

THE AGING SOCIAL BRAIN:

Neural and behavioral age-related changes in social cognition
and decision-making

O ENVELHECIMENTO E O CÉREBRO SOCIAL:

Alterações neuronais e comportamentais relacionadas com a
idade na cognição social e na tomada de decisão

CARINA SOFIA TEIXEIRA FERNANDES

TESE DE DOUTORAMENTO EM NEUROCIÊNCIAS APRESENTADA À FACULDADE DE
MEDICINA DA UNIVERSIDADE DO PORTO

PORTO 2019

**THIS PHD THESIS HAS BEEN SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR THE PHD DEGREE
IN NEUROSCIENCES AT THE FACULTY OF MEDICINE OF THE UNIVERSITY OF PORTO.**

**DISSERTAÇÃO DE CANDIDATURA AO GRAU DE DOUTOR APRESENTADA À FACULDADE DE MEDICINA DA
UNIVERSIDADE DO PORTO, NO ÂMBITO DO PROGRAMA DOUTORAL EM NEUROCIÊNCIAS**

CANDIDATE / CANDIDATA:

Carina Sofia Teixeira Fernandes

SUPERVISOR / ORIENTADOR:

Professor Doutor João Eduardo Marques-Teixeira

Professor Associado da Faculdade de Psicologia e Ciências da Educação da Universidade do Porto

CO-SUPERVISOR / COORIENTADORA:

Professora Doutora Isabel Pavão Martins

Professora Associada da Faculdade de Medicina da Universidade de Lisboa

This investigation was conducted in the Laboratory of Neuropsychophysiology of the Faculty of Psychology and Education Sciences of the University of Porto, and in the Language Research Laboratory of the Institute of Molecular Medicine of the Faculty of Medicine of the University of Lisbon.

The candidate performed this work with a grant from the “*Fundação para a Ciência e Tecnologia*” (SFRH/BD/112101/2015). The experimental work was funded by the “*Fundação BIAL*”

Constituição do júri, nomeado por despacho vice-reitoral de 20 de dezembro de 2018

Presidente

- Doutor Rui Manuel Bento de Almeida Coelho, Professor Catedrático da Faculdade de Medicina da Universidade do Porto

Vogais

- Doutor Rui Miguel Sales Pereira Mata, Professor Associado da University of Basel, Suíça;

- Doutora Adriana da Conceição Soares Sampaio, Professora Auxiliar da Escola de Psicologia da Universidade do Minho;

- Doutor João Carlos Bettencourt de Medeiros Relvas, Investigador Principal do i3S – Instituto de Investigação e Inovação em Saúde;

- Doutor João Eduardo Marques Teixeira, Professor Associado da Faculdade de Psicologia e Ciências da Educação da Universidade do Porto;

- Doutor Manuel Fernando dos Santos Barbosa, Professor Associado da Faculdade de Psicologia e Ciências da Educação da Universidade do Porto;

- Doutora Deolinda Maria Valente Alves Lima Teixeira, Professora Catedrática da Faculdade de Medicina da Universidade do Porto;

- Doutor António José de Bastos Leite, Professor Auxiliar da Faculdade de Medicina da Universidade do Porto.

According to the Article 8 of the Decree-Law 388/70 the following are part of this dissertation

Ao abrigo do Artigo 8 do Decreto-Lei 388/70 fazem parte desta dissertação as seguintes publicações

- Gonçalves, A. R., **Fernandes, C.**, Pasion, R., Ferreira-Santos, F., Barbosa, F., & Marques-Teixeira, J. (2018). Emotion identification and aging: Behavioral and neural age-related changes. *Clinical Neurophysiology*, 129(5), 1020-1029. <http://dx.doi.org/10.1016/j.clinph.2018.02.128>
- **Fernandes, C.**, Gonçalves, A. R., Pasion, R., Ferreira-Santos, F., Barbosa, F., Martins, I. P., & Marques-Teixeira, J. (2019). Age-related decline in emotional perspective-taking: its effect on the Late Positive Potential. *Cognitive, Affective, & Behavioral Neuroscience*, 19, 109-122. <http://dx.doi.org/10.3758/s13415-018-00648-1>
- Pasion, R., **Fernandes, C.**, Gonçalves, A. R., Ferreira-Santos, F., Páscoa, R., Barbosa, F., & Marques-Teixeira, J. (2018). The effect of aging on the (mis)perception of intentionality-an ERP study. *Social Neuroscience*, 1-13.
- **Fernandes, C.**, Pasion, R., Gonçalves, A. R., Ferreira-Santos, F., Barbosa, F., Martins, I. P., & Marques-Teixeira, J. (2018). Age differences in neural correlates of feedback processing after economic decisions under risk. *Neurobiology of Aging*, 65, 51-59. <http://dx.doi.org/10.1016/j.neurobiolaging.2018.01.003>
- **Fernandes, C.**, Gonçalves, A. R., Pasion, R., Ferreira-Santos, F., Barbosa, F., Martins, I. P., & Marques-Teixeira, J. (2019). Age-related changes in social decision-making: An electrophysiological analysis of unfairness evaluation in the Ultimatum Game. *Neuroscience Letters*, 692, 122-126. <http://dx.doi.org/10.1016/j.neulet.2018.10.061>

AGRADECIMENTOS

Em primeiro lugar gostaria de agradecer à Fundação para a Ciência e Tecnologia (SFRH/BD/112101/2015) por me ter fornecido o apoio financeiro necessário para a realização deste trabalho. Gostaria igualmente de agradecer à Fundação BIAL pelo financiamento atribuído ao projeto *Aging Social Brain* e ao projeto *Healthy aging and economic decision-making* (Ref. 249/2016).

Gostaria de agradecer aos meus orientadores, que partilharam comigo o seu tempo e conhecimento, e que me apoiaram incondicionalmente ao longo dos últimos anos. Ao Professor Marques-Teixeira, com quem aprendi, aprendo e continuarei a aprender nas novas etapas que nos esperam, agradeço pela oportunidade de o ter como orientador, por ter partilhado comigo a sua intelectualidade brilhante e a sua cultura enciclopédica. À Professora Isabel Pavão Martins, agradeço por todos os conselhos e conhecimentos científicos, pelas inúmeras sugestões e ideias perspicazes, pelo seu positivismo, motivação e energia contagiante.

Quero agradecer, por tudo, ao Professor Fernando Barbosa. Por todas as oportunidades, pelo apoio incondicional, pela constante partilha de conhecimento e por ser sempre uma base segura que nos permite explorar e estudar o que mais nos entusiasma. Agradeço, ainda, a todos os professores com quem me cruzei ao longo deste percurso de vinte anos de aprendizagem. De cada um deles levo conhecimentos para a vida e motivação para continuar, independentemente das dificuldades da profissão. Em especial, agradeço ao (eterno) Professor Frederico Marques, ao professor Rodrigo de Sá Nogueira Saraiva, à Professora Rosa Novo, ao Professor Branco Vasco e ao Dr. Jaime Grácio. Agradeço por me terem contagiado com a curiosidade científica e por me terem feito acreditar que era capaz.

O meu agradecimento mais profundo é para os meus pais, que sempre trabalharam arduamente para me dar a melhor educação e o amor mais incondicional. À minha querida amiga, colega e excelente neurocientista, Inês Mares, agradeço pelo amor e pelo apoio que não conhece fronteiras.

À Mariana Pereira e Rita Pasion, agradeço pela enorme amizade, por toda a paciência, pelo permanente sentido de humor até nas piores alturas, pela ajuda e incentivo constantes. Foi uma honra partilhar estes anos com elas. Aos restantes amigos do Laboratório de Neuropsicofisiologia, Cassilda Cunha Reis, Fernando Ferreira Santos, Pedro Almeida, David Tomé, Diana Moreira, Ana Rita Cruz, Tiago Paiva, Ana Gonçalves e Joana Melo e Castro, agradeço pela forma como me receberam no laboratório e por toda a ajuda que me deram desde então.

Aos meus amáveis e pacientes participantes dedico a minha enorme gratidão pelo contributo que deram a este estudo. Cresci mais um pouco com cada um deles, como profissional e ser humano. Agradeço também à Professora Doutora Maria Graça Pinto e à Dr.^a Isabel Barbosa da Faculdade de Letras da Universidade do Porto, pela enorme ajuda na divulgação desta investigação pelos alunos do Programa Universitário para Seniores.

Gostaria, ainda, de agradecer à Professora Deolinda Lima pela oportunidade de fazer parte do Programa Doutoral de Neurociências, e à minha querida amiga e colega de doutoramento Ana Freitas, pela sua visão positiva e contagiante do mundo.

Por último, mas não menos importante, agradeço ao Artur pelo amor e pela paciência, por ter tornado tudo mais fácil.

ABSTRACT / RESUMO

Older adults are at increased risk of cognitive deficits and neurological disease, but, paradoxically, they show preserved or even improved performance in emotional processing, in comparison with younger adults. These age-related changes likely shape social cognition and decision-making, but the neural and psychological mechanisms underlying these domains remain poorly understood during aging.

The present research aimed to analyze age-related changes in behavioral and neurophysiological correlates of social cognition and decision-making, as well as the role that cognitive functioning has in these domains. To this purpose, a sample of 30 younger, 30 middle-aged and 29 older adults performed a set of experimental tasks designed to examine five domains of social cognition and decision-making, during EEG recordings. These tasks assessed: (1) emotional identification; (2) theory of mind; (3) social perception; (4) decision-making under risk and (5) social decision-making.

Results showed that aging affects some domains of social cognition, preserving others. Specifically, aging appears to preserve emotional identification abilities, which can be mediated by an increased neural processing of the structural and emotional features of the face. However, aging appears to affect emotional perspective-taking abilities, which are fundamental to a preserved theory of mind. Older adults were also less accurate than younger adults at identifying the intentionality of social transgressions, which was found along with a N2 attenuation during the perception of accidental/intentional harms.

During decision-making under risk, older adults were less risk-averse than younger adults, preferring smaller losses associated with higher probabilities of losing. Regarding electrophysiological results, middle-aged and older adults had similar amplitudes of the feedback-related negativity after losses and non-losses, while younger adults had higher amplitudes after non-losses than after losses. Similarly, the amplitudes of the older adults' feedback-P3 did not differ between gains and non-gains, while younger and middle-aged adults had higher feedback-P3 after gains than after non-gains. Taken together, these results suggest that aging is accompanied by a decline in the ability to adjust economic decisions

according to the feedback, which may underlie older adults' preference for risk-taking. In the last task, older adults showed the best economic strategy, assessed through the Ultimatum Game. However, such strategy may be related with an age-related decline in the neural responses to unfair offers, as shown by similar amplitudes of the medial frontal negativity component after fair and unfair offers.

Interestingly, middle-aged adults were at an intermediate level between younger and older adults in all tasks, both in neural as in behavioral responses to social cues. This suggests that aging effects on social cognition start earlier in adult development, similarly to what happens to several neurocognitive processes.

With the exception of emotional identification, working memory and executive functions were correlated with social and decisional abilities. This finding is in accordance with previous results, which showed that neurocognition and social cognition are different, but related constructs.

O envelhecimento está associado a um risco aumentado de declínio cognitivo e doenças neurológicas, mas também a uma preservação ou até melhoria do funcionamento emocional. Estas alterações podem afetar a cognição social e a tomada de decisão, mas os mecanismos neuronais e psicológicos subjacentes a estes domínios estão pouco estudados no envelhecimento.

A presente investigação teve como objetivo analisar as alterações relacionadas com a idade nos correlatos comportamentais e neurofisiológicos da cognição social e da tomada de decisão, bem como o papel que funcionamento cognitivo desempenha nestes domínios. Para este efeito, 30 adultos mais novos, 30 adultos de meia idade e 29 adultos mais velhos realizaram, durante um registo eletroencefalográfico, um conjunto de tarefas experimentais construídas para avaliar cinco domínios da cognição social e da tomada de decisão. Estas tarefas avaliaram: (1) identificação emocional; (2) teoria da mente; (3) perceção social; (4) tomada de decisão económica em contexto de risco e (5) tomada de decisão económica em contexto social.

Os resultados evidenciaram que o envelhecimento afeta alguns domínios da cognição social, preservando outros. Especificamente, a identificação emocional não parece afetada pelo envelhecimento, o que pode ser mediado por um aumento do processamento neuronal das características estruturais e emocionais da face. No entanto, os adultos mais velhos demonstraram um pior desempenho na tarefa que avaliou a tomada de perspetiva emocional, a qual é fundamental para uma teoria da mente preservada. Os adultos mais velhos evidenciaram, ainda, pior performance na avaliação da intencionalidade de transgressões sociais, o que pode estar subjacente a uma atenuação do componente N2 dos potenciais relacionados com eventos.

Na tarefa de decisão económica em contexto de risco, os adultos mais velhos foram menos avessos ao risco do que os adultos mais jovens, preferindo apostar em valores menores, mas associados a uma maior probabilidade de perda. Relativamente aos resultados eletrofisiológicos, os adultos mais velhos e de meia idade demonstraram uma amplitude semelhante no componente *“negatividade relacionada com o feedback”* após perdas e não-perdas, enquanto os adultos mais jovens demonstraram uma amplitude maior

para não-perdas do que para perdas. Da mesma forma, nos adultos mais velhos, a amplitude do componente “feedback-P3” não diferiu depois de ganhos e não-ganhos, enquanto adultos mais jovens e de meia idade apresentaram um componente maior depois de ganhos do que depois de não-ganhos. Estes resultados sugerem que o envelhecimento pode ser acompanhado por um declínio na capacidade de ajustar decisões económicas aos resultados de decisões prévias, o que pode estar na base da preferência de adultos mais velhos por escolhas mais arriscadas. Na última tarefa, os adultos mais velhos demonstraram uma melhor estratégia económica em contexto social, avaliada pelo Jogo do Ultimato. No entanto, esta estratégia pode estar relacionada com um declínio na resposta neuronal a ofertas injustas, como foi evidenciado pela amplitude do componente “*negatividade medial-frontal*”.

Curiosamente, os resultados comportamentais e eletrofisiológicos dos adultos de meia idade ficaram num nível intermédio entre os resultados dos adultos mais jovens e mais velhos. Esta evidência sugere que os efeitos do envelhecimento na cognição social podem começar durante o desenvolvimento adulto, à semelhança do que acontece com vários processos neurocognitivos.

Com exceção da identificação emocional, as capacidades neurocognitivas de memória de trabalho e funcionamento executivo correlacionaram-se com a performance nos domínios da cognição social e decisão económica. Este resultado suporta evidências prévias que demonstram que a neurocognição e a cognição social estão relacionadas, apesar de serem constructos diferentes.

ABBREVIATIONS

ACC	anterior cingulate cortex
AVLT	Auditory Verbal Learning Test
BOLD	blood oxygen level-dependent
BSI	Brief Symptom Inventory
CBTT	Corsi Block-tapping task
dIPFC	dorsolateral prefrontal cortex
EEG	electroencephalography
ERP	event-related potential
FEE	facial expression of emotion
FRN	Feedback-related Negativity
fMRI	functional magnetic resonance imaging
HADS	Hospital Anxiety and Depression Scale
HAROLD	hemispheric asymmetry reduction in older adults
IFS	INECO Frontal Screening
INECO	Institute of Cognitive Neurology
LPP	Late Positive Potential
MFN	Medial Frontal Negativity
MoCA	Montreal Cognitive Assessment
NIMH	National Institute of Mental Health
PFC	prefrontal cortex
TMT	Trail Making Test
ToM	theory of mind
UG	Ultimatum Game
vmPFC	ventromedial prefrontal cortex
WHO	World Health Organization

TABLE OF CONTENTS

1. INTRODUCTION	1
1.1 THE AGING BRAIN	2
1.2 THE AFFECTIVE AGING BRAIN	7
1.3 AGING AND SOCIAL COGNITION	11
1.4 OVERVIEW OF THE STUDIES	14
1.5 REFERENCES	18
2. EXPERIMENTAL WORK	38
2.1 EMOTION IDENTIFICATION AND AGING: BEHAVIORAL AND NEURAL AGE-RELATED CHANGES	39
2.2 AGE-RELATED DECLINE IN EMOTIONAL PERSPECTIVE-TAKING: ITS EFFECT ON THE LATE POSITIVE POTENTIAL	50
2.3 THE EFFECT OF AGING ON THE (MIS)PERCEPTION OF INTENTIONALITY - AN ERP STUDY	65
2.4 AGE DIFFERENCES IN NEURAL CORRELATES OF FEEDBACK PROCESSING AFTER ECONOMIC DECISIONS UNDER RISK	80
2.5 AGE-RELATED CHANGES IN SOCIAL DECISION-MAKING: AN ELECTROPHYSIOLOGICAL ANALYSIS OF UNFAIRNESS EVALUATION IN THE ULTIMATUM GAME	90
3. FINAL CONSIDERATIONS	96
3.1. DISCUSSION	97
3.2. CONCLUSIONS	105
3.3. FUTURE PERSPECTIVES	107
3.4. REFERENCES	108
APPENDICES	117
APPENDIX 1	118
APPENDIX 2	129

1. INTRODUCTION

1.1 THE AGING BRAIN

For the first time in history, most people can live to their 60s and beyond (World Health Organization, 2015). However, this unprecedented demographic shift is accompanied by several social and health-related concerns, leading to the recognition of Aging as an important health topic. Accordingly, in 2002, the World Health Organization (WHO) released the *“Active ageing: a policy framework”*, in which active aging is defined as “the process of optimizing opportunities for health, participation and security in order to enhance quality of life as people age. (...) The word ‘active’ refers to continuing participation in social, economic, cultural, spiritual and civic affairs, not just the ability to be physically active or to participate in the labor force.” (World Health Organization, 2002, p. 12). Thereby, the WHO policy framework defined six main determinants of active aging: personal, behavioral, social, economic, health and social services, and the physical environment.

