is… 1) calmed down 2) terrified

9) Véronique fait un barbecue autour de sa piscine avec des amis et leurs enfants. Un des enfants, encore jeune, glisse, tombe dans la piscine et s'enfonce dans l'eau. Puis il refait surface en nageant.

Quand l'enfant refait surface en nageant, Véronique... 1) est soulagée 2) a peur

Véronique is making a barbecue around her swimming pool with friends and their children. One of the children, still young, slips, falls into the pool and sunks in the water. Then he resurfaces swimming.

When the child resurfaces swimming, Véronique is… 1) relieved 2) afraid

10) Benjamin a l'impression d'avoir brûlé la pizza qu'il est en train de cuire au four pour ses amis. En ouvrant le four, il voit que la pizza est tout juste bien cuite.

Quand Benjamin sort la pizza du four, il est... 1) réjoui 2) effarouché

Benjamin has the impression to have burned the pizza that he is cooking in the oven for his friends. When opening the oven, he sees that the pizza is just well cooked.

When Benjamin takes out the pizza from the oven, he is… 1) glad 2) frightened

11) Le soir, Théo s'aperçoit qu'il lui manque du rouge pour terminer une peinture pour son exposition le lendemain. Il se rappelle alors qu'il avait fait une réserve de peinture rouge dans l'armoire.

Quand Théo se rappelle de la réserve, il est... 1) content 2) anxieux

At night, Théo notices that he is missing some red to finish a painting for his exhibition the next day. He remembers that he did a stock of red painting in his cupboard.

When Théo remembers the stock, he is… 1) happy 2) anxious

12) Carlos a perdu son portefeuille à l'aéroport. Le soir même, la police a retrouvé le portefeuille avec tout son contenu et Carlos est invité à aller le chercher le lendemain.

Quand Carlos reçoit le coup de téléphone de la police, il est... 1) joyeux 2) craintif

Carlos lost his wallet at the airport. The same evening, the police found the wallet with all its content and Carlos is invited to pick it up the following morning.

When Carlos received the police phone call, he is… 1) joyful 2) fearful

13) Matthias s'élance en ski sur une piste raide et se rend compte qu'il ne sait pas encore bien freiner. Après un virage, il voit que la piste est longue et plate, et qu'il va pouvoir s'arrêter.

Après le virage, Matthias est... 1) rassuré 2) inquiet

Matthias is rushing forward on skis on a steep slope and realizes that he does not know well how to break. After a turn, he sees that the slope is long and flat, and that he will be able to stop.

After the turn, Matthias is… 1) reassured 2) worried

14) A la fin de la rédaction de son long rapport, l'ordinateur de Jonathan tombe en panne alors qu'il n'a pas de copie. Le service après-vente du magasin d'informatique réussit à récupérer le rapport.

Quand Jonathan récupère son rapport, il est... 1) enjoué 2) en détresse

At the end of the writing of his long report, the computer of Jonathan breakdowns while he had no copies. The after-sales service of the informatics shop manages to retrieve the report.

When Jonathan retrieves his report, he is… 1) cheerful 2) in distress

15) Charles coupe un arbre avec son frère dans son jardin. L'arbre penche de plus en plus sur la maison. Charles entend son frère l'appeler pour mettre en place un système de cordes qu'il a préparé pour bien diriger la chute de l'arbre.

Quand Charles voit le système de cordes, il est... 1) apaisé 2) oppressé

Charles is cutting a tree with his brother in his garden. The tree is tilting more and more over the house. Charles hears his brother calling him to set up a system of ropes that he had prepared to direct the fall of the tree.

When Charles sees the system of ropes, he is… 1) calmed down 2) oppressed

16) Au cœur de la tempête, Quentin ne voit pas terre et le mât du bateau se brise. La visibilité s'améliore et le port semble proche.

Quand Quentin aperçoit le port, il est... 1) content 2) soucieux

In the heart of the storm, Quentin does not see the land and the mast of the boat is breaking. The visibility improves and the harbor seems close.

