

Understanding the Social Brain

Neurocognitive effects of experiencing a Social Hierarchy.

Hernando Santamaría-García

TESI DOCTORAL UPF / 2013

Supervisor:

Dra. Nuria Sebastián-Gallés

Center for Brain and Cognition.

Department of Biomedicine



A mis abuelos, Blanca, Hernando y José Buenaventura, a mi tío Héctor Daniel.

A mi abuela Cecilia, por una vida llena de luz.

A Hernando,

A María del Rosario,

A Diego David,

A José Alejandro.

A Verónica.

AGRADECIMIENTOS

Gracias a Nuria Sebastián por esta oportunidad, por su confianza en este proyecto, por su constante respaldo, por su ánimo formativo.

Gracias a Gustavo Deco por su apoyo, y cercanía.

Gracias a Narcis Cardoner a Carles Soriano y a todo el equipo de Psiquiatría del Hospital de Bellvitge. Gracias al equipo de Neuro-imagen de la Clínica del Pilar.

Gracias especiales a Mario Pannuzi, Alba Ayneto, y a Miguel Burgaleta por trabajar y aprender conmigo.

A Adrian Ponce, Mario Pannunzi, Miguel Burgaleta, Marina Martínez, Andrea Insabato, Marco Pereáñez, Alveno Vitale, Alba Ayneto, Laura Démpere, Abeba Roessler, Larissa Albantakis, Gisela Pi, Karla Camacho, Volker Ressel, gracias por su amistad.

Gracias a mis compañeros del Speech Acquisition and Perception, Loreto Nacar, Yu Yin, Anna Bassora, Judith Schmitz, Pallabi Sengupta, Begoña Díaz, Ansgar Endress. Gracias a Albert Costa, Luca Bonatti, Salvador Soto, Juan Manuel Toro. Gracias a Fátima Vera, Alice Foucart, Manuela Ruzzoli, Matilde Fort, Xavier García, Cristina Baus, Carlos Romero, Paola Crespo, Ruggero Bettinardi, Sancho Moro, Emanuel Biau, Cristina Galusca, Panagiota Theodoni, Tristan Nakagawa, Tim Masquelier, Miguel Lechón, Julia Montes, Marco Calabria, Daniela Martínez, Nicolo Cesana, Francesca Branzi, Alexis Pérez y a todos los chicos del Center for Brain and Cognition. Un especial agradecimiento a Xavi Mayoral, a Silvia Blanch, a Cristina Cuadrado y a Florencia Nava por acudir y rescatarme de problemas.

Gracias a mis amigos en Barcelona, al escritor Leonardo Valencia, a Juan Pablo Ramírez Mahaluf, a Víctor Alarcón, Roberta Bertuccia, Alfredo Guzmán y a todo el equipo de contrabando radio. Gracias a José Miguel Méndez, Dussan Tomic, Miguel Pereira, David González, Alfonso de Lucas Buñuel y a todos a los chicos de la escuela de cine. Gracias Barcelona.

A Diego Santamaría-García, José Santamaría-García, Hernando Santamaría-Lozano y Scharito García-Bonilla, gracias por apoyarme y también claro, gracias por esperarme.

Gracias a mis amigos de toda la vida, tan cercanos a pesar de la distancia. Gracias a Verónica Salazar, por estar ahí, siempre. Gracias por acompañarme a aprender el valor de las ideas y de los sueños.

SUMMARY

The present research is aimed at analyzing how human's brain jointly computes cognitive and social interactions in presence of implicit social stimuli and/or in presence of socially neutral stimuli. First we analyzed the electrophysiological and neuroanatomical substrates involved in recognizing of explicit hierarchical stimuli. We observed that an early recognition of the social hierarchy that it is mediated by the morphology of a network of brain areas involved in automatic processing of social stimuli. Second we showed that social context modulates the early stages of processing of socially neutral stimulus including a visual discrimination task and a sentence comprehension task. Finally, we explored the impact of the social context in patients with recognized social sensitivity, as is the case of Obsessive Compulsive Disorder (OCD) patients. Crucially, we observed selective modulations of social context on the core cognitive processes involved in physiopathology of the OCD. Taken together, the studies presented in this dissertation provide new insights on how cognitive processes and social information interact.

RESUMEN

En la presente investigación analizamos la manera en la que el cerebro humano procesa la interacción entre procesos cognitivos y sociales, bien sea en presencia de estímulos socialmente implícitos y/o en presencia de estímulos socialmente neutros. Primero, hemos estudiado los sustratos electrofisiológicos, y neuroanatómicos implicados en el reconocimiento de estímulos socialmente implícitos. Mostramos un reconocimiento temprano de la jerarquía social, mediado por la morfología de una red de áreas cerebrales implicadas en el procesamiento automático de los estímulos sociales. Segundo, mostramos que el contexto social modula los estados tempranos del procesamiento de estímulos neutros, incluyendo en una tarea de discriminación visual, y una tarea de comprensión de oraciones. Finalmente, hemos explorado el impacto del contexto social en pacientes con una reconocida sensibilidad social, como es el caso de los pacientes con Trastorno Obsesivo Compulsivo. De forma crucial, encontramos que el contexto social modula selectivamente los procesos implicados en la fisiopatología del TOC. En conjunto, los estudios que presentamos en esta tesis aportan nuevos conocimientos en el estudio de cómo interactúan los procesos cognitivos con la información social.

PREFACE

Seminal works in Social Psychology suggested that social factors can deeply modulate cognitive processes. In the middle of the XX-th century, studies in Social Psychology reported that the presence of a social context can influence behaviour and mental processes in fellow individuals (Festinger & Hutte, 1954; Zajonc, 1965). (Festinger & Hutte, 1954) showed that comparing yourself to others, especially upward comparisons, favours self-improvement but also self-knowledge, an effect known under the name of social comparison process (Festinger & Hutte, 1954).

In the sixties (Zajonc, 1965) reported that in the presence of a social group, individuals can increase their performance, in particular, in motor tasks (Zajonc, 1965). This phenomenon was called social facilitation. These initial findings have been supported by more recent studies expanding social facilitation effects in other cognitive processes such as attention modulation and decision-making tasks. (Adler, Epel, Castellazzo, & Ickovics, 2000a; Amodio & Frith, 2006; Carver & Scheier, 1981; Frith & Frith, 2012). There are even studies supporting that the sole presence of others or the belief that one is being observed by others can induce changes in the brain mechanisms involved in decision-making processes. A watching pair of eyes, even if only in a photograph, is sufficient to increase pro-social behaviour (Amodio & Frith, 2006; Bateson, Nettle, & Roberts, 2006; Frith & Frith, 2012; Izuma, Saito, &

Sadato, 2010; Singer, Kiebel, Winston, Dolan, & Frith, 2004). In general, these studies have postulated that humans increase their level of self-attention / vigilance in the presence of other individuals and thus, they can adapt their behaviour to expected goals.

A recent article in child research suggests that this type of social effect is deeply rooted in our cognitive system. (Kovacs, Teglas, & Endress, 2010) showed that even in infants as young as 7 months, the mere presence of an external social agent automatically triggers powerful processes of belief computation that may be part of a “social sense” crucial to human societies (Kovacs et al., 2010).

All this evidence is suggesting that cognitive systems integrate social information and support the notion that cognition is mediated by the context (for a further review see (Amodio & Frith, 2006; Bateson et al., 2006; Carver & Scheier, 1981; Frith & Frith, 2012; Izuma et al., 2010; Singer et al., 2004; Zajonc, 1965)).

We consider that this evidence gives us enough background to support the assumption that a social construct can modulate different cognitive processes. However, so far it is unclear how this interaction takes place. Cognitive and social information could interact in different types of architectures. On the one hand, it might be that both types of information are processed in parallel. For this type of functional architecture, we would expect the neural networks to be quite independent and to interact only during the last steps of neural processing. On the other hand, another possible type of architecture could have the two types of

information interact from the onset. In this case, even in the early stages of processing, both types of information would influence each other. In any case, we cannot rule out the possibility that the interplay and permeability between both types of information may differ depending on the type of computation/process being performed. For instance, social processing in economic games could be integrated to other cognitive computations during decisional phases. In contrast, recognizing social threats, which could be considered to be a more automatic and biologically determined process, could be integrated during the earlier stages of processing.

The main objective of this dissertation is to test the hypothesis that there is an interaction between cognitive and social mechanisms even in "low-level" (early stages) processes. Up to this day, these processes have been considered less susceptible to social influences.

In this dissertation, we make use of social hierarchy to investigate the influence of social mechanisms on different cognitive processes. One of the most important social organizations with documented neurobiological influences is the establishment of hierarchical structures (Cummins, 2000; Ridgeway, 2006). Social organizations as the social hierarchy are crucial to survival, reproduction, and care for offspring and genetic legacy. Recent studies in social cognition and social neuroscience have shown neural correlates for the establishment of social hierarchy in different species, including humans. However, the specific

influence of social hierarchy on the regulation of cognitive processes remains relatively unexplored.

The present dissertation comprises six chapters. First in the introduction, we will review several studies and provide a state-of-the-art summary of the literature in the field of social hierarchy, on which our research is based. In this section, we will present a series of studies on how social hierarchies are built and what is their influence on the social functioning of a group. Furthermore, we will review studies in this field that assessed the neural basis of recognizing social status, as well as other studies focused on analyzing the neural basis of experiencing social hierarchy. Finally, we will present the general experimental procedure that we used to build the social context (social hierarchy). In the chapter two, a study on the neuroanatomical correlates underlying the process of perceiving implicit hierarchical social features by combining Event related Potentials (ERP) and structural magnetic resonance imaging (MRI) data is presented. In the third chapter, a study evaluating the influences of social context on the processing of socially neutral stimuli (visual discrimination task) is presented. In this study, we analyzed how the brain computes social influences on perceptual decision-making processes. In the chapter fourth, a study analyzing how language is processed depending on the social status of speaker is presented. Particularly, we evaluated if the social rank of a speaker could influence how listeners process and understand a socially neutral verbal message. In the fifth chapter, an investigation exploring the interplay between social and

cognitive processes in a context cognitively and socially altered as in the case of mental disorders is presented. More specifically, we analyzed how patients with Obsessive Compulsive Disorder process social hierarchy and how this social factor modulates different cognitive processes. Finally, in the last chapter I present a general discussion of this dissertation and the future directions proposed for this research.

TABLE OF CONTENTS

Summary	vii
Preface	xi
1. Introduction	
Recognizing and experiencing social hierarchies	19
1.1. Studies evaluating how/when hierarchical features are recognized	20
1.2. Studies evaluating biological effects of experiencing social hierarchy	24
1.3. Research strategy.....	28
2. Chapter two	
Neuro-anatomical substrates of recognize social hierarchy in humans. A simultaneous ERP and MRI study.....	31
3. Chapter three	
The role of social hierarchy on perceptual processes.....	59
4. Chapter four	
Effects of speaker's social hierarchy on sentence comprehension process	97

5.	Chapter five	
	Social hierarchy tunes performance monitoring and cognitive control in Obsessive Compulsive Disorder.....	133
6.	Discussion	167
	6.1. Summary of findings	168
	6.2. Towards an integrated conception of cognitive and social information.....	172
	6.3. Future directions.....	176
7.	References	181

1. INTRODUCTION

Recognizing and experiencing social hierarchies

“Sense of one’s place guides the occupants of a given social space towards the social positions adjusted to their properties, and towards the practices or goods which befit the occupants of that position.”

(Bourdieu Pierre, *Distinction*:

A Social Critique of the Judgement of Taste 1984. p. 466)

Social hierarchy is an ubiquitous principle of social organization across an extensive variety of animal species (ants, fish, birds, human and non-human primates) (Cummins, 2000; R. M. Sapolsky, 2004; R. M. Sapolsky, 2005). Hierarchical structures are crucial for regulating biological processes involved in survival, reproductive success, health, motivation, and, obviously, social behaviour (Adler & Ostrove, 1999; Adler, Epel, Castellazzo, & Ickovics, 2000b; Cummins, 2000; Ridgeway, 2006; R. M. Sapolsky, 2004; R. M. Sapolsky, 2005). Moreover, social hierarchies allow the stabilization of roles in a group by reducing risks and optimizing resources (Ridgeway, 2006).

From an evolutionary point of view, it has been proposed that species develop social hierarchies because of biological adaptation. These assumptions are based on Darwin’s theory of evolution, as presented in his book, ‘*On the Origin of Species by Means of*

Natural Selection, or the Preservation of Favoured Races in the Struggle for Life' (Darwin C, 1859). In this text, the author proposed that only certain gens of particular species are selected for survival. An important factor in the selection of those genes is, in fact, social hierarchy. The natural selection of genes of high-status members of a group has allowed species to adapt to threats in their environment (Adolphs, 2009; Amodio & Frith, 2006; Cummins, 2000; Ridgeway, 2006). Studies in animals have supported that a process of early and spontaneous recognition of hierarchical cues takes place in different species: ants and bees are able to recognize social status of their conspecifics from their appearance; fish can infer social rank by observation alone (Grosenick, Clement, & Fernald, 2007) and birds and primates infer social status from non-verbal cues such as eye gaze and body posture (Deaner, Khera, & Platt, 2005; R. M. Sapolsky, 2004; R. M. Sapolsky, 2005). Spontaneous recognition of social hierarchy across species suggests the existence of general biological mechanisms modulating the presence of social hierarchies.

1.1 Studies evaluating how/when hierarchical features are recognized

Consistent with the view of a biological origin for social hierarchies, there is evidence that humans spontaneously perceive hierarchical

patterns and as early as 15 months of age (Boyce, 2004; Cummins, 2000). (Mascaro & Csibra, 2012) found that toddlers are able to recognize dominant and submissive patterns in the interaction between two agents. These authors found that children understand these dominant or submissive characteristics to be stable attributes of a relationship, rather than internal attributes of the agents. They proposed that social dominance in human infants belongs to a “naïve sociology” mechanism. It is conceptual in nature and, thus, it forms part of an abstract representation of social life (Mascaro & Csibra, 2012). Thus social hierarchy is deeply rooted in humans both philo- and ontologically.

Humans make use of a highly sophisticated and complex collection of cues to convey information about social hierarchy. An array of physical features such as body size, facial shape, gender, age and attire (Van Berkum, van den Brink, Tesink, Kos, & Hagoort, 2008) can spontaneously convey implicit hierarchical features. At the behavioural level, body postures, facial cues (e.g., eye gaze) and vocal calls can also communicate rank and convey expectations about social behavior (Cummins, 2000; Foulsham, Cheng, Tracy, Henrich, & Kingstone, 2010; Galinsky et al., 2006; Galinsky, Magee, Inesi, & Gruenfeld, 2006; Huang, Galinsky, Gruenfeld, & Guillory, 2011; Oosterhof & Todorov, 2008; Todorov, Said, Engell, & Oosterhof, 2008; van Berkum, Zwitserlood, Hagoort, & Brown, 2003). On top of these likely biologically determined cues, humans also convey social hierarchy by means of culturally determined

traits. Multiple external and abstract representations such as mathematical or military symbols (as the number of stars or their size) also act as symbolic expressions of social hierarchy (Zink et al., 2008). As far as it seems, the process of judging an individual's status shares conceptual mechanisms with mental representations related to magnitude comparisons (Chiao et al., 2008; Chiao, 2010). Specifically, the knowledge of these representations in all domains is spatial, and symbolic (Chiao, Bordeaux, & Ambady, 2004; Chiao et al., 2009; Schubert, 2005).

The processing of indicators conveying information about social hierarchy must occur very rapidly and in a highly efficient way. The ability to deduce one's own status and the status of others is crucial for social interactions. These interactions require individuals to express and recognize social status signals. How individuals interpret these signals impacts implicit expectations and actions that consequently drive their social behaviour (Adler, Epel, Castellazzo, & Ickovics, 2000a; Cummins, 2000). Different studies have shown that the recognition of social hierarchy cues can occur within milliseconds after the appearance of the stimulus. For example, Chiao et al. (Chiao et al., 2008) showed that inferences of social dominance and submissive cues from facial expressions can occur within 170 ms after the stimulus onset, suggesting the existence of an early and automatic integration of this kind of social aspects (for a more thorough review of automatic social

processes see (Adolphs, 2009; Frith & Frith, 2012; Lieberman, 2007)).

Different studies have also provided evidence of a dedicated brain network responsible of recognizing social hierarchy in humans (Zink et al., 2008). In this article, the authors measured changes in the blood-oxygen-level-dependent (BOLD) signal when participants were viewing only pictures of other (simulated) players with a different hierarchical status. They found different brain activations when people saw photographs of individuals with a different social status. Brain activations were significantly higher in networks such as the occipital and parietal cortices, the ventral striatum, and the para-hippocampal cortex when participants saw the superior player's photograph. Furthermore, in this study the authors also employed a non-social experimental paradigm (see (Spitzer, Fischbacher, Herrnberger, Grön, & Fehr, 2007) for a similar paradigm), where the other human players were replaced by two computers. They confirmed several unique and dissociable activations in other areas, clearly distinguishing the social paradigm from the non-social paradigm. The specific activations observed only in the social paradigm were in the dorso-lateral prefrontal cortex (DLPFC), amygdala, thalamus, posterior cingulate cortex, and medial prefrontal cortex (MPFC). These effects have been corroborated by a recent study (Kumaran, Melo, & Duzel, 2012) showing a specificity for humans' social hierarchies in the neural activity in the amygdala. As it seems,

linear structure of both social and non-social hierarchies could be represented at different neural levels, particularly in the hippocampus.

Similarly, (Chiao et al., 2008) reported the neural correlates underlying the process of dominance and submissive positions recognition. The occipitotemporal, the fusiform and the lingual gyri, as well as the anterior portion of the superior temporal gyrus are involved in bodily and facial hierarchical recognition. They suggested that, activity within the fusiform gyrus, as well as in the posterior regions of the superior temporal gyrus increases in response to direct or mutual eye gaze, which is another well-known indicator of dominance (Chiao et al., 2004; Chiao et al., 2008; Chiao et al., 2009; Chiao, 2010). Important to our current goals, the studies just described also showed neural modulations in brain areas dedicated to process sensory and perceptual stimuli.

1.2 Studies evaluating biological effects of experiencing social hierarchy.

As said above, there are subsequent consequences related to the recognition of hierarchical features; in particular, recognizing hierarchical features can modify roles and behaviour, and in turn, can lead individuals to experience a hierarchical role themselves (Chiao et al., 2004; Chiao et al., 2008; Chiao et al., 2009; Chiao,

2010). Thus, when an individual recognizes another one's position, they are also identifying their own position (Zink et al., 2008). Two different strands of research have investigated the consequences of experiencing a specific hierarchical role: the neurobiological tradition and the neurocognitive approach.

There is solid evidence linking social hierarchy and health, morbidity and welfare (Adolphs, 2009; Amodio & Frith, 2006; Boyce, 2004; Cummins, 2000). Indeed, the neurobiological effects of experiencing specific social hierarchies can be observed in the modulation of different types of neurotransmitters. These studies even postulate that social hierarchy is responsible for the modulation of normal concentrations of serotonin and dopamine, its receptors and its precursors (Lesch et al., 1996; Moskowitz, Pinard, Zuroff, Annable, & Young, 2001; Nader et al., 2012; Schaechter & Wurtman, 1990). Similar studies have supported that experiencing a social status can also impact in modulating other neuroendocrine processes (Mehta, Jones, & Josephs, 2008; Mehta & Beer, 2010; Meyer-Lindenberg, Domes, Kirsch, & Heinrichs, 2011). Social status modulates automatic stress mechanisms regulated by cortisol release (Mehta et al., 2008) (Sherman et al., 2012); additionally social status can modulate basic hypothalamic neuropeptides as oxytocin, vasopressin and hormonal-modulators as testosterone (Mehta et al., 2008; Mehta & Beer, 2010; Meyer-Lindenberg et al., 2011).

Numerous studies have also provided evidence of the relevance of experiencing a social position on cognitive processes such as attention and executive function. Previous studies, have shown that high status individuals in many species receive more attention than low status individuals (Cummins, 2000; R. M. Sapolsky, 2004; R. M. Sapolsky, 2005). In 2010 (Foulsham et al., 2010) used eye tracker to show that humans gazed at high-status individuals much more often, and for longer periods than at low-status individuals. Regarding the effect of social status on the executive function, different studies showed how powerful individuals have advantages in distinguishing between what is and what is not goal-relevant in the environment (Boksem, Kostermans, & De Cremer, 2011; Boksem, Ruys, & Aarts, 2011; Boksem, Kostermans, Milivojevic, & De Cremer, 2012; Muscatell et al., 2012; Smith, Dijksterhuis, & Wigboldus, 2008; Smith, Jostmann, Galinsky, & van Dijk, 2008). In contrast, powerless individuals have difficulty distinguishing which is the relevant goal. Individuals in powerless roles have difficulties updating, inhibiting, planning and in performing other types of goal-directed tasks (Smith et al., 2008). (Boksem et al., 2012) also found that social status has an impact on how people monitor their environment and their performance. Using Event Related Potentials (ERPs), these authors found that while high-status individuals are more focused on rewarding outcomes, low-status subjects are more predisposed to processing outcomes in terms of potential threat and loss. These predispositions in low-status subjects may help maintain a stable

social hierarchy (Boksem et al., 2011; Boksem et al., 2011; Boksem et al., 2012).

Summarizing, there is at present evidence showing the existence of a dedicated brain network involved in the recognition (and representation) of human social hierarchies. There is also evidence showing the consequences of experiencing a specific social status on some cognitive domains, mostly related to the executive system. As we said above, the studies on the neural substrates of the recognition of human social hierarchies also showed a modulation in sensory-perceptual brain areas (occipital and parieto-occipital). These modulations, together with the early social effects reported by (Chiao et al., 2008) in face recognition (in the N170 ERP component) argue in favour of an early modulation of sensory-perceptual cognitive processes by social hierarchies. However, these early effects have been observed only for human faces. There is ample literature showing that human faces, likely because of evolutionary need, benefit from a special processing. Therefore, it is totally unknown how (and when) social information can affect the processing of socially neutral information. In this dissertation, we will investigate the hypothesis that social information shapes in a significant way different types of socially neutral information.

1. 3 Research strategy

It is well known that in everyday life, different hierarchical scenarios exist. It is clear that not only the presence of a relationship between a child and adult can create hierarchical social roles; we can consider other cases, such as the relationship between employees and their superiors, or the one between teachers and students.

As just said, the central goal of this dissertation is to investigate the influence of social hierarchies in the processing of socially neutral information. Therefore, our research strategy should be based on an experimental paradigm where stimuli would not intrinsically involve social information. That is, stimuli should be neutral and social information should be provided by the context where the stimuli appeared. To this purpose, we have adapted the procedure used by (Zink et al., 2008).

In our setting, the social hierarchy has been established through the online comparisons established by participants in relation to other simulated individuals, depending on their skills in a difficult visual discrimination task. Participants compared their performance on the task with one of the two other simulated players (of the same gender as the participant), one with a fixed superior rank (superior player) and the other with a fixed inferior

rank (inferior player) with respect to themselves. Thus, participants compared their performance with a highly skilled player (Superior simulated player) and with a lowly skilled player (Inferior simulated player). Furthermore, to reinforce features associated to social hierarchy, before the game, participants also saw brief video clips where the same simulated players described some social status features. These videos contained social and academic achievements consistent with the rankings in the game of the simulated players.

The game was not competitive in nature, mainly because we did not want performance on the task to be directly affected by outcomes of the simulated players. In fact, participants and the simulated players could win and lose in the same trial. The whole structure of this experiment was designed to increase participants' feeling of being involved in a realistic game and also to boost their motivation (for instance, participants were told that they would be invited to produce their own "video presentation" at the end of the session, that might be used with other participants).

In sum, we consider that this experimental paradigm allow us evaluate in a controlled way the cognitive processes related to perceive hierarchical social features and also the cognitive operations modulated by experience a role in a social hierarchy. Importantly, this way to build social hierarchy can reflects effects of a new social hierarchy, therefore it can inform us about how fast

and deep social hierarchy can modulate different cognitive operations. Further chapters will describe these modulations in cognitive process.

2. CHAPTER TWO

Neuroanatomical markers of social hierarchy recognition in humans. A combined ERP - MRI study.

Hernando Santamaría-García*; Miguel Burgaleta*; and Nuria Sebastián-Gallés

*These authors have equally contributed to this research.

This article has been submitted for publication to Current Biology (November 2013)

2.1 Abstract

Social hierarchy is a ubiquitous principle of social organization across an extensive variety of animal species. Although some progress has been made to understand how humans infer hierarchical identity, the neuroanatomical basis for perceiving key social dimensions of others remains relatively unexplored. Here, we combined Event Related Potentials (ERP) and structural Magnetic Resonance Imaging (sMRI) to reveal the cortical and subcortical anatomical substrates of early recognition of social hierarchies. We designed a covertly simulated hierarchical setting where participants performed a task either with a superior or with an inferior player. When presented with a picture of the superior

player (accompanied by three stars to confer higher rank), participants showed higher amplitude in the N170 component (usually associated to face processing) than when presented with a picture of the inferior player (one star, conferring lower rank). Crucially, the magnitude of this effect significantly correlated with brain morphology, estimated by means of surface-based morphometry and shape analysis. Our main result revealed a cortico-subcortical network, linked to the hierarchy effects over the N170 component, which comprised brain regions involved in perceiving social identity. This combination of ERP and MRI data provides a unique way for understanding the neuro-anatomical substrates of social hierarchy recognition in humans.

2.2 Introduction

Many animal species tend to display a hierarchical organization of individuals. Perception of cues depicting social hierarchy is biologically determined and is key in regulating survival, reproductive success, health, motivation, and social behaviour (Amodio & Frith, 2006; Boyce, 2004; Cummins, 2000; Ridgeway, 2006; R. M. Sapolsky, 2004). In humans, social hierarchy refers specifically to the ranking of individuals within a group as a function of power, prestige, social status, and resources (Cummins, 2000; Ridgeway, 2006). Hierarchical patterns are spontaneously

perceived very early in development (Boyce, 2004) and, as it is the case in other species, the ability to successfully recognize the social status of other individuals is a crucial skill that drives human interactions.