Considering these determinants, the scientific disciplines of Neuroscience and Psychology are in a privileged position to contribute to the active aging policies, by extending the knowledge about the neural, physiological, behavioral, affective, and cognitive changes that accompany aging. Indeed, the growth of psychological and biomedical research on aging followed this necessity, showing a five-fold increase over the last 30 years, as depicted in Figure 1. This research endeavor resulted in a better understanding of several neural and psychological aspects of aging, concerning to brain and cognitive function.

The most prominent cognitive change associated with aging is in memory, which can be broadly divided into short- (seconds to hours) and long-term (hours to lifetime) memory (McGaugh, 2000). Short-term memory can be further divided into immediate (or sensory) memory – associated with the passive retention of sensorial information – and working memory – associated with the active storage and manipulation of information (Maylor, 2005). Although aging affects both immediate and working memory, the effects are more pronounced in the latter (Maylor, 2005).

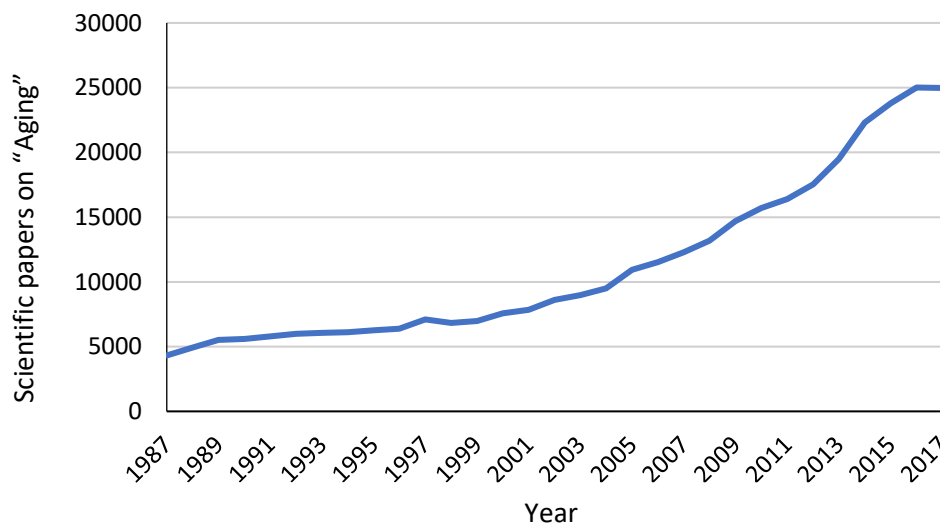


Figure 1. Number of scientific papers published in the last 30 years (1987-2017) retrieved from PubMed with the keyword "aging".

Regarding the long-term memory, it can be divided into declarative (or explicit) and non-declarative (or implicit) memory (Squire, 1992). The declarative memory is defined by the conscious recollection of facts and events, and encompasses semantic and episodic memory (Harada, Love, & Triebel, 2013). Semantic memory involves the general knowledge accumulated throughout life, including practical and general knowledge, facts, ideas, meanings or concepts. Episodic memory involves the memory for personally experienced events that occur at a specific place and time (Harada et al., 2013). Declarative memory can be contrasted with non-declarative memory, characterized by a non-conscious recall of information, which includes skills, habits, priming, associative and non-associative learnings (Squire, 1992). Although aging has an effect on both types of declarative memory, episodic memory shows a decline throughout the lifespan, while semantic memory shows a later decline in life (Rönnlund, Nyberg, Bäckman, & Nilsson, 2005). In contrast, non-declarative memory appears to be preserved across the lifespan (Lezak, Howieson, Loring, & Fischer, 2004).

Furthermore, aging selectively changes different processes of memory (Harada et al., 2013). It reduces acquisition (i.e., the ability to encode new information; Haaland, Price, & Larue, 2003) and retrieval (i.e., the ability to access newly learned information; Haaland et al., 2003), while preserves the retention of information that is successfully

learned (Whiting, Wythe, & Smith, 1997). However, all of these alterations in memory may be due to age-related changes in other cognitive domains, such as attention, processing speed (Luszcz & Bryan, 1999) or executive functioning (Darowski, Helder, Zacks, Hasher, & Hambrick, 2008). In fact, several cognitive changes reported in healthy aging are correlated with a decreased attention and a slower processing speed (Salthouse, 1992; Schretlen et al., 2000), which can negatively impact older adults' performance on several neuropsychological tests designed to measure other cognitive domains (Salthouse, 1992).

Processing speed is correlated with various indices of brain integrity, such as the volume of the dorsolateral prefrontal cortex (PFC; Raz, Briggs, Marks, & Acker, 1999) and white matter integrity (Madden, Whiting, Provenzale, & Huettel, 2004). However, a decline in this function does not explain all the cognitive changes associated with age, which can be accounted for a concomitant decline in executive functions (Schretlen et al., 2000). Executive functions are closely related to the integrity of prefrontal structures (Kimberg & Farah, 1993; Roberts & Pennington, 1996), and include processes such as hypothesis generation, response monitoring, working memory, set shifting, abstraction, inhibitory control, cognitive flexibility and planning (Diamond, 2013). According to the frontal lobe hypothesis (West, 1996), the PFC is one of the regions most affected by aging, resulting in an earlier and more pronounced decline in the cognitive abilities supported by this region (West, 1996). Despite the decline in these cognitive functions, aging preserves other abilities such as language, vocabulary and visuospatial skills (Haaland et al., 2003).

The above-mentioned age-related changes in neurocognition co-occur with several microscopic and macroscopic brain changes. The microscopic changes include the reduction of synaptic density, due to the pruning of dendrite arbors complexity, the reduction in dendrite length and the reduction in the number of neuritic spines (Dickstein et al., 2007; Hof & Morrison, 2004). Such changes, along with some neuronal loss (Anderton, 2002), result in a decrease of grey matter volume and integrity (Resnick, Pham, Kraut, Zonderman, & Davatzikos, 2003).

The grey matter loss appears to be greater in cortical than in subcortical structures (Jernigan et al., 2001; Walhovd et al., 2005), accelerates in old age (Raz &

Rodrigue, 2006), and results in an increase of the ventricular space and cerebrospinal fluid (Deary et al., 2009). This grey matter atrophy is most prominent in the PFC (e.g., Allen, Bruss, Brown, & Damasio, 2005; Good et al., 2001), hippocampus and medial temporal lobe (e.g., Bigler, Anderson, & Blatter, 2002; Du et al., 2006; Raz, Rodrigue, Head, Kennedy, & Acker, 2004; Walhovd et al., 2005). The prefrontal vulnerability is consistent with a pronounced age-related decline in functions such as processing speed, working memory and executive functions (Raz, Gunning-Dixon, Head, Dupuis, & Acker, 1998; West 1996), while the temporal vulnerability is associated with an age-related decline in episodic memory (Rodrigue & Raz, 2004; Rusinek et al., 2003; Verhaeghen, Marcoen, & Goossens, 1993).

The results regarding the white matter volume are less consistent. Some studies found a reduction of white matter volume with age (Allen et al., 2005; Guttmann et al., 1998; Jernigan et al., 2001; Walhovd et al., 2005), while others did not find any age-related differences (Blatter et al., 1995; Good et al., 2001; Jernigan et al., 1991; Pfefferbaum et al., 1994). The age of the older participants may have contributed to these discrepant results (Walhovd et al., 2011). While one study found that white matter volume was negatively correlated with age, but only from 70 years of age onwards (Courchesne et al., 2000), the subsequent studies found that, despite this later onset, the white matter loss was faster than the gray matter loss (Jernigan et al., 2001; Jernigan & Gamst, 2005). Thereby, the white matter volume tends to be relatively stable in healthy aging, having an abrupt decline around the age of 70 (Hedden & Gabrieli, 2004; Raz & Rodrigue, 2006; Sullivan & Pfefferbaum, 2006). The loss of white matter integrity appears to be particularly critical for cognition, due to a decreasing of the information transfer between different cortical regions (Sullivan & Pfefferbaum, 2006).

In addition to these structural changes, altered levels of some biomolecules can also affect the function of the aging brain (Deary et al., 2009). For instance, despite preserving the dopamine synthesis capacity (Karrer, Josef, Mata, Morris, & Samanez-Larkin, 2017), aging has an effect on the dopaminergic system by reducing the density of dopaminergic transporters, as well as D1 and D2 receptors in the frontal cortex and striatum (Li & Rieckmann, 2014; Nyberg & Bäckman, 2004). The dopaminergic system has received special attention due to its role in the reward prediction error and

consequent importance for learning, attention, and movement control. The midbrain dopaminergic neurons typically activate after inputs that are different from the expected (Schultz, 2013), and this signal provides a powerful tool to support reinforcement learning. The age-related dopaminergic reduction has been correlated with worse cognitive and motor performance, particularly regarding the executive functioning, episodic memory, processing speed (Bäckman, Lindenberger, Li, & Nyberg, 2010), attention and modulation of voluntary, fine motor responses (Volkow et al., 1998).

The levels of serotonin and brain-derived neurotrophic factor also decrease with the increasing age, affecting the regulation of synaptic plasticity and neurogenesis (Mattson, Maudsley, & Martin, 2004). Other age-related changes include increasing of monoamine oxidase (Volchegorskii, Shemyakov, Turygin, & Malinovskaya, 2004), calcium dysregulation (Toescu, Verkhatsky, & Landfield, 2004), mitochondrial dysfunction, production of reactive oxygen species (Melov, 2004), hypertension, vascular and microvascular changes, oxidative stress, inflammation and stress-related corticosteroid levels (Raz & Rodrigue, 2006; Whalley, Deary, Appleton, & Starr, 2004).

Despite these well-established cognitive and neural features of healthy aging, the studies unveiling the associations between structural brain changes and cognitive functions are few and elusive (Hedden & Gabrieli, 2004; Raz & Rodrigue, 2006; Sullivan & Pfefferbaum, 2006). These associations remain a challenge for Neurosciences, and both the reserve model as the compensation hypothesis may be hindering this work (Deary et al., 2009).

In the reserve model, *reserve* is defined as the capacity to buffer the harmful effects of brain damage or pathology, and it can be divided into brain and cognitive reserve (Marques-Teixeira, 2011). The *brain reserve* refers to the brain's ability to deal with its increasing damage, by increasing the number of additional synapses or redundant neural networks (Marques-Teixeira, 2011; Satz, 1993). On the other side, the *cognitive reserve* refers to the ability to use alternative strategies to perform an operation, when the typical strategies are not working properly (Stern, 2002). The reserve appears to be determined by early life cognitive ability, education level, life experience and occupational complexity (Whalley et al., 2004).

Regarding the compensation hypothesis (Reuter-Lorenz & Cappell, 2008), it proposes that the aging brain compensates structural losses by recruiting previously unrelated neural regions, particularly in the PFC and the contra-hemispheric areas (Hedden & Gabrieli, 2004; Sullivan & Pfefferbaum, 2006; Whalley et al., 2004). This recruitment results in a hemispheric asymmetry reduction in older adults (referred in the literature as HAROLD Model), and it is supported by neuroimaging results obtained in tasks assessing retrieval and encoding of episodic memory, retrieval of semantic memory, working memory, perception and inhibitory control (Cabeza, 2002; Deary et al., 2009; Reuter-Lorenz & Cappell, 2008). According to this model, older brains tend to show more symmetrical activation, which can be either due to a compensatory role of the brain (compensation view) or due to a difficulty in engaging specialized neural mechanisms (dedifferentiation view; Cabeza, 2002). Despite these dichotomous views, the compensation hypothesis has gained increasing support, since subsequent results have shown that equivalent performance between younger and older adults is accompanied by an over neural activation of older adults (Reuter-Lorenz & Cappell, 2008).

Thereby, both the reserve model as the compensation hypothesis might explain why normative age-related brain changes do not have a direct correlation with age-related cognitive decline (Deary et al., 2009). Moreover, longitudinal studies have shown that aging is marked by a high heterogeneity in cognitive performance (Persson et al., 2006; Persson et al., 2012), pointing to substantial individual differences among older adults. In fact, the development across the lifespan is influenced by an ongoing reciprocal interaction between the individual ontogeny and its surrounding context (Baltes, Reuter-Lorenz, & Rösler, 2006). Also, the brain structure and function depends on the individual genetic code, its unique life experience, and the past and current inner- and extra-organismic environment. Therefore, inter-individual differences in the architecture of the older adults' brain, even at the same age, are not surprising. Exploring these differences remains a major challenge for Neuroscience.

1.2 THE AFFECTIVE AGING BRAIN

The frontal theory of aging (West, 1996) postulates that the PFC is one of the regions most affected by aging, resulting in a more pronounced decline in the cognitive abilities supported by this region. However, this theory is not well fitted in what concerns to the older adults' affective abilities (Mather, 2016). Indeed, there is no overlap between the emotional abilities of older adults and those of patients with lesions in the ventromedial PFC (vmPFC). In several cases, patients with such lesions have impulsive and aggressive behaviors, feelings of anger (Grafman et al., 1996), and inability to maintain secure attachments (Damasio, Tranel, & Damasio, 1990). On the other hand, older adults tend to have less feelings of anger than younger adults (Birditt & Fingerman, 2005; Charles & Carstensen, 2008; Phillips, Henry, Hosie, & Milne, 2006), having also lower attachment anxiety (Chopik, Edelstein, & Fraley, 2013).

Earlier neuropsychological models of aging did not consider that the prefrontal lobes are subdivided into distinct areas, such as the vmPFC and dorsolateral PFC (dlPFC; MacPherson, Phillips, & Della Sala, 2002). Although these regions are closely connected between them, they are also connected with distinct parts of the brain. The dlPFC receives afferences from the primary sensory and motor regions, as well as the parietal cortex, while the vmPFC is connected to the limbic system (Adolphs, Tranel, Bechara, & Damasio, 1996; Rolls, 1996; Eslinger, 1999; Price, 1999). These areas can also be differentiated in terms of functional domains. While the dlPFC appears to support the executive functioning (Petrides & Milner, 1982), the vmPFC is involved in emotional contributions to social behavior and decision-making (Mather, 2016; Rolls, 1996).

Regarding the effects of aging in these areas, Phillips and Della Sala (1998) proposed that the dlPFC declines more during aging, while the vmPFC is more preserved. This hypothesis was posteriorly supported by a study that used tasks selected to induce abilities subserved by both regions, which showed that age-related impairments were significantly higher in the tasks related to the dlPFC (MacPherson et al., 2002). Phillips and Della Sala's hypothesis (1998) hypothesis was corroborated by subsequent results, which found negative correlations between increasing age and the cortical thickness of the frontal gyri, but not of the anterior cingulate cortex (ACC) or vmPFC (Fjell & Walhovd, 2010).

Besides the vmPFC and the ACC, healthy aging also appears to preserve the amygdala, an area involved in detecting emotionally relevant stimuli, given their novelty, level of threat or goal-related relevance. The amygdala also modulates other brain systems, leading to increased attention to those inputs and to a creation of long-lasting memory of them (Mather, 2016). This area is involved in the processing of anxiety and fear, but also in the processing of positive emotions and motivation (Mather, 2016).

Some studies did not find differences in the amygdala volume across the adult lifespan (Jernigan et al., 2001; Jiang et al., 2014; Shen et al., 2013), other studies found a negative association between amygdala volume and age (Allen et al., 2005; Curiati et al., 2009; Fjell et al., 2013; Laakso et al., 1995; Mu, Xie, Wen, Weng, & Shuyun, 1999), while other studies found a less pronounced reduction of amygdala during aging, in comparison with other regions (Good et al., 2001; Grieve, Clark, Williams, Peduto, & Gordon, 2005; Kalpouzos et al., 2009). Moreover, while some studies have reported no alteration in older adults' amygdala activation for novel and salient stimuli (such as faces; Wright, Dickerson, Feczko, Negeira, & Williams, 2007; Wright et al., 2008), other studies have found an age-related shift in the type of emotional stimuli that leads to increased amygdala activation (Erk, Walter, & Abler, 2008; Ge, Fu, Wang, Yao, & Long, 2014; Kehoe, Toomey, Balsters, & Bokde, 2013; Leclerc & Kensinger, 2011; Mather et al., 2004; Waldinger, Kensinger, & Schulz, 2011).

Interestingly, the functional connectivity of an amygdala-based network appears to increase with age, in comparison with other networks (such as the dorsal attention network; Tomasi & Volkow, 2012). The functional connectivity between the amygdala and the PFC may reflect a prefrontal regulation of anxiety and other emotional responses (Mather, 2016) since, among older adults, the activity of this network was correlated with more positive memories (Sakaki, Nga, & Mather, 2013) and less negative evaluations of pictures (St. Jacques, Dolcos, & Cabeza, 2010) during the processing of emotional material.