When Quentin sees the harbor, he is… 1) glad 2) concerned

17) Pendant sa première audition de théâtre, Thibault a l'impression d'avoir oublié son texte en voyant le grand jury. En quelques secondes, il respire profondément et se rappelle parfaitement de son texte.

Après avoir respiré profondément, Thibault est... 1) détendu 2) peureux

During his first theatre audition, Thibault has the impression to have forgotten his text when seeing the big jury. In few seconds, he takes a deep breath and remembers perfectly his text.

After having taken a deep breath, Thibault is… 1) relaxed 2) fearful

18) Dylan a l'impression d'avoir jeté les clés de la voiture avec la poubelle hier. Sa sœur arrive avec les clés à la main.

Quand Dylan voit sa sœur avec les clés, il est... 1) gai 2) tourmenté

Dylan has the impression to have thrown away his car keys with the trash yesterday. His sister arrives with the keys in her hand.

When Dylan sees his sister with the keys, he is… 1) happy 2) anguished

Others' Fear stories

1) Sylvie est en tête d'une course de chevaux importante et va bientôt franchir la ligne d'arrivée. Brusquement, le cheval glisse et projette Sylvie en arrière.

   Quand Sylvie sent le cheval glisser, elle est... 1) apeurée 2) joyeuse

   Sylvie is at the head of an important horse race and will soon reach the finishing line. Bluntly, the horse slips and throws Sylvie behind.

   When Sylvie feels the horse slipping, she is… 1) frightened 2) joyful

2) Magali dispose des fleurs magnifiques d'une surprise de son amoureux dans un vase précieux. Son nouveau chien ne fait pas attention aux objets et se rapproche du vase.

   Quand Magali voit le chien se rapprocher, elle... 1) a peur 2) est contente

   Magali is placing magnificent flowers from a surprise from her boyfriend in a precious vase. Her new dog does not take care of objects and moves closer to the vase.

   When Magali sees the dog moving closer, she… 1) is afraid 2) is glad

3) Hélène est en train de bercer tendrement son bébé qu'elle trouve très mignon. En le regardant attentivement, elle a l'impression qu'il s'est arrêté de respirer.

   Quand Hélène remarque cette anomalie, elle est... 1) paniquée 2) paisible

   Hélène is rocking gently her baby that she finds very cute. When looking at him carefully, she has the impression that he stopped breathing.

   When Hélène notices this anomaly, she is… 1) terrified 2) peaceful

4) Pendant ses vacances aux tropiques, Marylène se détend dans une splendide mer bleue au milieu de poissons colorés. Elle aperçoit sur la surface l'aileron d'un requin proche d'elle.

   Quand Marylène voit le requin, elle est... 1) horrifiée 2) insouciante

   During her tropical holidays, Marylène is relaxing into a splendid blue sea in the middle of colorful fishes. She sees on the surface a shark fin close to her.

When Marylène sees the shark, she is… 1) horrified 2) oblivious

5) Chantal se divertit devant son film comique préféré dans l'avion. L'avion entre dans des turbulences, semble très instable et le film s'est coupé.

Au moment des turbulences, Chantal est... 1) préoccupée 2) insouciante

Chantal is entertaining herself in front of her favorite comic movie on the plane. The plane goes into turbulences, seems very unstable and the movie stopped.

During the turbulences, Chantal is… 1) worried 2) unconcerned

6) Carole taille ses fleurs dans un coin du jardin. Ils ont poussé lentement et répandent enfin un parfum agréable. Elle voit la porte de sa maison ouverte et des inconnus se déplacer rapidement dedans en emportant des objets.

Quand Carole voit ces individus, elle est... 1) alarmée 2) gaie

Carole is pruning her flowers in a corner of the garden. They grew up slowly and are finally spreading a pleasant perfume. She sees the door of her house opened and unknown persons moving fast inside while taking objects away.