An array of physical features such as body size, facial shape, gender, age and attire can spontaneously convey implicit hierarchical features. At the behavioral level, body postures, facial cues (e.g., eye gaze) and vocal calls can also communicate rank and convey expectations about social behaviour (Foulsham et al., 2010; Oosterhof & Todorov, 2008; Van Berkum et al., 2008). Nevertheless, knowledge about how the brain perceives and processes such hierarchical cues is limited. ERP studies in humans have shown that social status is inferred as early as 200 ms after stimulus onset, when face processing takes place (Chiao et al., 2008). Furthermore, a network of brain regions sensitive to social cues appears to be consistently identified by functional brain imaging studies. This network includes the fusiform cortex, superior temporal gyrus/sulcus, intraparietal sulcus, ventromedial prefrontal cortex, and the basal ganglia (Chiao et al., 2008; Farrow et al., 2011; Golby, Gabrieli, Chiao, & Eberhardt, 2001; Grill-Spector, Knouf, & Kanwisher, 2004; Todorov, Mende-Siedlecki, & Dotsch, 2013; Zink et al., 2008).

In this vein, a current perspective in social neuroscience differentiates between controlled and automatic processes for integrating social information (Adolphs, 2009; Frith & Frith, 2012;

Lieberman, 2007). Automatic processes are related to activity in a set of dorsal network areas comprising superior temporal gyrus/sulcus, intraparietal sulcus, posterior cingulate cortex, anterior ventral temporal cortex and subcortical structures (ventral striatum, caudate, amygdala and hippocampus). In contrast, more controlled processes have been associated to activity in a set of frontal network areas such as prefrontal cortex, orbitofrontal cortex and anterior cingulate cortex (Adolphs, 2009; Frith & Frith, 2012; Lieberman, 2007).

In the present study we moved one step forward by focusing on how brain morphology correlates with hierarchy perception. Structural MRI-based morphometry techniques allow for neuroanatomy characterization at high resolution, and different metrics can be used to infer associations between cognitive measures and microstructural features of the gray matter. However, a major methodological issue is to obtain a fine-grained index that appropriately measures one's ability to perceive social status. High temporal sensitivity is necessary, given that cognitive processes involved in the hierarchy perception take place very early after stimulus onset, and during reduced time windows (200 ms; (Chiao et al., 2008)). For this reason, here we combined event-related potentials (ERP) and structural MRI, an approach that allowed us to a) assess individual differences in fine-grained temporal dynamics of hierarchy perception, and b) investigate the neuroanatomical correlates of such individual differences. In other

words, the magnitude of hierarchy-elicited effects over an ERP component can be linked to between-subjects variations in brain morphology, thus revealing with great detail the neuroanatomical basis of status perception. This method has the clear advantage of combining the high temporal resolution of ERP with the high spatial resolution of sMRI, and has been successfully used by others to study mainly higher-order cognition processes (Fjell, Walhovd, Fischl, & Reinvang, 2007; Ford et al., 1994; Walhovd et al., 2005; Westlye, Walhovd, Bjornerud, Due-Tonnessen, & Fjell, 2009). In addition, because of their low temporal resolution, fMRI studies may not be sensitive to those early processes identified by ERPs, but rather to later, protracted and/or compound processes involved in the hierarchy perception. Therefore, our approach is not only optimal to study the neuroanatomical substrates of status perception, but it also makes possible to better understand what brain regions are relevant for early, rapid processing of social hierarchy –a research question that cannot easily be answered with other approaches.

To achieve this we built an experimental social hierarchy following a similar procedure as (Zink et al., 2008) (see Fig. 1). Participants had to perform a difficult visual discrimination task with two covertly simulated players (of the same gender as the participant), one with a fixed superior rank (superior player, SP), and the other with a fixed inferior rank (inferior player, IP) with respect to the participant. To measure how participants perceived social status in

others, at each trial, ERP data were recorded while participants saw a photograph of either SP or IP and an explicit mark depicting social status: three stars for SP and one star for IP. We expected status-related differences (i.e., subtracting SP minus IP) in ERP components around 200 ms, roughly coinciding with the “face-selective” N170 component (Anaki, Zion-Golumbic, & Bentin, 2007; Eimer, 2011). However, we did not discard presence of effects related to social hierarchy in early ERP components as C1 (75 ms) or P100 (100-150ms) which can reflect a modulation of sensory - perceptual components (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Di Russo et al., 2012).

To characterize cortical morphology we applied surface-based morphometry and obtained two independent morphometric indices: cortical thickness (CTh) and cortical surface area (CSA). It has been proposed that CTh is sensitive to the amount of neuronal bodies, glial and capillary support, and dendritic arborization, whereas CSA may be related to the number and spacing of minicolumnar units of cells (Chklovskii, Mel, & Svoboda, 2004; la Fougere et al., 2011; Rakic, 1988; Thompson et al., 2007). Further, subcortical gray matter was investigated by means of subcortical shape analysis (Patenaude, Smith, Kennedy, & Jenkinson, 2011), a methodology that has been used mainly to study regional differences in subcortical morphology of patients diagnosed with Alzheimer’s disease, schizophrenia, Parkinson’s disease, or obsessive compulsive disorders (Chklovskii et al., 2004; la Fougere

et al., 2011; Qiu, Younes, Miller, & Csernansky, 2008; Thompson et al., 2007; Xu et al., 2008). This technique allowed us to investigate local variations, independent of global brain size, in the shape of caudate nucleus, nucleus accumbens, globus pallidus, putamen, thalamus, hippocampus and amygdala.

Based on the available fMRI evidence, we hypothesized significant associations between hierarchy-modulated ERP indices and the morphology of brain areas sensitive to social cues, namely, the fusiform cortex, superior temporal gyrus/sulcus, intraparietal sulcus, and the striatum (Chiao, 2010; Kumaran et al., 2012; Ly, Haynes, Barter, Weinberger, & Zink, 2011; Zink et al., 2008). Further, because we expected early modulations of salient hierarchical cues over ERP components, we hypothesized the involvement of automatic processing areas, but not of controlled processing regions (such as dorso lateral prefrontal cortex, orbito frontal cortex, among others; see (Lieberman, 2007)).

2.3 Methods

Participants

Twenty two right-handed participants (11 females) took part in this study. They were undergraduate students recruited at the Universitat Pompeu Fabra (Spain). Mean age was 23.39 (SD = 2.4 years; age range = 18–27 years). Participants were invited through an open call, voluntarily participated and received 10 Euros per

hour. All participants reported normal visual accuracy and none reported psychiatric or neurological conditions. Participants gave their informed consent prior to inclusion in the study, which conforms to the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Materials and Procedure

To build the hierarchical social context we implemented a procedure that has been proved successful in previous studies (Santamaría-García et al., 2013; Zink et al., 2008). We used brief samples of profile videos to establish initial hierarchical features followed by an interactive game to maintain the social hierarchy, where participants performed a visual discrimination task in presence of other (simulated) players. A schematic for the whole experiment design is depicted in Figure 1.

Profile videos. We created eight different videos (approximately 2 min each) depicting simulated players' profiles. The profiles crossed gender (male, female) and hierarchy (high, low status), and were interpreted by four confederates (two males, two females, 25 years old approximately). Each confederate followed two scripts in which personal, work and academic achievements of the characters were presented (Superior player reported many successes in the professional, academic, business and social fields, in contrast Inferior player reported low education, few job opportunities and social difficulties). Implicit cues related to social

superiority of the confederates were controlled to avoid substantial differences of age, facial expressions and attire.

Simulated game. Social Hierarchy was established based on simulation of performance in a difficult visual decision task through a computerized game following procedure of (Santamaría-García et al., 2013; Zink et al., 2008). In this game, participants played a visual discrimination task at the same time than one out of two simulated players. One of the simulated players performed, on average, better than the participant (superior player, SP) and through different manipulations consistently held a high rank status (for a more detailed description see (Santamaría-García et al., 2013; Zink et al., 2008)). The other simulated player performed worse and thus had a lower rank. Importantly, the same confederates previously displayed in social videos had a high or a low rank in the phase of game. Profiles of confederates (Superior and Inferior) were counterbalanced across participants. In each trial, after participants performed the visual task, feedback of their own performance, along with that of the simulated player, was displayed on the screen.

Hierarchical stimulus. At the beginning of every trial, we displayed a photograph of the simulated opponent with its corresponding ranking stars (three stars for SP and one star for IP). In the photograph, the simulated player maintained a neutral position and the gaze to the front. In our analyses we focused on these hierarchical stimuli.

Visual decision task. On a black background, we presented two rectangles of red dots, one at the top of the screen and the other at the bottom. Participants were situated approximately 50 cm in front of a 19-inch screen with an angle of vision of around 35°. All dots had the same diameter, shape and brightness. Each rectangle had a different percentage of red dots with over 1,000 dots in total. The percentage of red dots was complementary between the rectangles (e.g., if one had 49% of the dots, the other had 51%; see Fig. 1a). In every trial, we displayed screenshots of each rectangle with nine levels of dot percentages (44, 46, 48, 49, 51, 52, 54, 56)

Procedure. To control for possible interactions between gender and hierarchy, male participants played with male simulated participants, and female participants with female simulated players. Participants were first informed they would play a game based on a visual discrimination task, and were then notified that their performance would be compared with that of two players who had already completed the task and that the three players would be ranked according to their performance during the game. Participants were told that their performance could be compared with that of future participants.

Participants were situated in an electrically shielded room located in the neuroscience lab of the Center for Brain and Cognition (Universitat Pompeu Fabra, Barcelona) where electroencephalography (EEG) activity was registered.

The experiment began after electrode application. First, participants watched a 2-min video of the other players (see Fig. 1) to establish the initial hierarchy. Half of the participants were presented with the superior confederate, followed by the inferior confederate, while the other half were presented with the reverse order.

The game (see Fig. 1b) began immediately after training with five blocks of 36 trials (180 total, 90 with each simulated player). In each block (approximately 5 min), participants played nine consecutive trials twice with each player, followed by an updated ranking presentation. Participants could rest for up to 2 min between blocks. Rank order was fixed by manipulating the superior or inferior player's behaviour in order to maintain each participant in the middle of rank. Each trial lasted 5 s approximately. Each trial started with a 1-s presentation of the opponent's photograph (hierarchical stimulus) with its corresponding ranking stars. Next, participants performed the visual discrimination task, lasting 1 s. Feedback was then presented for 2 s: pictures of the participant and opponent above, and outcome (a coin meaning correct, an "X" meaning incorrect or a "time over" message) below. Both players could win or lose in a trial. The trial ended with the fixation cross for 1s.

A

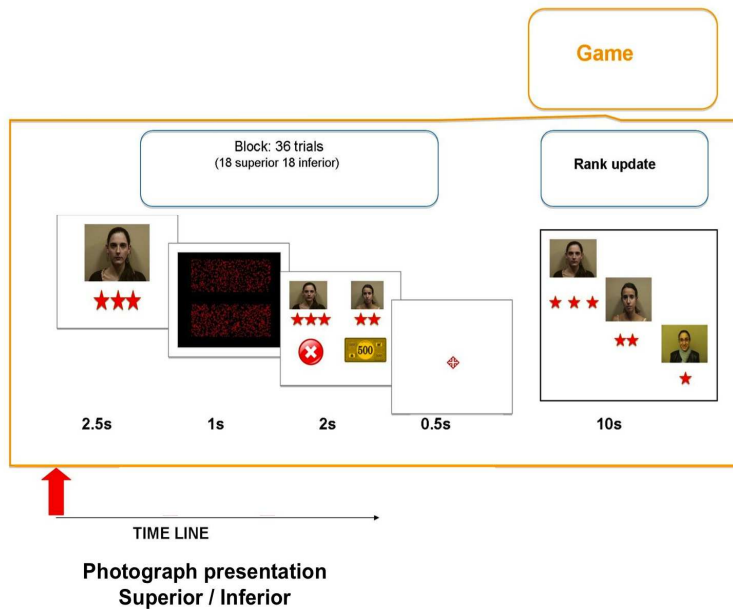


Figure 1: Hierarchy game structure. A. Game session started right after training and consisted of five blocks. Before the first block, we presented an artificial preliminary ranking to each participant with all participants in second position. Each block (5 min) constituted 36 trials and it was followed by an update on ranking. The 5.5-s trials were subdivided into two subgroups of 18 trials presented in random order; in each trial participants saw photograph of only one of the players, superior or inferior. Only one block of the game is represented. (B). ERP components were analyzed using photograph Stimulus locked potentials.

EEG/ERP recording

EEGs were recorded from 31 scalp sites. We placed two bipolar electrodes above and below the participant's left eye to record eye movements, two electrodes on the mastoids and a reference electrode on the nose. EEG recordings were digitized at 250 Hz. All

electrode impedances were below 3 KOhms. The EEG data were low- and high-pass filtered (30–0.03 Hz). We have used two different kinds of analyses: Stimulus locked and Response locked analysis. In Stimulus locked analysis, EEG was segmented into 1100-ms epochs ranging from 100 ms before stimulus onset to 1000 ms post onset (visual discrimination task). Before averaging, segments were baseline corrected by subtracting the mean amplitude of the pre-stimulus interval (-100–0 ms). All EEG data were semi-automatically screened offline for eye movements, muscle artefacts, electrode drifting and amplifier blocking. Segments containing such artefacts were discarded.

MRI acquisition: Structural MRI was acquired on a 1.5 T scanner (Signa; GE Medical Systems, Milwaukee, Wis). A 142-slice, three-dimensional, spoiled gradient-recalled acquisition sequence was obtained in the sagittal plane, with the following acquisition parameters: repetition time = 10.33 ms, echo time = 3.3 ms, inversion time = 600 ms, flip angle 10°, field of view 26 cm², matrix size 256 x 256 pixels, in-plane resolution 0.98 mm² and slice thickness 1.2 mm (no gap). Image quality control was performed before image processing.

MRI cortical processing: MRI images were processed by applying a fully automated pipeline, CIVET 1.1.9 (Kim et al., 2005; MacDonald, Kabani, Avis, & Evans, 2000) for the measurement of regional CT and CSA. CIVET was developed at the Montreal Neurological

Institute and was applied through the CBRAIN portal (cbrain.mcgill.ca). The pipeline comprised several steps, extensively detailed elsewhere (see, for instance, (S et al., 2009)): linear registration of native sMRI to the ICBM152 template (Mazziotta, Toga, Evans, Fox, & Lancaster, 1995); non-uniformity correction; tissue classification into GM, WM, cerebrospinal fluid (CSF) and background; pial and white matter surface fitting (40,962 vertices per hemisphere); non-linear surface registration to a high-resolution surface template in ICBM152 space; inverse registration of the surfaces into native space; CT calculation at each vertex with the t-link metric (Lerch & Evans, 2005); CT smoothing applying a 20 mm FWHM surface-based smoothing kernel; CSA calculation at each vertex as one-third of the total area of all triangular facets adjoining it; and surface area smoothing using a 40 mm FWHM surface-based smoothing kernel (Lyttelton et al., 2009).

Visual quality control of the native cortical surfaces was performed and all surface reconstructions were considered to be successful.

MRI subcortical processing: We applied the Bayesian Appearance Model (Patenaude et al., 2011), as implemented in FIRST which is part of the FSL package (FMRIB, Oxford, UK; <http://fsl.fmrib.ox.ac.uk/fsl>), to automatically segment the caudate nucleus, the nucleus accumbens, the globus pallidus, the putamen, and the thalamus. FIRST takes into account probabilistic information about shape and intensity of the segmented

structures. One advantage of this model over voxel-based morphometry alternatives is that it does not require tissue classification and arbitrary smoothing; instead, it is directly based on the geometry and location of the structure boundary and thus provides a robust estimation of anatomical boundaries and a higher sensitivity to regional variability. Based on manually segmented training data, FIRST creates a surface mesh for each sub-cortical structure using a deformable mesh model, the number of vertices for each structure being invariant, thus allowing for vertex-wise comparisons among subjects.

Visual quality control of the sub-cortical segmentations was performed and one participant was discarded because of poor segmentation of sub-cortical structures. A total sample size of $N = 21$ was included in further steps.

Statistical analysis of ERP and MRI data

ERP statistical analyses. Firstly, we analyzed the ERP components elicited when participants saw the hierarchical stimulus (photographs and stars of SP or IP). Secondly, the ERP components where we found statistical differences between SP and IP photographs was selected. For each component, we subtracted the component amplitude for SP minus that for IP, and used that difference score ($\Delta N170$) as an index of the hierarchy effect over that component. The mean averages were computed from at least

three electrodes where the component was located to stabilize the ERP measure.

Statistical analysis of cortical morphology.

Cortical vertex-wise analyses were carried out via permutation-based inference (Nichols & Holmes, 2002), implemented using the randomise tool of the FSL package (FMRIB, Oxford, UK; <http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Randomise>). For this purpose, the surface data were projected onto an ICBM152 2mm template by means of the appropriate function of the SurfStat Toolbox (<http://www.math.mcgill.ca/keith/surfstat/>), so that each vertex value was assigned to its nearest voxel while respecting the standard space of reference. Five thousand permutations were performed for each analysis. The association between difference scores and CT/CSA was analyzed at each vertex of the cortical surface, controlling for the effects of age, gender, and mean CT (for CT analyses) or total CSA (for CSA analyses). Controlling for mean CT or total CSA effects allowed improved sensitivity to detect local areas of significance unrelated to potential overall cortical effects. More specifically, the fitted regression equation at each vertex was:

$$CT \sim b_0 + b_1Age + b_2Gender + b_3MeanCT + b_4\Delta ERP + \epsilon,$$

where ΔERP represents the difference score for the ERP component of interest. A similar regression equation was fitted for CSA. t-statistic maps were produced at each vertex of the cortical surface, and the Threshold-Free Cluster Enhancement (TFCE; Smith

and Nichols, 2009) algorithm was applied to detect cluster-wise statistical signal while avoiding the setting of arbitrary cluster-forming thresholds. Finally, statistical maps were thresholded at $P < 0.05$ corrected for multiple comparisons (family-wise error rate below 5%).

Statistical analysis of subcortical morphology.

Vertex coordinates were analyzed in MNI space, where the structural images were finely registered and where structure models were generated. This allowed to minimize differences in pose and to provide relative deformation indices, orthogonal to the surface, adjusted for total brain size. More specifically, the fitted regression equation at each vertex was:

$$D_T \sim b_0 + b_1 \text{Age} + b_2 \text{Gender} + b_4 \Delta \text{ERP} + \varepsilon,$$

where D_T refers to the amount of vertex displacement perpendicular to the fitted surface. F statistics were computed vertex-wise, with the effects of age and gender being partialled out. As was the case for the cortical analyses, vertex-wise analyses were carried out via permutation-based inference (Nichols & Holmes, 2002), implemented using the randomise tool of the FSL package (FMRIB, Oxford, UK; <http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Randomise>). Five thousand permutations were performed for each analysis. The

TFCE algorithm was applied to detect cluster-wise statistical signal while avoiding the setting of arbitrary cluster-forming thresholds. Finally, statistical maps were thresholded at $P < 0.05$ corrected for multiple comparisons (family-wise error rate below 5%).

2.3.Results

ERP hierarchical modulations during opponent's photograph presentation

We performed an ANOVA with Social hierarchy (Superior and Inferior) as and electrodes (O1, O2, Oz for C1 and P1 components, and PO1, PO2, PZ, P3, P4 for N170 component) within-participants factors for each component (C1, P1 and N170). Analysis in C1 component and P1 component did not reveal significant effects (all test reflected $p > 0.1$). Analysis of the N170 component revealed a main effect of Social Hierarchy ($F_{1, 20} = 8.45$, $p < 0.01$) without other significant effects or interactions (Fig. 2). The N170 (a face-selective component; (Botzel & Grusser, 1989) was larger when participants saw the superior player's photograph and stars (Fig. 2). Because we only found a significant effect over the N170 component, further statistical analyses of MRI data were focused exclusively on $\Delta N170$.

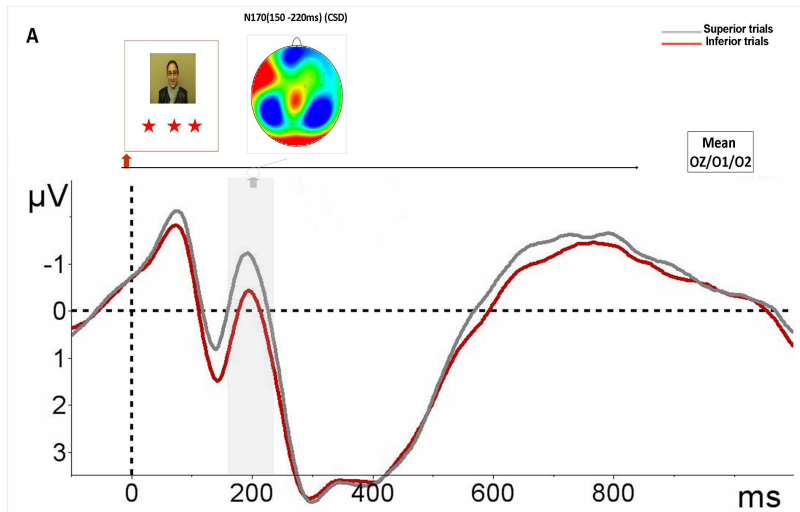


Figure. 2 Hierarchical effects in Event Related Components (ERP). ERP results (photograph stimulus-locked): differences in modulation of ERP components in presence of photograph of superior player (gray line) versus inferior (red line) player. Differences were observed on amplitudes of N170 component usually involved in face processing. The shaded areas demonstrate the time windows where the analysis reached statistical differences.

Cortical morphology correlates of hierarchy-modulated ERP components

We observed a significant positive correlation (FWE-corrected $P < 0.05$) between ΔN170 and CT in the right posterior cingulate cortex (MNI coordinates at the peak vertex: $x = -2, y = -20, z = 30$). With regard to CSA, a significant positive correlation was found in a region roughly covering the left transverse / superior temporal sulcus /gyrus ($x = 64, y = -36, z = 14$), whereas a negative association was observed in a cluster comprising the right insula,

ventral anterior temporal cortex and the anterior part of the fusiform gyrus ($x = -18, y = 12, z = -24$).

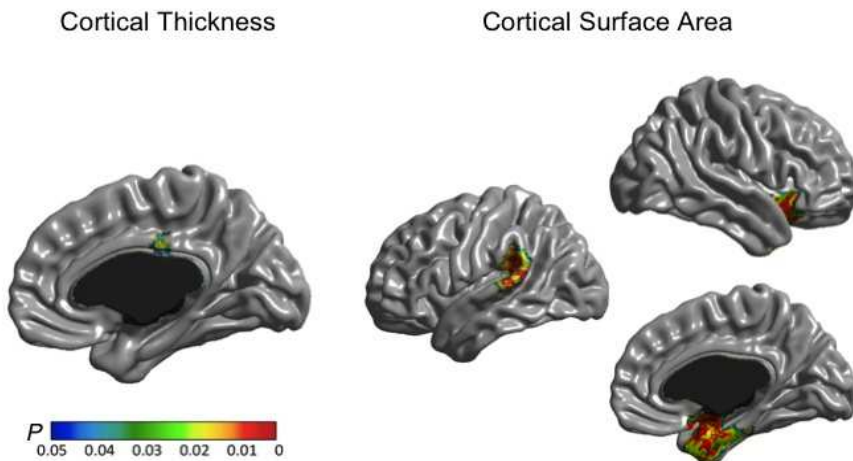


Figure 3. Cortical morphology results. Significant associations between $\Delta N170$ and cortical thickness (left) and cortical surface area (right). Results are corrected for multiple comparisons (family-wise error rate $< 5\%$).

Subcortical morphology correlates of hierarchy-modulated ERP components

We found a significant positive association (FWE-corrected $P < 0.05$) between the magnitude of vertex displacements in the dorsal

caudate and $\Delta N170$ (MNI coordinates at the peak vertex: $x = 20$, $y = -10$, $z = 24$). Neither negative associations nor other significant relationships were found between $\Delta N170$ and the shape of the other analyzed subcortical structures.

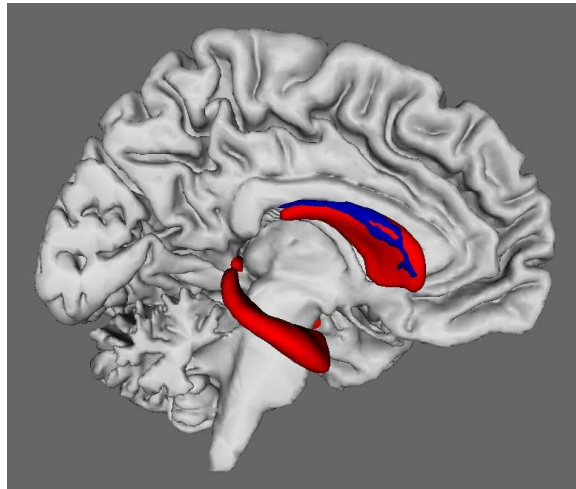


Figure 4. Subcortical morphology results. Significant associations between $\Delta N170$ and the shape of the right dorsal caudate nucleus. Results are corrected for multiple comparisons (family-wise error rate < 5%).

2.4 Discussion

Here, we combined Event Related Potentials (ERP) and structural Magnetic Resonance Imaging (sMRI) to reveal for the first time the cortical and subcortical anatomical substrates of early social status recognition. This combination of techniques provided a unique

approach for understanding the neuroanatomical basis of social hierarchy processing in humans.

In a first stage, we observed the expected modulations of social hierarchy over the N170 component, so that higher amplitudes were observed when we presented a picture of a superior player (SP), along with his or her corresponding status mark (three stars), than when we presented a picture of an inferior player (IP) accompanied by one star. (Chiao et al., 2008) demonstrated that humans are able to extract dominance and submission information from faces as early as 200 ms –which fits well with the N170 results reported here. N170 is not only involved in the process of face recognition (Eimer, 2011; Vuilleumier & Pourtois, 2007) but has also been linked to the identification of symbolic features as social information in faces (Eimer, 2011; Meaux, Roux, & Batty, 2013).