The preservation of brain regions involved in emotional processing is consistent with a wealth of data showing that older adults have a preserved ability to process emotional stimuli, even if different from younger adults (Mather et al., 2012). For instance, in comparison with younger adults, older adults showed an age-by-valence

interaction in attention (Mather & Carstensen, 2003) and memory (Charles, Mather, & Carstensen, 2003), which were increased to positive stimuli, and/or decreased to negative information. This pattern is known as the age-related *positivity effect* (Mather & Carstensen, 2005), and it was replicated by several subsequent studies (for a meta-analysis, see Reed, Chan, & Mikels, 2014). Older adults also exhibit better moods (Isaacowitz, Toner, & Neupert, 2009), and longitudinal studies showed that their levels of negative affect tend to decrease, while positive affect increases or decreases less than negative affect (Carstensen et al., 2011; Charles, Reynolds, & Gatz, 2001; Gruenewald, Mroczek, Ryff, & Singer, 2008).

As questioned by Cacioppo and colleagues (2011), can this positivity effect result from improved emotion-regulation processes, or is it a side effect of age-related decline in some neural functions that support attending and memorizing negative and potentially threatening information (Cacioppo, Berntson, Bechara, Tranel, & Hawley, 2011)? As mentioned above, not only the amygdala shows a less pronounced decline among healthy older adults, but it also appears to be more responsive to positive than negative stimuli in older than in younger adults (Erk et al., 2008; Ge et al., 2014; Kehoe et al., 2013; Leclerc & Kensinger, 2011; Mather et al., 2004; Waldinger et al., 2011). Therefore, it has been hypothesized that the amygdala continues to respond to emotional stimuli during aging, shifting the valence for those it is more responsive (stimuli with positive valence, rather than stimuli with negative valence; Mather, 2016). In support of this hypothesis, one study assessed the patterns of gaze direction of younger and older adults during the presentation of stimuli, and found that the positivity effect in visual attention only emerged 500 milliseconds after the stimulus onset, when processes of cognitive control could guide looking decisions (Isaacowitz, Allard, Murphy, & Schlangel, 2009; Knight et al., 2007).

These findings appear to suggest that the age-related positivity effect may be associated with improved emotion-regulation processes (Mather, 2016) and, consistent with this hypothesis, other studies showed that older adults had increased prefrontal activation than younger adults for emotional than neutral material (Nashiro, Sakaki, & Mather, 2012; St. Jacques, Bessette-Symons, & Cabeza, 2009). Moreover, older adults with greater positivity and emotional stability showed increased activity in the vmPFC

and ACC during the processing of negative emotional stimuli (Dolcos, Katsumi, & Dixon, 2014; Sakaki, Fryer, & Mather, 2014; Urry et al., 2006; Williams et al., 2006). Thereby, during aging, these regions can be activated both to increase the processing of positive stimuli as to reinterpret/distract from negative stimuli (Mather, 2016).

This conclusion appears to be supported by behavioral studies, which showed that higher executive functioning is correlated with higher positivity among older adults, but not among younger adults (Knight et al., 2007; Mather & Knight 2005; Petrican, Moscovitch, & Schimmack, 2008; Sasse, Gamer, Büchel, & Brassen, 2014; Simón, Suengas, Ruiz-Gallego-Largo, & Bandrés, 2013). Thus, they suggest that older adults are more likely to engage extra cognitive prefrontal resources to regulate emotions than younger adults are, and the socioemotional selectivity theory (Carstensen, Mikels, & Mather, 2006) can provide the reason. According to this theory, as time is perceived as more limited during aging, people prioritize more the emotional goals (Carstensen et al., 2006), which should lead to an increased focus on emotion regulation. Indeed, studies that manipulated time perspective revealed that a more limited time increases positivity in emotion identification (Kellough & Knight, 2012) and memory (Mather, 2016).

In sum, despite the well-documented age-related cognitive decline, older adults generally show higher levels of emotional well-being than younger adults do, an emotional paradox described as the positivity effect (Mather et al., 2012). Given that both cognitive and emotional processes are implicated in *social cognition* and *decision-making*, what happens to these domains during healthy aging? This question is the basis of the present research and will be discussed in detail in chapter 1.3.

1.3 AGING AND SOCIAL COGNITION

In close relation to the cognitive and emotional processing reviewed above, other topics have received little attention in aging research. Specifically, social cognition and economic decision-making have only very recently begun to be investigated in older adults (Harlé & Sanfey, 2012; Moran, 2013), despite their impact for the success of social interactions (Moran, 2013).

Social cognition broadly refers to the mental operations underlying social interactions, which allow us to understand and effectively interact with others (Kern &

Horan, 2010). According to one of its most consensual definitions, social cognition is “the ability to construct representations of the relations between oneself and others and to use those representations flexibly to guide social behavior” (Adolphs, 2001, p. 231). To this role, social cognition recruits several processes and neural structures that modulate behavioral responses to socially relevant stimuli (Adolphs, 2001). First, sensory and associative areas of the neocortex are involved in the perception of socially relevant stimuli (such as the superior temporal sulcus and the fusiform gyrus of the temporal lobe in the case of face perception). These regions work together with a network of structures that includes the amygdala, orbitofrontal cortex, cingulate cortex, and right somatosensory-related cortices, which mediate the relation between perception and several components of social cognitive processing. Finally, motor and premotor cortices and basal ganglia, as well as systems involved in emotional outputs such as the hypothalamus and periaqueductal gray, modulate effector systems that generate social behavior (Adolphs, 2001).

In Social Neurosciences, the study of social cognition is at the interface between basic perception processes and social behavior and includes research in several domains (Ochsner & Lieberman, 2001). In psychiatry, social cognition has been studied since the 1990s in populations with social dysfunction, such as patients with schizophrenia and other related disorders (Peyroux & Franck, 2016). The rapid expansion of research in this field has resulted in an increasingly diverse range of terminologies and definitions, leading to the National Institute of Mental Health (NIMH) to propose a consensus-building workshop, in order to integrate research in this area and to guide future research efforts (Green et al., 2008; Green, Olivier, Crawley, Penn, & Silverstein, 2005).

Based on recommendations of this group, social cognition can be divided into three broad domains: emotional perception, theory of mind (ToM), and social perception and knowledge. Emotional perception, also known as emotional recognition or emotional identification, is the ability to infer emotional information from the other’s facial expression, body posture, prosody, or from a combination of both (Marques-Teixeira, 2007). Theory of mind (ToM) or mentalizing is the ability to understand that others’ mental states can be different from ours, and to infer the content of these mental states (Baron-Cohen, Leslie, Frith, 1985; Leslie, 1987; Marques-Teixeira, 2007;

Premack & Woodruff, 1978). Social perception and knowledge refers to the ability to judge the cues of the behavior manifested in a given social context, to be aware of the roles and goals that characterize social situations and to guide social interactions (Greene & Haidt, 2002).

Regarding economic decision-making, this process involves the selection of a particular action from a set of alternatives, in order to achieve desired outcomes and avoid undesired ones (Barraclough, Conroy, & Lee, 2004). This selection can be made in individual or social contexts, and it is based on prior knowledge, goals, evidence about the outcomes, costs of risky choices, and evaluation of previous decisions (for a review see Gold & Shadlen, 2007). Individual decisions can occur under uncertainty (Hertwig & Erev, 2009; Yu & Dayan, 2005), when probabilities and possible outcomes are unknown and must be learned throughout experience, or under risk (Hertwig & Erev, 2009; Kahneman & Tversky, 1979), when these probabilities and outcomes are fully known, and the learning rate should be close to zero. Social economic decisions, on the other side, are dependent on others' decisions (Barraclough et al., 2004) and are highly influenced by social rewards (Beadle, Sheehan, Dahlben, & Gutchess, 2013).

Economic decision-making is highly dependent on brain regions involved in reward processing and value computation (Smith & Huettel, 2010). Specifically, dopaminergic regions such as the ventral striatum, the ventral tegmental area, and the vmPFC are part of a reward system that is essential to successful reward-based learning (Jocham, Klein, & Ullsperger, 2011; Marschner et al., 2005). Reward-based learning is, in turn, critical to form and update predictions about rewards (Schultz, 2006).

Healthy aging is characterized by a poorer performance in tests that assess neurocognitive abilities, such as memory (Rönnlund et al., 2005) and executive functions (West, 1996), but also by an increased positive affect (Mather, 2016) and a change in motivation (Carstensen et al., 2006). There is a consensus that neurocognition and social cognition are related, but different constructs (Penn, Corrigan, Bentall, Racenstein, & Newman, 1997), and studies that examined the neural underpinnings of neurocognitive and social cognitive abilities found semi-independent systems for processing nonsocial and social stimuli (e.g., Sachs, Steger-Wuchse, Kryspin-Exner, Gur, & Katschnig, 2004).

Regarding decision-making, several lines of research attributed age-related impairments in economic choices to a decline in neurocognition (particularly executive functions) and to changes in emotional reward processing (Liebherr, Schiebener, Averbek, & Brand, 2017).

Considering these relations, the evidence of cognitive decline would lead to expectations of deficits in social cognition and decision-making during aging, but the preserved emotional functioning would lead to expectations in the opposing prediction. These conflicting hypotheses are, in fact, according to conflicting findings of both impaired (e.g., Castelli et al., 2010) and preserved social cognitive (e.g., Happé, Winner, & Brownell, 1998) and decision-making skills (e.g., Keightley, Winocur, Burianova, Hongwanishkul, & Grady, 2006). Consequently, it is important to clarify how aging affects each domain of social cognition and economic decision-making, to identify the neural mechanisms that lead to the (eventual) age-related changes while assessing the relative contributions of cognitive factors to those domains.

1.4 OVERVIEW OF THE STUDIES

The main goal of the present research is to examine how social cognitive abilities and their respective underpinnings are affected by aging, as well as the relative contributions of cognitive factors to these skills. To achieve these goals, we conducted five empirical studies through which we examined the different components of social cognition and decision-making, at behavioral and neural levels, in a group of younger, middle-aged and older adults. The recruited participants underwent a neuropsychological assessment that aimed to confirm the inclusion and exclusion criteria, and to collect sociodemographic and neurocognitive data. Afterwards, the participants performed experimental tasks built to assess emotional identification, ToM, social perception, and social and economic decision-making. The results of the neuropsychological assessment were correlated with those obtained in each of the experimental tasks, in order to understand the relative impact of neurocognition in social cognition and decision-making.

Most research in this field relies either on neuropsychological or functional magnetic resonance imaging (fMRI) data, whereas electroencephalography (EEG) and related techniques are not as widely used.

The EEG captures, at the scalp level, the voltages generated by the summation of the excitatory postsynaptic potentials of the dendrites of the cortical pyramidal cells (Luck, 2005). Each pyramidal cell forms a small dipole, with a negativity around the apical dendrites and a positivity around the cell body. To measure the voltage of these small dipoles at the scalp level, they have to occur synchronously in a large number of cells spatially aligned. It is difficult to extract neural responses of specific cognitive processes from the raw EEG data, given that it reflects activity from multiple sources, associated with different neural processes, further masked by electrical noise.

To associate neural responses with the processing of specific events, a technique of averaging voltages occurring in a window time-locked to a specific event was developed (Luck, 2005). This method creates epochs limiting an event of interest, which are averaged to reduce nonspecific activity recorded in the EEG, maintaining all activity that is specific to the processing of the event (Luck, 2005). This averaging procedure generates series of positive and negative components temporally linked to an event onset, creating an event-related brain potential (ERP) waveform. Individual components are commonly labeled with a *P* or an *N*, signaling positive or negative deflections, respectively. Furthermore, components are either labeled according to their order in the waveform (e.g. P1, N1, P2), or to their latency in milliseconds (e.g. P100, N170). Other components can also be labeled according to their functionality and polarity, such as the feedback-related negativity (FRN), or according to their topography and polarity, such as the medial frontal negativity (MFN).

Thereby, the ERPs are a direct measure of neural activity. They are generated by the firing of cortical neurons in response to a specific event that precisely coincides with that neural activity. In contrast, the images obtained from fMRI are an indirect measure of neural activation, since they do not represent the neural activity, nor the moment when it occurred. Rather, the blood oxygen level-dependent (BOLD) signal represents changes in blood flow, inferred to occur as the result of oxygen-dependent neural activity that occurred within the preceding 4–6 seconds (Amodio, Bartholow, & Ito,

2014). Thereby, the higher temporal resolution of the ERPs makes them ideally suited for capturing rapidly unfolding cognitive and affective processes (Amodio et al., 2014; Lopes da Silva, 2014). They provide a powerful tool for probing the temporal dynamics of neural processes, being more informative about psychological mechanisms. With their precise temporal resolution (and sufficient spatial resolution), the ERPs offer the best approach to test several fundamental questions for social, cognitive and affective neuroscience (Amodio et al., 2014).

Of particular relevance for the present work, we will analyze ERPs time-locked to socially and emotionally relevant stimuli, such as facial expression of emotion, feedbacks delivered after economic decisions, or pictures displaying social interactions. Each subchapter of the experimental work will describe the empirical study conducted to assess age-related differences in each domain of social cognition and decision-making through an ERP methodology. Each article will describe previous findings on aging and that specific domain, the theoretical rationale of each ERP component, the hypothesis, methodology, results, and discussion.

Specifically, emotional identification (chapter 2.1) was assessed through a task in which participants identified categorical emotions displayed in facial expressions, rating also their levels of arousal and valence (Ferreira-Santos, 2013). Regarding neural responses, groups were compared in three stages of facial structure and affect processing: the initial visual processing, encoding of facial features, and decoding of emotional content, presumably indexed by the P100, N170, and N250 components, respectively (Wynn, Lee, Horan, & Green, 2008). The P100 is a positive occipital ERP component related to basic visual processing. The N170 is a negative occipitotemporal ERP component that appears to index the earliest stage of facial structure encoding (Bentin, Allison, Puce, Perez, & McCarthy, 1996), being also sensitive to the emotional content of a face (Hinojosa, Mercado, & Carretié, 2015). Finally, the N250 is negative frontocentral ERP component modulated by the emotional content of a face (Streit et al., 1999).

ToM was assessed through a task in which participants observed scenarios showing the interaction between two persons, and had to infer their emotional states (chapter 2.2). To this purpose, we adapt a task previously used in a fMRI study (Derntl

et al., 2009), in which participants observed scenarios showing two agents involved in social interactions, portraying emotional and neutral scenes. One person in each scenario was masked, and participants must infer his/her affective mental state based on the facial expression and body posture of the other (non-masked) intervenient, along with the contextual details. Then, a target facial expression of emotion (FEE) was displayed, and participants had to decide if the emotion presented by this target was congruent or incongruent with the emotion that they inferred during the scenario. For instance, in one of the scenarios, participants observed a man with an angry facial expression, holding a knife that was pointed to the person with the masked face. After the scenario, a FEE appeared and it could display fear (congruent condition) or one of the other basic emotions (incongruent condition). Through this experimental manipulation, we investigated perspective-taking abilities over the accuracy rates, while we assessed how these abilities modulated two ERP components that are typically influenced by the affective and evaluative congruency: the N170 and the Late Positive Potential (LPP; Diéguez-Risco, Aguado, Albert, & Hinojosa, 2013; 2015).

The third domain of social cognition (chapter 2.3) was assessed through a modified version of a standard Intention Inference Task (Decety & Cacioppo, 2012). During this task, participants watched series of three-frame video clips. The first frame established the scene; the second frame displayed an unintentional or an intentional harm, and the third frame confirmed the intentionality of the action. After the second frame, participants were asked to judge if the transgression was either intentional or accidental. Besides the accuracy rates, we compared groups regarding the P2, an ERP component that reflects selective attention and subsequent categorization and evaluation (Johannes, Münte, Heinze, & Mangun, 1995); the N2, an ERP component modulated by conflict detection, expectancy violation (Folstein & Van Petten, 2008) and affective evaluation of negative outcomes (Cui, Ma, & Luo, 2016); and the LPP, an ERP component that is considered to reflect critical processes of moral cognition (Wagner, Chaves, & Wolff, 2017).

Finally, economic decision-making was assessed through two experimental tasks. The first task examined age-related differences in risk aversion, by assessing participants' preference among two risky options (chapter 2.4). Besides the behavioral

decisions, we also aimed to analyze the neural mechanisms underlying feedback processing, through the analysis of the FRN and the feedback-P3. While the FRN appears to be sensitive to expectancy violations, the feedback-P3 appears to be sensitive to the arousing nature of the feedback (San Martín, 2012).

The second experimental task (chapter 2.5) assessed decision-making in social context through the participants' performance in the ultimatum game (UG; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). The UG involves two players: the proposer (who decides how to split an amount of money) and the responder (who accepts or rejects the proposer's offer). If the responder accepts the offer, the stake is divided as proposed, but if s/he rejects the offer, both players get nothing. During this task, we assessed participants' performance in the responder and proposer role. Moreover, during the responder role, we compared groups regarding the MFN, an ERP component that was recently proposed as an index of unfairness sensitivity (Boksem & De Cremer, 2010).