When Carole sees these persons, she is… 1) alarmed 2) merry

7) A son premier concert, Laura chante ses compositions longuement travaillées. Elle perçoit le fruit de ses efforts car elle est acclamée. Suite à un problème technique en plein milieu, le volume diminue et s'éteint.

Quand le volume diminue, Laura est pleine... 1) d'appréhension 2) de joie

At her first concert, Laura is singing her compositions that she had worked on for a long time. She perceives the fruits of her efforts as she is cheered. Because of a technical problem in the middle, the volume diminishes and turns off.

When the volume diminishes, Laura is full of… 1) apprehension 2) joy

8) Christiane fait du surf sur une nouvelle planche dont elle avait envie depuis plusieurs mois. Elle n'arrive pas à suivre une grosse vague, se fait engloutir et emporter.

Quand Christiane se fait engloutir, elle est... 1) effrayée 2) calme

Christiane is surfing on a new surfboard that she was looking for since several months. She does not manage to follow a big wave, is submerged and taken away.

When Christiane is submerged, she is… 1) frighten 2) calm

9) Amandine écoute attentivement un conte. Une belle princesse vit avec ses parents aimants dans son royaume merveilleux. Une méchante sorcière arrive et l'enlève pour lui faire du mal.

Quand Amandine entend parler de la sorcière, elle est... 1) épouvantée 2) soulagée

Amandine is listening carefully to a fairy tale. A beautiful princess lives with her loving parents in her wonderful kingdom. A nasty witch comes and kidnaps her to hurt her.

When Amandine hears about the witch, she is… 1) scared 2) relieved

10) Après une dure journée, Noam se prélasse doucement sur un hamac qu'il a accroché haut à deux palmiers sur la plage. Une corde de soutien du hamac casse et le hamac s'effondre.

Quand la corde casse, Noam est... 1) affolé 2) radieux

After a hard day, Noam is lounging quietly on a hamac that he had hooked up high to two palm trees on the beach. A support rope of the hamac breaks and the hamac falls down.

When the rope breaks, Noam is… 1) distraughted 2) radiant

11) Thomas admire le paysage de soleil couchant pendant son jogging. Des éclairs surgissent dans le ciel et il pleut. La foudre se rapproche de lui rapidement et il voit qu'il a oublié ses clés.

Quand Thomas remarque qu'il a oublié les clés, il a... 1) des frissons 2) le sourire

Thomas is admiring the sunset landscape meanwhile he is going jogging. Bolts of lightnings appears suddenly in the sky and it rains. The lightning gets closer to him and he sees that he forgot the keys.

When Thomas notices that he forgot the keys, he has 1) shivers 2) a smile

12) Luc aime cuisiner pour ses amis. Il a préparé un plat qui sent très bon. En nettoyant son plan de travail, il fait tomber le couteau vers son pied.

Quand le couteau tombe, Luc est... 1) terrifié 2) ravi

Luc likes to cook for his friends. He prepared a dish that smells very good. When cleaning his kitchen counter, he drops the knife towards his foot.

When the knife drops, Luc is… 1) terrified 2) pleased

13) Lucien, passionné de lions, fait un safari et découvre par chance une famille. Il prend des photos impressionnantes en se rapprochant. Un lion le remarque et commence à courir vers lui.

Quand Lucien voit le lion se rapprocher de lui, il est... 1) terrorisé 2) détendu

Lucien, passionate by lions, is doing a safari and discovers by chance a family. He is taking impressive pictures while moving closer. A lion sees him and starts to run towards him.

When Lucien sees the lion getting closer to him, he is… 1) terrorized 2) relaxed

14) Au casino, Nicolas gagne beaucoup d'argent en tirant les bonnes cartes et imagine tout ce qu'il va acheter. Il mise une forte somme et pioche une combinaison de cartes probablement perdante.