In a second stage, we have focused our analyses on brain morphology related to modulation in N170 component. Results provided strong support for an effect of social hierarchy over N170. As we predicted, such an early index of status processing was strongly related to the morphology of areas involved in automatic, rather than controlled, integration of social information processing –i.e., superior temporal gyrus/sulcus, posterior cingulate cortex, anterior ventral temporal cortex at cortical level and the caudate nucleus at subcortical level (Adolphs, 2009; Frith & Frith, 2012; Lieberman, 2007).

In regard to STS, previous studies have shown that STS plays a role in mentalizing other's social status (Adolphs, 2009; Muscatell et al., 2012), and previous fMRI studies showed higher activations in STS when participants perceived social dominance orientation in others (Marsh, Blair, Jones, Soliman, & Blair, 2009; Yamakawa, Kanai, Matsumura, & Naito, 2009). Further, recent connectivity analyses have supported that the superior temporal cortex could be also implicated in processing social and emotional cues related with social status (Marsh et al., 2009). Second, right posterior cingulate cortex and right insula are implicated in a salience network that facilitates the detection of relevant social stimuli (Menon & Uddin, 2010; Sugiura et al., 2012; Zink et al., 2008).

Negative correlations were observed between $\Delta N170$ and brain morphology in a cluster comprising the antero-ventral temporal lobe, fusiform gyrus and right insula. Low insular activity has been observed in subjects with poor sensitivity to unfairness situations (Montague & Lohrenz, 2007; Rilling JK, 2011) and, along this line, high insular activity is linked with inequity aversion (Hsu, Anen, & Quartz, 2008). A recent article (Farrow et al., 2011) also reported that individuals expressing preference for social distance judgments (e.g., hierarchical relations), as opposed to social alliance judgments, exhibited deactivations in insular regions. Therefore, it is well possible that a reduced insular region entails an increased preference and/or reactivity to hierarchical settings (that are unequal by definition).

These negative correlations may also reflect a higher sensitivity to the emotional component involved in the hierarchy perception. Indeed, hierarchy recognition is associated with increased arousal, nervousness, high stress and emotional reactivity (Boyce, 2004; Mehta et al., 2008). The experience of social status modifies modulation of automatic stress mechanisms, regulated by cortisol release (Mehta et al., 2008). Previous fMRI studies showed that negative affectivity and social inhibition scores increase with deactivation of a network comprising the temporal pole, right insula and fusiform gyrus, among other areas (Kret, Denollet, Grèzes, & de Gelder, 2011). Similar results have been reported in healthy adolescents, who showed deactivation in the same set of areas during passive viewing of emotional faces (Perez-Edgar et al., 2007). Therefore, functional deactivations in the cited areas may imply a higher sensitivity to detect hierarchy identity –as measured by $\Delta N170$. Our results are in agreement with this notion, in the sense that participants with reduced morphology in these areas would exhibit a major susceptibility to external social and emotional features, such as hierarchical cues.

At the subcortical level, the caudate nucleus plays a crucial role in salience processing of perceptual stimulus (Zink, Pagnoni, Chappelow, Martin-Skurski, & Berns, 2006; Zink et al., 2008). Correlations between right caudate and $\Delta N170$ confirms that evaluation of hierarchical identity in faces is a highly salient process (Zink et al., 2008) that depends, in part, on the recruitment of structures implicated in reward-processing and saliency (Mende-

Siedlecki, Said, & Todorov, 2013). The reported striatal involvement is in agreement as well with an fMRI study reporting activations in right caudate nucleus during the recognition of social-emotional faces in healthy individuals with high anxiety scores (Gaebler, Daniels, Lamke, Fydrich, & Walter, 2013).

Importantly, it is of note that all the significant regions observed here has traditionally been related to particular face processing. Areas such as the fusiform gyrus (fusiform face area (Haxby, Hoffman, & Gobbini, 2000) antero ventral temporal cortex (Nasr & Tootell, 2012), right insula (Eger, Moretti, Dehaene, & Sirigu, 2013), superior temporal gyrus/sulcus (Haxby et al., 2001; Haxby, Hoffman, & Gobbini, 2002) and right caudate nucleus (Morita et al., 2013; Sugiura et al., 2012) have been involved in integrate different features of faces (for a further review see (Haxby et al., 2001)).

In this context, the so-called Fusiform Face Area (lateral part of right fusiform gyrus) is known to be involved in the recognition of individual identity (Kanwisher, McDermott, & Chun, 1997; Kanwisher & Yovel, 2006; Kawasaki et al., 2012), whereas the superior temporal sulcus (STS), posterior cingulate cortex and insula are relevant in recognizing contextual social information associated to faces (Eisenberger, Lieberman, & Williams, 2003; Muscatell et al., 2012); as well as for extracting social information integrated in faces (Muscatell et al., 2012). Along this vein, a recent study (Eger et al., 2013) has suggested that anterior insula and posterior cingulate cortex contain fine-grained information shaped

by prior social interactions that allow for categorisation of faces according to their learned social status.

Thus, hierarchical effects over N170 involved regions associated to processing contextual social and emotional information (that is sometimes extracted from faces, but not necessarily), as well as brain areas implicated in face processing. Importantly, here we used an experimental paradigm where social hierarchy was inferred through symbolic cues (stars) accompanying neutral faces, and not by facial features per se. Therefore, we speculate that hierarchical symbols had an effect over the face-sensitive N170 component, perhaps because status and face information are integrated during that time window in order to infer SP or IP's hierarchical identity. Alternatively, the observed N170 effect could possibly arise from an earlier inference of the hierarchy status through the symbolic stars, which would exert further modulation (e.g., enhancement) over face processing. Future research will need to focus on this particular issue to better understand the specific contributions and potential interactions of face and social brain regions during hierarchy perception.

A final comment must be made with regard to the differences between cortical thickness and surface area, given that CT was related to Δ N170 in the cingulate cortex, whereas CSA covaried with Δ N170 in the STS, insular cortex and fusiform gyrus. CT is generally considered as an index of neuron density, dendritic arborization and glial support; CSA, on the other hand, is thought

to depend on the number and spacing of neuronal minicolumns (la Fougere et al., 2011; Rakic, 1988; Thompson et al., 2007). A straightforward consequence of such distinction is that the reported results may differ in the microstructural features that drive the observed anatomical correlations. An important implication of this possible difference in cellular underpinnings is that some of the associations found are more prone to be explained by environmental effects, whereas others would be driven by genetic factors to a higher extent (Burgaleta, Diaz, Baus, & Sebastian-Galles, in press). More specifically, CT associations may be more sensitive to environmental pressures, given that CT-related microstructures such as glial and capillary support, as well as dendritic arborisation (Thompson et al., 2007), dendritic and spine rearrangement and elimination (Petanjek, Judas, Kostovic, & Uylings, 2008) and gliogenesis (Dong & Greenough, 2004) are sensitive to learning and experience, whereas CSA-related results are likely to be under a higher genetic control, given that CSA is thought to depend on neurogenesis and neuronal migration, and such processes are known to suffer little modifications after term gestation (Hill et al., 2010). Because most of the results at the cortical level of analysis were found for CSA, it raises the question of to what extent is social status recognition under genetic control, and whether appropriate training would allow modulating the effect of social hierarchy over other cognitive processes (Santamaría-García et al., 2013).

2.5 Conclusion

In the present study, we reveal for the first time the cortical and subcortical anatomical substrates of early social status recognition. We conclude that such early processes are captured by the N170 component, likely reflecting the first stages in the inference of social identity, and that individual differences in the hierarchical effect over N170 is predicted by the morphology of brain regions associated with the automatic processing of social information. These results highlight the power of combining ERP and structural MRI data to understand the neuro-anatomical basis of social hierarchy processing in humans.

2.6 Acknowledgments: This research was supported by grants from the Spanish Ministerio de Economía y Competitividad (Consolider-Ingenio2010-CDS-2007-00012) and the Catalan Government (SGR 2009-1521). M.B. was funded by the postdoctoral “Alianza 4 Universidades” fellowship (A4U-4-2011). N.S.G. received the prize “ICREA Acadèmia”.

3. CHAPTER THREE

The role of social hierarchy on perceptual processes.

Santamaría-García H, Pannunzi M, Ayneto A, Deco G & Sebastián-Gallés N.

["If you are good, I get better": the role of social hierarchy in perceptual decision-making.](#)

Soc Cogn Affect Neurosci. 2014 Oct; 9(10): 1489-97. DOI: 10.1093/scan/nst133

4. CHAPTER FOUR

Effects of speaker's social hierarchy on sentence comprehension. A week has seven days, depending on who says it.

Hernando Santamaría-García; Alba Ayneto; and Nuria Sebastián-Gallés.

This article has been submitted for publication in Journal of Neuroscience (November 2013)

4.1 Abstract

How much influence does the speaker have on how humans understand a message? Common sense tells us that we are less likely to be influenced if we think that statements are true. Here we have analyzed the effects of social hierarchy on the perceived credibility of sentences that vary in their degree of plausibility. We obtained two types of responses: behavioural overt plausibility judgements and electrophysiological, unconscious responses (modulations of the N400 component). Sentences were uttered by two speakers with different hierarchical statuses (as previously established through a hierarchical video game). Participants heard three subsets of sentences with different plausibility values

depending on the last word (highly, intermediately and lowly-plausibility). No traces of social hierarchy effects were detected in participants' overt judgements. However, brain activity in response to differences in plausibility was modulated by the social status of the speaker. When listening to the superior speaker, the modulation of the N400 component followed the expected pattern (inverse relationship between amplitudes and sentence plausibility). However, when participants heard the inferior speaker, the amplitude of the N400 for highly-plausible sentences matched that of the intermediate plausibility (increased amplitude). This pattern was not due to decreased attention to the inferior speaker. Reducing attention to speech resulted in an overall decrement of the N400 responses and in delayed latencies. Results are interpreted as indicating that participants did not trust low ranking speakers, even if they uttered highly plausible sentences. The observed effects may reflect the existence of prejudices. The present results have important implications for educational practice.

4.2 Introduction

People tend to give different value to what others say, and this often depends on the extent to which we perceive our interlocutor as a reliable source. Therefore, the perceived social hierarchy is important in making judgments about others, and it can be a

determinant factor in modulating trust (Lount Jr. & Pettit, 2012). Social hierarchies emerge spontaneously early in life, as young as 2 years of age (Boyce, 2004), and they play a fundamental role in shaping social behaviour (Cummins, 2000; Festinger & Hutte, 1954). The influence of social hierarchies extends beyond the domain of social behaviour and recently it has been shown to influence different cognitive processes such as attention, perceptual processes (Foulsham et al., 2010; Santamaría-García et al., 2013; Zink et al., 2008) and executive function mechanisms (Boksem et al., 2012; Smith et al., 2008). As it seems, sensory perceptual stimuli coming from high-ranking individuals could be favoured by an enhanced attentional and perceptual process (Santamaría-García et al., 2013; Zink et al., 2008).

The relationship between language processing and social hierarchies was established a long time ago. Indeed, it is well known that language (in particular speech) is a natural marker of social class (Adler & Ostrove, 1999; Cazden, 1968). Replacing Eliza Doolittle's low class accent by an upper class one was one of the major tasks (and achievements) of Professor Henry Higgins in the popular play "My Fair Lady". There is a bulk of studies indicating that listeners evaluate speakers based on their verbal proficiency. All the reviewed data in this topic have been collected by asking participants to produce overt responses concerning speakers' reliability. Such evaluations have an impact on the attributed reliability of what is said and on the listener's general confidence in the speaker. In general, most of these studies have been focused on

evaluating influences of the speaker's social status through certain language aspects such as accent or the usage of grammatical structures (Glaeser & Laibson, 2000; Jay, Routh, & Brantley, 1980; Kang, O, Donald, L. R., 2009; Kraus, Piff, & Keltner, 2009; Seligman, 1972).

The influence of social stereotypes on language comprehension has also been observed when measuring brain responses. A study (Van Berkum et al., 2008) reported modulations of ERP responses as a function of consistency between the identity of the speaker and the message. Indeed, sentences such as "I have a large tattoo on my back" elicited different electrophysiological responses depending on the upper or lower accent of the speaker. These effects are deeply rooted in human cognition and can be observed in early childhood. Einav et al., (Einav & Robinson, 2011) observed that children as young as 3-4 years of age estimate the consistency of what other people say by exhibiting selective trust based on different features of the speaker, such as relative age, familiarity, verbal proficiency and self-confidence. These features closely match those observed in research with adults (see also (Corriveau & Harris, 2009; Harris & Corriveau, 2011; Jaswal & Neely, 2006)). Together these investigations both with adults and children, suggest that humans differently judged the reliability of individuals according to its social value.

Nevertheless, so far, it is unclear how much these judgements are influenced by post-decisional mechanisms related to prejudice. Additionally, these responses reflect participants' beliefs about

their trust in a speaker, however evidence of on-line direct processing of speakers' reliability of socially neutral utterances is lacking at present. It may be the case that sentences uttered by high and low status individuals are processed in the same way, and that late stage decision related mechanisms drive the differences in our phenomenological experience. Confirmatory biases would affect participants' responses. Nevertheless, it may also be the case that how much we trust a speaker alters basic mechanisms of sentence processing. Indeed, there is ample literature indicating that we pay more attention to high status individuals (Foulsham et al., 2010; Zink et al., 2008). Attention is a well-known mechanism that facilitates sentence integration processes (among others) (Kiefer & Brendel, 2006; Kutas & Federmeier, 2011; Relander, Rama, & Kujala, 2009). Because we are more alert and we integrate better the information high status individuals convey, we may consider their messages more reliable. Electrophysiological responses and in particular Event-Related Potentials (ERP) provide the high temporal (millisecond) resolution necessary to tackle this question. Furthermore, previous research has established the correspondence between different ERP components and the operation of specific language-related processes (for reviews (Hagoort, P., Baggio, G., Willems, R.M., 2009; Kutas & Federmeier, 2011)).

Of particular interest is the so-called N400 component. The N400 is an Event-Related-Potential (ERP) component peaking around 400 ms after word presentation. Although there is some debate

concerning its specific origin, previous research has firmly established that it is sensitive to semantic anomalies (Kutas & Hillyard, 1980; Kutas & Hillyard, 1984; Kutas & Federmeier, 2011). In sentential contexts, semantically anomalous (or less plausible or predictable) words elicit reliably larger N400 responses than non-anomalous (or more plausible or predictable) ones. It has been argued that these modulations of the N400 component reflect differences in the ease with which a particular word can be integrated with the preceding context (Hagoort, P., Baggio, G., Willems, R.M., 2009; Kutas & Hillyard, 1980; Kutas & Federmeier, 2011). Although the N400 is elicited in an automatic way, its amplitude can be also modulated by attentional factors (Kiefer & Brendel, 2006; Kutas & Federmeier, 2011; Relander et al., 2009).

Here we want to assess when information about the social status of the speaker influences the unfolding interpretation of a sentence. If the previously reported differences in speakers' reliability reflect post decisional effects, no differences in the N400 component should be observed as a function of speakers' status. Differences should be observed at later time windows, preceding the response, thus reflecting the decision biases. However, if speakers' status influences the integration of sentential information, one should observe a modulation of the N400 component depending on the status of the speaker. In general, low-ranking speakers (with low attributed reliability) should elicit larger N400 responses, as compared to high-ranking ones (with high attributed reliability); reflecting the higher difficulties in integrating sentential

information in this context. In the present study, we will compare the processing of sentences with varying degrees of plausibility (see Methods) uttered by two different speakers whose statuses will be determined by the outcome of a visual perception task. One methodological feature of previous studies exploring social factors in language processing is that often, different sentences were used in different experimental situations (i.e. in the van Berkum et al study (Van Berkum et al., 2008), the sentence “I have a large tattoo on my back” pronounced by an upper or lower class accent had to be realized in two different stimuli). This fact may introduce some unwanted biases, as participants’ prejudices or preferences may alter their responses. A more controlled experimental situation is to use the same stimuli across hierarchical conditions. Here, we used sentences free of social stereotypes that only differ in plausibility, irrespective of who is speaking.

Following common practice where hierarchies are induced through game playing, here we have used a previous procedure (Santamaría-García et al., 2013) to create a social hierarchy through a computerized game based on participants' performance in a visual discrimination task. As described below, before listening to the sentences, participants played a visual discrimination game at the same time as two simulated players. One of the simulated players played, on average, better than the participant and through different manipulations consistently held a higher-ranking status. The other simulated player played worse and had a lower rank in the hierarchy. Importantly, the same confederates were

counterbalanced across participants. Confederates with a higher rank for some participants would be the lower ranking player for others.

4.3. Methods

Participants: Forty participants (20 females 20 males; mean age = 23, 39; age range 18 – 27 years) took part in the experiment 1. Thirty eight right-handed participants, (twenty females) took part in the experiment 2 (mean age = 20, 38; age range 18 – 27 years). All participants were students at the University Pompeu Fabra in Barcelona. Participants were recruited using an open call. Participation was voluntary. No selected participants reported having had any language-learning pathology or suffering from psychiatric or neurological disorders. All participants gave their informed consent prior to their inclusion in the study. The study conformed to The Code of Ethics of the World Medical Association (Declaration of Helsinki). Participants were paid for their participation in the experiment, 10 euros per hour.

Stimuli: We recorded 360 sentences in Spanish varying in plausibility with the last word regarding the precedent fragment. Sentences varied between 7 and 15 words in length. Sentence duration was 4.08 s on average (sd = 551ms). Two male and two female (mean age 27 years) native speakers of Spanish (of the same

age range of the experimental participants) recorded the sentences. Stimuli were digitized and down-sampled to 16 kHz. Stimuli by each Speaker were recorded in a single session. Four experienced Spanish-native independent judges checked for the correct pronunciation of every sentence. Stimuli were edited with Cool Edit (Syntrillium Software Corp., Phoenix, AZ), and individual stimuli files were created for each sentence. No silences were left at the beginning or end of each file.

To determine the plausibility of each sentence, we ran a pilot study where 20 participants (10 females) evaluated the sentences. Participants were asked to determine using a two-alternative choice test, on a total of 480 sentences, which of these sentences were plausible or implausible based on the relevance of the last word with respect to the previous context (the “critical word”). A sentence was considered plausible or implausible when all participants considered it so. A sentence was classified as intermediate-plausible when participants were split concerning its plausibility (40% to 60% of participants considered it plausible). The final sample of stimuli was constituted by 120 stimuli of each type.

Across the different speakers, the critical words were matched in duration (highly-plausible sentences, critical word mean = 548 ms, sd = 133 ms; low-plausible sentences critical word 549 ms sd = 130ms; intermediate-plausible sentences critical word = 557 sd =136ms). Two equivalent lists of sentences were created, so that participants heard half of the stimuli uttered by one speaker and half of the stimuli by another speaker. The lists were matched in

terms of number of words, sentence length and critical word and duration. Separate ANOVAS on each measure did not show any difference between lists or speaker (4 speakers).

Apparatus: All of the stimuli were delivered binaurally through headphones (Sennheiser HD 435 Manhattan) at an intensity of 70 dB. To perform the tasks in the study, participants used a custom-made joystick with an up/down lever based on mouse hardware. The ERPs were recorded from the scalp by using tin electrodes mounted in an electrocap (Electro-Cap International). The ERP register and the ERP analyses were conducted using the Brain Vision Analyzer Software package (v. 1.05; Brain Products).

EEG Recording and Analysis: Participants were placed in an electrically shielded room at the Neuroscience Laboratories (Centre for Brain and Cognition, University Pompeu Fabra) where the EEG activity was registered. The EEGs were recorded from 31 scalp positions using the BB cap configuration from v. 1.05, Brain Products. We placed two bipolar electrodes above and underneath the left eye to record eye movements. We also used two bipolar electrodes in the area of mastoids of each side. An electrode placed on the participant's nose was used as reference channel. The common EEG/ electro-oculogram (EOG) reference was attached to the tip of the nose. The electrophysiological signals were filtered on-line with a band pass of 0.1–100 Hz and digitized at a rate of 500 Hz. Eye movements were corrected by means of independent

component analyses (ICA) (v. 1.05; Brain Products). All impedances were below 3 KOhms. The EEG data was low- and high-pass filtered (0.03 Hz to 30 Hz) and afterwards segmented into 1000 ms epochs, ranging from -100 ms before to 900 ms after the onset of the critical word (last word of each sentence). Epochs with EEG exceeding either +/-100 μV at any channel, activity $<0.5 \mu\text{V}$, or voltage step/sampling $>50 \mu\text{V}$ within intervals of 200 ms were automatically rejected off-line. In all cases, epochs included a pre-stimulus baseline of 100 ms and were 900 ms long. Base line was corrected and lineal DC detrend procedure was performed on the individual segments. Individual ERPs were digitally band-pass filtered between 0.1 and 30 Hz (with a slope of 12 dB/oct). The 900-ms epochs were averaged in reference to the 100-ms pre-stimulus baseline.

Procedure Experiment 1 (Hierarchical Speakers). The experiment consisted of two phases. In the first one, the hierarchical social context was created. In the second one, the sentence comprehension process was evaluated (see Fig.1 for a full description of the experimental procedure).

Setting the social hierarchy phase: To control for possible interactions between gender and hierarchy, male participants performed the experiment with male simulated participants, and female participants with female ones. Participants watched a short video (two minutes) of two other simulated players. We used the

videos to establish initial hierarchical features. Four different videos depicting four profiles were created. The four profiles corresponded to the crossing of gender (male/female) by hierarchy (high/low status). Four confederates (two males and two females) interpreted the videos.

Each confederate recreated the superior profile and the inferior profile following two scripts where the personal, work and academic achievements of the characters were presented. Implicit cues related to social status of the confederates were controlled to avoid big differences in terms of age, face expressions, or attire. Half of the participants saw one same-gender confederate as a superior player and another same-gender as an inferior player; while for the other half of the participants confederate's rank was reversed. To reinforce confederates' and participants' ranks, whenever their pictures were displayed, there were one to three red stars below the pictures indicating their ranks (one star indicating the lowest rank and three stars the highest rank). Participants were also invited to make their own video at the end of the experiment and made believe that it would be used with other participants. Videos lasted 2 minutes approximately.

To maintain the social hierarchy, participants performed a visual discrimination task using a computerized game. In the visual task, participants saw two rectangles with different percentages of red dots. They had up to 1 second to decide which rectangle contained more red dots using the corresponding lever (up/down) of the joystick. In each trial, participants performed the visual task

comparing their performance with one of each player seen in the social videos (Superior or Inferior). The nature of the game was non-competitive because in the same trial the participant and the simulated player could win, lose or have a different outcome. Performances in the game of the superior and inferior players were simulated to maintain the hierarchical order. A game trial started with the photograph of the corresponding simulated player in the trial (Superior or Inferior) with its corresponding ranking in stars. Then, the two rectangles with the red dots were presented and participants performed the visual task. After the participants responded, participant and player's feedback were presented. The trial ended with the presentation of the fixation cross. The game phase was sub-divided in 5 blocks; each block had 36 trials. After each block, a screen with the updated rank was presented. Participants were always placed in the second position to maintain the hierarchy. Participants played 90 trials with the superior player and 90 with the inferior (see Fig 1 panel A).

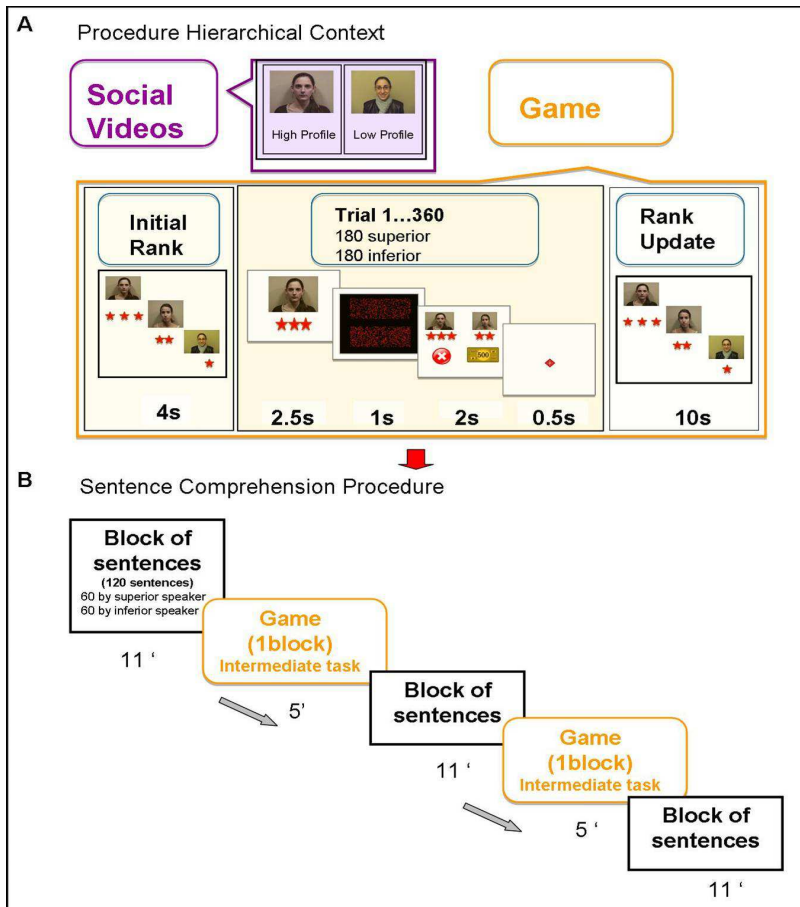


Figure 1. General Procedure. Panel A shows the procedure used to build up the hierarchical context. The procedure had two phases: the Social Videos and the Game session. In the Social Videos, two confederates simulated the superior and the inferior player. In the game phase, the participants performed a visual discrimination task comparing their performance to the hierarchical players. Panel B presents the general structure of the sentence comprehension phase. Participants heard three blocks of sentences. In each block, participants heard 120 sentences, 60 by each Speaker (Superior and Inferior). After each block of sentences, participants played a new block of the game to refresh the hierarchical context.