1.5 REFERENCES

- Adolphs, R. (2001). The neurobiology of social cognition. *Current Opinion in Neurobiology*, 11(2), 231-239. [http://dx.doi.org/10.1016/S0959-4388\(00\)00202-6](http://dx.doi.org/10.1016/S0959-4388(00)00202-6)
- Adolphs, R., Tranel, D., Bechara, A., & Damasio, H. (1996). Neuropsychological approaches to reasoning and decision-making. In A. R. Damasio (Ed.). *Neurobiology of decision-making* (pp. 157–179). Berlin: Springer-Verlag.
- Allen, J. S., Bruss, J., Brown, C. K., & Damasio, H. (2005). Normal neuroanatomical variation due to age: the major lobes and a parcellation of the temporal region. *Neurobiology of Aging*, 26(9), 1245-1260. <http://dx.doi.org/10.1016/j.neurobiolaging.2005.05.023>
- Amodio, D. M., Bartholow, B. D., & Ito, T. A. (2013). Tracking the dynamics of the social brain: ERP approaches for social cognitive and affective neuroscience. *Social Cognitive and Affective Neuroscience*, 9(3), 385-393. <http://dx.doi.org/10.1093/scan/nst177>
- Anderton, B. H. (2002). Ageing of the brain. *Mechanisms of Ageing and Development*, 123(7), 811-817. [http://dx.doi.org/10.1016/S0047-6374\(01\)00426-2](http://dx.doi.org/10.1016/S0047-6374(01)00426-2)

- Bäckman, L., Lindenberger, U., Li, S. C., & Nyberg, L. (2010). Linking cognitive aging to alterations in dopamine neurotransmitter functioning: recent data and future avenues. *Neuroscience & Biobehavioral Reviews*, 34(5), 670-677.
<http://dx.doi.org/10.1016/j.neubiorev.2009.12.008>
- Baltes, P. B., Reuter-Lorenz, P. A., & Rösler, F. (2006). *Lifespan development and the brain: The perspective of biocultural co-constructivism*. New York, USA: Cambridge University Press.
- Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a "theory of mind"? *Cognition*, 21(1), 37-46. [http://dx.doi.org/10.1016/0010-0277\(85\)90022-8](http://dx.doi.org/10.1016/0010-0277(85)90022-8)
- Barracough, D. J., Conroy, M. L., & Lee, D. (2004). Prefrontal cortex and decision making in a mixed-strategy game. *Nature Neuroscience*, 7(4), 404-410.
- Beadle, J. N., Sheehan, A. H., Dahlben, B., & Gutchess, A. H. (2013). Aging, empathy, and prosociality. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, 70(2), 213-222. <http://dx.doi.org/10.1093/geronb/gbt091>
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8(6), 551-565. <http://dx.doi.org/10.1162/jocn.1996.8.6.551>
- Bigler, E. D., Andersob, C. V., & Blatter, D. D. (2002). Temporal lobe morphology in normal aging and traumatic brain injury. *American Journal of Neuroradiology*, 23(2), 255-266.
- Birditt, K. S., & Fingerman, K. L. (2005). Do we get better at picking our battles? Age group differences in descriptions of behavioral reactions to interpersonal tensions. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, 60(3), 121-128. <http://dx.doi.org/10.1093/geronb/60.3.P121>
- Blatter, D. D., Bigler, E. D., Gale, S. D., Johnson, S. C., Anderson, C. V., Burnett, B. M., ... & Horn, S. D. (1995). Quantitative volumetric analysis of brain MR: normative database spanning 5 decades of life. *American journal of Neuroradiology*, 16(2), 241-251.

- Boksem, M. A., & De Cremer, D. (2010). Fairness concerns predict medial frontal negativity amplitude in ultimatum bargaining. *Social Neuroscience*, 5(1), 118-128. <http://dx.doi.org/10.1080/17470910903202666>
- Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: the HAROLD Model. *Psychology and Aging*, 17(1), 85-100. <http://dx.doi.org/10.1037//0882-7974.17.1.85>
- Cacioppo, J. T., Berntson, G. G., Bechara, A., Tranel, D., & Hawkley, L. C. (2011). Could an aging brain contribute to subjective well-being? The value added by a social neuroscience perspective. In A. Todorov, S. T. Fiske, & D. A. Prentice (Eds.), *Social neuroscience: Toward understanding the underpinnings of the social mind* (pp. 249-262). New York: Oxford University Press.
- Carstensen, L. L., Mikels, J. A., & Mather, M. (2006). Aging and the intersection of cognition, motivation, and emotion. In J. E. Birren, & K. W. Schaie (Eds.), *Handbook of the psychology of aging* (pp. 343-362). San Diego, CA: Academic.
- Carstensen, L. L., Turan, B., Scheibe, S., Ram, N., Ersner-Hershfield, H., Samanez-Larkin, G. R., ... & Nesselroade, J. R. (2011). Emotional experience improves with age: evidence based on over 10 years of experience sampling. *Psychology and Aging*, 26(1), 21-33. <http://dx.doi.org/10.1037/a0021285>
- Castelli, I., Baglio, F., Blasi, V., Alberoni, M., Falini, A., Liverta-Sempio, O., ... & Marchetti, A. (2010). Effects of aging on mindreading ability through the eyes: an fMRI study. *Neuropsychologia*, 48(9), 2586-2594. <http://dx.doi.org/10.1016/j.neuropsychologia.2010.05.005>
- Charles, S. T., & Carstensen, L. L. (2008). Unpleasant situations elicit different emotional responses in younger and older adults. *Psychology and Aging*, 23(3), 495-504. <http://dx.doi.org/10.1037/a0013284>
- Charles, S. T., Mather, M., & Carstensen, L. L. (2003). Aging and emotional memory: the forgettable nature of negative images for older adults. *Journal of Experimental Psychology: General*, 132(2), 310-324. <http://dx.doi.org/10.1037/0096-3445.132.2.310>

- Charles, S. T., Reynolds, C. A., & Gatz, M. (2001). Age-related differences and change in positive and negative affect over 23 years. *Journal of Personality and Social Psychology*, 80(1), 136-151. <http://dx.doi.org/10.1037/0022-3514.80.1.136>
- Chopik, W. J., Edelstein, R. S., & Fraley, R. C. (2013). From the cradle to the grave: Age differences in attachment from early adulthood to old age. *Journal of Personality*, 81(2), 171-183. <http://dx.doi.org/10.1111/j.1467-6494.2012.00793.x>
- Courchesne, E., Chisum, H. J., Townsend, J., Cowles, A., Covington, J., Egaas, B., ... & Press, G. A. (2000). Normal brain development and aging: quantitative analysis at in vivo MR imaging in healthy volunteers. *Radiology*, 216(3), 672-682. <http://dx.doi.org/10.1148/radiology.216.3.r00au37672>
- Cui, F., Ma, N., & Luo, Y. J. (2016). Moral judgment modulates neural responses to the perception of other's pain: an ERP study. *Scientific Reports*, 6, 1-8.
- Curiati, P. K., Tamashiro, J. H., Squarzoni, P., Duran, F. L. S., Santos, L. C., Wajngarten, M., ... & Busatto, G. F. (2009). Brain structural variability due to aging and gender in cognitively healthy Elders: results from the Sao Paulo Ageing and Health study. *American Journal of Neuroradiology*, 30(10), 1850-1856. <http://dx.doi.org/10.3174/ajnr.A1727>
- Damasio, A. R., Tranel, D., & Damasio, H. (1990). Individuals with sociopathic behavior caused by frontal damage fail to respond autonomically to social stimuli. *Behavioural Brain Research*, 41(2), 81-94. [http://dx.doi.org/10.1016/0166-4328\(90\)90144-4](http://dx.doi.org/10.1016/0166-4328(90)90144-4)
- Darowski, E. S., Helder, E., Zacks, R. T., Hasher, L., & Hambrick, D. Z. (2008). Age-related differences in cognition: The role of distraction control. *Neuropsychology*, 22(5), 638-644. <http://dx.doi.org/10.1037/0894-4105.22.5.638>
- Deary, I. J., Corley, J., Gow, A. J., Harris, S. E., Houlihan, L. M., Marioni, R. E., ... & Starr, J. M. (2009). Age-associated cognitive decline. *British Medical Bulletin*, 92(1), 135-152. <http://dx.doi.org/10.1093/bmb/ldp033>
- Decety, J., & Cacioppo, S. (2012). The speed of morality: a high-density electrical neuroimaging study. *Journal of Neurophysiology*, 108(11), 3068-3072. <http://dx.doi.org/10.1152/jn.00473.2012>

- Derntl, B., Finkelmeyer, A., Toygar, T. K., Hülsmann, A., Schneider, F., Falkenberg, D. I., & Habel, U. (2009). Generalized deficit in all core components of empathy in schizophrenia. *Schizophrenia Research*, 108(1-3), 197-206.
<http://dx.doi.org/10.1016/j.schres.2008.11.009>
- Diamond, A. (2013). Executive functions. *Annual Review of Psychology*, 64, 135-168.
<http://dx.doi.org/10.1146/annurev-psych-113011-143750>
- Dickstein, D. L., Kabaso, D., Rocher, A. B., Luebke, J. I., Wearne, S. L., & Hof, P. R. (2007). Changes in the structural complexity of the aged brain. *Aging Cell*, 6(3), 275-284. <http://dx.doi.org/10.1111/j.1474-9726.2007.00289.x>
- Diéguez-Risco, T., Aguado, L., Albert, J., & Hinojosa, J. A. (2013). Faces in context: modulation of expression processing by situational information. *Social Neuroscience*, 8(6), 601–620. <http://dx.doi.org/10.1080/17470919.2013.834842>
- Diéguez-Risco, T., Aguado, L., Albert, J., & Hinojosa, J. A. (2015). Judging emotional congruency: Explicit attention to situational context modulates processing of facial expressions of emotion. *Biological Psychology*, 112, 27-38.
<http://dx.doi.org/10.1016/j.biopsycho.2015.09.012>
- Dolcos, S., Katsumi, Y., & Dixon, R. A. (2014). The role of arousal in the spontaneous regulation of emotions in healthy aging: a fMRI investigation. *Frontiers in Psychology*, 5, 1-12. <http://dx.doi.org/10.3389/fpsyg.2014.00681>
- Du, A. T., Schuff, N., Chao, L. L., Kornak, J., Jagust, W. J., Kramer, J. H., ... & Weiner, M. W. (2006). Age effects on atrophy rates of entorhinal cortex and hippocampus. *Neurobiology of Aging*, 27(5), 733-740.
<http://dx.doi.org/10.1016/j.neurobiolaging.2005.03.021>
- Erk, S., Walter, H., & Abler, B. (2008). Age-related physiological responses to emotion anticipation and exposure. *Neuroreport*, 19(4), 447-452.
<http://dx.doi.org/10.1097/WNR.0b013e3282f5d92f>
- Eslinger, P. J. (1999). Orbital frontal cortex: Historical and contemdorarv views about its behavioral and physiological significanc;. An introduction to special topic papers: Part I. *Neurocase*, 5(3), 225-229.
<http://dx.doi.org/10.1080/13554799908402727>

- Ferreira-Santos, F. (2013). *Modulation of event-related potentials by facial expressions of emotion in infants (at 9, 16, and 24 months) and adults: Contributions for the understanding of the ontogenesis of emotional face processing* (Doctoral dissertation). Retrieved from: <http://hdl.handle.net/10216/68002>
- Fjell, A. M., & Walhovd, K. B. (2010). Structural brain changes in aging: courses, causes and cognitive consequences. *Reviews in the Neurosciences*, 21(3), 187-222. <http://dx.doi.org/10.1515/REVNEURO.2010.21.3.187>
- Fjell, A. M., Westlye, L. T., Grydeland, H., Amlien, I., Espeseth, T., Reinvang, I., ... & Alzheimer Disease Neuroimaging Initiative. (2013). Critical ages in the life course of the adult brain: nonlinear subcortical aging. *Neurobiology of Aging*, 34(10), 2239-2247. <http://dx.doi.org/10.1016/j.neurobiolaging.2013.04.006>
- Folstein, J. R., & Van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: a review. *Psychophysiology*, 45(1), 152-170. <http://dx.doi.org/10.1111/j.1469-8986.2007.00602.x>
- Ge, R., Fu, Y., Wang, D., Yao, L., & Long, Z. (2014). Age-related alterations of brain network underlying the retrieval of emotional autobiographical memories: an fMRI study using independent component analysis. *Frontiers in Human Neuroscience*, 8, 629, 1-17. <http://dx.doi.org/10.3389/fnhum.2014.00629>
- Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. *Annual Review of Neuroscience*, 30, 535-574. <http://dx.doi.org/10.1146/annurev.neuro.29.051605.113038>
- Good, C. D., Johnsrude, I. S., Ashburner, J., Henson, R. N., Fristen, K. J., & Frackowiak, R. S. (2001). A voxel-based morphometric study of ageing in 465 normal adult human brains. *Neuroimage*, 14(1), 21-36. <http://dx.doi.org/10.1006/nimg.2001.0786>
- Grafman, J., Schwab, K., Warden, D., Pridgen, A., Brown, H. R., & Salazar, A. M. (1996). Frontal lobe injuries, violence, and aggression: a report of the Vietnam Head Injury Study. *Neurology*, 46(5), 1231-1238. <http://dx.doi.org/10.1212/WNL.46.5.1231>
- Green, M. F., Olivier, B., Crawley, J. N., Penn, D. L., & Silverstein, S. (2005). Social cognition in schizophrenia: recommendations from the measurement and

treatment research to improve cognition in schizophrenia new approaches conference. *Schizophrenia Bulletin*, 31(4), 882-887.

<http://dx.doi.org/10.1093/schbul/sbi049>

Green, M. F., Penn, D. L., Bentall, R., Carpenter, W. T., Gaebel, W., Gur, R. C., ... & Heinssen, R. (2008). Social cognition in schizophrenia: an NIMH workshop on definitions, assessment, and research opportunities. *Schizophrenia Bulletin*, 34(6), 1211-1220. <http://dx.doi.org/10.1093/schbul/sbm145>

Greene, J., & Haidt, J. (2002). How (and where) does moral judgment work?. *Trends in Cognitive Sciences*, 6(12), 517-523.

Grieve, S. M., Clark, C. R., Williams, L. M., Peduto, A. J., & Gordon, E. (2005). Preservation of limbic and paralimbic structures in aging. *Human Brain Mapping*, 25(4), 391-401. <http://dx.doi.org/10.1002/hbm.20115>

Gruenewald, T. L., Mroczek, D. K., Ryff, C. D., & Singer, B. H. (2008). Diverse pathways to positive and negative affect in adulthood and later life: An integrative approach using recursive partitioning. *Developmental Psychology*, 44(2), 330-343. <http://dx.doi.org/10.1037/0012-1649.44.2.330>

Guttmann, C. R., Jolesz, F. A., Kikinis, R., Killiany, R. J., Moss, M. B., Sandor, T., & Albert, M. S. (1998). White matter changes with normal aging. *Neurology*, 50(4), 972-978. <http://dx.doi.org/10.1212/WNL.50.4.972>

Haaland, K. Y., Price, L., & Larue, A. (2003). What does the WMS-III tell us about memory changes with normal aging?. *Journal of the International Neuropsychological Society*, 9(1), 89-96. <http://dx.doi.org/10.1017/S1355617703910101>

Happé, F. G., Winner, E., & Brownell, H. (1998). The getting of wisdom: theory of mind in old age. *Developmental Psychology*, 34(2), 358-362. <http://dx.doi.org/10.1037/0012-1649.34.2.358>

Harada, C. N., Love, M. C. N., & Triebel, K. L. (2013). Normal cognitive aging. *Clinics in Geriatric Medicine*, 29(4), 737-752. <http://dx.doi.org/10.1016/j.cger.2013.07.002>

Harlé, K. M., & Sanfey, A. G. (2012). Social economic decision-making across the lifespan: an fMRI investigation. *Neuropsychologia*, 50(7), 1416-1424. <http://dx.doi.org/10.1016/j.neuropsychologia.2012.02.026>

- Hedden, T., & Gabrieli, J. D. (2004). Insights into the ageing mind: a view from cognitive neuroscience. *Nature Reviews Neuroscience*, 5(2), 87-96.
- Hertwig, R., & Erev, I. (2009). The description–experience gap in risky choice. *Trends in Cognitive Sciences*, 13(12), 517-523. <http://dx.doi.org/10.1016/j.tics.2009.09.004>
- Hinojosa, J. A., Mercado, F., & Carretié, L. (2015). N170 sensitivity to facial expression: A meta-analysis. *Neuroscience & Biobehavioral Reviews*, 55, 498-509. <http://dx.doi.org/10.1016/j.neubiorev.2015.06.002>
- Hof, P. R., & Morrison, J. H. (2004). The aging brain: morphomolecular senescence of cortical circuits. *Trends in Neurosciences*, 27(10), 607-613. <http://dx.doi.org/10.1016/j.tins.2004.07.013>
- Isaacowitz, D. M., Allard, E. S., Murphy, N. A., & Schlangel, M. (2009). The time course of age-related preferences toward positive and negative stimuli. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, 64(2), 188-192. <http://dx.doi.org/10.1093/geronb/gbn036>
- Isaacowitz, D. M., Toner, K., & Neupert, S. D. (2009). Use of gaze for real-time mood regulation: effects of age and attentional functioning. *Psychology and Aging*, 24(4), 989-994. <http://dx.doi.org/10.1037/a0017706>
- Jernigan, T. L., Archibald, S. L., Berhow, M. T., Sowell, E. R., Foster, D. S., & Hesselink, J. R. (1991). Cerebral structure on MRI, Part I: Localization of age-related changes. *Biological Psychiatry*, 29(1), 55-60. [http://dx.doi.org/10.1016/0006-3223\(91\)90210-D](http://dx.doi.org/10.1016/0006-3223(91)90210-D)
- Jernigan, T. L., Archibald, S. L., Fennema-Notestine, C., Gamst, A. C., Stout, J. C., Bonner, J., & Hesselink, J. R. (2001). Effects of age on tissues and regions of the cerebrum and cerebellum. *Neurobiology of Aging*, 22(4), 581-594. [http://dx.doi.org/10.1016/S0197-4580\(01\)00217-2](http://dx.doi.org/10.1016/S0197-4580(01)00217-2)
- Jernigan, T. L., & Gamst, A. C. (2005). Changes in volume with age—consistency and interpretation of observed effects. *Neurobiology of Aging*, 26(9), 1271-1274. <http://dx.doi.org/10.1016/j.neurobiolaging.2005.05.016>
- Jiang, J., Sachdev, P., Lipnicki, D. M., Zhang, H., Liu, T., Zhu, W., ... & Trollor, J. (2014). A longitudinal study of brain atrophy over two years in community-dwelling older

individuals. *Neuroimage*, 86, 203-211.