Quand Nicolas découvre ses nouvelles cartes, il est... 1) préoccupé 2) tranquille

At the casino, Nicolas is winning a lot of money by pulling the good cards and is imagining everything that he is going to buy. He bets a high sum of money and draws a probably losing card combination.

When Nicolas discovers his new cards. He is… 1) preoccupied 2) relaxed

15) Lucas est à l'aéroport pour le début de son tour du monde rêvé depuis son enfance. A la sécurité, il ne trouve pas son passeport.

Quand il cherche son passeport, Lucas est... 1) stressé 2) riant

Lucas is at the airport for the beginning of his world round trip that he has been dreaming about since childhood. At the security gate, he does not find his passport.

When he searches for his passport, Lucas is… 1) stressed 2) laughing

16) Michel tourne un film près du trottoir avec sa nouvelle caméra et s'émerveille des nouvelles fonctions. Un scooter le frôle à toute allure et il tombe avec sa caméra sur la chaussée.

Quand le scooter frôle Michel, il éprouve de... 1) la crainte 2) l'amusement

Michel is shooting a movie near the sidewalk with his new camera and is amazed with the new functionalities. A scooter brushes past him very quickly and he falls with his camera on the road.

When the scooter brushes Michel, he feels 1) fear 2) amusement

17) Ludovic fait une randonnée au milieu d'un désert de sable. Il apprécie marcher sur du sable en contemplant l'étendue. Voulant boire, il s'aperçoit que l'eau de sa gourde mal rebouchée s'est répandue dans son sac.

Quand Ludovic s'aperçoit que l'eau s'est répandue, il est... 1) effrayé 2) serein

Ludovic is hiking in the middle of a sand desert. He appreciates walking on the sand while contemplating the stretch. Wanting to drink, he notices that the water of his not well recapped flask has spread in his bag.

When Ludovic notices that the water has spread, he is… 1) frightened 2) relaxed

Others' Belief stories

1) Virginie a rangé le chocolat dans l'armoire. Ensuite elle a quitté la pièce. Marc a déplacé le chocolat de l'armoire au frigo. Une demi-heure plus tard, Virginie est retournée dans la pièce.

   Virginie s'attend à trouver le chocolat dans... 1) l'armoire 2) le frigo

   Virginie put her chocolate away in the cupboard. Then she went outside. Marc moved the chocolate from the cupboard into the fridge. Half an hour later, Virginie came back inside.

   Virginie expects to find her chocolate in the... 1) cupboard 2) fridge

2) Susie a parqué sa voiture de sport dans l'allée. En pleine nuit, Paul a déplacé la voiture dans le garage pour garer son monospace dans l'allée. Susie s'est réveillée tôt le matin.

   Susie voit dans l'allée... 1) un monospace 2) une voiture de sport

   Susie parked her red sports car in the driveway. In the middle of the night, Paul moved her car into the garage to make room for his minivan. Susie woke up early in the morning.

   Susie sees in the driveway... 1) a sports car 2) a minivan

3) Jean a dit à Marie qu'il a perdu ses clés. Il est sorti pour chercher dans la voiture. Soudainement Marie voit les clés derrière le canapé.

   Au moment où Marie rentre, Jean... 1) sait... 2) ne sait pas... où se trouvent les clés

   John told Mary that he had lost his keys. The two of them searched the house with no luck. Then Mary went outside to look in the car. Suddenly John noticed his keys behind the sofa.

   By the time Mary comes in, John... 1) knows 2) doesn't know … where the keys are

4) Anne a mis des lasagnes dans le plat bleu. Anne partie, Michel est rentré à la maison et a mangé les lasagnes. Ensuite il a mis des spaghettis dans le plat bleu et l'a remis dans le frigo.

   Anne pense que le plat bleu contient des... 1) lasagnes 2) spaghettis

   Anne made lasagna in the blue dish. After Anne left, Michel came home and ate the lasagna. Then he filled the blue dish with spaghetti and replaced it in the fridge.