Sentence Comprehension Phase: This phase started with 24 practice trials to familiarize participants with the procedure and the kinds of sentences. Half of the practice sentences were produced by the high-ranking speaker and the other half by the other speaker (4 sentences of each type). Sentences were presented in blocks (60 sentences by each block). Each trial started with the display of the photograph of the corresponding speaker in the trial (Superior or Inferior). After one second, sentences were presented (the photograph disappeared at the end of the sentence). Participants had up to 2.5 s after sentence completion to determine its plausibility by using the corresponding level of the joystick (up = plausible/down= implausible). A trial ended with the presentation of a fixation cross lasting 0.5s (see Fig 2 panel A). Participants heard a total of 180 sentences in total said by each speaker (60 highly-plausible, 60 intermediately-plausible and 60 lowly-plausible sentences). A block of sentences was composed by 120 sentences. Each one of the Speakers said 60 sentences in total (20 sentences of each type). Order of presentation of each sentence within each block was fully randomized. Presentation of speakers was counterbalanced within each block. The hierarchical role of each speaker was counterbalanced among the participants. The sentences were presented in three blocks lasting approximately 13 minutes each. Each block was constituted by 120 sentences; each speaker enunciated 60 sentences. After each block of sentences, participants took part in 2 new blocks of game trials: one of them between the first and second block of sentences and the other one

between the second and third block of sentences. Participants took part in these blocks of game trials to refresh the social hierarchy (see Fig 1 Panel B).

Procedure Experiment 2 (Attentional conditions):

Setting game phase: Here, participants took part in a game phase following a similar procedure as in the condition 1. However, hierarchical features were taken out. Pictures of simulated players were replaced by one of two colorful squares and participants did not compare their performance with other players. We maintained this phase to preserve the time course and overall structure of the experiment.

Sentence comprehension Phase: This phase was divided in two parts, one of Reduced attention and other of Normal attention. Sentences were presented in the same number and structure as in the previous experiment (180 sentences said by each speaker, 60 sentences of each plausibility type). In the first part of the experiment participants had to watch and pay attention to a silent film while half of the experimental sentences were presented (Reduced attention condition). To ensure that participants were paying attention to the film, they were asked quite difficult questions about what happened in the video (see (Relander et al., 2009) for an analogous procedure to manipulate attention in a sentence comprehension task while measuring the N400 response).

In the second part of the Sentence comprehension phase, the same procedure as in the previous experiment was adopted, except that no information about other players was presented and therefore, no social information was provided (Normal attention condition). The experimental procedure followed the one described in the previous experiment, except for the differences just mentioned (see Figure 2. Panel B).

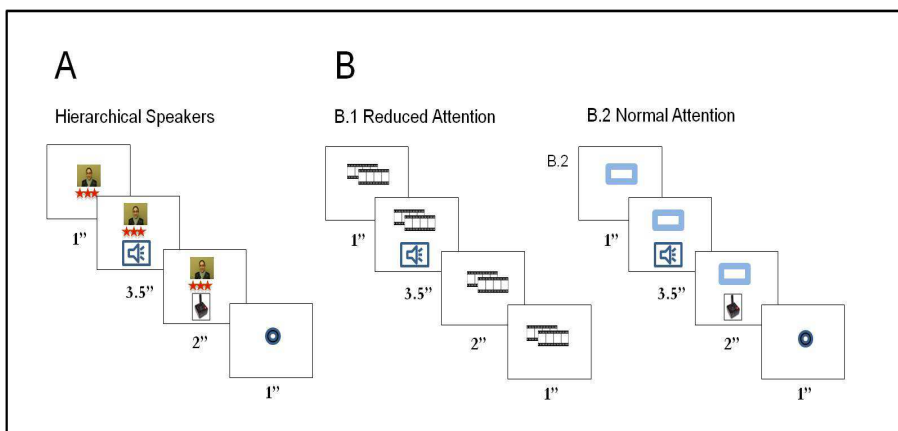


Figure 2. Procedure of the sentence comprehension phase in each experiment. Panel A shows the procedure of a trial in the hierarchical condition (Hierarchical Speakers). Each trial started with the display of the photograph of the corresponding speaker in the trial (Superior or Inferior). After sentences were presented (the photograph disappeared at the end of the sentence). After sentence completion, participants determined its plausibility by using the corresponding level of the joystick. A trial ended with the presentation of a fixation cross. Panel B shows the procedure of a trial in Experiment 2 (Attentional conditions i.e., Reduced and Normal). In Reduced attention condition (B.1), participants watched silent video clips and simultaneously heard the sentences. In Normal attention condition (B.2), a photo of the speaker was replaced by a neutral rectangle (green or blue) to avoid the hierarchical cues. Participants were required to actively attend to sentences and determine its plausibility. Structure of trial in this condition followed as in experiment 1 (Panel A).

4.4 Experiment 1

The experiment consisted of two phases. In the first one, we created the hierarchical social context and, in the second one, we evaluated the sentence comprehension process (see Fig 1). At the sentence comprehension phase, participants listened to the same sentences, but they were interpreted as coming from a high or a low status speaker depending on the outcome of the previous phase.

Forty right-handed participants (20 females) took part in this condition (mean age = 23.39; age range 18 – 27 years). Initially, participants watched a short video of two other simulated players (superior and inferior) lasting approximately 2 minutes each. We used short video-clips to establish the initial hierarchical features (see Methods). To maintain the social hierarchy, participants performed a visual discrimination task in the context of an interactive computer game. In the visual task, participants saw two rectangles with different percentages of red dots. In each trial, after participants had performed the visual task, feedback on their own performance along with that of one of the two other players seen in the social videos (superior or inferior) were displayed on the screen. Performances of the superior and inferior players in the game were simulated to maintain the hierarchical order. Afterwards, participants performed a sentence comprehension task where they had to perform a “yes/no” plausibility judgment at the

end of each sentence. Participants heard sentences spoken by the same players from the previous phase. The high-ranking speaker (superior) produced half of the practice sentences and the low-ranking speaker (inferior) produced the other half (four sentences of each plausibility level).

Sentences were presented in blocks. Then participants heard a total of 180 sentences said by each speaker. They heard 60 highly plausible: “Carlos bought an umbrella to protect himself from the rain” (Carlos compró un paraguas para cubrirse de la lluvia), 60 intermediately plausible: “The children play football at the airport” (Los niños juegan al fútbol en el aeropuerto) and 60 low plausibility sentences: “The Italian ate spaghettis with shoes” (El italiano comió los spaguettis con los zapatos). After each block of sentences, participants performed one new block of the visual game. The goal of these additional visual game blocks was to refresh participants’ memory of the social hierarchy (see Fig 1 Panel B). Participants were exposed to confederates (simulated players) of their own gender (two equivalent sets of materials were created) (see Methods for a further description).

4.4.1 Results

Behavioural Data: A 2 (gender) by 2 (speakers’ hierarchy) by 3 (sentence plausibility) mixed factors ANOVA was run on participants’ plausibility judgments. We only found a main effect of

sentence plausibility [$F(2,78) = 19.62$ $p < 0.01$]. No other effects or interactions were significant. A parallel analysis on the reaction times yielded a main effect of sentence plausibility [$F(2,78) = 48.02$ $p < 0.01$], in the absence of other significant effects or interactions. Participants were both consistent in classifying highly and lowly-plausible sentences. They were faster in classifying the low-plausible sentences (348 ms on average after the end of the word) than the highly-plausible sentences (397 ms on average after the end of the word). Intermediate-plausible sentences were classified as plausible in an average of 51 ± 2 % of cases. Participants were slower to classify this type of sentence (426 ms in average after end of word)(see Table.1).

ERP Data: Only participants with more than 70% artifact-free trials were included in the analyses. Following this criterion, two participants (2 males) were excluded and two new participants were evaluated. We analyzed latencies and mean amplitudes in N400 time window (250 to 450 ms after the onset of the critical word, i.e., the last word, with a duration of 551 ± 110 ms) in central electrodes (CZ, P3, P4, PZ) as previously described to evaluate N400 effects (Nieuwland & Van Berkum, 2008; van Berkum, Brown, Hagoort, & Zwitserlood, 2003; Van Berkum et al., 2008). In regard to latencies measures, the mean peak of latency for the N400 in each subset of sentence with Superior Speaker was 353 ms in average; while for the Inferior speaker was: 355 ms in average. To analyze the latency measures, we ran an ANOVA of the peak latency in milliseconds of the N400 using hierarchy of speaker

(Superior and Inferior), sentence plausibility (highly, intermediately, lowly), electrode (CZ, P3, P4, PZ) and gender (male, female) as factors. The analyses did not reveal any significant effect (see Table 1 & Fig. 3,4).

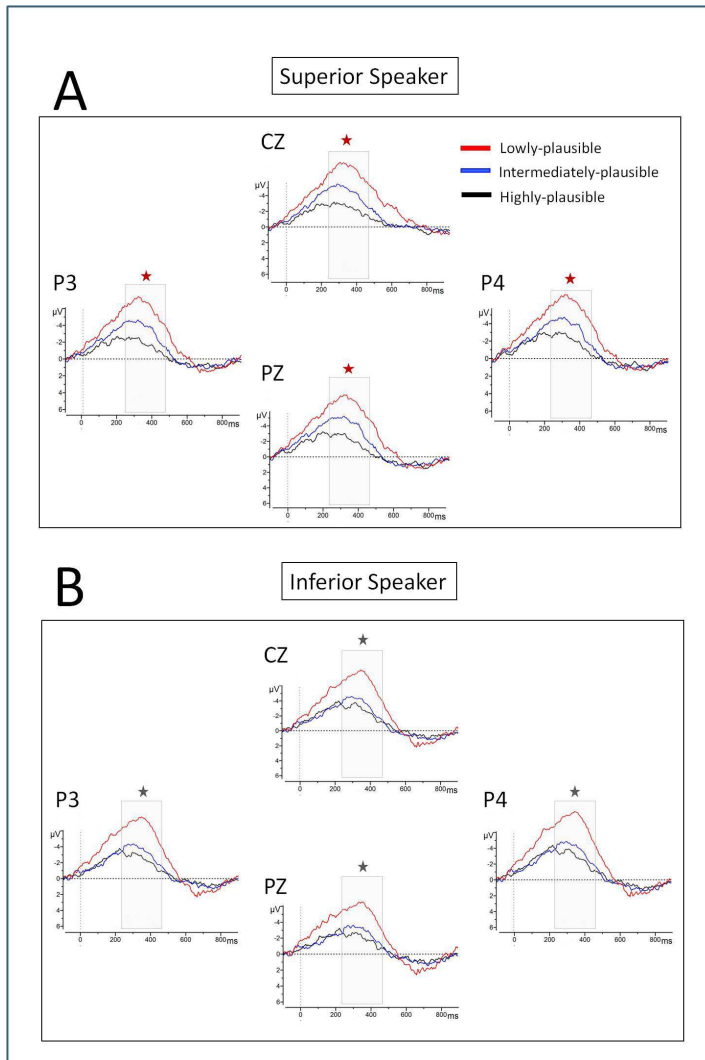


Figure 3. Modulation of N400 in Experiment 1 (Hierarchical Speakers). Panel A shows the N400 modulations for the Superior Speaker. The graph shows N400 modulation on central electrodes by each sentence type: highly-plausible (black), intermediately-

plausible (blue), and lowly - plausible (red). The N400 was significantly different in each sentence type. Shaded area is showing the time window where the differences reached statistical differences. Panel B shows the N400 modulations for the Inferior Speaker, the N400 in highly-plausible and intermediate-plausible sentences was equivalent. The red star depicts statistical differences between each sentence type (superior player). The black star depicts the absence of statistical difference between highly and intermediately plausible sentences.

Concerning to amplitude measures, an ANOVA of mean amplitudes of N400, using the same factors described for latency (see above), revealed a significant main effect of sentence plausibility [$F(2, 78) = 98.01, p < 0.01$]. Further, we obtained a significant interaction between sentence plausibility and hierarchy of the speaker [$F(2, 78) = 3.96, p < 0.05$]. No other effects or interactions reached significance levels. Accordingly, we analyzed separately the effects of sentence plausibility for each type of hierarchy of the speaker. In the case of the superior speaker the three kinds of sentences were significantly different from each other (all t-tests $p < 0.01$). In contrast, for the inferior speaker, we found statistical differences only between low-plausible sentences and the other two kinds of sentences (intermediate- and highly-plausible) (both t-tests $p < 0.01$), but we did not find any difference between the intermediate-plausible and highly-plausible sentences (t-test $p > 0.1$). We also compared the modulations of the N400 in each sentence type by comparing the two speakers. Only in the case of highly-plausible sentences was the N400 component differently modulated depending on the social hierarchy of the speaker

($p < 0.01$). The amplitude of the N400 component was larger when sentences were pronounced by the inferior speaker than when they were pronounced by the superior speaker (see Fig 3, 4). Social hierarchy has modulated only the ERP responses in the N400 component, supporting the view that social factors influence sentence interpretation. Indeed, when participants heard the superior speaker, the modulation of the N400 component followed the expected pattern (inverse relationship between amplitude and sentence plausibility) (Kutas & Hillyard, 1980; Kutas & Hillyard, 1984; Kutas & Federmeier, 2011). However, when participants heard the inferior speaker the amplitude of the N400 in highly-plausible sentences matched that of intermediate plausibility for the same speaker (increased amplitude)(see Table.1).

Two possible explanations are possible. First, the pattern of results may reflect social prejudices against the reliability of low-ranking individuals and constitute a specific signature of processing of social information. Second, the results can be the result of secondary effects of processing of social information. Indeed, they can reflect reduced attention to low-ranking individuals when compared to high-ranking ones (Foulsham et al., 2010). It may be argued that diminished attention to low-ranking individuals may particularly affect the integration of information in highly - plausible sentences. It cannot be discarded that the incongruence in low and intermediate - plausible sentences may be enough to automatically trigger the N400 response, even with reduced attention (identifying

the words “eating”, “spaghettis” and “shoes” may suffice to detect inconsistencies). However, processing of highly-plausible ones would require more extensive parsing. Data from participants’ reaction times partially support this possibility, as participants were slower in responding to highly - plausible sentences (397 ms in average) than to low - plausible ones (348 ms in average) (although participants were even slower in the intermediate - plausible sentences, whose processing was not modified by the hierarchy of the speaker)(see Table. 1). To test this second hypothesis a new experiment was run where attention, and not the social factors, was manipulated.

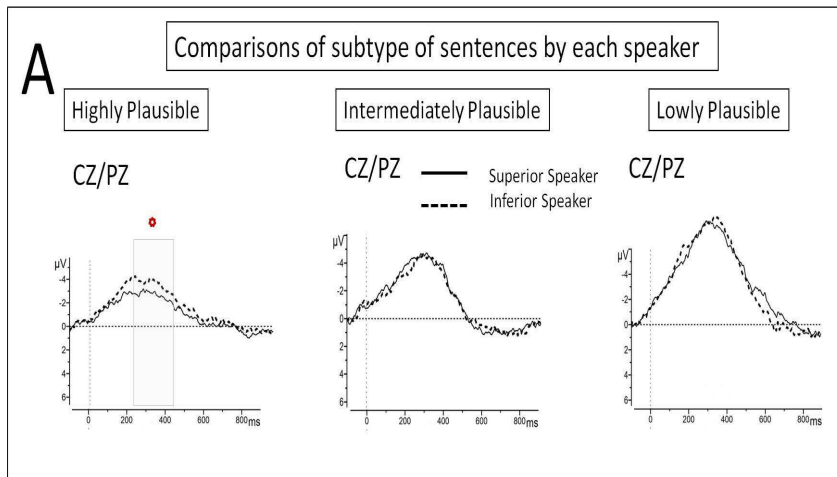


Figure 4. Modulation of N400 in Experiment 1 by each type of sentence. The graph shows N400 modulation in an average of central electrodes (CZ/PZ) by each type of sentence in presence of each speaker (superior speaker (solid line) and inferior speaker (dash line)). The left panel shows N400 modulations in highly – plausible sentences, the middle panel in intermediately plausible sentences and the right

panel modulations in the lowly plausible ones. The red symbol depicts statistical differences.

4.5 Experiment 2

In this experiment, participants' N400 responses to the same sentences as in the previous experiment were compared in two different Attentional conditions. In the first part of the experiment, participants had to watch and pay attention to a silent film while half of the experimental sentences were presented (Reduced attention condition). To ensure that participants were paying attention to the film, they were asked complex questions about what they had seen in the video (see (Relander et al., 2009) for an analogous procedure designed to manipulate attention in a sentence comprehension task while measuring the N400 response).

In the second part of the experiment, the same procedure as in the experiment 1 was adopted, except that no information about other players was presented and therefore, participants had no access to social information (Normal attention condition). Otherwise, the experimental setup was identical to the one in the previous experiment

Thirty eight right-handed participants, (twenty females) took part in this experiment (mean age = 20, 38; age range 18 – 27 years) (see Methods and Figure 2. Panel B).

4.5.1 Results

Behavioural data: Participants' plausibility judgments were only evaluated for the Normal attention condition, as only under this condition participants were asked to provide a response in this regard. A 2 (gender) by 3 (sentence plausibility) mixed factors ANOVA was run on participants' plausibility judgments. We only found a main effect of sentence plausibility [$F(2,74) = 9.25$ $p < 0.01$]. No other effects or interactions reached significance levels. A parallel analysis on the reaction times also yielded a main effect of sentence plausibility [$F(2,74) = 6.02$ $p < 0.01$], in absence of other significant effects. Plausibility judgments and Reaction times followed the same pattern as in the previous experiment. Participants were faster in classifying the low-plausibility sentences (304 ms on average) than the highly plausible ones (312 ms on average) and intermediately plausible sentences elicited the slowest reaction times (338 ms on average)(see Table 1). Intermediately plausible sentences were classified as plausible in 51+/-4 % of cases, on average.

ERP data: We analyzed latencies and mean amplitudes in N400 time windows (250 to 450 ms after the onset of the critical word i.e., the last word, with a duration of 551 +/-110 ms) in central electrodes (CZ, P3, P4, PZ) as previously described to evaluate N400

effects (Nieuwland & Van Berkum, 2008; van Berkum et al., 2003; Van Berkum et al., 2008). In regard to latencies measures, the mean peak of latency for the N400 in each sub set of sentence in Normal attention condition was: 318 ms in average; while for the Reduced attention condition was 357 ms in average (see Table 1 & Fig. 5). The ANOVA of the peak latency in milliseconds of the N400, using each Attention Condition (Reduced and Normal), Sentence Plausibility (high, intermediate, low), electrode (CZ, P3, P4, PZ) and gender (male, female) as factors only revealed a main effect of Attention Condition [$F(1, 37) = 24.08$ $p < 0.01$]. No other effects or interactions reached significant values. The peak of latency for the N400 in Normal attention condition peaked significantly earlier than in the Reduced attention condition (see Table 1 & Fig. 5).

The ANOVA of mean amplitudes of N400, using the same factors described for latency (see above), revealed a significant main effect of the Attention Condition [$F(1, 37) = 6.83$ $p < 0.01$] (amplitudes were lower in the Reduced attention condition), and a main effect of Sentence Plausibility [$F(2, 74) = 9.01$ $p < 0.001$] without any significant interactions. Modulation of the N400 component in both Attentional Conditions (Reduced and Normal) followed the same (and expected) pattern showing an inverse relationship between amplitudes and sentence plausibility in each Attentional Condition (see Fig. 5).

Two different analyses pooling the data of both experiments supported the conclusion that the selective increase in the N400 component for highly-plausibility sentences uttered by low-ranking individuals (reported in experiment 1) did not simply reflect diminished attention to those speakers. First, we ran two independent ANOVA on the latencies and on the mean amplitudes of the N400 in each condition in central electrodes (CZ, P3, P4, PZ), as previously described (Nieuwland & Van Berkum, 2008; van Berkum et al., 2003; Van Berkum et al., 2008). To do so, we assumed that listening to high-ranking individuals corresponded to the Normal attention condition and listening to low-ranking individuals corresponded to the Reduced attention condition. The factors of analysis used were Experiment (Hierarchy and Attention), Condition (Normal attention/Superior and Reduced attention/Inferior), Sentence Plausibility (high, intermediate, low) and Electrode (CZ, P3, P4, PZ). The analyses on the latencies revealed a main effect of Experiment [$F(1, 76) = 13.01$, $p < 0.01$]. This effect was modulated by the interaction between Experiment * Condition [$F(1, 76) = 19.02$, $p < 0.00$] and Experiment * Sentence Plausibility [$F(2, 152) = 3.00$, $p < 0.05$]. No other effects or interactions reached significant values.

The analysis on mean amplitudes of N400 revealed a main effect of Experiment [$F(1, 76) = 8.038$, $p < 0.01$]. This effect was modulated by the interactions between Experiment * Condition [$F(1, 76) = 7.25$, $p < 0.01$], Experiment * Sentence Plausibility [$F(2, 152) = 35.12$

$p < 0.01$], and, crucially, the triple interaction between Experiment * Condition * Sentence Plausibility [$F(2, 152) = 6.96$ $p < 0.01$] was also significant.

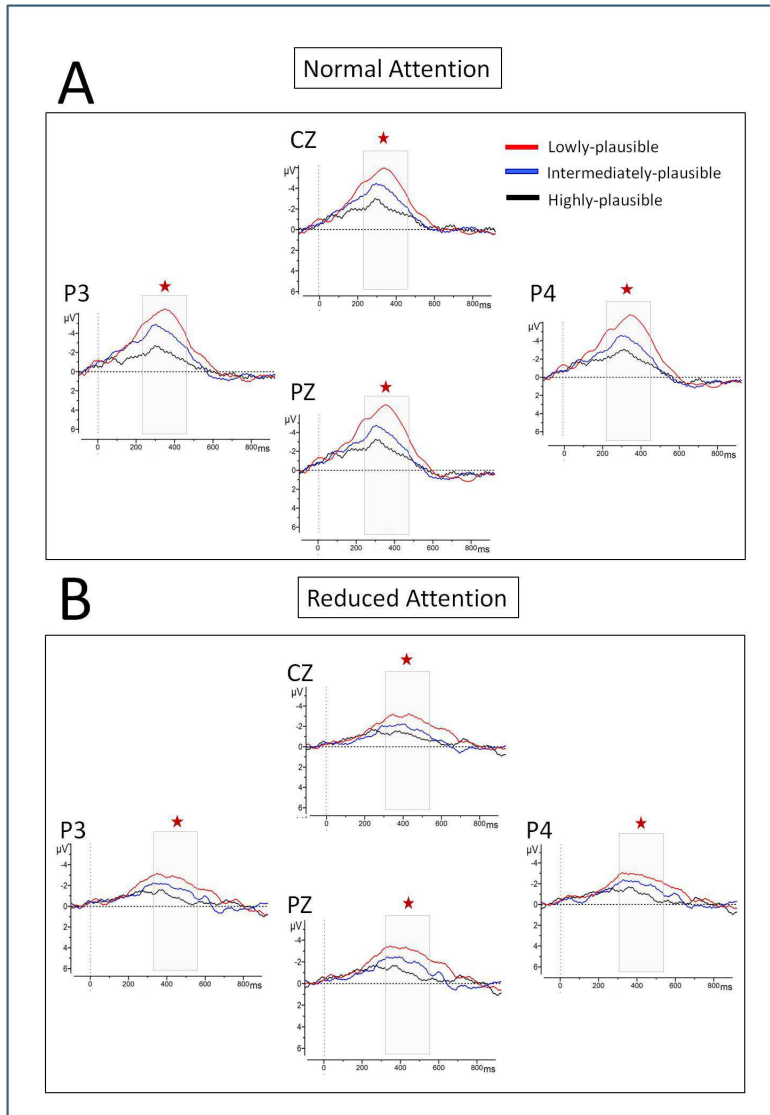


Figure 5. Modulation of N400 in Experiment 2 (Attentional conditions). Panel A shows the N400 modulations in the Normal

attention condition. Panel B shows the N400 modulations in the Reduced attention condition. The graph shows N400 modulation on central electrodes by each sentence type: highly-plausible (black), intermediately-plausible (blue), and lowly-plausible (red). The N400 was significantly different in each sentence type. Shaded area is showing the time window where the differences reached statistical differences.

To rule out the possibility that the different patterns observed in the Reduced attention and the Inferior conditions were due to overall reductions in amplitude in the Reduced attention condition, an additional analysis was performed normalizing scores. In this analysis, we considered the N400 responses to low plausibility sentences as the baseline for each Hierarchical or Attentional condition, and then computed the percentage of reduction of the N400 for each sentence condition (intermediate and high plausibility in comparison to its respective baseline). This new analysis yielded the same results as the previous one: there were equivalent differences between highly and intermediate - plausible sentences for all conditions, except when the sentences were uttered by the Inferior Speaker: (Normal attention [$F(1, 37) = 20.36$ $p < 0.01$]; Superior Speaker [$F(1, 39) = 31.65$ $p < 0.00$] Reduced attention [$F(1, 37) = 4.58$ $p < 0.05$]), Inferior Speaker ([$F(1, 39) = 1.36$ $p > 0.21$]).

The results of this experiment show that reducing attention to speech induces an overall reduction and delay in the N400 response, in line with previous research (33). Although the N400 response was significantly reduced, it showed the expected pattern

of reverse amplitude as a function of sentence plausibility both in the Reduced and the Normal attention conditions, indicating that sentences were semantically processed in both Attentional conditions. Important to our goals, the differences in the N400 responses for highly - plausible sentences when they were uttered by a low Status individual compared to the Reduced attention condition point to the direction that the pattern of results observed in experiment 1 reflected the brain's specific response to social information.

		SUPERIOR SPEAKER			INFERIOR SPEAKER		
		Highly plausible	Intermediately plausible	Lowly plausible	Highly plausible	Intermediately plausible	Lowly plausible
Experiment 1							
ERP responses	Mean of latency peak of N400 (ms)	360 ms ± 55	340 ms ± 51	370 ms ± 66	350 ms ± 40	347 ms ± 45	361 ms ± 65
	Mean amplitudes of N400 (250-450ms)(mV)	-2,28	-3,24	-5,94	-2,99	-3,07	-5,58
Behavioral	Reaction times (ms)	393ms ± 12	422 ± 12	348 ± 11	401 ms ± 14	430 ± 28	349 ± 26
		NORMAL ATTENTION			REDUCED ATTENTION		
		Highly plausible	Intermediately plausible	Lowly plausible	Highly plausible	Intermediately plausible	Lowly plausible
Experiment 2							
ERP responses	Mean peak of latency of N400 (ms)	312 ms ± 82	304 ms ± 51	338 ms ± 52	332 ms ± 87	368 ms ± 86	371 ms ± 81
	Mean amplitudes of N400 (250-450ms)(mV)	-2,46	-3,58	-5,76	-1,16	-2,09	-3,18
Behavioral	Reaction times (ms)	442ms ± 26	462 ms ± 22	416 ± 21	N/A	N/A	N/A

Table 1. Values of each type of ERP measure (latencies and mean amplitudes) in each sub set of sentences in each experiment.