<http://dx.doi.org/10.1016/j.neuroimage.2013.08.022>

Jocham, G., Klein, T. A., & Ullsperger, M. (2011). Dopamine-mediated reinforcement learning signals in the striatum and ventromedial prefrontal cortex underlie value-based choices. *Journal of Neuroscience*, 31(5), 1606-1613.

<http://dx.doi.org/10.1523/JNEUROSCI.3904-10.2011>

Johannes, S., Münte, T. F., Heinze, H. J., & Mangun, G. R. (1995). Luminance and spatial attention effects on early visual processing. *Cognitive Brain Research*, 2(3), 189-205. [http://dx.doi.org/10.1016/0926-6410\(95\)90008-X](http://dx.doi.org/10.1016/0926-6410(95)90008-X)

Kahneman, D., & Tversky, A. (2013). Prospect theory: An analysis of decision under risk. *Econometrica: Journal of the Econometric Society*, 47, 263-291.

<http://dx.doi.org/10.2307/1914185>

Kalpouzos, G., Chételat, G., Baron, J. C., Landeau, B., Mevel, K., Godeau, C., ... & Desgranges, B. (2009). Voxel-based mapping of brain gray matter volume and glucose metabolism profiles in normal aging. *Neurobiology of Aging*, 30(1), 112-124. <http://dx.doi.org/10.1016/j.neurobiolaging.2007.05.019>

Karrer, T. M., Josef, A. K., Mata, R., Morris, E. D., & Samanez-Larkin, G. R. (2017). Reduced dopamine receptors and transporters but not synthesis capacity in normal aging adults: a meta-analysis. *Neurobiology of Aging*, 57, 36-46.

<http://dx.doi.org/10.1016/j.neurobiolaging.2017.05.006>

Kehoe, E. G., Toomey, J. M., Balsters, J. H., & Bokde, A. L. (2013). Healthy aging is associated with increased neural processing of positive valence but attenuated processing of emotional arousal: an fMRI study. *Neurobiology of Aging*, 34(3), 809-821. <http://dx.doi.org/10.1016/j.neurobiolaging.2012.07.006>

Keightley, M. L., Winocur, G., Burianova, H., Hongwanishkul, D., & Grady, C. L. (2006). Age effects on social cognition: faces tell a different story. *Psychology and Aging*, 21(3), 558-572. <http://dx.doi.org/10.1037/0882-7974.21.3.558>

Kellough, J. L., & Knight, B. G. (2011). Positivity effects in older adults' perception of facial emotion: The role of future time perspective. *Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, 67(2), 150-158.

<http://dx.doi.org/10.1093/geronb/gbr079>

- Kern, R. S., & Horan, W. P. (2010). Definition and measurement of neurocognition and social cognition. In V. Roder, & A. Medalia (Eds.), *Neurocognition and social cognition in schizophrenia patients* (pp. 1-22). Basel, Switzerland: Karger Publishers.
- Kimberg, D. Y., & Farah, M. J. (1993). A unified account of cognitive impairments following frontal lobe damage: The role of working memory in complex, organized behavior. *Journal of Experimental Psychology: General*, 122(4), 411-428.
- Knight, M., Seymour, T. L., Gaunt, J. T., Baker, C., Nesmith, K., & Mather, M. (2007). Aging and goal-directed emotional attention: distraction reverses emotional biases. *Emotion*, 7(4), 705-714. <http://dx.doi.org/10.1037/1528-3542.7.4.705>
- Laakso, M. P., Partanen, K., Lehtovirta, M., Hallikainen, M., Hänninen, T., Vainio, P., ... & Soininen, H. (1995). MRI of amygdala fails of diagnose early Alzheimer's disease. *Neuroreport*, 6(17), 2414-2418. <http://dx.doi.org/10.1097/00001756-199511270-00032>
- Leclerc, C. M., & Kensinger, E. A. (2011). Neural processing of emotional pictures and words: A comparison of young and older adults. *Developmental Neuropsychology*, 36(4), 519-538. <http://dx.doi.org/10.1080/87565641.2010.549864>
- Leslie, A. M. (1987). Pretense and representation: The origins of "theory of mind". *Psychological Review*, 94(4), 412-426. <http://dx.doi.org/10.1037/0033-295X.94.4.412>
- Lezak, M. D., Howieson, D. B., Loring, D. W., & Fischer, J. S. (2004). *Neuropsychological assessment (4th ed.)*. New York: Oxford University Press.
- Li, W., van Tol, M. J., Li, M., Miao, W., Jiao, Y., Heinze, H. J., ... & Walter, M. (2014). Regional specificity of sex effects on subcortical volumes across the lifespan in healthy aging. *Human Brain Mapping*, 35(1), 238-247. <http://dx.doi.org/10.1002/hbm.22168>
- Liebherr, M., Schiebener, J., Averbek, H., & Brand, M. (2017). Decision Making under Ambiguity and Objective Risk in Higher Age—A Review on Cognitive and

- Emotional Contributions. *Frontiers in Psychology*, 8, 1-12.
<http://dx.doi.org/10.3389/fpsyg.2017.02128>
- Lopes da Silva, F. (2013). EEG and MEG: relevance to neuroscience. *Neuron*, 80(5), 1112-1128. <http://dx.doi.org/10.1016/j.neuron.2013.10.017>
- Luck, S. J. (2005). *An Introduction to the Event-Related Potential Technique*. London, England: MIT press.
- Luszcz, M. A., & Bryan, J. (1999). Toward understanding age-related memory loss in late adulthood. *Gerontology*, 45, 2-9. <http://dx.doi.org/10.1159/000022048>
- MacPherson, S. E., Phillips, L. H., & Della Sala, S. (2002). Age, executive function and social decision making: a dorsolateral prefrontal theory of cognitive aging. *Psychology and Aging*, 17(4), 598-609. <http://dx.doi.org/10.1037/0882-7974.17.4.598>
- Madden, D. J., Whiting, W. L., Provenzale, J. M., & Huettel, S. A. (2004). Age-related changes in neural activity during visual target detection measured by fMRI. *Cerebral Cortex*, 14(2), 143–155. <http://dx.doi.org/10.1093/cercor/bhg113>.
- Marques-Teixeira, J. (2007). Neurocognição, cognição social e funcionamento social na esquizofrenia. *Mental Health*, 9(6), 7-10.
- Marques-Teixeira, J. (2011). Reserva cognitiva e esquizofrenia. *Mental Health*, 13(1), 6-10.
- McGaugh, J. L. (2000). Memory--a century of consolidation. *Science*, 287(5451), 248-251. <http://dx.doi.org/10.1126/science.287.5451.248>
- Marschner, A., Mell, T., Wartenburger, I., Villringer, A., Reischies, F. M., & Heekeren, H. R. (2005). Reward-based decision-making and aging. *Brain Research Bulletin*, 67(5), 382-390. <http://dx.doi.org/10.1016/j.brainresbull.2005.06.010>
- Mather, M. (2016). The affective neuroscience of aging. *Annual Review of Psychology*, 67, 213-238. <http://dx.doi.org/10.1146/annurev-psych-122414-033540>
- Mather, M., Canli, T., English, T., Whitfield, S., Wais, P., Ochsner, K., ... & Carstensen, L. L. (2004). Amygdala responses to emotionally valenced stimuli in older and younger adults. *Psychological Science*, 15(4), 259-263.
<http://dx.doi.org/10.1111/j.0956-7976.2004.00662.x>

- Mather, M., & Carstensen, L. L. (2003). Aging and attentional biases for emotional faces. *Psychological Science*, 14(5), 409-415. <http://dx.doi.org/10.1111/1467-9280.01455>
- Mather, M., & Carstensen, L. L. (2005). Aging and motivated cognition: The positivity effect in attention and memory. *Trends in Cognitive Sciences*, 9(10), 496-502. <http://dx.doi.org/10.1016/j.tics.2005.08.005>
- Mather, M., & Knight, M. (2005). Goal-directed memory: The role of cognitive control in older adults' emotional memory. *Psychology and Aging*, 20(4), 554-570. <http://dx.doi.org/10.1037/0882-7974.20.4.554>.
- Mather, M., Mazar, N., Gorlick, M. A., Lighthall, N. R., Burgeno, J., Schoeke, A., & Ariely, D. (2012). Risk preferences and aging: The “certainty effect” in older adults' decision making. *Psychology and Aging*, 27(4), 801-816. <http://dx.doi.org/10.1037/a0030174>
- Mattson, M. P., Maudsley, S., & Martin, B. (2004). BDNF and 5-HT: a dynamic duo in age-related neuronal plasticity and neurodegenerative disorders. *Trends in Neurosciences*, 27(10), 589-594. <http://dx.doi.org/10.1016/j.tins.2004.08.001>
- Maylor, E. A. (2005). Age-related changes in memory. In M. L. Johnson (Ed.). *The Cambridge handbook of age and ageing* (pp. 200-208). New York: Cambridge University Press.
- Melov, S. (2004). Modeling mitochondrial function in aging neurons. *Trends in Neurosciences*, 27(10), 601-606. <http://dx.doi.org/10.1016/j.tins.2004.08.004>
- Moran, J. M. (2013). Lifespan development: The effects of typical aging on theory of mind. *Behavioural Brain Research*, 237, 32-40. <http://dx.doi.org/10.1016/j.bbr.2012.09.020>
- Mu, Q., Xie, J., Wen, Z., Weng, Y., & Shuyun, Z. (1999). A quantitative MR study of the hippocampal formation, the amygdala, and the temporal horn of the lateral ventricle in healthy subjects 40 to 90 years of age. *American Journal of Neuroradiology*, 20(2), 207-211.
- Nashiro, K., Sakaki, M., & Mather, M. (2012). Age differences in brain activity during emotion processing: Reflections of age-related decline or increased emotion regulation. *Gerontology*, 58(2), 156-163. <http://dx.doi.org/10.1159/000328465>

- Nyberg, L., & Baäcckman, L. (2004). Cognitive ageing: a view from brain imaging. In R. Dixon, L. Baäcckman, & L. Nilsson (Eds.). *New frontiers in cognitive ageing* (pp. 135-160). Oxford: Oxford University Press.
- Ochsner, K. N., & Lieberman, M. D. (2001). The emergence of social cognitive neuroscience. *American Psychologist*, 56(9), 717-734.
<http://dx.doi.org/10.1037/0003-066X.56.9.717>
- Penn, D. L., Corrigan, P. W., Bentall, R. P., Racenstein, J., & Newman, L. (1997). Social cognition in schizophrenia. *Psychological Bulletin*, 121(1), 114.
<http://dx.doi.org/10.1038/nrn4005>
- Persson, J., Nyberg, L., Lind, J., Larsson, A., Nilsson, L. G., Ingvar, M., & Buckner, R. L. (2006). Structure–function correlates of cognitive decline in aging. *Cerebral Cortex*, 16(7), 907-915. <http://dx.doi.org/10.1093/cercor/bhj036>
- Persson, J., Pudas, S., Lind, J., Kauppi, K., Nilsson, L. G., & Nyberg, L. (2012). Longitudinal structure–function correlates in elderly reveal MTL dysfunction with cognitive decline. *Cerebral Cortex*, 22(10), 2297-2304.
<http://dx.doi.org/10.1093/cercor/bhr306>
- Petrican, R., Moscovitch, M., & Schimmack, U. (2008). Cognitive resources, valence, and memory retrieval of emotional events in older adults. *Psychology and Aging*, 23(3), 585-594. <http://dx.doi.org/10.1037/a0013176>
- Petrides, M., & Milner, B. (1982). Deficits on subject-ordered tasks after frontal-and temporal-lobe lesions in man. *Neuropsychologia*, 20(3), 249-262.
[http://dx.doi.org/10.1016/0028-3932\(82\)90100-2](http://dx.doi.org/10.1016/0028-3932(82)90100-2)
- Peyroux, E., & Franck, N. (2016). Improving social cognition in people with schizophrenia with RC2S: two single-case studies. *Frontiers in Psychiatry*, 7, 66.
<http://dx.doi.org/10.3389/fpsy.2016.00066>
- Pfefferbaum, A., Mathalon, D. H., Sullivan, E. V., Rawles, J. M., Zipursky, R. B., & Lim, K. O. (1994). A quantitative magnetic resonance imaging study of changes in brain morphology from infancy to late adulthood. *Archives of Neurology*, 51(9), 874-887. <http://dx.doi.org/10.1001/archneur.1994.00540210046012>

- Phillips, L. H., & Della Sala, S. (1998). Aging, intelligence, and anatomical segregation in the frontal lobes. *Learning and Individual Differences*, 10(3), 217-243.
[http://dx.doi.org/10.1016/S1041-6080\(99\)80131-9](http://dx.doi.org/10.1016/S1041-6080(99)80131-9)
- Phillips, L. H., Henry, J. D., Hosie, J. A., & Milne, A. B. (2006). Age, anger regulation and well-being. *Aging and Mental Health*, 10(3), 250-256.
<http://dx.doi.org/10.1080/13607860500310385>
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind?. *Behavioral and Brain Sciences*, 1(4), 515-526.
<http://dx.doi.org/10.1017/S0140525X00076512>
- Price, J. L. (1999). Networks within the orbital and medial prefrontal cortex. *Neurocase*, 5(3), 231-241. <http://dx.doi.org/10.1080/13554799908402728>
- Raz, N., Briggs, S. D., Marks, W., & Acker, J. D. (1999). Age-related deficits in generation and manipulation of mental images: II. The role of dorsolateral prefrontal cortex. *Psychology and Aging*, 14(3), 436-444. <http://dx.doi.org/10.1037/0882-7974.14.3.436>
- Raz, N., Gunning-Dixon, F. M., Head, D., Dupuis, J. H., & Acker, J. D. (1998). Neuroanatomical correlates of cognitive aging: evidence from structural magnetic resonance imaging. *Neuropsychology*, 12(1), 95.
- Raz, N., & Rodrigue, K. M. (2006). Differential aging of the brain: patterns, cognitive correlates and modifiers. *Neuroscience & Biobehavioral Reviews*, 30(6), 730-748.
<http://dx.doi.org/10.1016/j.neubiorev.2006.07.001>
- Raz, N., Rodrigue, K. M., Head, D., Kennedy, K. M., & Acker, J. D. (2004). Differential aging of the medial temporal lobe a study of a five-year change. *Neurology*, 62(3), 433-438.
<http://dx.doi.org/10.1212/01.WNL.0000106466.09835.46>
- Reed, A. E., Chan, L., & Mikels, J. A. (2014). Meta-analysis of the age-related positivity effect: age differences in preferences for positive over negative information. *Psychology and Aging*, 29(1), 1-15.
<http://dx.doi.org/10.1037/a0035194>
- Resnick, S. M., Pham, D. L., Kraut, M. A., Zonderman, A. B., & Davatzikos, C. (2003). Longitudinal magnetic resonance imaging studies of older adults: a shrinking

- brain. *Journal of Neuroscience*, 23(8), 3295-3301.
<http://dx.doi.org/10.1523/JNEUROSCI.23-08-03295.2003>
- Reuter-Lorenz, P. A., & Cappell, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, 17(3), 177-182. <http://dx.doi.org/10.1111/j.1467-8721.2008.00570.x>
- Roberts, R. J. & Pennington, B. F. (1996). An interactive framework for examining prefrontal cognitive processes. *Developmental Neuropsychology*, 12(1), 105–126.
<http://dx.doi.org/10.1080/87565649609540642>
- Rodrigue, K. M., & Raz, N. (2004). Shrinkage of the entorhinal cortex over five years predicts memory performance in healthy adults. *Journal of Neuroscience*, 24(4), 956-963. <http://dx.doi.org/10.1523/JNEUROSCI.4166-03.2004>
- Rolls, E. T. (1996). The orbitofrontal cortex. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 351, 1433–1444.
<http://dx.doi.org/10.1098/rstb.1996.0128>
- Rönnlund, M., Nyberg, L., Bäckman, L., & Nilsson, L. G. (2005). Stability, growth, and decline in adult life span development of declarative memory: cross-sectional and longitudinal data from a population-based study. *Psychology and Aging*, 20(1), 3-18. <http://dx.doi.org/10.1037/0882-7974.20.1.3>
- Rusinek, H., De Santi, S., Frid, D., Tsui, W. H., Tarshish, C. Y., Convit, A., & de Leon, M. J. (2003). Regional brain atrophy rate predicts future cognitive decline: 6-year longitudinal MR imaging study of normal aging. *Radiology*, 229(3), 691-696.
<http://dx.doi.org/10.1148/radiol.2293021299>
- Sachs, G., Steger-Wuchse, D., Kryspin-Exner, I., Gur, R. C., & Katschnig, H. (2004). Facial recognition deficits and cognition in schizophrenia. *Schizophrenia Research*, 68(1), 27-35. [http://dx.doi.org/10.1016/S0920-9964\(03\)00131-2](http://dx.doi.org/10.1016/S0920-9964(03)00131-2)
- Sakaki, M., Fryer, K., & Mather, M. (2014). Emotion strengthens high-priority memory traces but weakens low-priority memory traces. *Psychological Science*, 25(2), 387-395. <http://dx.doi.org/10.1177/0956797613504784>
- Sakaki, M., Nga, L., & Mather, M. (2013). Amygdala functional connectivity with medial prefrontal cortex at rest predicts the positivity effect in older adults'