   Anne thinks the blue dish contains... 1) lasagna 2) spaghetti

5) Aline est allée au travail à pied. Quand Georges s'est réveillé, il a vu la voiture d'Aline dans l'allée. La chambre d'Aline est calme et sombre. Georges sait que quand Aline est malade, elle se repose dans une chambre sombre.

   En réalité Aline est... 1) allée au travail à pied 2) malade

Aline walked to work today. When George woke up, he saw her car in the drive. Her room was quiet and dark. George knows that when Aline is sick, she lies down in a dark room.

In fact Amy... 1) was sick 2) walked to work

6) Quand Sophie a quitté Martin, il dormait profondément sur la plage. Plus tard, il se réveille et décide d'aller nager.

   Maintenant Sophie croit que Martin est en train de... 1) dormir 2) nager

When Sophie left Martin he was deep asleep on the beach. A few minutes later a huge wave woke him. Seeing that Sophie was gone Jacob decided to go swimming.

Sophie now believes that Martin is... 1) swimming 2) sleeping

7) Les filles ont laissé de la glace dans le congélateur avant d'aller dormir. Pendant la nuit, une coupure de courant dans la cuisine a fait fondre la glace.

   Quand les filles se réveillent elles pensent que la glace est... 1) congelée 2) fondue

The girls left ice cream in the freezer before they went to sleep. Overnight the power to the kitchen was cut and the ice cream melted.

When they get up the girls believe the ice cream is... 1) melted 2) frozen

8) Marc a dit à Andrea qu'il allait faire les boutiques pour s'acheter des sandales. Au magasin de chaussures, Marc a remarqué une paire de bottes et les a achetées au lieu des sandales.

   En réalité le sac de Marc contient des... 1) bottes 2) sandales

Marc told Andrea that he was going shopping for sandals. At the shoe store, Marc noticed a very nice pair of boots on sale, and bought them instead.

Marc's shoestore bag really contains... 1) boots 2) sandals

9) Au zoo, Camille voit le panneau "pingouins" à côté de l'étang. Cette semaine, des flamants roses y séjournent. Jane n'a jamais vu de pingouin ou de flamant rose, et pense que ces oiseaux sont des pingouins.

Les vrais pingouins sont... 1) déplacés 2) à côté de l'étang

At the zoo, Jane sees the sign that says 'penguins'. This week, flamingos are being held in this pond. Jane has never seen penguins or flamingos before, and thinks these birds are penguins.

Real penguins are... 1) black and white 2) bright pink

10) Serge est en train de parler à ses parents de son professeur de mathématiques. Sa mère sort pour aller chercher la lessive et Serge parle maintenant de son professeur de physique à son père.

Quand elle revient la mère de Serge pense qu'il parle de son professeur de... 1) mathématiques 2) physiques

Serge has always liked the snackfood called 'goldfish'. He asked his mother to buy some goldfish when she went to the supermarket. Serge's mother came home with real pet fish.

Serge's mom thought that Serge wanted... 1) real fish 2) snackfood

11) David sait qu'Arnaud n'aime pas les chats. Arnaud est dans le grenier et s'exclame en retrouvant un jouet de son enfance. David entend Arnaud pousser un cri.

David croit qu'Arnaud pense avoir vu... 1) un chat 2) un jouet

David knows that Arnaud is very scared of spiders. Arnaud, alone in the attic, sees a shadow move and thinks it is a burglar. David hears Arnaud cry for help.

David assumes that Arnaud thinks he has seen... 1) a burglar 2) a spider

12) Ce magasin est géré par un faussaire de bijoux très habile; tous les bijoux sont en verre. Denise vient d'y acheter une bague avec une pierre rouge. Elle l'a payée des centaines de francs.

La pierre rouge de la bague de Denise est en... 1) verre 2) rubis

This store is run by a cunning counterfeit jeweler; all the jewels are glass. Denise has just bought a ring here, with a beautiful red stone. She paid hundreds of dollars for it.