4.6 Discussion

The present study investigated the brain's responses to sentences uttered by speakers whose social hierarchy was determined through their relative performance in a visual perception task. Although participants' overt responses concerning the plausibility of a sentence did not depend on who uttered it, participants were engaged in the task, as reflected by the modulation of the N400 component as a function of speakers' social hierarchy. Although the pattern of the N400 was the expected one for the case of the

superior speaker, a different pattern emerged when the speaker had a lower rank. Neural responses to highly-plausible sentences yielded increased N400 responses, matching those of intermediate-plausible sentences. A follow up experiment allowed ruling out the possibility that the increase in the N400 component for highly-plausible sentences uttered by low-ranking individuals simply reflected diminished attention to those speakers. Reducing attention to the sentences resulted in a general diminution of amplitudes of the N400 and in slower latencies in all sentence types (Kiefer & Brendel, 2006; Kutas & Federmeier, 2011; Relander et al., 2009) (see Table 1 & Fig.5).

As said, the N400 component has been thought to reflect the ease of semantic integration of a word into the global meaning of the sentence. We argued that participants would experience more difficulties integrating information coming from inferior speakers. Supporting this assumption, previous studies have shown that information that comes from non-reliable persons seems more difficult to integrate (van Berkum, Hagoort, & Brown, 1999; Van Berkum et al., 2008; White, Crites, Taylor, & Corral, 2009). Here we did not observe a general modulation but a very specific effect for low-status speakers.

The lack of hierarchical effects for low-plausible sentences likely reflects the fact that strong semantic inconsistencies are salient enough to make sentence interpretation difficult, regardless of the speaker. The reduced integration of highly-plausible words into the sentence meaning observed for inferior speakers could reflect the

emergence of an automatic prejudice leading listeners to consider inferior speakers as less reliable informants.

Given that we have used sentences describing probable or improbable situations, but not sentences with fixed truth-values, we favour an explanation of the present results in terms of participants' lack of trust in inferior speakers. This lack of trust could not be observed in intermediate and low probability sentences, as they were improbable, regardless of the speaker. Our results show that it does not matter who says a sentence such as "The Italian ate spaghetti with shoes" as it always will sound odd. Because participants considered low status speakers unreliable sources, high probability sentences became "suspicious" and therefore, less likely to be true. That is, to our participants it mattered who said sentences such as "Carlos bought an umbrella to protect himself from the rain", they found it less likely to be true (to integrate its meaning) if uttered by a low status individual. An alternative explanation (not excluding the preceding one) is that participants evaluated highly-plausible sentences uttered by low status speakers as unexpected situations. Particularly, we consider that the N400 modulation in highly-plausible sentences may reflect the impact of social evaluations, a form of social prejudice.

As mentioned, although we observed different patterns in the N400 responses as a function of the social status of the speakers, participants' overt responses were not affected by the social status. Previous studies on trust and trustworthiness using different economic games have reported that equivalent behavioural

responses (i.e., reaction times) can trigger dissociable ERP responses (Boudreau, McCubbins, & Coulson, 2009). The pattern of N400 modulations observed here is likely to reflect the automatic processing of sentences taking place before decisional mechanisms involved in the generation of overt responses. Overt responses, but not the N400, would be affected by decisional or post decisional mechanisms (Baetens, der Cruyssen, Achtziger, Vandekerckhove, & Van Overwalle, 2011; Osterhout, Bersick, & McLaughlin, 1997; White et al., 2009).

In contrast with other studies addressing the impact of trust, we observed social effects even when no information was given concerning the potential reliability of the speakers (they were just better or worse at performing a visual discrimination game). The usual way trust is studied is through the participants' involvement in joint action tasks, such as cooperation in economic games. Our results show that not only is interaction between participants not needed to elicit changes in trust, but that individuals over-generalize information from one domain (hierarchy in visual discrimination skills) to reliability of verbal utterances.

Finally, the present results may provide relevant information for educational practice. In many Western societies, the status of teachers has been challenged and downgraded. Indeed, there was a time when teaching commanded a serious status in the community, but in some places this is no longer the case. The countries that consistently achieve highest scores in educational attainment are those where teaching is held in highest social esteem. In Finland,

South Korea, and China, teaching is placed among the most respected professions. In these countries, teachers' status is high and students perceive and know this. Although effectiveness of educational systems is complex and multifaceted, the present results may indicate less effective teaching where teachers hold a low status. Indeed, the classical studies on social learning have shown that trust and confidence are crucial factors in human learning, cooperation, leadership and school effectiveness (Bandura, 1977; Rotter, 1945). The effects of low status may start very precociously as indicated by recent results on the development of trust. These studies have demonstrated that at as early as four years of age, infants do not treat the information provided by every person equally; they monitor the past accuracy of informants and use this information when deciding which informant to trust (Corriveau & Harris, 2009; Einav & Robinson, 2011; Harris & Corriveau, 2011; Jaswal & Neely, 2006). The questions of how early humans generalize status from one domain of knowledge to another, or whether information shared by inferior members may negatively influence the learning process are unanswered.

4.7 Acknowledgements.

This research was supported by grants from the Spanish Ministerio de Economía y Competitividad (PSI 2012 - 34071), (Consolider-Ingenio2010-CDS-2007-00012); and the Catalan Government (SGR 2009-1521).

5. CHAPTER FIVE

Social tuning of error monitoring and cognitive control in Obsessive Compulsive Disorder

Hernando Santamaría-García¹, Carles Soriano-Mas², Miguel Burgaleta¹, Alba Ayneto¹, Pino Alonso², José M. Menchón², Narcis Cardoner², Nuria Sebastián-Gallés¹

1. Center for Brain and Cognition, Universitat Pompeu Fabra, Barcelona, Spain.

2. OCD Clinical and Research Unit, Psychiatry Department, Hospital de Bellvitge-IDIBELL, Barcelona, Spain; CIBERSAM (Centro de Investigación Biomédica en Red de Salud Mental), Barcelona, Spain.

This article has been submitted for publication to JAMA Psychiatry (November 2013).

5.1 Abstract

INTRODUCTION: Obsessive Compulsive Disorder (OCD), a mental disorder mainly characterized by obsessive thoughts and compulsive behaviours, often entails a high sensitivity to social evaluations. These symptoms are related to alterations in performance monitoring functions such as error monitoring and cognitive control. Nevertheless, we have limited knowledge about how social environments affect such monitoring processes in OCD patients.

METHODS: In this study we experimentally created a previously validated hierarchical social scenario in which OCD and control participants performed a visual decision task while playing in presence of a simulated superior player (showing the highest performance) or inferior player (lowest performance). Event Related Potentials (ERP) were recorded during the task in order to evaluate the effect of the hierarchical environment on performance monitoring and as complementary analyses the effects of these social context on cognitive control and motor control.

RESULTS: We found a significant interaction between group and social hierarchy in all the four analyzed components (ERN, Pe, frontal N2 and LPR-r). Also, all components showed the same pattern of interaction. First, effects of social hierarchy were only observed in the patients group. Second, patients and controls only differed when playing in presence of the superior player, while showing equivalent responses in presence of the inferior player.

DISCUSSION: Our main results revealed that, for patients only, social context strongly modulated the Error-Related Negativity, an ERP component that is considered an endo-phenotype of OCD. Specifically, playing in presence of an inferior player reduced ERN signals to the levels observed in control participants. This effect was accompanied by OCD-specific social modulations of cognitive and motor control components (frontal N2 and Lateralized Readiness Potentials). Our results have important implications to understand how social context can directly affect cognitive

functioning in OCD; moreover, we consider that these findings could have an impact on the therapeutics.

5.2. Introduction

Obsessive Compulsive Disorder (OCD) is a mental disorder characterized by a disturbed fronto-striatal brain activity. Fronto-striatal circuits are essential for behavioral regulation mechanisms such as error monitoring, cognitive control and motor control – processes that have been postulated to be at the core of OCD alterations (Chamberlain, Blackwell, Fineberg, Robbins, & Sahakian, 2005; Dittrich & Johansen, 2013; Purcell, Maruff, Kyrios, & Pantelis, 1998; Trivedi et al., 2008). Indeed, behavioural evidence shows that OCD patients are impaired across a range of tests of inhibitory function such as cognitive inhibition and attentional set shifting tasks, and they display inability to inhibit motor tasks related to compulsive behaviour (Chamberlain et al., 2007; Penades et al., 2007; van den Heuvel et al., 2005).

As in other disorders with anxiety symptoms, OCD is also associated with an increased sensitivity to social evaluations, leading to impairments in social functioning (Calkins, Berman, & Wilhelm, 2013a; Carrasco et al., 2013; Peng et al., 2012). Indeed, OCD patients display disruptions in their ability to interact with other individuals and generally show inflexibility (Harrison et al.,

2012) and anxiety symptoms related to social evaluations (Boulougouris, Chamberlain, & Robbins, 2009; Chamberlain et al., 2008; Chamberlain & Menzies, 2009a; Grisham, Henry, Williams, & Bailey, 2010). A growing body of evidence demonstrates that people with anxiety symptoms and social worries, such as OCD patients, tend to adopt inferiority roles in social encounters, and they can respond to social dominance threat with signs of pronounced social submission, feelings of incompetence, pessimism and lack of self-efficacy (Johnson, Leedom, & Muhtadie, 2012; Maner, Miller, Schmidt, & Eckel, 2008).

Different studies have provided compelling evidence of the impact of social context on cognitive functioning in healthy subjects. To demonstrate such effects, researchers have focused mainly on the construct of social hierarchy, a key social domain that is involved in different biological processes such as survival, reproductive success, motivation and social behaviour regulation (Chiao et al., 2009; Cummins, 2000; R. M. Sapolsky, 2004). Recognizing and experiencing a role within a social hierarchy can influence a wide array of cognitive processes, such as sensory-perceptual mechanisms (Santamaría-García et al., 2013), decision making (Rilling JK, 2011) and feedback assessment (Boksem et al., 2012). Furthermore, recent research shows that assuming a social role may have an impact on some executive functions, namely, updating, inhibiting, planning and performing goal-focused tasks (Galinsky et al., 2006; Gruenfeld, Inesi, Magee, & Galinsky, 2008;

Huang et al., 2011; Smith et al., 2008; Whitson & Galinsky, 2008).

Given the altered social sensitivity of OCD patients, and because social hierarchy is known to affect in healthy subjects executive functions impaired in OCD, the current research addresses to what extent the social context may influence the fronto-striatal activity underlying core cognitive processes in OCD such as increased self-monitoring behaviours, difficulties in cognitive control and disrupted motor control mechanisms. For this purpose we will use Event-Related Potentials (ERP), an electroencephalographic technique known to reliably reflect error monitoring, cognitive control and motor control activity both in healthy subjects and patients. In particular, error monitoring activity is captured by the Error Related Negativity (ERN) and Error Positivity (Pe) components (Christ, Falkenstein, Heuer, & Hohnsbein, 2000; Danielmeier, Wessel, Steinhauser, & Ullsperger, 2009a; Falkenstein, Hohnsbein, & Hoormann, 1995; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000a) mechanisms of cognitive control and conflict adaptation can be measured by the frontal N2 (Folstein & Van Petten, 2008b) component; and finally motor control and inhibition processes are reflected in the Lateralized Readiness Potentials (LRP-r) (Ibanez et al., 2012; Melloni et al., 2012; Tollner et al., 2012).

Larger amplitudes in ERN and Pe have been reported in OCD patients, reflecting an amplified error-monitoring processing (Carrasco et al., 2013; Chamberlain et al., 2008; Fishman & Ng,

2013a). The ERN component is a robust, trait-like electrophysiological index of functioning of the error-detection system (including the anterior cingulate cortex) and is considered as a quantitative endophenotype independent of current diagnostic status or treatment effects (Chamberlain & Menzies, 2009a; Riesel, Endrass, Kaufmann, & Kathmann, 2011; Suchan, Jokisch, Skotara, & Daum, 2007). Additionally, the Pe component has been described as an index of awareness in detecting errors and it has been associated to activity in the posterior cingulate cortex (Endrass et al., 2010; Endrass, Koehne, Riesel, & Kathmann, 2013). These alterations in error processing underlie OCD's obsessive thoughts, concern over mistakes, high expectations from other people's evaluations and repetitive behaviours. Given the well established role of the ERN/Pe as a neuromarker of OCD, the main goal of this research is to assess to what extent the social context can modulate the OCD-specific error monitoring components compared to healthy subjects.

Furthermore, recent studies have suggested that probably disruptions in cognitive and motor control mechanisms also stem from OCD's fronto-striatal dysfunction. Larger amplitudes in N2 are associated to high conflict adaptation and improved cognitive control (Chamberlain et al., 2008; Dittrich & Johansen, 2013; Folstein & Van Petten, 2008b), and OCD patients show lower negativities in the N2 fronto-central component, which arguably reflect their impaired cognitive control skills (Dittrich & Johansen,

2013; Purcell et al., 1998). The LRP-r component, in turn, captures cognitive control processes that extend into immediate control of action, such as cancelling a prepared response encompassing response inhibition, response conflict, and error monitoring (Johannes, Wieringa, Mantey, Nager, Rada, Muller-Vahl, Emrich, Dengler, Munte, & Dietrich, 2001a; Tollner et al., 2012; Ulrich & Miller, 2001). Available evidence shows altered LRP-r in OCD patients, which has been hypothesized to stem as well from a dysfunctional fronto-striatal circuit, and likely underlies impairments in motor inhibition related to compulsive behaviour (de Wit et al., 2012; Menzies et al., 2007; Penades et al., 2007). Thus, a complementary goal in this research will be to explore how the social context can modulate the N2 and LRP-r components in OCD patients.

In this study a sample of OCD patients and healthy controls took part in an experimental implementation of a previously validated hierarchical social scenario (see (Santamaría-García et al., 2013; Zink et al., 2008)). During this paradigm, ERP data were recorded while participants played a game consisting on a difficult visual decision task (numerosity) in the presence of simulated inferior or superior players. Playing in presence of an inferior player was expected to confer a superiority position to the participant, whereas playing in presence of a superior player would have the opposite effect (Santamaría-García et al., 2013). Opponent's superiority or inferiority was first induced by means of profile

videos in which personal, work and academic achievements were presented. In addition, performance and ranking feedback was provided during the task and opponent's performance was simulated to be higher or lower than the participant's performance, for the superior and inferior player respectively.

We expected a different pattern of social modulation of ERN in patients and controls according to the social context where errors were performed, i.e., in presence of a superior or an inferior player (inferiority or superiority position, respectively). In addition, we also expected influences of social hierarchy in patients compared to controls on ERP components related to cognitive control (N2) and motor preparation (LRP-r). For OCD patients we expected lower amplitudes with the inferior player compared to the superior player for the ERN/Pe and LRP-r components, and the inverse pattern for the N2 component (denoting, respectively, reduction of error detection hyperactivity, enhanced motor control and better cognitive control when patients adopt a superiority position). Finally, we hypothesized that, if the social effect is indeed a key factor for OCD cognitive impairments, then the OCD pattern of brain activity when performing the task in a superiority position should tend to approach the brain activity levels observed for control participants.

5.3 Methods

Participants: Sixteen (right-handed) outpatients with OCD (8 females; mean age 35.25, range 27 – 40 years) were recruited from the OCD Clinic at the Bellvitge University Hospital (Barcelona, Spain). All patients fulfilled DSM-IV criteria for OCD (APA, 1984) for a period of at least one year. Diagnoses were made on the basis of structured interviews conducted independently by two trained psychiatrists using the Structured Clinical Interview for DSM-IV Axis I Disorders-Clinician Version (SCID-CV)(First et al., 1997). Exclusion criteria were age under 18 or over 65 years, psychoactive substance abuse/dependence (either current or in the past six months), mental retardation, psychotic or bipolar disorders, severe organic or neurological pathology, or any contraindication to MRI scanning. Comorbid major depression and other anxiety disorders were not considered an exclusion criterion provided that OCD was the main diagnosis and the primary reason for seeking assistance. All the patients had been taking stable doses of medication for at least 3 months prior to the time of scanning. Sixteen (right-handed) healthy controls from the same socio-demographic environment and with a comparable age and gender distribution (8 females; mean age 33.59; age range 29 – 40 years) were also included. Each control subject underwent the Structured Clinical Interview for DSM-IV non-patient version to exclude the presence of any Axis I psychiatric disorder. Remaining exclusion criteria were the same as

those applied to OCD patients. Table 1 provides the socio-demographic and clinical information of the study participants. Written informed consent was obtained from each study participant after a full description of the study, which was conducted in compliance with national legislation and the principles set out in the Declaration of Helsinki. The study was also approved by the ethics committee of Bellvitge University Hospital and for the ethics committee of the Center for Brain and Cognition of the Pompeu Fabra University.

Variable	Mean (SD), range
Age, yrs a	33.1 (8.3), 24-47
Gender, m/f b	37/32
Education, yrs c	13.75 (2.8), 5-19
HDRS	11.7 (4.8), 6-18
HARS	18.1 (4.4), 16-26
Age at onset of OCD, yrs	18.8 (7.9), 5-40
Duration of illness, yrs	12.8 (9.4), 1-45
Y-BOCS-Total	25.4 (2.4), 21-30
Comorbid mood/anxiety disorders	no. (% cases)
Bipolar disorder type II	1 (6)
Social phobia	1 (6)
Major depressive disorder	1 (6)
Medication at time of study	no. (% cases)
Medication-free (> 4 weeks)	2 (12)
Clomipramine	2 (12)
Escitalopram	5 (31)
Fluoxetine	2 (12)
Fluvoxamine	2 (12)
Sertraline	1 (6)
Paroxetine	1 (6)

Table 1. Clinical Characteristics of sixteen OCD patients

Abbreviations: HDRS, Hamilton Depression Rating Scale; HARS, Hamilton Anxiety Rating Scale; Y-BOCS, Yale-Brown Obsessive-

Compulsive Scale; DY-BOCS, Dimensional Yale-Brown Obsessive-Compulsive Scale.

Materials: In order to build the hierarchical social context we used a procedure validated in previous studies (Santamaría-García et al., 2013; Zink et al., 2008). We used brief videos to introduce simulated players' profiles and establish the initial hierarchical features, followed by an interactive game in which the participants performed a visual discrimination task in the presence of other (simulated) players and received updated information about both participant's and opponent's performance.

A total of eight different video profiles (approximately 2 min each) were created. The profiles crossed gender (male, female) and hierarchy (high, low status), and were interpreted by four confederates (two males, two females). Each confederate followed two scripts (high or low status) that presented the character's personal, work and academic achievements. Implicit cues related to the social superiority of the confederates were controlled to avoid substantial differences in age, facial expressions and attire. Each participant saw two video profiles, one for the superior player and one for the inferior player. Half of the participants saw the superior and then the inferior confederate, while the other half saw them in the reverse order.

Participants then performed the visual discrimination task in the context of a computerized game. The task was first performed in a

neutral context followed by the implementation of the task within a hierarchical social context, where participants performed the task in presence of two simulated players (see Fig. 1). One of the simulated players performed, on average, better than the participant, thus consistently holding a higher rank status. The other simulated player showed lower performance, and hence had a lower rank status. The status simulated during the profile videos was consistent with the simulated ranking during the game. The role played by confederates was counterbalanced across participants. Importantly, the nature of the game was non-competitive because the participant and the simulated players could win, lose or have different outcomes in the same trial. The whole experiment was designed to increase participants' feeling of being involved in a realistic game.

In each trial of the visual discrimination task, we presented two rectangles of red dots (of constant diameter, shape and brightness) on a black background, one at the top of the screen, and the other at the bottom. The two rectangles contained a different number of dots, and participants were asked to decide which rectangle contained more dots. The sum of the dots displayed in the two rectangles was 1000 dots, each rectangle having a different percentage of this total amount. The percentage of red dots was complementary between the rectangles (e.g., if one had 49% of the dots, the other had 51%; see Fig. 1). We created nine levels of dot percentages (44, 46, 48, 49, 51, 52, 54, 56). The visual

discrimination task and the dynamic game structure were designed using MATLAB version 7.9.0 (R2009b) with the Psychophysics Toolbox version 3.0.8.

Procedure: To control for possible interactions between gender and hierarchy, male participants played with male simulated participants, and female participants with females. Participants were first informed that they would play a visual decision game, and then were notified that their performance would be compared with that of the two players who already completed the task, and that all three players would be ranked depending on their performance during the game. The participants were told that their performance could be compared with that of future participants as well.

All participants were tested in an electrically-shielded testing room in the Neuroscience laboratories of the Center for Brain and Cognition (Pompeu Fabra University, Barcelona, Spain) where electro-encephalography (EEG) activity was recorded. Participants were situated approximately 50 cm in front of a 19-inch screen, at an angle of vision of around 35°. The experiment began after electrode application.

In order to be familiarized with the visual task, all the participants were required to perform 70 trials (see Fig. 1) of the task in a

neutral context. This set of trials was used as a baseline measure (“social-free” scenario) of the performance of each participant. Afterward, participants performed the visual discrimination task in the hierarchical social context. The game began right after training, including five blocks of 36 trials each (180 total, 90 in presence of each simulated player). In each block (approximately 5 min), the participants played nine consecutive trials in presence of a simulated player followed by nine trials in presence of the other simulated player, and this sequence was repeated once, followed then by the presentation of the updated ranking. Rank order was set by adjusting the superior or inferior player’s behaviour following the algorithm developed by (Santamaría-García et al., 2013).

Each trial of the game started with a 2 s presentation of the opponent’s photograph, along with three or one ranking stars (for the superior and inferior player respectively), followed by the visual discrimination task. The dot rectangles were presented for 1 s. Participants then decided which rectangle contained more dots and answered with the corresponding joystick movement (up or down) using their right hand. Behavioural Reaction times (RT) and accuracy were recorded. They were given feedback upon their response that stayed on the screen for 2 s. The feedback consisted of pictures of the participant with the opponent above, and the outcome (a coin meaning correct, an “X” meaning incorrect or a “time over” message) below. Both participant and simulated player

could win or lose in a trial. The trial ended with a fixation cross for 0.5 s. The participants could rest for up to 2 min between blocks.

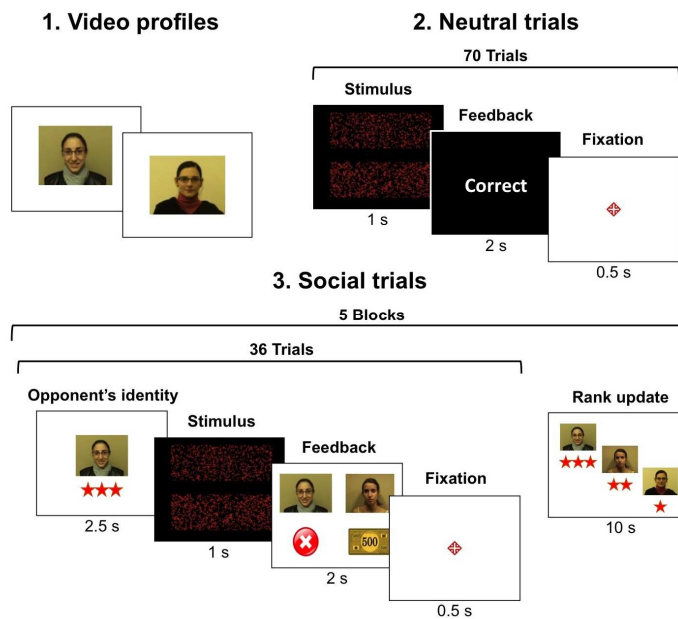


Figure 1. General Procedure. Two procedures built social hierarchy, the Social Videos and the Game session. During the Social Videos, two confederates simulated the superior and the inferior player. During the game session, participants first performed 70 trials in neutral context (here, hierarchical scenario was avoided). During the game phase, the participants performed a visual discrimination task while comparing their performance to the hierarchical players. Panel B shows the timeline during which the ERP components were studied. We evaluated stimulus- and response-locked potentials of the visual task.

EEG/ERP methods: The EEGs were recorded from 31 scalp sites. We placed two bipolar electrodes above and below each participant's left eye to record eye movements, two electrodes on the mastoids, and a reference electrode on the nose. The EEG

recordings were digitized at 250 Hz. All electrode impedances were below 3 KOhms. The EEG data were low- and high-pass filtered (30-0.03 Hz). We performed two types of analyses: Stimulus-locked (for N2 component) and response-locked (for ERN/Pe and LRP-r components) analyses. For stimulus-locked analyses, the EEG were segmented into 1100-ms epochs ranging from 100 ms before stimulus onset, to 1000 ms post onset. Before averaging, segments were baseline-corrected by subtracting the mean amplitude of the pre-stimulus interval (-100-0 ms). In the response-locked analysis, the EEG data was segmented into 1100-ms epochs ranging from 200 ms before response onset to 900 ms post response. Before averaging, segments were baseline-corrected by subtracting the mean amplitude of the pre-stimulus interval (-200–50 ms) as done in previous studies (Falkenstein et al., 1995; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000a). All the EEG data were semi-automatically screened offline for eye movements and muscle artefacts. The segments containing such artefacts were rejected: We rejected a similar proportion of segments (around 5%) in both groups (patients and controls).

Error monitoring components: The ERN component was studied in the time window 50-200 ms after error-response, and the Pe component was analyzed between 500-650 ms upon error-response. Both components were studied in the same group of frontocentral electrodes (F3, F4, FZ), following previous studies (Carrasco et al., 2013; Endrass et al., 2013; Falkenstein et al., 1995;

Falkenstein, Hoormann, Christ, & Hohnsbein, 2000a; Fishman & Ng, 2013a). Mean amplitudes in these electrodes were averaged. Note that we previously found no significant differences in modulation of ERN and Pe in these electrodes ($p > 0.1$).