- memory. *Journal of Cognitive Neuroscience*, 25(8), 1206-1224.
http://dx.doi.org/10.1162/jocn_a_00392
- Salthouse, T. A. (1992). Influence of processing speed on adult age differences in working memory. *Acta Psychologica*, 79(2), 155-170.
[http://dx.doi.org/10.1016/0001-6918\(92\)90030-H](http://dx.doi.org/10.1016/0001-6918(92)90030-H)
- San Martín, R. (2012). Event-related potential studies of outcome processing and feedback-guided learning. *Frontiers in Human Neuroscience*, 6, 304.
<http://dx.doi.org/10.3389/fnhum.2012.00304>
- Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the ultimatum game. *Science*, 300(5626), 1755-1758. <http://dx.doi.org/10.1126/science.1082976>
- Sasse, L. K., Gamer, M., Büchel, C., & Brassen, S. (2014). Selective control of attention supports the positivity effect in aging. *PloS One*, 9(8), e104180.
<http://dx.doi.org/10.1371/journal.pone.0104180>
- Satz, P. (1993). Brain reserve capacity on symptom onset after brain injury: a formulation and review of evidence for threshold theory. *Neuropsychology*, 7(3), 273-295. <http://dx.doi.org/10.1037//0894-4105.7.3.273>
- Schretlen, D., Pearlson, G. D., Anthony, J. C., Aylward, E. H., Augustine, A. M., Davis, A., & Barta, P. (2000). Elucidating the contributions of processing speed, executive ability, and frontal lobe volume to normal age-related differences in fluid intelligence. *Journal of the International Neuropsychological Society*, 6(1), 52-61.
<http://dx.doi.org/10.1017/S1355617700611062>
- Schultz, W. (2006). Behavioral theories and the neurophysiology of reward. *Annual Review Psychology*, 57, 87-115.
<http://dx.doi.org/10.1146/annurev.psych.56.091103.070229>
- Schultz, W. (2013). Updating dopamine reward signals. *Current Opinion in Neurobiology*, 23(2), 229-238. <http://dx.doi.org/10.1016/j.conb.2012.11.012>
- Shen, J., Kassir, M. A., Wu, J., Zhang, Q., Zhou, S., Xuan, S. Y., ... & Hu, J. (2013). MR volumetric study of piriform-cortical amygdala and orbitofrontal cortices: the aging effect. *PloS One*, 8(9), e74526.
<http://dx.doi.org/10.1371/journal.pone.0074526>

- Simón, T., Suengas, A. G., Ruiz-Gallego-Largo, T., & Bandrés, J. (2013). Positive bias is a defining characteristic of aging to the same extent as declining performance. *International Journal of Psychology*, 48(4), 704-714.
<http://dx.doi.org/10.1080/00207594.2012.718781>
- Smith, D. V., & Huettel, S. A. (2010). Decision neuroscience: neuroeconomics. *Wiley Interdisciplinary Reviews: Cognitive Science*, 1(6), 854-871.
<http://dx.doi.org/10.1002/wcs.73>
- Squire, L. R. (1992). Declarative and nondeclarative memory: Multiple brain systems supporting learning and memory. *Journal of Cognitive Neuroscience*, 4(3), 232-243. <http://dx.doi.org/10.1162/jocn.1992.4.3.232>
- St. Jacques, P., Bessette-Symons, B., & Cabeza, R. (2009). Functional neuroimaging studies of aging and emotion: fronto-amygdalar differences during emotional perception and episodic memory. *Journal of the International Neuropsychological Society*, 15(6), 819-825.
<http://dx.doi.org/10.1017/S1355617709990439>
- St. Jacques, P., Dolcos, F., & Cabeza, R. (2010). Effects of aging on functional connectivity of the amygdala during negative evaluation: a network analysis of fMRI data. *Neurobiology of Aging*, 31(2), 315-327.
<http://dx.doi.org/10.1016/j.neurobiolaging.2008.03.012>
- Stern, Y. (2002). What is cognitive reserve? Theory and research application of the reserve concept. *Journal of the International Neuropsychological Society*, 8(3), 448-460. <http://dx.doi.org/10.1017/S1355617702813248>
- Streit, M., Ioannides, A. A., Liu, L., Wölwer, W., Dammers, J., Gross, J., ... & Müller-Gärtner, H. W. (1999). Neurophysiological correlates of the recognition of facial expressions of emotion as revealed by magnetoencephalography. *Cognitive Brain Research*, 7(4), 481-491. [http://dx.doi.org/10.1016/S0926-6410\(98\)00048-2](http://dx.doi.org/10.1016/S0926-6410(98)00048-2)
- Sullivan, E. V., & Pfefferbaum, A. (2006). Diffusion tensor imaging and aging. *Neuroscience & Biobehavioral Reviews*, 30(6), 749-761.
<http://dx.doi.org/10.1016/j.neubiorev.2006.06.002>

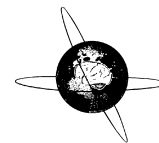
- Toescu, E. C., Verkhatsky, A., & Landfield, P. W. (2004). Ca^{2+} regulation and gene expression in normal brain aging. *Trends in Neurosciences*, 27(10), 614-620. <http://dx.doi.org/10.1016/j.tins.2004.07.010>
- Tomasi, D., & Volkow, N. D. (2012). Aging and Functional Brain Networks. *Molecular Psychiatry*, 17(5), 471-558. <http://dx.doi.org/10.1038/mp.2011.81>
- Urry, H. L., Van Reekum, C. M., Johnstone, T., Kalin, N. H., Thurow, M. E., Schaefer, H. S., ... & Davidson, R. J. (2006). Amygdala and ventromedial prefrontal cortex are inversely coupled during regulation of negative affect and predict the diurnal pattern of cortisol secretion among older adults. *Journal of Neuroscience*, 26(16), 4415-4425. <http://dx.doi.org/10.1523/JNEUROSCI.3215-05.2006>
- Verhaeghen, P., Marcoen, A., & Goossens, L. (1993). Facts and fiction about memory aging: A quantitative integration of research findings. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, 48(4), 157-171. <http://dx.doi.org/10.1093/geronj/48.4.P157>
- Volchegorskii, I. A., Shemyakov, S. E., Turygin, V. V., & Malinovskaya, N. V. (2004). The age dynamics of monoamine oxidase activity and levels of lipid peroxidation products in the human brain. *Neuroscience and Behavioral Physiology*, 34(4), 303-305.
- Volkow, N. D., Gur, R. C., Wang, G. J., Fowler, J. S., Moberg, P. J., Ding, Y. S., ... & Logan, J. (1998). Association between decline in brain dopamine activity with age and cognitive and motor impairment in healthy individuals. *American Journal of Psychiatry*, 155(3), 344-349. <http://dx.doi.org/10.1176/ajp.155.3.344>
- Wagner, N. F., Chaves, P., & Wolff, A. (2017). Discovering the neural nature of moral cognition? Empirical, theoretical, and practical challenges in bioethical research with electroencephalography (EEG). *Journal of Bioethical Inquiry*, 14(2), 299-313. <http://dx.doi.org/10.1007/s11673-017-9780-2>
- Waldinger, R. J., Kensinger, E. A., & Schulz, M. S. (2011). Neural activity, neural connectivity, and the processing of emotionally valenced information in older adults: links with life satisfaction. *Cognitive, Affective, & Behavioral Neuroscience*, 11(3), 426-436. <http://dx.doi.org/10.3758/s13415-011-0039-9>

- Walhovd, K. B., Fjell, A. M., Reinvang, I., Lundervold, A., Dale, A. M., Eilertsen, D. E., ... & Fischl, B. (2005). Effects of age on volumes of cortex, white matter and subcortical structures. *Neurobiology of Aging*, 26(9), 1261-1270.
<http://dx.doi.org/10.1016/j.neurobiolaging.2005.05.020>
- Walhovd, K. B., Westlye, L. T., Amlien, I., Espeseth, T., Reinvang, I., Raz, N., ... & Dale, A. M. (2011). Consistent neuroanatomical age-related volume differences across multiple samples. *Neurobiology of aging*, 32(5), 916-932.
<http://dx.doi.org/10.1016/j.neurobiolaging.2009.05.013>
- West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin*, 120(2), 272–292. <http://dx.doi.org/10.1037/0033-2909.120.2.272>
- Whalley, L. J., Deary, I. J., Appleton, C. L., & Starr, J. M. (2004). Cognitive reserve and the neurobiology of cognitive aging. *Ageing Research Reviews*, 3(4), 369-382.
<http://dx.doi.org/10.1016/j.arr.2004.05.001>
- Whiting, I. V., Wythe, L., & Smith, A. D. (1997). Differential age-related processing limitations in recall and recognition tasks. *Psychology and Aging*, 12(2), 216-224.
<http://dx.doi.org/10.1037/0882-7974.12.2.216>
- Williams, L. M., Brown, K. J., Palmer, D., Liddell, B. J., Kemp, A. H., Olivieri, G., ... & Gordon, E. (2006). The mellow years?: neural basis of improving emotional stability over age. *Journal of Neuroscience*, 26(24), 6422-6430.
<http://dx.doi.org/10.1523/JNEUROSCI.0022-06.2006>
- Wright, C. I., Dickerson, B. C., Feczko, E., Negeira, A., & Williams, D. (2007). A functional magnetic resonance imaging study of amygdala responses to human faces in aging and mild Alzheimer's disease. *Biological Psychiatry*, 62(12), 1388-1395.
<http://dx.doi.org/10.1016/j.biopsych.2006.11.013>
- Wright, C. I., Negreira, A., Gold, A. L., Britton, J. C., Williams, D., & Barrett, L. F. (2008). Neural correlates of novelty and face-age effects in young and elderly adults. *Neuroimage*, 42(2), 956-968.
<http://dx.doi.org/10.1016/j.neuroimage.2008.05.015>

- World Health Organization (2002). Active ageing: A policy framework. Geneva: World Health Organization. Retrieved from <http://apps.who.int/iris/handle/10665/67215>.
- World Health Organization (2015). *World report on ageing and health*. World Health Organization. Retrieved from http://apps.who.int/iris/bitstream/handle/10665/186463/9789240694811_eng.pdf?sequence=1.
- Wynn, J. K., Lee, J., Horan, W. P., & Green, M. F. (2008). Using event related potentials to explore stages of facial affect recognition deficits in schizophrenia. *Schizophrenia Bulletin*, 34(4), 679-687. <http://dx.doi.org/10.1093/schbul/sbn047>
- Yu, A. J., & Dayan, P. (2005). Uncertainty, neuromodulation, and attention. *Neuron*, 46(4), 681-692. <http://dx.doi.org/10.1016/j.neuron.2005.04.026>

2. EXPERIMENTAL WORK

2.1 EMOTION IDENTIFICATION AND AGING: BEHAVIORAL AND NEURAL AGE-RELATED CHANGES



Emotion identification and aging: Behavioral and neural age-related changes



Ana R. Gonçalves^{a,*}, Carina Fernandes^{a,b,c}, Rita Pasion^a, Fernando Ferreira-Santos^a, Fernando Barbosa^a, João Marques-Teixeira^a

^a Laboratory of Neuropsychophysiology, Faculty of Psychology and Education Sciences, University of Porto, Rua Alfredo Allen, 4200-135 Porto, Portugal

^b Faculty of Medicine, University of Porto, Al. Prof. Hernâni Monteiro, 4200-319 Porto, Portugal

^c Language Research Laboratory, Institute of Molecular Medicine, Faculty of Medicine, University of Lisbon, Av. Professor Egas Moniz, 1649-028 Lisboa, Portugal

ARTICLE INFO

Article history:

Accepted 18 February 2018

Available online 9 March 2018

Keywords:

Emotion identification

Aging

Event-related potentials

Positivity effect

Compensation hypothesis

HIGHLIGHTS

- Younger, middle-aged, and older adults show similar accuracy in identifying facial expressions of emotion.
- Older adults showed a larger-amplitude and preponderantly left-hemispheric N170 event-related potential component.
- Compensatory mechanisms may explain age-equivalent performance in emotion identification.

ABSTRACT

Objective: Aging is known to alter the processing of facial expressions of emotion (FEE), however the impact of this alteration is less clear. Additionally, there is little information about the temporal dynamics of the neural processing of facial affect.

Methods: We examined behavioral and neural age-related changes in the identification of FEE using event-related potentials. Furthermore, we analyze the relationship between behavioral/neural responses and neuropsychological functioning. To this purpose, 30 younger adults, 29 middle-aged adults and 26 older adults identified FEE.

Results: The behavioral results showed a similar performance between groups. The neural results showed no significant differences between groups for the P100 component and an increased N170 amplitude in the older group. Furthermore, a pattern of asymmetric activation was evident in the N170 component. Results also suggest deficits in facial feature decoding abilities, reflected by a reduced N250 amplitude in older adults. Neuropsychological functioning predicts P100 modulation, but does not seem to influence emotion identification ability.

Conclusions: The findings suggest the existence of a compensatory function that would explain the age-equivalent performance in emotion identification.

Significance: The study may help future research addressing behavioral and neural processes involved on processing of FEE in neurodegenerative conditions.

© 2018 International Federation of Clinical Neurophysiology. Published by Elsevier B.V. All rights reserved.

1. Introduction

Emotion identification is a key element of nonverbal communication, with emotions often expressed through changes in facial expression, eye contact, body posture and movement. Across the life span, accurate identification of emotional expressions is

essential for successful interpersonal functioning (Carstensen et al., 1997). Inferring the emotions that others are experiencing is an important feature in avoiding conflict and providing social support. Furthermore, intact emotion identification skills are essential to regulate behavior. For instance, individuals may selectively attend and approach to positive stimuli to elicit positive feelings and avoid negative ones (Gross et al., 2006).

The dynamic integration theory attributes the “positivity effect” to greater cognitive demands required to process negative

* Corresponding author.

E-mail address: anasgoncalves@fpce.up.pt (A.R. Gonçalves).

information (Labouvie-Vief, 2003). A body of research suggests an age-related “positivity effect” (Mather and Carstensen, 2005), that is, a tendency for older adults to attend to, and better remember, positive information relative to neutral and negative information. Socio-emotional Selectivity Theory (Carstensen et al., 1999) indicates that significant developmental changes occur in adults’ regulation and processing of affect. According to this theory, the preserved emotional processing and functioning in old age is due to a motivational shift toward emotional regulation goals (i.e., achieving positive affect) as older adults begin to view their lifetime as limited (Carstensen et al., 1999).

Previous studies have indicated that there are age-related differences in how young and older adults process emotional facial expressions (e.g., Leigland et al., 2004; Mather and Knight, 2005). Ruffman et al. (2008) performed a meta-analysis to examine age differences in emotion identification across four modalities – faces, voices, bodies/contexts, and matching of faces to voices – and found an age-related decline across all emotions and modalities with the exception of happiness. However, the mean effect sizes in the faces modality range from 0.07 to 0.34 across all emotions, reflecting inconsistencies among findings in the studies included. Also, following studies (García-Rodríguez et al., 2009; Orgeta, 2010; Suzuki and Akiyama, 2013) report inconsistent findings that raise questions about the effects of aging on emotion identification.

Human aging is accompanied by the decline of various cognitive abilities (for a review, see Salthouse, 2009). For example, sustained attention and working memory decrease with age (Gazzaley et al., 2007; Park et al., 1996). Importantly, these cognitive abilities seem to be relevant to the performance in emotion identification tasks (Lambrecht et al., 2012). However, beyond this well-known age-related cognitive decline, which might influence emotion identification, the impact of aging on emotional processing is less clear (García-Rodríguez et al., 2009; Orgeta, 2010; Suzuki and Akiyama, 2013). Furthermore, there is little information on neural temporal dynamics of facial affect processing. The current study examines facial affect processing in aging using event-related potentials (ERPs).

It has been suggested that processing of faces and facial affect can be roughly divided into three stages: the initial visual processing, encoding of facial features, and decoding of emotional content, presumably indexed by the P100, N170, and N250 ERP components respectively (Wynn et al., 2008). The P100 is a positive waveform peaking approximately after 80–120 ms post-stimulus at occipital sites. It is one of the earliest components identified with basic visual processing (Wynn et al., 2008). The N170 is a negative waveform peaking approximately 150–180 ms post-stimulus in occipito-temporal sites. This component is indicated as the earliest stage of facial structure encoding (Bentin et al., 1996) and is sensitive to the emotional content of a face (Almeida et al., 2014, 2016; Hinojosa et al., 2015). Also sensitive to this content, the N250 is a negative ERP peaking at approximately 250 ms in fronto-central sites (Streit et al., 1999). There are also studies that report emotion modulation of even earlier components, such as the C1, thought to be generated within the primary visual cortex (Halgren et al., 2000; Pourtois et al., 2004).