The red stone in Denise's ring is... 1) ruby 2) glass

13) Marthe est chargée de réserver un voyage à Malte pour elle et son mari. Sur internet, elle voit une promotion pour la Crête et lui fait une surprise en changeant de destination.

Le mari de Marthe croit qu'ils vont... 1) à Malte 2) en Crête

Marthe is in charge of booking a trip to Malta for herself and for her husband. On the internet, she sees an offer for Crete and makes him a surprise by changing destination.

The husband of Marthe believes that they are going… 1) to Malta 2) to Crete

14) Pendant le sommeil de Jean, son chat est sorti et s'est promené dans la boue.

A son réveil, Jean s'attend à voir son chat... 1) propre 2) sale

During Jean's sleep, his cat went outside and walked in the mud.

When he wakes up, Jean expects to see his cat… 1) clean 2) dirty

15) Amanda a préparé les affaires de skis pour Pierre. Arrivé en haut de la montagne, il s'aperçoit que la neige est verglacée et décide de rentrer pour retrouver Amanda.

Amanda croit que Pierre... 1) fait du ski 2) rentre

Amanda prepared the ski gears for Pierre. Arrived at the top of the mountain, he realizes that the snow is icy and decides to come back to meet Amanda.

Amanda believes that Pierre… 1) is skiing 1) is coming back

16) Une erreur de fabrication a inversé les couleurs d'un test d'alcoolémie et l'erreur n'a pas encore été signalée aux policiers. Lors d'un contrôle, les policiers lisent sur le test que Sandra a bu de l'alcool.

En réalité, Sandra... 1) n'a pas bu d'alcool 2) a bu de l'alcool

A manufacture error has inverted the colors of an alcohol level test and the error has not been signaled yet to policemen. During a control, policemen read on the test that Sandra drank alcohol.

In reality, Sandra… 1) did not drink alcohol 2) drank alcohol

17) Aujourd'hui, l'entreprise accueille un grand groupe de visiteurs. D'habitude, il n'y a personne à la machine à café et Thomas n'a pas à attendre pour prendre son café.

Lors de la pause-café, Thomas va... 1) attendre 2) ne pas attendre

Today, the company is welcoming a group of visitors. Usually, there is nobody at the coffee machine and Thomas does not have to wait to grab his coffee.

During the coffee break, Thomas is… 1) going to wait 2) not going to wait

18) Valentine se fait aborder dans la rue par un garçon et lui donne un faux numéro de téléphone.

Lorsque le garçon appelle, la personne qui répond est... 1) inconnue 2) Valentine

Valentine is approached on the street by a man and gives him a wrong telephone number.

When the man calls, the person who answers is… 1) unknown 2) Valentine

Photo stories

1) On a pris une photo d'une pomme bien mûre sur un arbre. Après quelques instants, un grand coup de vent a fait tomber la pomme de l'arbre.

Sur la photo, la pomme est... 1) sur l'arbre 2) par terre

A photograph was taken of an apple hanging on a tree branch. The film took half an hour to develop. In the meantime, a strong wind blew the apple to the ground.

The developed photograph shows the apple on the… 1) ground 2) branch.

2) Voici un dessin de notre cabane que j'ai fait il y a 3 ans. C'était avant l'ouragan. On en a construite une nouvelle l'été dernier mais on l'a peinte en rouge plutôt qu'en bleu.

La cabane sur le dessin est de couleur... 1) bleue 2) rouge

Here is a drawing she made of the original tree house, three years ago. That was before the storm. We built a new tree house last summer, but we painted it red instead of blue.

The treehouse in the drawing is... 1) red 2) blue.

3) Il y a 3 mois, il y a eu une éruption d'un volcan sur cette île forestière des Caraïbes. Tout ce qui reste sont ces pierres volcaniques. Des photos satellite montrent l'île avant l'éruption.