Frontal N2 component: The frontal N2 component was studied in the range of 250-350ms after stimulus onset, in frontocentral electrodes (FZ /F3/F4 and CZ). We chose these sets of electrodes and time windows based on the topographical distribution of grand averaged ERP activity and on previous studies (Folstein & Van Petten, 2008a; Ibanez et al., 2012). Mean amplitudes in these electrodes were averaged, as no significant differences in modulation of N2 were found between these electrodes ($p > 0.1$).

Lateralized Readiness Potentials: LRP-r waveforms were calculated using the difference in contralateral-ipsilateral activation for C3 and C4 electrode pairs in each hemisphere, following previous studies (Tollner et al., 2012; Ulrich & Miller, 2001). LRP-r components were computed using a baseline of -800 to -600 ms for response-locked averages. Given that participants used their right hand to respond, we computed a contralateral (C3) – ipsilateral (C4) difference waveform. Such waveform was extracted separately for each condition (trials in presence of superior player vs. trials in presence of inferior player). LRP-r amplitudes and latencies were measured from the resulting difference waves. As recommended by Mille et al., 1998 (Miller, Patterson, & Ulrich, 1998), we used the 90% of the maximum LRP-r activation as optimal criteria for defining LRP-r onset latencies. The amplitudes

of the LRP-r were calculated by averaging five sample points before and after the maximum deflection obtained in the time window of 100-20 ms pre-response. We controlled noise on latency measure using a low-pass filter prior to the latency measures (Gaussian impulse response function, half-amplitude cut-off =23.2 Hz, full width at half maximum =18.8 ms), furthermore, incorrect trials and trials with artefacts were excluded prior to averaging following previous studies (Tollner et al., 2012; Ulrich & Miller, 2001).

Statistical Analyses

Separate analyses of variance (ANOVA) on the amplitude and latency of each component were conducted with Group (patients vs. controls) as between-subjects factor, and Hierarchy (superior and inferior) as within-subjects factors. For the sake of completeness, we used a similar design to study potential effects over behavioural measures (RT and accuracy).

5.4. Results

Analyses were performed on the latency and amplitudes of the different components. Significant results were only observed in the analyses on the amplitude of the different components.

Effects of Group (patients vs. controls) over ERP components

A significant main effect of Group was observed for the amplitudes of all components (ERN: $F_{1, 31} = 6.32$, $p < 0.01$; Pe: $F_{1, 31} = 7.02$, $p < 0.01$; N2: $F_{1, 31} = 5.67$, $p < 0.01$; LRP-r: $F_{1, 31} = 4.54$, $p < 0.01$) (See Fig. 2).

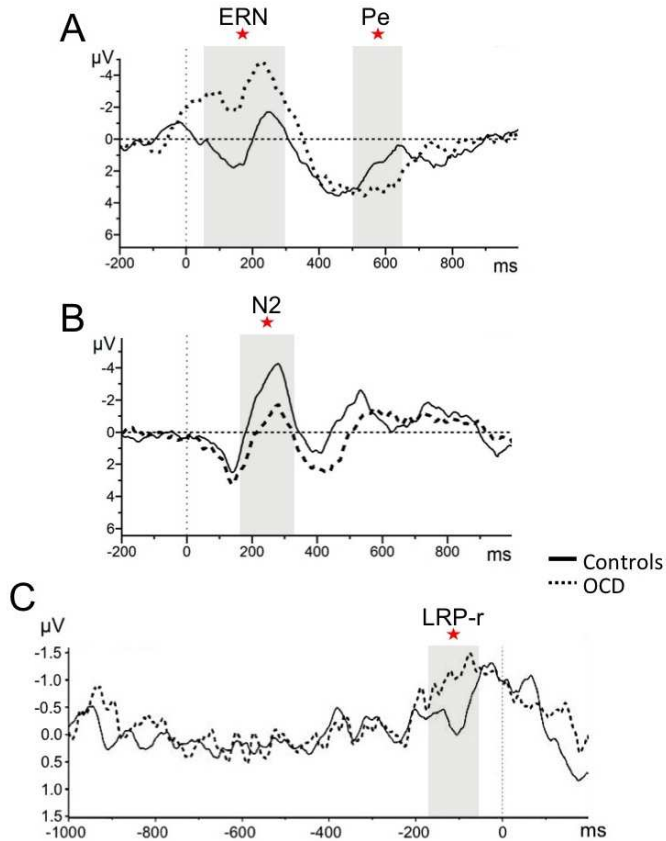


Figure 2. Baseline differences between OCD patients and controls in ERN/Pe, N2 and LRP-r. Group differences (patients vs. controls) for ERN and Pe (Panel A), N2 (Panel B) and LRP-r (Panel C). Larger amplitudes were found for patients compared to controls in ERN/Pe and LRP-r, whereas controls displayed higher N2 amplitudes than patients. * $p < 0.05$.

Group-by-Hierarchy interactions over ERP components

The Group by Hierarchy interaction was significant in all the four analyzed components (all $p < 0.01$). Also, all components showed the same pattern of interaction. First, effects of social hierarchy were only observed in the patients group. Second, patients and controls only differ when playing in presence of the superior player, while showing equivalent responses in presence of the inferior player (table 2 displays the different statistical values, see also figures 3, 4 and 5).

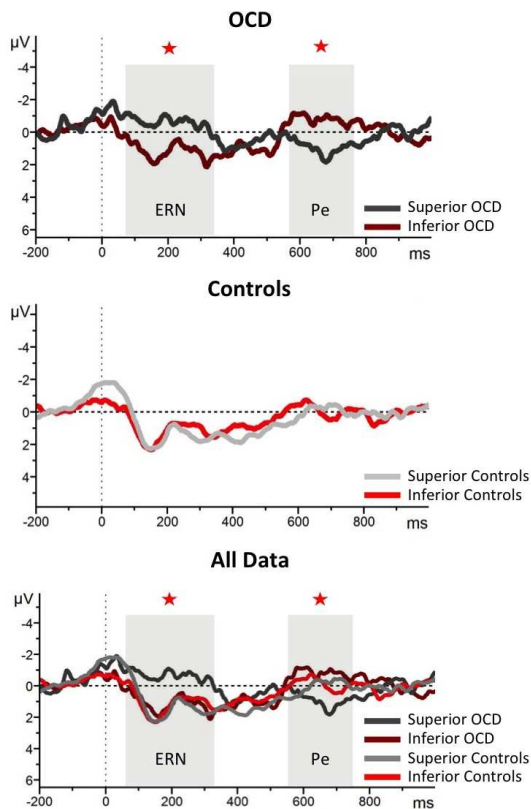


Figure 3. Social effects on Error-Monitoring processes

Panel A shows modulations on the ERN and the Pe components elicited by social hierarchy. Shaded areas indicate significant differences ($p < 0.05$). Panel B shows no significant effects of

Hierarchy in controls. For visualization purposes, panel C shows panels A and B superimposed, illustrating the significant Group x Hierarchy interaction for both ERN and Pe components. Squared regions indicate the windows of significant interactions ($p < 0.05$).

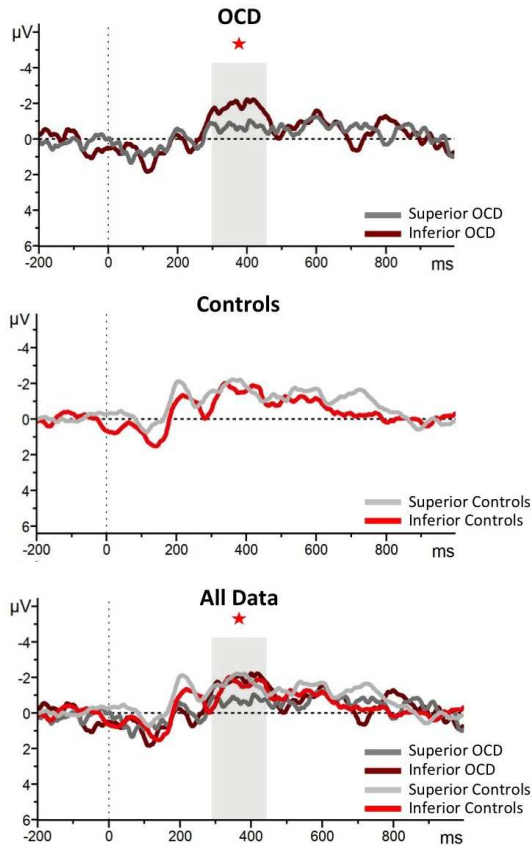


Figure 4. The effects of the presence of social hierarchy on N2 component. Panel A and B show effects of social hierarchy on N2 component in fronto-central electrodes for patients and controls, respectively. Shaded areas indicate significant differences ($p < 0.05$). For visualization purposes, panel C shows panels A and B superimposed, illustrating the significant Group x Hierarchy interaction for N2 amplitudes. * $p < 0.05$.

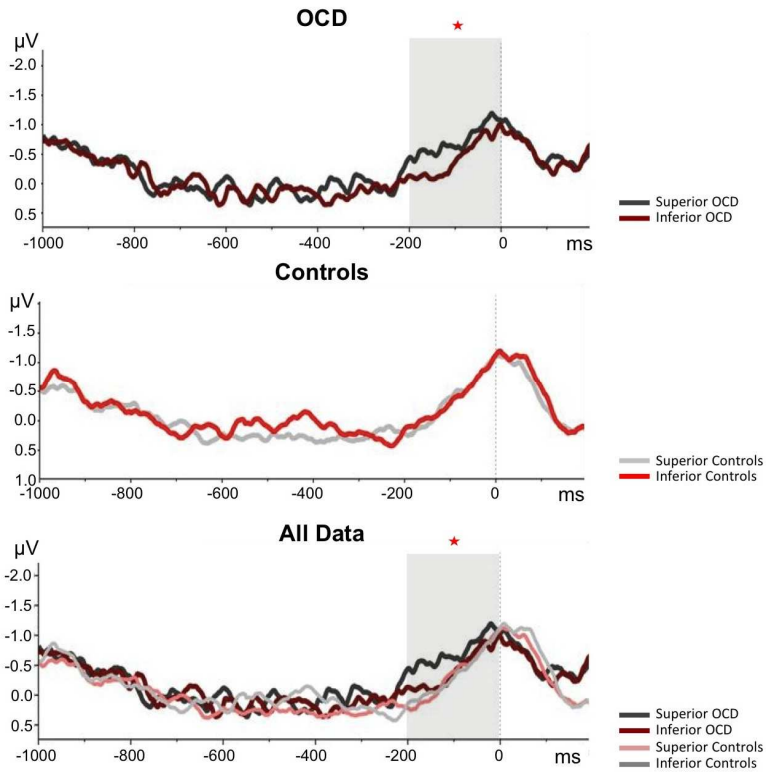


Figure 5. The effects of the presence of social hierarchy on a perceptual decision-making task. Lateralized Readiness Potentials (response-locked) LRP-r.

Panel A and B shows the waveforms elicited in LRP-r for patients and controls, respectively. In the patient group, but not in controls, we observed statistical differences on LRP-r amplitudes between trials played with the superior and with the inferior player. For visualization purposes, panel C shows panels A and B superimposed, illustrating the significant Group x Hierarchy interaction for both ERN and Pe components. * $p < 0.05$.

Behavioural effects

As an ancillary aside, we performed separate 2 x 2 ANOVAs (Group x Hierarchy) for accuracy and RT during the visual discrimination task. The analysis of accuracy rates yielded a main effect of Group ($F_{1, 31} = 8.44, p < 0.001$). On average, we observed lower accuracy in the patient group. No other effects or interactions reached significant levels. There was however a trend for the main effect of Hierarchy in OCD, suggesting a better accuracy in trials performed with inferior player ($p < 0.1$)(see Fig. 6). With regard to the RT analysis, we also observed a Group effect ($F_{1, 31} = 6.29, p < 0.01$). On average, OCD patients were slower than healthy controls. No other effects or interactions reached significant levels (see Fig. 6).

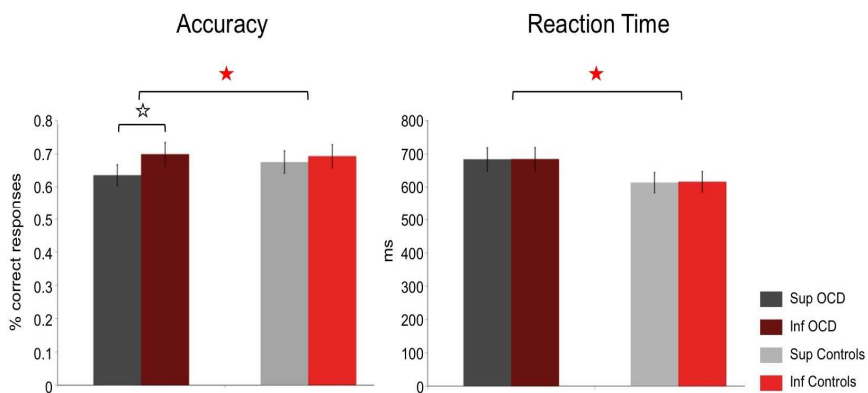


Figure 6. Behavioural effects of social hierarchy on participants' performance: The left side shows the average accuracy scores for each group (OCD patients and controls) and hierarchical condition (trials played with a superior player and trials played with an inferior player). We observed a main effect of Group ($p < 0.05$). A trend-level effect of Hierarchy was found for the OCD group ($p < 0.1$) (black star). The right side shows the average RTs for each group and hierarchical condition. We also observed a main effect of Group ($p < 0.05$). Error bars represent s.e.m. * $p < 0.05$.

ERP component		OCD		Controls		Stat.	Group*Hierarchy	Planned t-test	
		Superior	Inferior	Superior	Inferior			OCD_sup > Controls_sup	OCD_inf > Controls_inf
ERN	Mean	-1.21	1.57	1.54	1.57	<i>F</i> _{1, 31} = 7.95,		<i>t</i> (1, 15) = 4.93	<i>t</i> (1, 15) = 0.28
	SD	2.8	2.3	2.5	2.7	Sig. <i>p</i> < 0.01		<i>p</i> < 0.01	ns
Pe	Mean	1.52	-0.74	-0.52	-0.49	<i>F</i> _{1, 31} = 5.97,		<i>t</i> (1, 15) = 2.02	<i>t</i> (1, 15) = 0.59
	SD	2.2	2.1	2.0	2.2	Sig. <i>p</i> < 0.05		<i>p</i> < 0.05	ns
N2	Mean	-0.05	-1.99	-1.92	-2.01	<i>F</i> _{1, 31} = 6.73,		<i>t</i> (1, 15) = 2.01	<i>t</i> (1, 15) = 0.40
	SD	4.1	4.4	3.8	3.6	Sig. <i>p</i> < 0.01		<i>p</i> < 0.05	ns
LRP-r	Mean	-0.65	-0.29	-0.21	-0.19	<i>F</i> _{1, 31} = 3.83,		<i>t</i> (1, 15) = 2.05	<i>t</i> (1, 15) = 0.82
	SD	0.9	1.0	1.1	1.2	Sig. <i>p</i> < 0.05		<i>p</i> < 0.05	ns

Table 2. Mean amplitudes and statistical values of each component in each group.

5.5. Discussion

Can social context influence the core cognitive processes involved in the physiopathology of OCD? More specifically, how does a social hierarchy scenario affect OCD's fronto-striatal alterations such as error monitoring, cognitive control and motor control processes? Here we addressed these questions by analyzing ERP data in a social hierarchy context, and observed striking differences

between OCD patients and healthy controls in the way contextual social information modulates error-monitoring, cognitive control and motor control brain activity. Crucially, performing a visual discrimination task in a superiority position reduced the levels of aberrant ERP signals in OCD patients to match the normal brain activity patterns of healthy controls. The following paragraphs will discuss these results in detail.

Error monitoring disruption is known to be crucial to explain the symptoms in OCD (Carrasco et al., 2013; Endrass et al., 2010; Melloni et al., 2012). Unsurprisingly, we found larger amplitudes in the ERN and Pe components in patients when compared to healthy controls, consistently with the usual pattern reported in previous studies (Carrasco et al., 2013; Endrass et al., 2010; Endrass et al., 2013) (see Fig 2). Amplified error signals (larger ERN and Pe) in OCD have been hypothesized to underlie obsessive thoughts, concern over mistakes, high expectations from people's evaluations and repetitive behaviours (Chamberlain et al., 2008; Chamberlain & Menzies, 2009b). Hyperactivity in a fronto-striatal network comprising the orbitofrontal cortex, the anterior cingulate cortex and the basal ganglia (BG), among other areas (Calkins, Berman, & Wilhelm, 2013a; Carrasco et al., 2013; Chamberlain et al., 2008; Chamberlain & Menzies, 2009b; Harrison et al., 2012; Melloni et al., 2012; Piras et al., 2013) is linked to excessive generation of internal error signals, higher self-supervision and susceptibility to external evaluations, giving rise to the

characteristic symptoms of OCD (intrusive, obsessive and ruminative thoughts) (Barclay, Bransford, Franks, McCarrel, & Nitsch, 1974; Chamberlain et al., 2008; Segalas et al., 2013; Vriend et al., 2013).

Crucially, whereas normative baseline differences (during neutral trials) were observed between patients and controls in the ERP-based cognitive functioning. Crucially, we observed social effects on error-monitoring processes, reflected in ERN and Pe modulations (see Fig.3). Lower ERN and Pe amplitudes displayed by patients in the presence of an inferior player is consistent with an explanation assuming that OCD patients are highly sensitive to the social context and that their abnormal error sensitivity and awareness is reduced when adopting a superiority position. In healthy populations there is evidence suggesting that different emotional, affective or motivational factors might affect the amplitude of the ERN response (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000b; van Veen & Carter, 2006). For instance, the ERN may be influenced by certain personality traits characterized by a higher emotional reaction to errors (e.g., high neuroticism) (Fishman & Ng, 2013b)., Consistently, our results suggest that social context is of special value in the specific case of OCD patients, so that increased social sensitivity translates into a higher emotional load associated with the hierarchical scenario. Facing an inferior opponent (when the patient has a superior role position) may indeed decrease social anxiety and/or impact the emotional

evaluation of the social context, thus reducing abnormal error-monitoring processes. This interpretation fits well with the fact that ERN responses in OCD elicited during the game in presence of the inferior player were not significantly different from ERN responses in controls. In other words, adopting a superiority role diminished OCD patients' ERN signals to those levels observed for healthy participants. Conversely, the fact that we did not observe significant social effects in the control group may be explained by the non-competitive nature of the game (both the participant and the simulated player could win or lose a trial simultaneously), which may not exert an emotional pressure of enough magnitude as to influence their error monitoring processes. As we have mentioned before, there are several studies showing effects of social hierarchy in how a stimulus is processed. In contrast, in OCD patients social hierarchy affected the core cognitive processes involved in physiopathology of OCD, namely the performance monitoring mechanisms.

We moved one step beyond by showing that social effects were not specific to the ERN, but extended into components indexing cognitive and motor control. To measure cognitive control we focused on the frontal N2 component (Folstein & Van Petten, 2008a; Yeung, Botvinick, & Cohen, 2004). We confirmed previous evidence showing that OCD patients display lower negativities in the N2 fronto-central component, indexing poor cognitive control and conflict adaptation (Dittrich & Johansen, 2013; Folstein & Van

Petten, 2008a; Melloni et al., 2012). Importantly, whereas no effects of social hierarchy over N2 amplitudes were found in controls (consistently with our previous work (Santamaría-García et al., 2013), patients exhibited larger N2 amplitudes in presence of inferior players than in presence of superior players. As it was the case for the ERN results, it is of note that OCD-specific amplitudes of frontal N2 in presence of inferior players were not significantly different from the N2 amplitudes observed in healthy controls.

Regarding our motor control analyses, we observed larger LRP-r amplitudes in OCD patients vs. controls during the neutral trials confirming the difficulties in motor inhibition and motor control mechanisms (larger LRP-r amplitudes in OCD vs. controls) in these patients (Johannes, Wieringa, Mantey, Nager, Rada, Muller-Vahl, Emrich, Dengler, Munte, & Dietrich, 2001b). Interestingly, and following the pattern of results found for ERN/Pe and N2, OCD-specific social hierarchy modulations on the LRP-r provided additional information about how social context affects control mechanisms in patients, extending into motor preparation and motor control mechanisms (Johannes, Wieringa, Mantey, Nager, Rada, Muller-Vahl, Emrich, Dengler, Munte, & Dietrich, 2001b). The social context significantly modulated LRP-r, so that performing the task in presence of an inferior player induced LRP-r signals that were equivalent to those observed for controls. This effect suggests enhanced motor control and inhibition when the patients had a superiority social role with respect to the simulated player.

This result can be interpreted in light of recent evidence demonstrating a tight coupling between emerging decision variables and preparatory activation in cortical motor areas. Indeed, activity in the pre-supplementary motor area (pre-SMA) is correlated with the amount of accumulated evidence in decision phases (Gluth, Rieskamp, & Buchel, 2013; Tollner et al., 2012). Lower LRP-r amplitudes in presence of the inferior player could therefore be indicative of decreased accumulation and demands of motor evidence in a social context where patients had a higher social position, leading to an increased motor inhibition process in this context.

It is noteworthy that patients displayed a similar pattern of ERP modulations in neutral trials as in trials performed in presence of a superior player. Given the high social sensitivity of OCD, patients likely assume a submissive role by default and the mere fact of participating in an experimental situation (allegedly a social scenario of implicit performance evaluation per se) would have a negative effect over their error monitoring and cognitive/motor control functioning. Of special interest is that, whereas the OCD-specific amplified ERN is considered as a reliable measure of baseline alteration of the error-detection system, our results raise the question of whether the standard “testing” assessment in this population already represents a scenario of social pressure that could account for the increased ERN signal. This possibility has

important implications regarding the integration of social factors in the assessment and pathophysiology of OCD.

At the behavioural level we observed a trend in performance suggesting a better accuracy in trials performed with inferior players in OCD patients. Although behavioural information is not very informative in this context (as it is not able to disentangle the main cognitive processes of interest as is the case with the ERP technique), this result suggests a potential transfer from the experimental social setting to the actual patient's behaviour, which opens the door to additional research on the impact of the social context on the behavioural OCD symptoms as well as on therapeutic options based on the simulation of this kind of social scenarios.

Here we observed a social modulation of three key cognitive processes in OCD, yet the specific way in which such processes interact in a social context remains to be determined. Previous research has shown that ERN, N2 and LRP-r interact among each other (Danielmeier, Wessel, Steinhauser, & Ullsperger, 2009b; Rodriguez-Fornells, Kurzbuch, & Munte, 2002; Yeung & Cohen, 2006), but no causal relationships have been postulated. It might be the case that a more effective cognitive control in a superiority position would be followed by an increased motor preparation and a decreased post-response error monitoring. Equally, decreased error-monitoring may lead to decreased difficulties in cognitive

control and motor inhibition. Disentangling the cognitive chain of events underlying the social modulations of action monitoring and control in OCD should be object of further research.

Finally, our results open the door to further investigating to what extent social, emotional or motivational factors can modulate a component postulated as an endo-phenotype in OCD. The reported effects suggest that OCD patients could benefit from social relationships where they can adopt powerful or superiority roles; by contrast, submissive scenarios may be a source of increased anxiety and concerns over mistakes, likely disturbing their cognitive functioning. Additionally, it is of note that the social effects described here could be common to different disorders involving fronto-striatal hiperactivity, and further research will be necessary to ascertain whether the observed social modulations are OCD-specific. Research in this field would provide new evidences about how neuro-cognitive function is modulated by the social context, and it can have important implications for the therapeutic choices.

5.6. Conclusion

All in all, we observed that in OCD patients, error-monitoring processes were importantly modulated in the presence of a social

hierarchy. To our knowledge, this is the first evidence showing social effects on ERN in a group of patients with disrupted error monitoring processes. Here we provide novel evidence showing that the functioning of the error-detection system in OCD is affected by the presence of a social context, likely suggesting a modulation of the activity of the fronto-striatal network (Chamberlain & Menzies, 2009b; Melloni et al., 2012) by experiencing social role in a hierarchy. Furthermore, this effect extends into relevant neuromarkers of cognitive and motor control. This profile of alterations is consistent with the sensitivity to social evaluations described in OCD (Bystritsky et al., 2001; Calkins, Berman, & Wilhelm, 2013b) and contributes significantly to our understanding of how the social environment of OCD patients impacts cognitive processes.

5.7. Acknowledgements

This research was supported by grants from the Spanish Ministerio de Economía y Competitividad (JCI-2009-04492; SEJ2009-09072; SAF2010-16085; Consolider-Ingenio2010-CDS-2007-00012), the Carlos III Health Institute (PI09/01331, PI10/01753, PI10/01003, CP10/00604, CIBER-CB06/03/0034) and the Catalan Government (SGR 2009-1521 and 2009-1554). C. Soriano-Mas is funded by a 'Miguel Servet' contract from the Carlos III Health Institute (CP10/00604). N. Sebastián-Gallés received the "ICREA Acadèmia" prize for excellence in research, funded by the Generalitat de Catalunya. We thank Mario Pannunzi for his assistance with the development of the computerized game used here.

6. DISCUSSION

In this dissertation, we analyzed how and when cognitive and social processing interacts. Through several studies, we showed that social information has a selective influence of cognitive processing and it affects even early stages of stimuli encoding processing where only automatic (low-level) processing is thought to take place.

The articles that compose this dissertation provide new insights on how social and cognitive processes interplay in two different contexts, namely, in presence of stimuli with implicit social information (first article), and crucially, in presence of socially neutral stimuli (a visual discrimination task and a sentence comprehension task, in the second and third articles, respectively). Lastly, we analyzed the interplay between social and cognitive factors in patients with high susceptibility to social evaluations such as OCD patients.

In the following, I summarize the main results of each empirical article. In the remaining sections I discuss the findings of all the experimental studies and I propose some future directions for this research.

6.1. Summary of findings

Neuroanatomical substrates of the recognition of social hierarchy in humans.