Several studies used the N170 to examine age-related changes in face perception. Larger N170 amplitudes for faces vs. objects, representing generic face sensitivity, were found identically in young and older adults (Gao et al., 2009). However, the typical lateralization of the N170, with larger amplitudes over the right relative to the left hemisphere (Bentin et al., 1996; Eimer, 2011), has been reported to be less marked in older adults (Gao et al., 2009). This pattern may result from an attempt to compensate for age-related decline (Komes et al., 2014). Liao et al. (2017) used event-related potentials (ERPs) to investigate the effects of age on neural temporal dynamics of processing task-relevant facial

expressions and their relationship to cognitive functions. Analyzing the amplitudes of the P100, N170, P200 and N250 components, the authors found that older people may exert more effort in structural encoding for negative faces, there are different response patterns for the categorization of different facial emotions, and cognitive functioning may be related to facial emotion categorization deficits observed in older adults. Hilimire et al. (2014) examined the neural temporal dynamics of the positivity effect using event-related potentials (ERPs). The results revealed that within the first 130 ms young adults show an FcEP (frontocentral emotional positivity) to negative emotional expressions, whereas older adults show an FcEP to positive emotional expressions. These results constitute additional evidence that the age-related positivity effect in emotion processing can be associated to early automatic processes in the processing of emotional facial expressions. Across these studies, a common pattern of attenuated N170 lateralization effect in older adults was evident.

In spite of the considerable literature on emotion identification and aging, the impact of aging on emotional processing is far from being clear. The studies revealed inconsistent findings regarding behavioral performance and the knowledge about neural temporal dynamics of facial affect processing is still scarce. Additionally, most studies only compared older and younger adults’ behavioral and neural responses, which does not allow examining whether age-related changes occur gradually across the lifespan or have to do with specific changes in old age.

To examine behavioral and neural age-related changes in the identification of facial expressions, we compared ERPs elicited by emotional faces in three age groups – younger adults, middle-aged adults and older adults – examining the three stages of face and facial affect processing: basic visual processing of faces (using the P100), facial feature encoding (using the N170), and decoding of facial features used to identify an emotion (using the N250). By exploring these three stages of face and facial affect processing, we expect to gain a better understanding of when deficits, if they exist, occur in the course of processing facial affect identification in older adults. Furthermore, we analyze the relationship between behavioral/neural responses and neuropsychological functioning. Understanding the behavioral and neural processes involved on processing of facial affect identification across aging is essential to clarify the same processes in neurodegenerative conditions. Considering the inconsistent findings across studies on age differences in emotion identification, besides the age-related decline reported by a previous meta-analysis (Ruffman et al., 2008), a specific directional hypothesis is difficult to support. However, according to the attenuated lateralization of the N170 found in older adults, and assuming that it results from an attempt to compensate for age-related decline (Komes et al., 2014), we may expect an identical behavioral performance between groups. Regarding neuropsychological functioning, if unimpaired performance on identifying facial expressions is a consequence of a compensatory mechanism for general decline of cognitive function associated with old age (Komes et al., 2014), we anticipated that cognitive abilities would not show a significant correlation with performance in identifying FEE.

2. Methods

2.1. Participants

A total of 183 participants were recruited from the community and local University to three groups: younger adults (20–35 years); middle-aged adults (40–55 years); older adults (60–75 years). Participants were included if they had more than four years of formal education and excluded if they reported: uncorrected visual

Table 1
Mean (and SD) values of sociodemographic and neuropsychological data of the participants.

	Younger adults	Middle-aged adults	Older adults	<i>F</i>	χ^2	<i>p</i>
<i>Sociodemographic data</i>						
<i>n</i>	30	29	26			
Gender (<i>n</i> females)	15	15	13		0.55	.758
Age (years)	26.6 (4.0)	47.9 (7.3)	65.0 (4.0)	344		.000 ^{a,b,c}
Years of education	16.3 (2.3)	15.6 (4.8)	13.9 (4.7)	1.78		.175
Handedness (<i>n</i> right)	28	28	26		1.76	.414
<i>Neuropsychological data</i>						
MoCA	27.9 (1.5)	26.8 (2.1)	25.4 (2.2)	11.0		.000 ^{a,b}
IFS	24.6 (2.5)	24.4 (3.0)	22.6 (3.2)	3.92		.024 ^a
CBTT	17.8 (2.9)	17.0 (3.5)	14.9 (3.5)	5.72		.005 ^{a,b}
TMT	35.4 (17.5)	39.9 (18.9)	59.0 (25.1)	9.66		.000 ^{a,b}
AVLT	66.3 (9.1)	60.6 (11.7)	51.8 (9.4)	10.4		.000 ^{a,b}
Phonemic fluency	38.8 (8.7)	37.5 (12.7)	35.4 (11.0)	0.43		.650
Semantic fluency	20.9 (4.2)	20.0 (6.0)	18.3 (4.9)	1.96		.147
HADS depression	2.9 (2.5)	4.0 (3.6)	3.8 (2.4)	1.18		.312
HADS anxiety	6.0 (3.3)	5.9 (3.6)	5.1 (3.8)	0.36		.696
BSI	27.0 (20.7)	28.0 (21.0)	23.7 (17.0)	0.32		.723

Note. MoCA: Montreal Cognitive Assessment; IFS: Institute of Cognitive Neurology Frontal Screening; CBTT: Corsi Block-Tapping Task; TMT: Trail Making Test; AVLT: Auditory Verbal Learning Test; HADS: Hospital Anxiety and Depression Scale; BSI: Brief Symptom Inventory. ^asignificant differences between younger and older adults; ^bbetween middle-aged adults and older adults; ^cbetween younger and middle-aged adults.

impairments ($n = 3$); a score inferior to 22 (cutoff for mild cognitive impairment; Freitas et al., 2014) in the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005; $n = 6$); use of psychotropic medication ($n = 15$); and history of brain injury, neurological or psychiatric diagnosis ($n = 25$). Moreover, 46 participants dropped out the study at the end of the neuropsychological assessment. Data from three older adults were not included in the analysis due to a computer error in saving data. Thus, the final sample was composed by 30 younger, 29 middle-aged, and 26 older adults (see Table 1 for sociodemographic data). They each gave written, informed consent and received 20€ (gift card).

The study was approved by the local Ethics Committee.

2.2. Measures

2.2.1. Self-report measures

Anxiety and depression traits were measured by the Hospital Anxiety and Depression Scale (HADS; Snaith and Zigmond, 1994; Portuguese version by Pais-Ribeiro et al., 2007), and psychopathological symptomatology by the Brief Symptom Inventory (BSI; Derogatis, 1993; Portuguese version by Canavarro, 1999).

2.2.2. Neuropsychological measures

Executive functioning was assessed using the Trail Making Test (TMT; Armitage, 1946; normative data by Cavaco et al., 2013a), and the INECO Frontal Screening (IFS; Torralva et al., 2009; Portuguese version by Moreira et al., 2014). Semantic fluency and phonemic fluency tests were used to assess non-motor processing speed, language production and executive functions (Strauss et al., 2006; Portuguese versions by Cavaco et al., 2013b). Short-term memory was assessed by the Corsi Block-Tapping Task (CBTT; Wechsler, 2008), while verbal, immediate and episodic memory were tested using the Auditory Verbal Learning Test (AVLT; Boake, 2000; Portuguese version by Cavaco et al., 2015).

2.2.3. Stimuli

The stimuli comprised 20 examples each of angry, neutral/calm, happy and surprised expressions selected from the NimStim Face Stimulus Set (Tottenham et al., 2009). These specific emotional categories were selected in order to allow mapping of the affective space by including both low and high arousal exemplars of happy and angry faces and slightly pleasant and unpleasant exemplars of neutral and surprised faces. Emotional expressions of each cate-

gory were selected considering the following criteria: (1) proportion of correct identification of the portrayed emotion was superior to 75%, based on normative data from Tottenham et al. (2009), specifically the mean proportion of correct identification for happiness was 98.9% ($SD = 1.5\%$), anger 93.5% ($SD = 6.0\%$), surprise 92.9% ($SD = 2.9\%$), and calm 86.8% ($SD = 7.0\%$); (2) arousal/valence of the images was lower than the first quartile (Q1) of the corresponding pooled distribution or higher than the third quartile (Q3) of the same distribution (based on reference data from a previous affective ratings study by Ferreira-Santos (2013)). The actors included men and women and were ethnically diverse young adults.

2.3. Procedure

Each image was shown twice, in random order within repetition block, with no response timeout. In each trial, a 500 ms fixation cross was presented at the center of the screen, followed by a 1000 ms face stimulus, and then by the 500 ms fixation cross. Next, an unlimited duration screen with nine emotion labels (anger, disgust, fear, happiness, sadness, calm, neutral, surprise and none of the others) was presented until key press. During this screen, participants used a response box to choose an emotion label to match the stimulus expression. Participants viewed the images on a computer screen from a distance of 115 cm. E-Prime (Psychology Software Tools, Pittsburgh, PA, USA) was used to control the experiment and collect responses. After a block of three practice trials, participants completed two blocks of 80 experimental trials each.

Participants were also asked to rate each emotion 'for each of the dimensions of affective arousal and affective valence' (Ferreira-Santos, 2013). For that purpose, the above procedure was repeated with the response screen presenting 'a modified 7-point version of the Self-Assessment Manikin (SAM) rating scales (Bradley and Lang, 1994)' (Ferreira-Santos, 2013). Participants used a response box to choose a rating from 1 (low arousal or negative valence) to 7 (high arousal or positive valence). The presentation of facial stimuli was randomly ordered, and the response (arousal/valence or valence/arousal) was counter-balanced between participants. After a block of three practice trials, participants completed one block of 80 experimental trials. The emotion identification and the rating experimental tasks were counterbalanced.

All participants were tested individually in two sessions to avoid fatigue effects. In the first (screening) session, a semi-structured interview and the MoCA were conducted to assess inclusion criteria. All the neuropsychological tests and self-report measures were then administered in a random order between participants. Participants meeting the inclusion criteria were invited to participate on a second session, in which the emotion identification task was performed simultaneously to EEG recording. The AVLTL was administered in this session to avoid the possible interference of word lists from other tests with the later evocation and recognition of words from the AVLTL. This second session was part of a larger research protocol with a duration of approximately 240 min (including breaks), requiring all experimental tasks to be randomized. After the placement of the EEG cap, participants read the instructions and completed a practice block.

2.3.1. EEG recording and pre-processing

EEG data was recorded on the acquisition software NetStation V4.5.2 (2008, Electrical Geodesics Inc., Eugene, OR, USA – EGI) using a 128-electrode Hydrocel Geodesic Sensor Net with a Net Amps 300 amplifier (EGI). Impedances were kept below 50 kOhm for all electrodes (high-input impedance system). Data were recorded with a sampling rate of 500 Hz and the electrodes were referenced to the vertex (Cz).

The EEG raw data were pre-processed in the EEGLAB (version 11; Delorme and Makeig, 2004), a MATLAB toolbox (2017, The Mathworks Inc., Natick, MA, USA). Continuous EEG recordings were down-sampled to 250 Hz, band-pass filtered (0.2–30 Hz), bad channels were interpolated (up to a maximum of 10% of the electrodes), and submitted to an Independent Components Analysis (ICA) decomposition. Correction of eye blinks, saccades, and cardiac activity was done by subtracting the corresponding independent component activity from the data, followed by visual inspection to ensure the correction did not alter the signals outside the time windows of the artifacts. The signal was re-referenced to the average of the electrodes. EEG records were segmented into 1000 ms epochs (–200 to 800 ms) and visually inspected for manual artefact rejection. All epochs were baseline corrected (200 ms pre-stimulus) and averaged by condition (age group and emotional category) for each participant.

2.3.2. ERP data analysis

Inspection of ERP grand-average was done to ensure that the expected ERP morphology was present. The mean amplitudes for each ERP component were extracted as the average of the 200 voltage samples around the peak amplitude in the [100, 130] ms time-window for the P100, [120, 220] ms for the N170 and [215, 300] ms for the N250. Electrodes were chosen based on those examined in other studies (Wynn et al., 2008 for P100 and N250; Almeida et al., 2016 for N170). For P100, the activity from O1 (left hemisphere) and O2 (right hemisphere) was analyzed. For N170, the P7 (left hemisphere) and P8 (right hemisphere) electrodes were analyzed. For N250, the C3, F3, and FC1 (left hemisphere) and C4, F4, and FC2 (right hemisphere) electrodes were examined. Analysis of peak amplitudes and latencies could provide additional information, but given the limited signal-to-noise ratio of the present study, we opted to use mean amplitudes as a more reliable way of quantifying the ERP components of interest (Luck, 2014).

2.3.3. Data analysis

One-way ANOVAs were computed to analyze group differences in neuropsychological performance and self-report measures.

To compare group performance on emotion identification and on the ratings for arousal and valence, we used mixed factors ANOVAs followed by post hoc analyses when appropriate. The identification scores and ratings were used as dependent measures, the

age group (younger adults, middle-aged adults, older adults) as between participants factor, and emotion (anger, calm, happiness, surprise) as within-participant factor.

The electrophysiological data were analyzed by mixed factors ANOVAs with age group (younger adults, middle-aged adults, older adults) as a between participants factor, and hemisphere (left, right) and emotion (anger, calm, happiness, surprise) as within-participant factors. The mean amplitudes for each ERP component were used as a dependent measure. When appropriate we performed post hoc analyses.

To test the influence of cognitive decline in behavioral performance and ERPs modulation, a Linear Regression Model was computed given the shared variance across tests (all $r > .121$, except for the non-significant association between TMT and phonemic fluency). Scores of cognitive tests (raw scores) in which differences between groups were detected (IFS, CBTT, TMT, AVLTL) were entered as main predictors of behavioral measures and P100, N170, and N250 modulation (independent models). For P100, N170 and N250 modulation, the model was applied to each electrode or electrode cluster examined in the ERP data analysis. The model was computed only for older adults since it was our group of interest. To further explore and clarify the results, the analysis was extended to the younger and middle-aged adults groups whenever necessary.

The association between behavioral and electrophysiological data was analyzed using linear mixed models (LMM) given that measures for different emotions were not independent. P100, N170, and N250 mean amplitudes for each hemisphere were modeled as a function of the accuracy of emotional identification as a fixed effect and *participants* and *emotional category* random effects. The correlation coefficient for the association between each mean amplitude and identification scores was then calculated based on the fixed effect t-score estimates of the LMM. The analysis was performed only for older adults.

The threshold for statistical significance was set at $\alpha = .05$ for all analyses. Violations of sphericity were corrected via the Greenhouse-Geisser method. Significant ANOVA main effects were quantified using Bonferroni-corrected post hoc comparisons. LMM modeling was performed in R 3.4.2 (R Core Team, 2017), using the nlme package (version 3.1–131; Pinheiro et al., 2017). The remaining statistical analysis was performed using SPSS 24 (IBM Corp., Armonk, NY, USA).

3. Results

3.1. Behavioral results

Neuropsychological data analysis revealed no differences between groups in semantic fluency, phonemic fluency, anxiety, depression, nor psychopathological symptomatology (all $F \leq 1.96$, all $p \geq .147$). However, group differences were observed on IFS, $F(2,80) = 3.92$, $p = .024$, CBTT, $F(2,80) = 5.72$, $p = .005$, TMT, $F(2,80) = 9.66$, $p < .001$, and AVLTL, $F(2,77) = 10.4$, $p < .001$. Older adults were outperformed in these neuropsychological tests compared to the younger groups (see Table 1).

Mean emotion identification scores, and mean ratings for arousal and valence are shown in Table 2. These were examined using mixed factors ANOVAs. The results showed that young, middle age and older were equally accurate in their responses, $F(2, 81) = 2.80$, $p = .067$. However, a main effect of emotion, $F(3, 79) = 29.9$, $p < .001$, $\eta_p^2 = 0.269$, revealed that the identification of all emotions was significantly different from each other (all $p < .001$). The identification of happiness (M accuracy = 85.9%, $SD = 18.7$) was significantly higher than surprise ($M = 75.2\%$, $SD = 22.4$), anger ($M = 69.8\%$, $SD = 20.3$), and calm ($M = 60.2\%$, $SD = 19.8$); the identifica-

Table 2

Mean (and SD) of emotion identification accuracy and ratings for arousal and valence for the three age groups.

		Accuracy (%)				Arousal ¹			Valence ¹	
		YA	A	AO	YA	A	OA	YA	A	AO
Happiness	M (SD)	91.9 (8.24)	80.9 (26.3)	81.3 (22.4)	4.93 (1.10)	4.97 (1.04)	5.09 (1.11)	5.84 (0.51)	5.60 (0.72)	5.61 (0.72)
Calm	M (SD)	59.0 (5.80)	58.5 (27.3)	63.7 (20.7)	2.58 (0.85)	3.04 (1.11)	3.30 (0.99)	3.77 (0.35)	3.59 (0.56)	3.52 (0.55)
Anger	M (SD)	78.0 (13.6)	65.9 (24.1)	61.8 (23.3)	4.96 (0.82)	5.24 (0.86)	5.30 (1.12)	2.25 (0.53)	2.32 (0.71)	2.51 (1.12)
Surprise	M (SD)	79.5 (17.6)	74.7 (27.6)	68.0 (21.4)	4.73 (0.87)	4.79 (0.66)	5.00 (1.13)	3.91 (0.58)	3.76 (0.67)	4.00 (0.90)

Note. YA = younger adults; A = adults; OA = older adults. ¹Likert scale ranging from 1 (low arousal/very unpleasant) to 7 (high arousal/very pleasant).

tion of surprise was significantly higher than the other two, and so on. The data analysis also showed that the interaction age group $\times$ emotion was not statistically significant, $F(6, 158) = 1.63$, $p = .163$.