Sur ces photos satellite, l'île est recouverte de... 1) végétation 2) pierres

A volcano erupted on this Caribbean island three months ago. Barren lavarock is all that remains. Satellite photographs show the island as it was before the eruption.

The island itself is covered in... 1) rock 2) vegetation.

4) Des vieilles cartes des îles près de Tahiti sont affichées au musée Maritime. Depuis, l'érosion a continué son cours et a tout effacé sauf 3 îles.

Près de Tahiti, aujourd'hui il y a... 1) trois îles 2) beaucoup d'îles

Old maps of the islands near Tahiti are displayed in the Maritime museum. Erosion has since taken its toll, washing away all but the three largest islands.

Near Tahiti today there are... 1) three islands 2) many islands.

5) Sargent a peint la berge sud de la rivière en 1885. En 1910 un énorme barrage a été construit, inondant tout le bassin de la rivière, détruisant l'ancienne forêt. Maintenant toute la zone est sous l'eau.

Sur le tableau de Sargent, la berge sud de la rivière est... 1) arborisé 2) inondée

Sargent famously painted the south bank of the river in 1885. In 1910 a huge dam was built, flooding out the whole river basin, killing the old forests. Now the whole area is under water.

In the painting the south bank of the river is... 1) wooded 2) flooded.

6) Ce plan montre le premier étage. Une photocopie a été envoyée hier à l'architecte. Le plan contenait une erreur: la porte de la cuisine manquait. Elle a été rajoutée ce matin.

La photocopie de l'architecte... 1) n'inclut pas... 2) inclut......la porte de la cuisine

This map shows the ground floor plan. A photocopy was sent to the architect yesterday. The map initially had a flaw: the kitchen door was missing. It was added to the map this morning.

The architect's photocopy... 1) includes 2) doesn't include …the kitchen door.

7) Sous l'effet du vieillissement, le projecteur de lumière blanche projette plutôt une lumière beige. La table renvoit du beige uniquement quand elle est éclairée avec ce vieux projecteur.

En réalité, la table est... 1) blanche 2) beige

Because of aging, the white light spotlight is rather projecting beige light. The table is reflecting beige light only when illuminated with this old spotlight.

The table is actually... 1) white 2) beige.

8) Pour détecter les intrus, le laboratoire utilise un système automatique de détection de bruit. Pendant la nuit, dans le laboratoire vide, un courant d'air fait claquer une porte.

En réalité, cette nuit... 1) il n'y avait personne... 2) il y avait quelqu'un......dans le laboratoire

To detect intruders, the lab uses an automated system for recording noise. In the empty lab one night, a door was slammed by a draught.

In fact there was... 1) someone 2) no one …in the lab that night

9) Quand cette photo a été prise, le garçon était à deux mètres et une fontaine à 600 mètres de distance de l'appareil. Sur la photo le garçon a la même taille que la fontaine.

    En réalité, le garçon est... 1) plus petit... 2) plus grand......que la fontaine

When this photograph was taken, the boy in it was two meters away from the camera. The Eiffel tower is beside the boy in the photo; it was about 600 meters away.

In 'real life' the boy is... 1) bigger 2) smaller …than the Eiffel tower

10) Les cartouches d'encre de couleur viennent de se vider, mais l'imprimante a continué à imprimer. Elle a imprimé une image grise d'un jardin verdoyant.

    Sur l'image d'origine, l'herbe est... 1) verte 2) grise

The color printer cartridge just ran out of blue ink, but kept printing without it. It printed a picture of a healthy grass lawn from that screen over there.

In the original picture, the grass in the image is... 1) greed 2) yellow.

11) Cette partie du jardin est censée être réservée aux roses; c'est écrit sur le panneau. Récemment, le jardin tout entier a été envahi par des pissenlits.

    Selon le panneau, ces fleurs sont des... 1) roses 2) pissenlits

This part of the garden is supposed to be reserved for the roses; it's labeled accordingly. Recently the garden has run wild, and dandelions have taken over the entire flower bed.