In this article, we conducted a research to explore the recognition process of implicit hierarchical stimuli. That is, human faces accompanied by hierarchical cues depicting different hierarchical roles (one star for an inferior individual and three stars for a

superior individual). We combined ERP and structural MRI analyses to elucidate how early hierarchical stimuli are recognized and which neuroanatomical structures are involved in this recognition. Based on previous studies showing the high relevance of social roles in human behaviour, we hypothesized an early recognition of social hierarchy mediated by the morphology of brain areas implicated in an automatic processing of social stimulus.

Following our predictions, hierarchical information affected the amplitude of the N170 component, a specific face recognition component. Furthermore, the social modulation of the N170 component correlated with the morphology (volume and thickness) of a network of dorsal brain areas, formerly described as implicated in the automatic processing of implicit social features of faces. This network includes the superior temporal gyrus/sulcus, the posterior cingulate cortex, the anterior ventral temporal cortex at cortical level, and the caudate nucleus at subcortical level. We conclude that the early processing of social hierarchy recognition (as captured by the N170 component), is reflecting the first stages in the inference of social identity, and that there is a relationship between individual differences in the hierarchical effect, as measured by the N170, and the morphology of brain regions associated with the automatic processing of social information.

The role of social hierarchy on perceptual processes

This research was conducted to evaluate the effects of the social context on the processing of a socially neutral task. We combined behavioural and ERP analyses to elucidate how early the interplay between cognitive and social factors takes place in the processing of a socially neutral visual discrimination task.

First, we observed that the presence of the social context influences participants' performance. In particular, we found that participants were faster, maintaining a similar accuracy level, when performing the task in the presence of a superior player. Second, the analyses of the ERP data allowed us disentangle what stages of the information processing chain are more influenced by the social context, either the perceptual stages or the decisional stages. Importantly, we only observed social effects on the amplitudes of early ERP components (N1 and early phases of the P300 components), usually implicated in the perceptual encoding of stimuli. Additionally, the absence of social effects on response-related ERP components, together with the results of a computational modelling of participants' responses provided converging support that most probably social context plays a role only in the perceptual encoding stages.

Effects of speaker's social hierarchy on sentence comprehension process

In this study we analyzed if the social rank of a speaker could influence how listeners process and understand a verbal message. We used behavioural and ERP responses to analyze how listeners listened to sentences of different values of plausibility (highly, intermediately and lowly plausible) uttered by speakers of different social rank (superior and inferior ranks).

We observed that participants' overt responses concerning the plausibility of a sentence did not depend on who uttered it. However, we observed important modulations on the N400 component (a component related to the degree of semantic integration) as a function of the speakers' social hierarchy. The expected pattern of the N400 response (an inverse relationship between sentence plausibility and N400 amplitude) was found for sentences uttered by the superior speaker. However, we observed a different pattern of N400 responses when an individual with low social rank uttered the sentences. In this case, the neural responses to highly plausible sentences yielded increased N400 amplitudes, matching sentences of intermediate plausibility. In a follow up study, we discarded that the presence of social effects on the N400 were only due to changes in the attention level. Therefore we concluded that participants experienced more difficulties to integrate highly plausible sentences uttered by inferior speakers. We favoured an interpretation of the differences in the N400 component when uttered by a high or a low rank individual as reflecting the emergence of an automatic social

prejudice leading listeners to consider inferior speakers as less reliable informants.

Social hierarchy tunes error monitoring and cognitive control in patients with Obsessive Compulsive Disorder.

In our final study, we evaluated to what extent social context affects the cognitive processes in patients in whom it has been reported a high sensitivity to external social evaluations, such as of OCD patients. To this purpose, we combined behavioural and ERP analyses to evaluate how patients and healthy controls process a neutral visual discrimination task in presence of a social context (an adaptation of the task developed in the second experimental series of this dissertation – chapter three).

Our data clearly showed a contrasting pattern of effects between OCD patients and healthy controls. In OCD patients, the social context selectively affected the core cognitive processes involved in the pathophysiology of OCD, namely the error monitoring process, cognitive control and the motor inhibition process. Only in OCD patients, the social context strongly modulated the Error-Related Negativity, an ERP component that is considered an endophenotype of OCD. Importantly, playing in presence of an inferior player reduced ERN signals to the levels observed in control participants. This effect was accompanied by OCD-specific social modulations of cognitive and motor control components (frontal

N2 and Lateralized Readiness Potentials). Because performing the task in presence of an inferior player induced patients' ERP waveforms match those found in healthy controls, we concluded that experiencing a superiority position reduced excessive error monitoring activity and enhanced cognitive and motor control mechanisms.

6.2 Towards an integrated conceptualization of cognitive and social processing

Our results highlight the importance of social information in the modulation of highly selective neurocognitive processes. First, the results of the first article support that humans integrate early in the processing the social features in presence of implicit hierarchical stimuli. These results are in agreement with previous studies that support that humans quickly recognize hierarchical features in natural stimuli such as human faces and even in external abstract symbols as medals or stars. However, our results go one step forward linking the early recognition of social hierarchy (as early as 170 ms) with the morphology of a network of brain areas implicated in the automatic processing of social stimuli. Given that in our daily life we are constantly facing social stimulus and as we have said, this recognition allows regulate our social

behaviour it is understandable the presence of an early and automatic integration of these social features.

Probably, the central contribution of the present dissertation is to show that even in the processing of socially neutral stimuli (patterns of dots in the visual discrimination and neutral sentences in the language comprehension task) the social context modulates early phases of the information processing, thus affecting the way in which the stimuli are encoded.

So far, different approaches in Cognitive Psychology (Gazzaniga, 2013; Osherson, 1981; Shettleworth, 2012; Treisman & Kanwisher, 1998) have postulated that the adult brain may process social information in a globally modular and sequential way, with social information usually integrated in the late phases of the processing. These approaches basically postulate the existence of more "peripheral" processes, in which the sensory and perceptual encoding of stimulus are integrated first, while the contextual information associated to a stimulus is only integrated afterwards, even if the stimulus has implicit social marks. Following this view, when we see an image of a country flag, for instance, an individual should first integrate the formal aspects of this image (size, colour, shape, etc), and, only after that, integrate the contextual information related to this object (i.e., feeling associated to the flag of Colombia). Similarly, in the field of speech perception, it has always been postulated that the acoustic, linguistic and formal

aspects of language are processed first, and only afterwards, the pragmatic aspects of language (such as social information or identity related to voices).

Our results challenge this line of argumentation and suggest that social information is probably integrated in parallel with other types of information. In fact, in the second article (chapter three) we showed that even in the processing of socially neutral stimuli (dots in a visual discrimination task), the social context mainly modulates the perceptual stages of the information chain. Along this vein, in the third article (chapter four) we provided evidence showing that the social context also has an impact on how neutral sentences are processed. Although the social context did not affect participants' overt responses, we observed that participants processed the sentences depending on speakers' social status. It is important to highlight that independently of the type of task (visual discrimination or sentence comprehension) the social context mainly modulated early stages of the processing, where stimuli are encoded rather than late stages of processing that are more related to decisional or mechanisms of response re-evaluation.

The study of OCD patients also supports that social effects are highly selective, i.e. affect specific aspects of the processing. The presence of a social hierarchy in OCD patients resulted in a particular modulation of those re-evaluation processes, particularly involved in the physiopathology of the OCD, such as error

monitoring, cognitive control and motor inhibition control. The previous literature has suggested that individuals with anxiety symptoms and social worries, such as OCD patients, tend to adopt inferiority roles in social encounters, and they can respond to social dominance threat with signs of pronounced social submission, feelings of incompetence, pessimism and lack of efficacy. We observed that social context modulated neuromarkers of abnormal cognitive functioning in OCD patients, including the ERN which is considered an endophenotype of OCD. Furthermore, we observed that when OCD patients performed the task in presence of inferior individuals had similar ERP responses to those found in healthy controls. Thus, we conclude that experiencing a superiority position reduced excessive error monitoring activity and enhanced cognitive and motor control mechanisms. To our knowledge these results may have important consequences to the study of the role of social factors in other mental disorders. A deep understanding of how social information can help in maintaining or controlling symptoms in mental disorders may give a strong alternative to the symptom-driven classification of mental disorders as provided by traditional Psychiatry and it could open the door to investigate new therapeutic choices.

The present dissertation does not provide information about how much of the reported hierarchy-induced effects are due to changes in arousal or attention. Nevertheless, we have provided convincing evidences suggesting a high selectivity and specificity of social

effects on cognitive process. If the social effects were only due to attention or arousal, we should have found a general and nonspecific modulation of different ERP components usually affected by these factors (like the P1 or N2, or the late phases of the P300 in the case of the visual discrimination task). Furthermore, in the third study (social effects on sentence comprehension, chapter four) the results of a follow up experiment (Experiment 2) ruled out the possibility that the effects related to speakers' social hierarchy simply reflected changes in the attention level to the speakers.

6.3 Future Directions

Social hierarchy vs. social reward

Further research is needed to assess to what extent social hierarchy can influence cognitive mechanisms such as attention, arousal, motivation and goal –directed behaviour mediated by social rewards. One possibility is that favouring perception or saliency in the presence of superior individuals entails an implicit social reward. This interpretation is consistent with previous evidence showing an enhanced activation of the reward circuitry when processing photographs of superior individuals. Individuals with a low social position experience more social threats and punishment, especially the threat of being evaluated unfavourably

by those with a higher status (superior). Accordingly, it would be also interesting to know how cognitive functions are modulated / tuned in contexts of reward or punishment and/or in freeze- flight - fight situations.

Stable vs. Unstable hierarchies

When we originally planned this dissertation, we included different studies with unstable social hierarchies. We acknowledge the limitations of the present enterprise as our data only refers to stable social hierarchies. It is a total unanswered question how the present results in particular those referring to OCD patients, would generalize to unstable social situations.

The ontogeny of experiencing social hierarchies

Another interesting field to be explored is the emergence and development of the recognition of social hierarchy in childhood. It would be also interesting to evaluate the consequences of experiencing social roles in childhood. It would be of particular interest for educational settings to know how social roles influence perceptual and attentional processes, working memory and

decision-making processes, which are considered to be the most important processes involved in learning.

Classical studies on learning have shown that social factors such as trust, confidence and leadership are pivotal factors in human learning. The questions of whether information shared by inferior or superior members of a social rank can influence the learning process remain at present to be answered.

Genetic factors underlying the processing of social hierarchies.

Recent genetic studies (Chiao, 2010; Munafo, Clark, & Flint, 2005) suggests that the functional polymorphism of the serotonin transporter gene (5-HTTLPR) (this gene is responsible for serotonin reuptake at the synapse) can explain the interaction between genetic and environmental factors that shape the neural processing of social hierarchies and its consequences on behaviour. Modifications in the expression of the serotonin transporter gene have been associated to increased negative emotions, heightened anxiety, harm, and avoidance fear, and also to higher amygdala activations in response to negative stimuli. The kind of studies we have carried out in the present dissertation combined with genetic information may help to shed new light on the investigation of mental disorders.

7. REFERENCES

- Adler, N. E., Epel, E. S., Castellazzo, G., & Ickovics, J. R. (2000a). Relationship of subjective and objective social status with psychological and physiological functioning: Preliminary data in healthy white women. *Health Psychology Official Journal of*

- the Division of Health Psychology, American Psychological Association, 19(6), 586-592.*
- Adler, N. E., Epel, E. S., Castellazzo, G., & Ickovics, J. R. (2000b). Relationship of subjective and objective social status with psychological and physiological functioning: Preliminary data in healthy white women. *Health Psychology Official Journal of the Division of Health Psychology, American Psychological Association, 19(6), 586-592.*
- Adler, N. E., & Ostrove, J. M. (1999). Socioeconomic status and health: What we know and what we don't. *Annals of the New York Academy of Sciences, 896, 3-15.*
- Adolphs, R. (2009). The social brain: Neural basis of social knowledge. *Annual Review of Psychology, 60, 693-716.*
- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience, 7(4), 268-277.*
- Anaki, D., Zion-Golumbic, E., & Bentin, S. (2007). Electrophysiological neural mechanisms for detection, configural analysis and recognition of faces. *Neuroimage, 37(4), 1407-1416.*
- Baetens, K., der Cruyssen, L. V., Achtziger, A., Vandekerckhove, M., & Van Overwalle, F. (2011). N400 and LPP in spontaneous trait inferences. *Brain Research, 1418, 83-92.*
- Bandura, A. (1977). *Social learning theory. General Learning Press.*

- Barclay, J. R., Bransford, J. D., Franks, J. J., McCarrel, N. S., & Nitsch, K. (1974). Comprehension and semantic flexibility. *Journal of Verbal Learning and Verbal Behavior*, *13*, 471-481.
- Bateson, M., Nettle, D., & Roberts, G. (2006). Cues of being watched enhance cooperation in a real-world setting. *Biology Letters*, *2*(3), 412-414.
- Boksem, M. A., Kostermans, E., & De Cremer, D. (2011). Failing where others have succeeded: Medial frontal negativity tracks failure in a social context. *Psychophysiology*, *48*(7), 973-979.
- Boksem, M. A., Kostermans, E., Milivojevic, B., & De Cremer, D. (2012). Social status determines how we monitor and evaluate our performance. *Social Cognitive and Affective Neuroscience*, *7*(3), 304-313.
- Boksem, M. A., Ruys, K. I., & Aarts, H. (2011). Facing disapproval: Performance monitoring in a social context. *Social Neuroscience*, *6*(4), 360-368.
- Botzel, K., & Grusser, O. J. (1989). Electric brain potentials evoked by pictures of faces and non-faces: A search for "face-specific" EEG-potentials. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *77*(2), 349-360.
- Boudreau, C., McCubbins, M. D., & Coulson, S. (2009). Knowing when to trust others: An ERP study of decision making after receiving information from unknown people. *Social Cognitive and Affective Neuroscience*, *4*(1), 23-34.

- Boulougouris, V., Chamberlain, S. R., & Robbins, T. W. (2009). Cross-species models of OCD spectrum disorders. *Psychiatry Research, 170*(1), 15-21.
- Boyce, W. T. (2004). Social stratification, health, and violence in the very young. *Annals of the New York Academy of Sciences, 1036*, 47-68.
- Bradley, M. M., Sabatinelli, D., Lang, P. J., Fitzsimmons, J. R., King, W., & Desai, P. (2003). Activation of the visual cortex in motivated attention. *Behavioral Neuroscience, 117*(2), 369-380.
- Burgaleta, M., Diaz, B., Baus, C., & Sebastian-Galles, N. (in press). Brain structure is related to speech perception abilities in bilinguals. *Brain Structure and Function*,
- Bystritsky, A., Liberman, R. P., Hwang, S., Wallace, C. J., Vapnik, T., Maindment, K., et al. (2001). Social functioning and quality of life comparisons between obsessive-compulsive and schizophrenic disorders. *Depression and Anxiety, 14*(4), 214-218.
- Calkins, A. W., Berman, N. C., & Wilhelm, S. (2013a). Recent advances in research on cognition and emotion in OCD: A review. *Current Psychiatry Reports, 15*(5), 357-013-0357-4.
- Calkins, A. W., Berman, N. C., & Wilhelm, S. (2013b). Recent advances in research on cognition and emotion in OCD: A review. *Current Psychiatry Reports, 15*(5), 357-013-0357-4.
- Carrasco, M., Hong, C., Nienhuis, J. K., Harbin, S. M., Fitzgerald, K. D., Gehring, W. J., et al. (2013). Increased error-related brain

- activity in youth with obsessive-compulsive disorder and other anxiety disorders. *Neuroscience Letters*, 541, 214-218.
- Carver, C. S., & Scheier, M. F. (1981). The self-attention-induced feedback loop and social facilitation. *Journal of Experimental Social Psychology*, 17(6), 545-568.
- Cazden, C. B. (1968). Three sociolinguistic views of the language and speech of lower-class children--with special attention to the work of basil bernstein. *Developmental Medicine and Child Neurology*, 10(5), 600-612.
- Chamberlain, S. R., Blackwell, A. D., Fineberg, N. A., Robbins, T. W., & Sahakian, B. J. (2005). The neuropsychology of obsessive compulsive disorder: The importance of failures in cognitive and behavioural inhibition as candidate endophenotypic markers. *Neuroscience and Biobehavioral Reviews*, 29(3), 399-419.
- Chamberlain, S. R., Fineberg, N. A., Menzies, L. A., Blackwell, A. D., Bullmore, E. T., Robbins, T. W., et al. (2007). Impaired cognitive flexibility and motor inhibition in unaffected first-degree relatives of patients with obsessive-compulsive disorder. *The American Journal of Psychiatry*, 164(2), 335-338.
- Chamberlain, S. R., & Menzies, L. (2009a). Endophenotypes of obsessive-compulsive disorder: Rationale, evidence and future potential. *Expert Review of Neurotherapeutics*, 9(8), 1133-1146.
- Chamberlain, S. R., & Menzies, L. (2009b). Endophenotypes of obsessive-compulsive disorder: Rationale, evidence and future

- potential. *Expert Review of Neurotherapeutics*, 9(8), 1133-1146.
- Chamberlain, S. R., Menzies, L., Hampshire, A., Suckling, J., Fineberg, N. A., del Campo, N., et al. (2008). Orbitofrontal dysfunction in patients with obsessive-compulsive disorder and their unaffected relatives. *Science (New York, N.Y.)*, 321(5887), 421-422.
- Chiao, J. Y. (2010). Neural basis of social status hierarchy across species. *Current Opinion in Neurobiology*, 20(6), 803-809.
- Chiao, J. Y., Adams, R. B., Tse, P. U., Lowenthal, L., Richeson, J. A., & Ambady, N. (2008). Knowing who's boss: fMRI and ERP investigations of social dominance perception. *Group Processes & Intergroup Relations GPIR*, 11(2), 201-214.
- Chiao, J. Y., Bordeaux, A. R., & Ambady, N. (2004). Mental representations of social status. *Cognition*, 93(2), B49-57.
- Chiao, J. Y., Harada, T., Oby, E. R., Li, Z., Parrish, T., & Bridge, D. J. (2009). Neural representations of social status hierarchy in human inferior parietal cortex. *Neuropsychologia*, 47(2), 354-363.
- Chklovskii, D. B., Mel, B. W., & Svoboda, K. (2004). Cortical rewiring and information storage. *Nature*, 431(7010), 782-788.
- Christ, S., Falkenstein, M., Heuer, H., & Hohnsbein, J. (2000). Different error types and error processing in spatial stimulus-response-compatibility tasks: Behavioural and electrophysiological data. *Biological Psychology*, 51, 129-150.

- Corriveau, K., & Harris, P. L. (2009). Choosing your informant: Weighing familiarity and recent accuracy. *Developmental Science*, *12*(3), 426-437.
- Cummins, D. (2000). How the social environment shaped the evolution of the mind. *Synthese*, *122* (1/2), 3-28,
- Danielmeier, C., Wessel, J. R., Steinhauser, M., & Ullsperger, M. (2009a). Modulation of the error-related negativity by response conflict. *Psychophysiology*, *46*(6), 1288-1298.
- Danielmeier, C., Wessel, J. R., Steinhauser, M., & Ullsperger, M. (2009b). Modulation of the error-related negativity by response conflict. *Psychophysiology*, *46*(6), 1288-1298.
- De Wit, S. J., de Vries, F. E., van der Werf, Y. D., Cath, D. C., Heslenfeld, D. J., Veltman, E. M., et al. (2012). Presupplementary motor area hyperactivity during response inhibition: A candidate endophenotype of obsessive-compulsive disorder. *The American Journal of Psychiatry*, *169*(10), 1100-1108.
- Deaner, R. O., Khera, A. V., & Platt, M. L. (2005). Monkeys pay per view: Adaptive valuation of social images by rhesus macaques. *Current Biology : CB*, *15*(6), 543-548.
- Di Russo, F., Martinez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex (New York, N.Y.: 1991)*, *13*(5), 486-499.
- Di Russo, F., Martinez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping*, *15*(2), 95-111.

- Di Russo, F., Stella, A., Spitoni, G., Strappini, F., Sdoia, S., Galati, G., et al. (2012). Spatiotemporal brain mapping of spatial attention effects on pattern-reversal ERPs. *Human Brain Mapping, 33*(6), 1334-1351.
- Dittrich, W. H., & Johansen, T. (2013). Cognitive deficits of executive functions and decision-making in obsessive-compulsive disorder. *Scandinavian Journal of Psychology, 54*(5), 393-400.
- Dong, W. K., & Greenough, W. T. (2004). Plasticity of nonneuronal brain tissue: Roles in developmental disorders. *Mental Retardation and Developmental Disabilities Research Reviews, 10*(2), 85-90.
- Eger, E., Moretti, L., Dehaene, S., & Sirigu, A. (2013). Decoding the representation of learned social roles in the human brain. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior,*
- Eimer, M. (2011). The face-sensitivity of the n170 component. *Frontiers in Human Neuroscience, 5,* 119.
- Einav, S., & Robinson, E. J. (2011). When being right is not enough: Four-year-olds distinguish knowledgeable informants from merely accurate informants. *Psychological Science, 22*(10), 1250-1253.
- Eisenberger, N. I., Lieberman, M. D., & Williams, K. D. (2003). Does rejection hurt? an fMRI study of social exclusion. *Science (New York, N.Y.), 302*(5643), 290-292.

- Endrass, T., Koehne, S., Riesel, A., & Kathmann, N. (2013). Neural correlates of feedback processing in obsessive-compulsive disorder. *Journal of Abnormal Psychology*,
- Endrass, T., Schuermann, B., Kaufmann, C., Spielberg, R., Kniesche, R., & Kathmann, N. (2010). Performance monitoring and error significance in patients with obsessive-compulsive disorder. *Biological Psychology*, *84*(2), 257-263.
- Falkenstein, M., Hohnsbein, J., & Hoormann, J. (1995). Event-related potential correlates of errors in reaction tasks. *Electroencephalography and Clinical Neurophysiology Supplement*, *44*, 287-296.
- Falkenstein, M., Hoormann, J., Christ, S., & Hohnsbein, J. (2000a). ERP components on reaction errors and their functional significance: A tutorial. *Biological Psychology*, *51*, 87-107.
- Falkenstein, M., Hoormann, J., Christ, S., & Hohnsbein, J. (2000b). ERP components on reaction errors and their functional significance: A tutorial. *Biological Psychology*, *51*(2-3), 87-107.
- Farrow, T. F., Jones, S. C., Kaylor-Hughes, C. J., Wilkinson, I. D., Woodruff, P. W., Hunter, M. D., et al. (2011). Higher or lower? the functional anatomy of perceived allocentric social hierarchies. *Neuroimage*, *57*(4), 1552-1560.
- Festinger, L., & Hutte, H. A. (1954). An experimental investigation of the effect of unstable interpersonal relations in a group. *Journal of Abnormal and Social Psychology*, *49*, 513-512.

- Fishman, I., & Ng, R. (2013a). Error-related brain activity in extraverts: Evidence for altered response monitoring in social context. *Biological Psychology, 93*(1), 225-230.
- Fishman, I., & Ng, R. (2013b). Error-related brain activity in extraverts: Evidence for altered response monitoring in social context. *Biological Psychology, 93*(1), 225-230.
- Fjell, A. M., Walhovd, K. B., Fischl, B., & Reinvang, I. (2007). Cognitive function, P3a/P3b brain potentials, and cortical thickness in aging. *Human Brain Mapping, 28*(11), 1098-1116.
- Folstein, J. R., & Van Petten, C. (2008a). Influence of cognitive control and mismatch on the N2 component of the ERP: A review. *Psychophysiology, 45*(1), 152-170.
- Folstein, J. R., & Van Petten, C. (2008b). Influence of cognitive control and mismatch on the N2 component of the ERP: A review. *Psychophysiology, 45*(1), 152-170.
- Ford, J. M., Sullivan, E. V., Marsh, L., White, P. M., Lim, K. O., & Pfefferbaum, A. (1994). The relationship between P300 amplitude and regional gray matter volumes depends upon the attentional system engaged. *Electroencephalography and Clinical Neurophysiology, 90*(3), 214-228.
- Foulsham, T., Cheng, J. T., Tracy, J. L., Henrich, J., & Kingstone, A. (2010). Gaze allocation in a dynamic situation: Effects of social status and speaking. *Cognition, 117*(3), 319-331.
- Frith, C. D., & Frith, U. (2012). Mechanisms of social cognition. *Annual Review of Psychology, 63*, 287-313.

- Gaebler, M., Daniels, J. K., Lamke, J. P., Fydrich, T., & Walter, H. (2013). Heart rate variability and its neural correlates during emotional face processing in social anxiety disorder. *Biological Psychology, 94*(2), 319-330.
- Galinsky, A. D., Magee, J. C., Inesi, M. E., & Gruenfeld, D. H. (2006). Power and perspectives not taken. *Psychological Science, 17*(12), 1068-1074.
- Gazzaniga, M. S. (2013). Shifting gears: Seeking new approaches for mind/brain mechanisms. *Annual Review of Psychology, 64*, 1-20.
- Glaeser, E., & Laibson, D. I. (2000). Measuring trust. *The Quarterly Journal of Economics 115* (3): 811-846,
- Gluth, S., Rieskamp, J., & Buchel, C. (2013). Classic EEG motor potentials track the emergence of value-based decisions. *Neuroimage, 79*, 394-403.
- Golby, A. J., Gabrieli, J. D., Chiao, J. Y., & Eberhardt, J. L. (2001). Differential responses in the fusiform region to same-race and other-race faces. *Nature Neuroscience, 4*(8), 845-850.
- Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience, 7*(5), 555-562.
- Grisham, J. R., Henry, J. D., Williams, A. D., & Bailey, P. E. (2010). Socioemotional deficits associated with obsessive-compulsive symptomatology. *Psychiatry Research, 175*(3), 256-259.
- Grosenick, L., Clement, T. S., & Fernald, R. D. (2007). Fish can infer social rank by observation alone. *Nature, 445*(7126), 429-432.