According to the label, these flowers are... 1) roses 2) dandelions.

12) La biographie décrit la chambre telle qu'elle l'était en 1965. Les murs étaient recouverts d'un papier peint foncé. Ensuite le papier peint a été remplacé par de la peinture couleur crème.

    Dans la biographie, les murs de la chambre sont... 1) foncés 2) clairs

The biography describes the room as it was in 1965. Originally the walls were covered in dark wallpaper. By 1965 the paper had been stripped and replaced with cream paint.

The biography says that the room was... 1) light 2) dark.

13) Un dépliant du parc naturel a été édité quand il y avait un panda dans le parc. Un deuxième panda vient de rejoindre le parc.

Dans le dépliant, il est mentionné la présence dans le parc de... 1) un panda 2) deux pandas

A leaflet of the natural park was edited when there was one panda in the park. A second panda just joined the park.

In the leaflet, it is mentioned the presence in the park of… 1) one panda 2) two pandas

14) L'activité du cerveau d'un patient est enregistrée pour détecter des crises épileptiques, à l'aide d'électrodes placées sur la tête. Après plusieurs jours d'enregistrement, l'appareil est arrêté. Le patient a présenté une crise épileptique quelques heures après cet arrêt.

L'enregistrement de l'activité du cerveau de ce patient montre... 1) un tracé normal 2) une crise épileptique.

A patient's brain activity is recorded to detect epileptic seizures, with electrodes placed on the head. After several days of recording, the machine is stopped. The patient had an epileptic seizure few hours after this stop.

The recording of this patient's brain activity shows… 1) a normal signal 2) a seizure

15) Les journaux d'hier ont indiqué la valeur du franc suisse par rapport à l'euro. Le franc suisse a pris de la valeur ce matin, et égalise la valeur de l'euro.

Ces journaux ont indiqué que le franc suisse a une valeur... 1) plus basse que l'euro 2) égale à l'euro.

Yesterday journals indicated swiss franc value compared to euro. Swiss franc value increased this morning, and equals euro value.

Those journals indicated that swiss franc has a value… 1) lower than euro 2) equal to euro.

16) Le détecteur d'humidité des plantes a envoyé un signal de basse humidité dans l'après-midi. Le jardinier est venu arroser les plantes le soir.

Le détecteur d'humidité des plantes indique actuellement un taux d'humidité... 1) bon 2) bas

The detector of plant humidity sent a signal of low humidity in the afternoon. The gardener came to water the plants in the evening.

The humidity detector currently indicates a level of humidity… 1) good 2) low

17) Un pull en laine est décrit de taille large sur l'étiquette. Lors du premier lavage, l'acheteur s'est trompé de température et a mis une température chaude ce qui rétrécit la laine.

Aujourd'hui, le pull de cet acheteur est de taille... 1) Moyenne 2) Large

A wool sweater is described as large size on the label. During the first washing, the purchaser made a mistake in the temperature and put a hot temperature that shrinks the wool.

Today, the size of the sweater of this purchaser is… 1) Medium 2) Large

18) Un opéra a été enregistré en version classique en 1990. En 2014, un producteur a convaincu le compositeur de reprendre cet opéra en version rock'n'roll et de faire une tournée.

La tournée de cet opéra en 2014 est en version... 1) reprise rock'n'roll 2) originale classique

An opera has been recorded in a classic version in 1990. In 2014, a producer convinced the composer to go back over this opera in a rock'n'roll version and to do a tour.

The tour of this opera in 2014 is a version… 1) rock'n'roll remake 2) original classic

4.2 Influence of Emotions on Pain and Empathy for Pain

Qiao-Tasserit, Emilie, Corrado Corradi-Dell'Acqua, and Patrik Vuilleumier. 2018. "The Good, the Bad, and the Suffering. Transient Emotional Episodes Modulate the Neural Circuits of Pain and Empathy." *Neuropsychologia* (May):1–17.