- Gruenfeld, D., Inesi, M., Magee, J., & Galinsky, A. (2008). Power and the objectification of social targets. *J Pers Soc Psychol*, 2008 Jul;95(1):111-27,
- Guinote, A. (2007). Power and goal pursuit. *Personality & Social Psychology Bulletin*, 33(8), 1076-1087.
- Hagoort, P., Baggio, G., Willems, R.M. (2009). Semantic unification, In the cognitive neurosciences, ed. MS Gazzaniga. Pp. 819–36. Boston, MA: MIT Press. 4th Ed.
- Harris, P. L., & Corriveau, K. H. (2011). Young children's selective trust in informants. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 366(1567), 1179-1187.
- Harrison, B. J., Pujol, J., Soriano-Mas, C., Hernandez-Ribas, R., Lopez-Sola, M., Ortiz, H., et al. (2012). Neural correlates of moral sensitivity in obsessive-compulsive disorder. *Archives of General Psychiatry*, 69(7), 741-749.
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science (New York, N.Y.)*, 293(5539), 2425-2430.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4(6), 223-233.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry*, 51(1), 59-67.

- Hill, J., Inder, T., Neil, J., Dierker, D., Harwell, J., & Van Essen, D. (2010). Similar patterns of cortical expansion during human development and evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(29), 13135-13140.
- Hsu, M., Anen, C., & Quartz, S. R. (2008). The right and the good: Distributive justice and neural encoding of equity and efficiency. *Science (New York, N.Y.)*, *320*(5879), 1092-1095.
- Huang, L., Galinsky, A. D., Gruenfeld, D. H., & Guillory, L. E. (2011). Powerful postures versus powerful roles: Which is the proximate correlate of thought and behavior? *Psychological Science*, *22*(1), 95-102.
- Ibanez, A., Melloni, M., Huepe, D., Helgiu, E., Rivera-Rei, A., Canales-Johnson, A., et al. (2012). What event-related potentials (ERPs) bring to social neuroscience? *Social Neuroscience*, *7*(6), 632-649.
- Izuma, K., Saito, D. N., & Sadato, N. (2010). The roles of the medial prefrontal cortex and striatum in reputation processing. *Social Neuroscience*, *5*(2), 133-147.
- Jaswal, V. K., & Neely, L. A. (2006). Adults don't always know best: Preschoolers use past reliability over age when learning new words. *Psychological Science*, *17*(9), 757-758.
- Jay, S. M., Routh, D. K., & Brantley, J. C. (1980). Social class differences in children's comprehension of adult language. *Journal of Psycholinguistic Research*, *9*(3), 205-217.

- Johannes, S., Wieringa, B. M., Mantey, M., Nager, W., Rada, D., Muller-Vahl, K. R., et al. (2001a). Altered inhibition of motor responses in tourette syndrome and obsessive-compulsive disorder. *Acta Neurologica Scandinavica*, *104*(1), 36-43.
- Johannes, S., Wieringa, B. M., Mantey, M., Nager, W., Rada, D., Muller-Vahl, K. R., et al. (2001b). Altered inhibition of motor responses in tourette syndrome and obsessive-compulsive disorder. *Acta Neurologica Scandinavica*, *104*(1), 36-43.
- Johnson, S. L., Leedom, L. J., & Muhtadie, L. (2012). The dominance behavioral system and psychopathology: Evidence from self-report, observational, and biological studies. *Psychological Bulletin*, *138*(4), 692-743.
- Kang, O, Donald, L, R. (2009). Reverse linguistic stereotyping: Measuring the effect of listener expectations on speech evaluation. *Journal of Language and Social Psychology* 2009 *28*: 441,
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience The Official Journal of the Society for Neuroscience*, *17*(11), 4302-4311.
- Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *361*(1476), 2109-2128.
- Kawasaki, H., Tsuchiya, N., Kovach, C. K., Nourski, K. V., Oya, H., Howard, M. A., et al. (2012). Processing of facial emotion in

- the human fusiform gyrus. *Journal of Cognitive Neuroscience*, 24(6), 1358-1370.
- Kiefer, M., & Brendel, D. (2006). Attentional modulation of unconscious "automatic" processes: Evidence from event-related potentials in a masked priming paradigm. *Journal of Cognitive Neuroscience*, 18(2), 184-198.
- Kiesel, A., Miller, J., Jolicoeur, P., & Brisson, B. (2008). Measurement of ERP latency differences: A comparison of single-participant and jackknife-based scoring methods. *Psychophysiology*, 45(2), 250-274.
- Kim, J. S., Singh, V., Lee, J. K., Lerch, J., Ad-Dab'bagh, Y., MacDonald, D., et al. (2005). Automated 3-D extraction and evaluation of the inner and outer cortical surfaces using a laplacian map and partial volume effect classification. *Neuroimage*, 27(1), 210-221.
- Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, 38(3), 557-577.
- Kovacs, A. M., Teglas, E., & Endress, A. D. (2010). The social sense: Susceptibility to others' beliefs in human infants and adults. *Science (New York, N.Y.)*, 330(6012), 1830-1834.
- Kraus, M. W., Piff, P. K., & Keltner, D. (2009). Social class, sense of control, and social explanation. *Journal of Personality and Social Psychology*, 97(6), 992-1004.
- Kret, M. E., Denollet, J., Grèzes, J., & de Gelder, B. (2011). The role of negative affectivity and social inhibition in perceiving social threat: An fMRI study. *Neuropsychologia*, 49(5), 1187-1193.

- Kumaran, D., Melo, H. L., & Duzel, E. (2012). The emergence and representation of knowledge about social and nonsocial hierarchies. *Neuron*, 76(3), 653-666.
- Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, 62, 621-647.
- Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science*, 207, 203-205.
- Kutas, M., & Hillyard, S. A. (1984). Brain potentials during reading reflect word expectancy and semantic association. *Nature*, 307, 161-163.
- La Fougere, C., Grant, S., Kostikov, A., Schirmacher, R., Gravel, P., Schipper, H. M., et al. (2011). Where in-vivo imaging meets cytoarchitectonics: The relationship between cortical thickness and neuronal density measured with high-resolution [18F]flumazenil-PET. *Neuroimage*, 56(3), 951-960.
- Lerch, J. P., & Evans, A. C. (2005). Cortical thickness analysis examined through power analysis and a population simulation. *Neuroimage*, 24(1), 163-173.
- Lesch, K. P., Bengel, D., Heils, A., Sabol, S. Z., Greenberg, B. D., Petri, S., et al. (1996). Association of anxiety-related traits with a polymorphism in the serotonin transporter gene regulatory region. *Science (New York, N.Y.)*, 274(5292), 1527-1531.

- Lieberman, M. D. (2007). Social cognitive neuroscience: A review of core processes. *Annual Review of Psychology, 58*, 259-289.
- Lount Jr., R. B., & Pettit, N. C. (2012). The social context of trust: The role of status. *Organizational Behavior and Human Decision Processes, 117*(1), 15-23.
- Ly, M., Haynes, M. R., Barter, J. W., Weinberger, D. R., & Zink, C. F. (2011). Subjective socioeconomic status predicts human ventral striatal responses to social status information. *Current Biology : CB, 21*(9), 794-797.
- Lytelton, O. C., Karama, S., Ad-Dab'bagh, Y., Zatorre, R. J., Carbonell, F., Worsley, K., et al. (2009). Positional and surface area asymmetry of the human cerebral cortex. *Neuroimage, 46*(4), 895-903.
- MacDonald, D., Kabani, N., Avis, D., & Evans, A. C. (2000). Automated 3-D extraction of inner and outer surfaces of cerebral cortex from MRI. *Neuroimage, 12*(3), 340-356.
- Maner, J. K., Miller, S. L., Schmidt, N. B., & Eckel, L. A. (2008). Submitting to defeat: Social anxiety, dominance threat, and decrements in testosterone. *Psychological Science, 19*(8), 764-768.
- Marsh, A. A., Blair, K. S., Jones, M. M., Soliman, N., & Blair, R. J. (2009). Dominance and submission: The ventrolateral prefrontal cortex and responses to status cues. *Journal of Cognitive Neuroscience, 21*(4), 713-724.
- Mascaro, O., & Csibra, G. (2012). Representation of stable social dominance relations by human infants. *Proceedings of the*

National Academy of Sciences of the United States of America,
109(18), 6862-6867.

Mazziotta, J. C., Toga, A. W., Evans, A., Fox, P., & Lancaster, J. (1995). A probabilistic atlas of the human brain: Theory and rationale for its development. the international consortium for brain mapping (ICBM). *Neuroimage*, 2(2), 89-101.

Meaux, E., Roux, S., & Batty, M. (2013). Early visual ERPs are influenced by individual emotional skills. *Social Cognitive and Affective Neuroscience*,

Mehta, P. H., & Beer, J. (2010). Neural mechanisms of the testosterone-aggression relation: The role of orbitofrontal cortex. *Journal of Cognitive Neuroscience*, 22(10), 2357-2368.

Mehta, P. H., Jones, A. C., & Josephs, R. A. (2008). The social endocrinology of dominance: Basal testosterone predicts cortisol changes and behavior following victory and defeat. *Journal of Personality and Social Psychology*, 94(6), 1078-1093.

Melloni, M., Urbistondo, C., Seden, L., Gelormini, C., Kichic, R., & Ibanez, A. (2012). The extended fronto-striatal model of obsessive compulsive disorder: Convergence from event-related potentials, neuropsychology and neuroimaging. *Frontiers in Human Neuroscience*, 6, 259.

Mende-Siedlecki, P., Said, C. P., & Todorov, A. (2013). The social evaluation of faces: A meta-analysis of functional neuroimaging studies. *Social Cognitive and Affective Neuroscience*, 8(3), 285-299.

- Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: A network model of insula function. *Brain Structure & Function*, 214(5-6), 655-667.
- Menzies, L., Achard, S., Chamberlain, S. R., Fineberg, N., Chen, C. H., del Campo, N., et al. (2007). Neurocognitive endophenotypes of obsessive-compulsive disorder. *Brain : A Journal of Neurology*, 130(Pt 12), 3223-3236.
- Meyer-Lindenberg, A., Domes, G., Kirsch, P., & Heinrichs, M. (2011). Oxytocin and vasopressin in the human brain: Social neuropeptides for translational medicine. *Nature Reviews.Neuroscience*, 12(9), 524-538.
- Miller, J., Patterson, T., & Ulrich, R. (1998). Jackknife-based method for measuring LRP onset latency differences. *Psychophysiology*, 35(1), 99-115.
- Montague, P. R., & Lohrenz, T. (2007). To detect and correct: Norm violations and their enforcement. *Neuron*, 56(1), 14-18.
- Morita, T., Tanabe, H. C., Sasaki, A. T., Shimada, K., Kakigi, R., & Sadato, N. (2013). The anterior insular and anterior cingulate cortices in emotional processing for self-face recognition. *Social Cognitive and Affective Neuroscience*,
- Moskowitz, D. S., Pinard, G., Zuroff, D. C., Annable, L., & Young, S. N. (2001). The effect of tryptophan on social interaction in everyday life: A placebo-controlled study. *Neuropsychopharmacology : Official Publication of the American College of Neuropsychopharmacology*, 25(2), 277-289.

- Munafo, M. R., Clark, T., & Flint, J. (2005). Does measurement instrument moderate the association between the serotonin transporter gene and anxiety-related personality traits? A meta-analysis. *Molecular Psychiatry*, *10*(4), 415-419.
- Muscatell, K. A., Morelli, S. A., Falk, E. B., Way, B. M., Pfeifer, J. H., Galinsky, A. D., et al. (2012). Social status modulates neural activity in the mentalizing network. *Neuroimage*, *60*(3), 1771-1777.
- Nader, M. A., Nader, S. H., Czoty, P. W., Riddick, N. V., Gage, H. D., Gould, R. W., et al. (2012). Social dominance in female monkeys: Dopamine receptor function and cocaine reinforcement. *Biological Psychiatry*, *72*(5), 414-421.
- Nasr, S., & Tootell, R. B. (2012). Role of fusiform and anterior temporal cortical areas in facial recognition. *Neuroimage*, *63*(3), 1743-1753.
- Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping*, *15*(1), 1-25.
- Nieuwland, M. S., & Van Berkum, J. J. (2008). The interplay between semantic and referential aspects of anaphoric noun phrase resolution: Evidence from ERPs. *Brain and Language*, *106*(2), 119-131.
- Oosterhof, N. N., & Todorov, A. (2008). The functional basis of face evaluation. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(32), 11087-11092.

- Osherson, D. N. (1981). Modularity as an issue for cognitive science. *Cognition*, 10(1-3), 241-242.
- Osterhout, L., Bersick, M., & McLaughlin, J. (1997). Brain potentials reflect violations of gender stereotypes. *Memory & Cognition*, 25(3), 273-285.
- Overbeck, J. R., & Park, B. (2006). Powerful perceivers, powerless objects: Flexibility of powerholders' social attention. *Organizational Behavior and Human Decision Processes*, 99(2), 227-243.
- Patenaude, B., Smith, S. M., Kennedy, D. N., & Jenkinson, M. (2011). A bayesian model of shape and appearance for subcortical brain segmentation. *Neuroimage*, 56(3), 907-922.
- Penades, R., Catalan, R., Rubia, K., Andres, S., Salamero, M., & Gasto, C. (2007). Impaired response inhibition in obsessive compulsive disorder. *European Psychiatry : The Journal of the Association of European Psychiatrists*, 22(6), 404-410.
- Peng, Z., Lui, S. S., Cheung, E. F., Jin, Z., Miao, G., Jing, J., et al. (2012). Brain structural abnormalities in obsessive-compulsive disorder: Converging evidence from white matter and grey matter. *Asian Journal of Psychiatry*, 5(4), 290-296.
- Perez-Edgar, K., Roberson-Nay, R., Hardin, M. G., Poeth, K., Guyer, A. E., Nelson, E. E., et al. (2007). Attention alters neural responses to evocative faces in behaviorally inhibited adolescents. *Neuroimage*, 35(4), 1538-1546.
- Petanjek, Z., Judas, M., Kostovic, I., & Uylings, H. B. (2008). Lifespan alterations of basal dendritic trees of pyramidal neurons in the

- human prefrontal cortex: A layer-specific pattern. *Cerebral Cortex (New York, N.Y.: 1991)*, 18(4), 915-929.
- Piras, F., Piras, F., Chiapponi, C., Girardi, P., Caltagirone, C., & Spalletta, G. (2013). Widespread structural brain changes in OCD: A systematic review of voxel-based morphometry studies. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*,
- Polich, J., & Criado, J. R. (2006). Neuropsychology and neuropharmacology of P3a and P3b. *International Journal of Psychophysiology : Official Journal of the International Organization of Psychophysiology*, 60(2), 172-185.
- Polich, J., & Kok, A. (1995). Cognitive and biological determinants of P300: An integrative review. *Biological Psychology*, 41(2), 103-146.
- Purcell, R., Maruff, P., Kyrios, M., & Pantelis, C. (1998). Cognitive deficits in Obsessive–Compulsive disorder on tests of Frontal–Striatal function. *Biological Psychiatry*, 43(5), 348-357.
- Qiu, A., Younes, L., Miller, M. I., & Csernansky, J. G. (2008). Parallel transport in diffeomorphisms distinguishes the time-dependent pattern of hippocampal surface deformation due to healthy aging and the dementia of the alzheimer's type. *Neuroimage*, 40(1), 68-76.
- Rakic, P. (1988). Specification of cerebral cortical areas. *Science*, 241, 170-176.
- Ratcliff, R. (1978). A theory of memory retrieval. *Psychological Review*, 85, 59–108.,

- Ratcliff, R., & McKoon, G. (2008). The diffusion decision model: Theory and data for two-choice decision tasks. *Neural Computation, 20*(4), 873-922.
- Relander, K., Rama, P., & Kujala, T. (2009). Word semantics is processed even without attentional effort. *Journal of Cognitive Neuroscience, 21*(8), 1511-1522.
- Ridgeway, C., L. (2006). Status construction theory. Pp. 301-323 in *Contemporary Social Psychological Theories, Edited by P. J. Burke. Stanford University Press,*
- Riesel, A., Endrass, T., Kaufmann, C., & Kathmann, N. (2011). Overactive error-related brain activity as a candidate endophenotype for obsessive-compulsive disorder: Evidence from unaffected first-degree relatives. *The American Journal of Psychiatry, 168*(3), 317-324.
- Rilling JK, S. A. (2011). The neuroscience of social decision-making. *Annu Rev Psychol. 2011; 62:23-48,*
- Rodriguez-Fornells, A., Kurzbuch, A. R., & Munte, T. F. (2002). Time course of error detection and correction in humans: Neurophysiological evidence. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience, 22*(22), 9990-9996.
- Rojas, M., Masip, D., Todorov, A., & Vitria, J. (2011). Automatic prediction of facial trait judgments: Appearance vs. structural models. *PloS One, 6*(8), e23323.
- Rotter, J. B. (1945). *Social learning and clinical psychology.* [] *Prentice-Hall.,*

- S, K., Y, A. D., Rj, H., Ij, D., Oc, L., C, L., et al. (2009). Positive association between cognitive ability and cortical thickness in a representative US sample of healthy 6 to 18 year-olds. *Intelligence*, 37(2), 145-155.
- Santamaría-García, H., Pannunzi, M., Ayneto, A., Deco, G., & Sebastián-Gallés, N. (2013). "If you are good, I get better": The role of social hierarchy in perceptual decision-making. *Social Cognitive and Affective Neuroscience*,
- Sapolsky, R. M. (2004). Social status and health in humans and other animals. *Annu. Rev. Anthropol.* 33, 393–418,
- Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science (New York, N.Y.)*, 308(5722), 648-652.
- Schaechter, J. D., & Wurtman, R. J. (1990). Serotonin release varies with brain tryptophan levels. *Brain Research*, 532(1-2), 203-210.
- Schubert, T. W. (2005). Your highness: Vertical positions as perceptual symbols of power. *Journal of Personality and Social Psychology*, 89(1), 1-21.
- Segalas, C., Alonso, P., Orbegozo, A., Real, E., Subira, M., Lopez-Sola, C., et al. (2013). Brain structural imaging correlates of olfactory dysfunction in obsessive-compulsive disorder. *European Archives of Psychiatry and Clinical Neuroscience*,
- Seligman, C., R. (1972). The effects of speech style and other attributes on teachers' attitudes toward pupils. *Language in Society*, 1, 131-142,

- Sherman, G. D., Lee, J. J., Cuddy, A. J., Renshon, J., Oveis, C., Gross, J. J., et al. (2012). Leadership is associated with lower levels of stress. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(44), 17903-17907.
- Shettleworth, S. J. (2012). Modularity, comparative cognition and human uniqueness. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1603), 2794-2802.
- Singer, T., Kiebel, S. J., Winston, J. S., Dolan, R. J., & Frith, C. D. (2004). Brain responses to the acquired moral status of faces. *Neuron*, *41*(4), 653-662.
- Smith, P. K., Dijksterhuis, A., & Wigboldus, D. H. (2008). Powerful people make good decisions even when they consciously think. *Psychological Science*, *19*(12), 1258-1259.
- Smith, P. K., Jostmann, N. B., Galinsky, A. D., & van Dijk, W. W. (2008). Lacking power impairs executive functions. *Psychological Science*, *19*(5), 441-447.
- Smith, P. K., & Trope, Y. (2006). You focus on the forest when you're in charge of the trees: Power priming and abstract information processing. *Journal of Personality and Social Psychology*, *90*(4), 578-596.
- Spitzer, M., Fischbacher, U., Herrnberger, B., Grön, G., & Fehr, E. (2007). The neural signature of social norm compliance. *Neuron*, *56*(1), 185-196.

- Suchan, B., Jokisch, D., Skotara, N., & Daum, I. (2007). Evaluation-related frontocentral negativity evoked by correct responses and errors. *Behavioural Brain Research, 183*(2), 206-212.
- Sugiura, M., Sassa, Y., Jeong, H., Wakusawa, K., Horie, K., Sato, S., et al. (2012). Self-face recognition in social context. *Human Brain Mapping, 33*(6), 1364-1374.
- Thompson, P. M., Hayashi, K. M., Dutton, R. A., Chiang, M. C., Leow, A. D., Sowell, E. R., et al. (2007). Tracking alzheimer's disease. *Annals of the New York Academy of Sciences, 1097*, 183-214.
- Todorov, A., Mende-Siedlecki, P., & Dotsch, R. (2013). Social judgments from faces. *Current Opinion in Neurobiology, 23*(3), 373-380.
- Todorov, A., Said, C. P., Engell, A. D., & Oosterhof, N. N. (2008). Understanding evaluation of faces on social dimensions. *Trends in Cognitive Sciences, 12*(12), 455-460.
- Tollner, T., Rangelov, D., & Muller, H. J. (2012). How the speed of motor-response decisions, but not focal-attentional selection, differs as a function of task set and target prevalence. *Proceedings of the National Academy of Sciences of the United States of America, 109*(28), E1990-9.
- Treisman, A. M., & Kanwisher, N. G. (1998). Perceiving visually presented objects: Recognition, awareness, and modularity. *Current Opinion in Neurobiology, 8*(2), 218-226.
- Trivedi, J. K., Dhyani, M., Goel, D., Sharma, S., Singh, A. P., Sinha, P. K., et al. (2008). Neurocognitive dysfunction in patients with

- obsessive compulsive disorder. *African Journal of Psychiatry*, 11(3), 204-209.
- Ulrich, R., & Miller, J. (2001). Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs. *Psychophysiology*, 38(5), 816-827.
- Van Berkum, J. J., Brown, C. M., Hagoort, P., & Zwitterlood, P. (2003). Event-related brain potentials reflect discourse-referential ambiguity in spoken language comprehension. *Psychophysiology*, 40(2), 235-248.
- van Berkum, J. J., Hagoort, P., & Brown, C. M. (1999). Semantic integration in sentences and discourse: Evidence from the N400. *Journal of Cognitive Neuroscience*, 11(6), 657-671.
- Van Berkum, J. J., van den Brink, D., Tesink, C. M., Kos, M., & Hagoort, P. (2008). The neural integration of speaker and message. *Journal of Cognitive Neuroscience*, 20(4), 580-591.
- van Berkum, J. J., Zwitterlood, P., Hagoort, P., & Brown, C. M. (2003). When and how do listeners relate a sentence to the wider discourse? evidence from the N400 effect. *Brain Research.Cognitive Brain Research*, 17(3), 701-718.
- van den Heuvel, O. A., Veltman, D. J., Groenewegen, H. J., Cath, D. C., van Balkom, A. J., van Hartkamp, J., et al. (2005). Frontal-striatal dysfunction during planning in obsessive-compulsive disorder. *Archives of General Psychiatry*, 62(3), 301-309.
- van Veen, V., & Carter, C. S. (2006). Error detection, correction, and prevention in the brain: A brief review of data and theories.

Clinical EEG and Neuroscience : Official Journal of the EEG and Clinical Neuroscience Society (ENCS), 37(4), 330-335.

Vandekerckhove, J., & Tuerlinckx, F. (2007). Fitting the ratcliff diffusion model to experimental data. *Psychonomic Bulletin & Review*, 14(6), 1011-1026.

Vandekerckhove, J., & Tuerlinckx, F. (2008). Diffusion model analysis with MATLAB: A DMAT primer. *Behavior Research Methods*, 40(1), 61-72.

Vogel, E. K., & Luck, S. J. (2000). The visual N1 component as an index of a discrimination process. *Psychophysiology*, 37(2), 190-203.

Vriend, C., de Wit, S. J., Remijnse, P. L., van Balkom, A. J., Veltman, D. J., & van den Heuvel, O. A. (2013). Switch the itch: A naturalistic follow-up study on the neural correlates of cognitive flexibility in obsessive-compulsive disorder. *Psychiatry Research*, 213(1), 31-38.

Vuilleumier, P., & Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: Evidence from functional neuroimaging. *Neuropsychologia*, 45(1), 174-194.

Walhovd, K. B., Fjell, A. M., Reinvang, I., Lundervold, A., Fischl, B., Salat, D., et al. (2005). Cortical volume and speed-of-processing are complementary in prediction of performance intelligence. *Neuropsychologia*, 43(5), 704-713.

- Wascher, E., Hoffmann, S., Sanger, J., & Grosjean, M. (2009). Visuo-spatial processing and the N1 component of the ERP. *Psychophysiology*, *46*(6), 1270-1277.
- Westlye, L. T., Walhovd, K. B., Bjornerud, A., Due-Tonnessen, P., & Fjell, A. M. (2009). Error-related negativity is mediated by fractional anisotropy in the posterior cingulate gyrus--a study combining diffusion tensor imaging and electrophysiology in healthy adults. *Cerebral Cortex (New York, N.Y.: 1991)*, *19*(2), 293-304.
- White, K. R., Crites, S. L., Jr, Taylor, J. H., & Corral, G. (2009). Wait, what? assessing stereotype incongruities using the N400 ERP component. *Social Cognitive and Affective Neuroscience*, *4*(2), 191-198.
- Whitson, J. A., & Galinsky, A. D. (2008). Lacking control increases illusory pattern perception. *Science (New York, N.Y.)*, *322*(5898), 115-117.
- Woodman, G. F., & Luck, S. J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology. Human Perception and Performance*, *29*(1), 121-138.
- Xu, Y., Valentino, D. J., Scher, A. I., Dinov, I., White, L. R., Thompson, P. M., et al. (2008). Age effects on hippocampal structural changes in old men: The HAAS. *Neuroimage*, *40*(3), 1003-1015.

- Yamakawa, Y., Kanai, R., Matsumura, M., & Naito, E. (2009). Social distance evaluation in human parietal cortex. *PloS One*, *4*(2), e4360.
- Yeung, N., Botvinick, M. M., & Cohen, J. D. (2004). The neural basis of error detection: Conflict monitoring and the error-related negativity. *Psychological Review*, *111*(4), 931-959.
- Yeung, N., & Cohen, J. D. (2006). The impact of cognitive deficits on conflict monitoring. predictable dissociations between the error-related negativity and N2. *Psychological Science*, *17*(2), 164-171.
- Zajonc, R. B. (1965). Social facilitation. *Science (New York, N.Y.)*, *149*(3681), 269-274.
- Zink, C. F., Pagnoni, G., Chappelow, J., Martin-Skurski, M., & Berns, G. S. (2006). Human striatal activation reflects degree of stimulus saliency. *Neuroimage*, *29*(3), 977-983.
- Zink, C. F., Tong, Y., Chen, Q., Bassett, D. S., Stein, J. L., & Meyer-Lindenberg, A. (2008). Know your place: Neural processing of social hierarchy in humans. *Neuron*, *58*(2), 273-283.