Regarding arousal and valence ratings, no significant differences were found between the age groups (arousal: $F(2, 80) = 1.59$, $p = .211$; valence: $F < 1$). Again, a main effect of emotion, $F(3, 78) = 193$, $p < .001$, $\eta_p^2 = 0.458$, followed by post hoc analyses, revealed that calm elicited significantly lower arousal ratings (all $p < .001$). The valence ratings were also significantly different between emotions, $F(3, 78) = 399$, $p < .001$, $\eta_p^2 = 0.754$, with the exception of calm and surprise comparison ($p = .112$; for the remaining comparisons $p < .001$). The interaction age group $\times$ emotion was not statistically significant neither for arousal, $F(6, 156) = 1.13$, $p = .346$, nor valence ratings, $F(6, 156) = 1.22$, $p = .304$.

The Linear Regression analysis, computed for older adults, showed no significant main predictors of performance on emotion identification, Adj $R^2 = .149$, $F(4, 22) = 1.96$, $p = .143$ (all $\beta < .46$, $p > .059$), among the neuropsychological abilities tested (IFS, CBTT, TMT, AVLTT).

3.2. Electrophysiological results

Mean amplitudes for P100, N170 and N250 components are presented in Table 3.

The repeated measures ANOVA revealed no significant differences on the P100 mean amplitude across age groups, $F(2, 82) = 1.31$, $p = .275$. The analysis also showed that none of the interactions – age group $\times$ emotion, age group $\times$ hemisphere, and age group $\times$ emotion $\times$ hemisphere – was statistically significant for P100 mean amplitude (all $F < 1$).

For the N170 component, significant differences were found on the mean amplitude across age groups, $F(2, 82) = 5.36$, $p = .006$, $\eta_p^2 = 0.116$. The older adults group had a significantly increased N170 amplitude compared to the younger adults group ($p = .010$) (Fig. 1). A main effect of emotion was not found on the N170 mean amplitude across age groups, $F(3, 80) = 1.83$, $p = .140$. Additionally, a significantly age group $\times$ hemisphere interaction emerged, $F(2, 82) = 7.35$, $p = .001$, $\eta_p^2 = 0.039$. The paired samples t-test revealed marginally significant differences on the N170 mean amplitude between the hemispheres of younger adults, $t(29) = 1.89$, $p = .069$. The right hemisphere had an increased N170 amplitude compared to the left hemisphere. Furthermore, significant differences were found between the hemispheres of middle-aged adults, $t(28) = 2.49$, $p = .019$; the right hemisphere had a significantly increased N170 amplitude compared to the left hemisphere (Fig. 1). The analysis also showed marginally significant differences between the two hemispheres in the older adults group $t(25) = -2.06$, $p = .050$. The left hemisphere of older adults had an increased N170 amplitude compared to the right hemisphere (Fig. 1). The remaining interactions – age group $\times$ emotion and age group $\times$ emotion $\times$ hemisphere – were not statistically significant (all $p > .069$).

Significant differences were found on the N250 mean amplitude across age groups, $F(2, 82) = 21.3$, $p < .001$, $\eta_p^2 = 0.342$. The older adults group presented a significantly reduced N250 amplitude

compared to both younger adults and middle-aged adults (both $p < .001$) (Fig. 2). Regarding interactions – age group $\times$ emotion, age group $\times$ hemisphere and age group $\times$ emotion $\times$ hemisphere – no significant effects were found (all $F < 2.20$, $p > .117$).

The Linear Regression model, computed for older adults, was significant for P100 at the right hemisphere, $F(4, 18) = 3.58$, $p = .026$. IFS was a main predictor of P100 modulation at the right hemisphere (Adj $R^2 = .189$, $\beta = .47$, $p = .017$). To further explore this result, we extended the analysis to younger and middle-aged adults. For younger adults, the model was significant for P100 modulation at both hemispheres (right hemisphere: $F(4, 23) = 3.35$, $p = .027$; left hemisphere: $F(4, 23) = 3.30$, $p = .028$). AVLTT was a main predictor of P100 modulation at both hemispheres (right hemisphere: Adj $R^2 = .259$, $\beta = .36$, $p = .046$; left hemisphere: Adj $R^2 = .255$, $\beta = .42$, $p = .021$) and IFS was a main predictor of P100 modulation at the left hemisphere (Adj $R^2 = .255$, $\beta = .39$, $p = .049$).

The Linear Regression model, computed for older adults, was neither significant for N170 (right hemisphere: $F < 1$, all $\beta < .38$, $p > .142$; left hemisphere: $F < 1$, all $\beta < .41$, $p > .093$) nor N250 (right hemisphere: $F < 1$, all $\beta < .13$, $p > .285$; for left hemisphere: Adj $R^2 = .089$, $F(4, 18) = 1.54$, $p = .233$, all $\beta < .36$, $p > .043$) components.

3.3. Association between behavioral and electrophysiological results

The LMM model, performed for older adults, showed a significant association between the mean amplitudes at the right hemisphere of N170 components and behavioral performance in the emotion identification task, $r = -.280$, $p = .014$. Increased N170 amplitudes (i.e., more negative amplitudes, as this is a negative going component) at the right hemisphere of older adults are weakly associated with improved behavioral performance (Fig. 3). For the P100 and N250 components, no significant association was found between behavioral and electrophysiological measures (all $r < .092$, $p > .195$).

4. Discussion

In the present study, younger, middle-aged and older adults were presented with faces displaying different emotional expressions and asked to identify the corresponding emotional category and rate each emotion, for arousal and valence.

Our results did not reveal age differences in emotion identification, contrarily to a substantial set of literature showing emotion identification deficits in older adults (see meta-analysis by Ruffman et al., 2008). This equivalent performance across age groups may be explained by neural compensatory mechanisms (as discussed below). Furthermore, it is worth noting that previous studies found that younger and older adults did not differ on their identification of emotions considered to have positive valence, such as happy expressions (e.g., Calder et al., 2003; Murphy and Isaacowitz, 2010; Phillips et al., 2002). These results are inconsistent with the positivity effect that concerns the relative difference between older and younger people in attention to and memory for positive as opposed to negative material. Nevertheless, a positivity

Table 3Mean (and SD) ERP amplitudes (μ V) by group, condition, and electrode.

Age group/component	Electrode	Happiness	Calm	Anger	Surprise
Younger adults					
P100 component	O1	2.85 (1.87)	2.75 (1.84)	2.60 (1.72)	2.23 (2.00)
	O2	2.73 (2.11)	3.03 (1.92)	3.00 (1.87)	2.28 (2.39)
N170 component	P7	0.88 (1.77)	1.58 (1.92)	0.81 (2.03)	1.02 (1.73)
	P8	0.49 (1.91)	1.12 (2.55)	0.26 (2.38)	0.25 (1.94)
N250 component	C3	−1.04 (1.60)	−1.18 (1.47)	−1.04 (1.75)	−0.39 (1.63)
	F3	−2.84 (2.64)	−3.40 (2.70)	−2.78 (2.78)	−2.59 (3.23)
	FC1	−2.24 (2.60)	−3.04 (2.33)	−2.15 (2.52)	−1.70 (3.30)
	C4	−0.95 (1.58)	−0.75 (1.48)	−0.72 (1.61)	−0.88 (1.75)
	F4	−3.37 (2.56)	−3.08 (2.57)	−3.22 (2.56)	−3.35 (2.82)
	FC2	−2.25 (2.82)	−2.09 (2.48)	−1.75 (2.56)	−1.93 (2.48)
Middle-aged adults					
P100 component	O1	3.18 (2.26)	2.90 (2.46)	2.87 (2.66)	2.71 (2.82)
	O2	2.87 (1.90)	2.63 (2.24)	2.81 (2.19)	2.73 (2.70)
N170 component	P7	0.43 (1.98)	0.44 (2.16)	0.50 (2.35)	0.20 (2.72)
	P8	−1.01 (3.28)	−0.81 (3.44)	−0.81 (3.79)	−1.13 (4.58)
N250 component	C3	0.57 (2.07)	0.01 (2.06)	0.13 (1.87)	0.37 (1.96)
	F3	−2.11 (3.53)	−2.14 (3.54)	−2.12 (3.56)	−1.70 (3.89)
	FC1	−1.16 (2.87)	−1.28 (3.52)	−1.00 (2.82)	−0.98 (3.84)
	C4	−0.05 (1.73)	−0.06 (1.72)	0.11 (1.80)	0.09 (1.73)
	F4	−2.03 (3.32)	−1.96 (3.18)	−1.61 (3.76)	−1.81 (3.40)
	FC2	−1.26 (3.01)	−1.42 (3.00)	−0.86 (3.06)	−0.74 (3.33)
Older adults					
P100 component	O1	2.01 (4.01)	1.28 (4.54)	1.70 (5.33)	1.52 (4.36)
	O2	2.36 (4.62)	1.75 (4.80)	2.06 (3.91)	2.13 (3.48)
N170 component	P7	−1.82 (4.56)	−0.63 (3.15)	−1.78 (2.92)	−3.26 (4.74)
	P8	−0.40 (3.01)	0.39 (4.30)	−0.46 (3.01)	0.19 (4.47)
N250 component	C3	0.64 (4.03)	0.82 (1.89)	1.15 (2.18)	1.52 (1.57)
	F3	0.38 (4.65)	−0.04 (4.20)	0.12 (3.48)	0.73 (4.34)
	FC1	1.94 (3.74)	1.57 (4.03)	1.09 (3.19)	2.36 (3.14)
	C4	2.05 (4.76)	2.91 (3.24)	2.82 (2.85)	2.87 (3.28)
	F4	0.98 (4.26)	1.78 (3.46)	1.01 (3.96)	1.59 (3.78)
	FC2	1.53 (4.50)	1.74 (5.75)	2.09 (3.14)	2.02 (3.49)

effect is evident in older adults since they had a better performance on the identification of emotions with positive valence compared to emotions with negative valence. Regarding the ratings of arousal and valence, age differences were not found which means that older adults considered positive/negative images as positive/negative as younger and middle-aged adults did.

Consistent with numerous studies (e.g., Leppänen et al., 2003; Wells et al., 2016), an effect of emotion emerged in our study: happiness was better recognized, followed by surprise, anger, and calm. This pattern of results is consistent with a ‘happy face advantage’, an effect repeatedly observed of happy or smiling faces being recognized more quickly and more accurately than any other facial expression (Kirita and Endo, 1995; Wells et al., 2016).

Regarding electrophysiological data, the lack of significant differences between groups in the P100 component may imply that neural processes underlying deficits in facial emotion identification in older adults occurs at a later stage of visual processing.

In the present analysis, an age group effect emerged for the N170 component that is consistent with the compensation hypothesis. An overactivation was recorded for the N170 component of older adults comparatively to the younger adults group. In many studies, overactivation is accompanied by age-equivalent performance, raising the possibility that the additional neural activity serves a beneficial, compensatory function without which performance decrements would occur (Reuter-Lorenz and Cappell, 2008). In our study, the increased N170 amplitude recorded in the group of older adults may serve as evidence for such compensatory mechanism, which would explain equivalent performance across age groups.

The results also revealed an age group by hemisphere interaction for the N170 component evidencing an asymmetric hemisphere activation in middle-aged adults. Although reaching only marginal significance, younger and older adults also presented this

pattern of asymmetric activation. However, younger and middle-aged adults had an increased N170 amplitude at the right hemisphere compared to the left hemisphere, whereas older adults had the opposite asymmetry, i.e., an increased N170 amplitude at the left hemisphere compared to the right hemisphere. The pattern of asymmetric hemisphere activation recorded across age groups is in line with the previously reported. In fact, right hemisphere specialization for face recognition (in right handed persons) has been reported to be present very early in life and to undergo little change with age (see review by Chung and Thomson, 1995).

A lower amplitude was recorded for the N250 component of older adults comparatively to the younger adults group suggesting deficits in facial feature decoding abilities. Age-related underactivation is typically interpreted as a sign of impairment due to poor or underutilized strategies, or due to structural changes such as atrophy (Reuter-Lorenz and Cappell, 2008). However, in our study the underactivation was not found in association with poor behavioral performance suggesting that this component may not contribute to the identification of emotional expressions, at least not as much as the N170 component.

At this point, it is important to note that neurophysiological age-related changes seem to occur gradually across the lifespan since significant differences in ERP components arose only when younger and older adults were compared.

The current sample of older adults exhibited a significant disadvantage in several neuropsychological tests (TMT, IFS, AVLT, CBTT) compared to the younger groups. This disadvantage was not reflected in emotion identification, suggesting that in our study neuropsychological functioning did not influence the emotion identification ability. In fact, the linear regression model did not reveal any significant predictor of emotion identification performance among the neuropsychological functions that were measured.

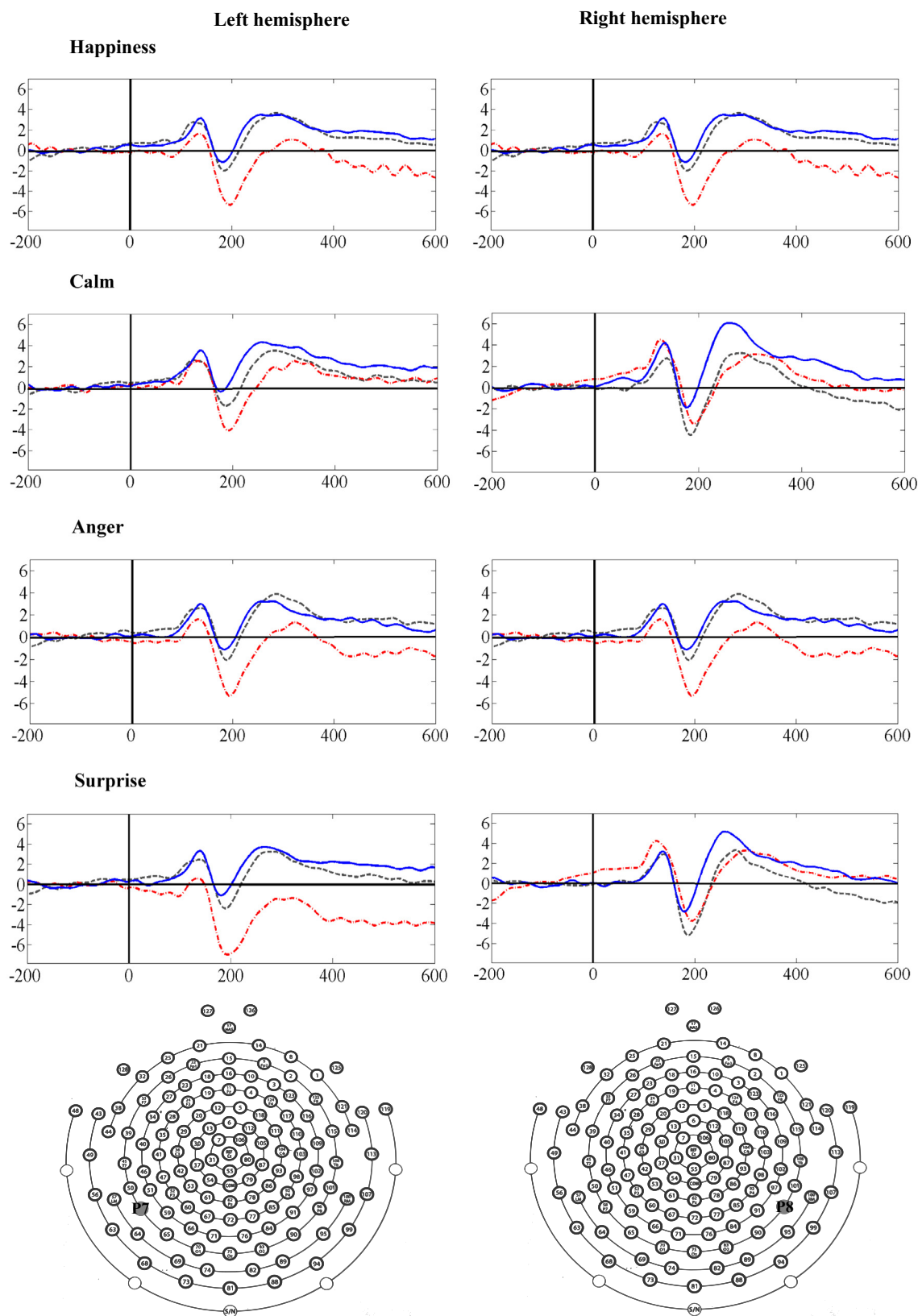


Fig. 1. ERP of the N170 component for each group at P7 (left hemisphere) and P8 (right hemisphere). Solid lines (blue) = younger adults, broken lines (black) = middle-aged adults, broken and dotted lines (red) = older adults. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

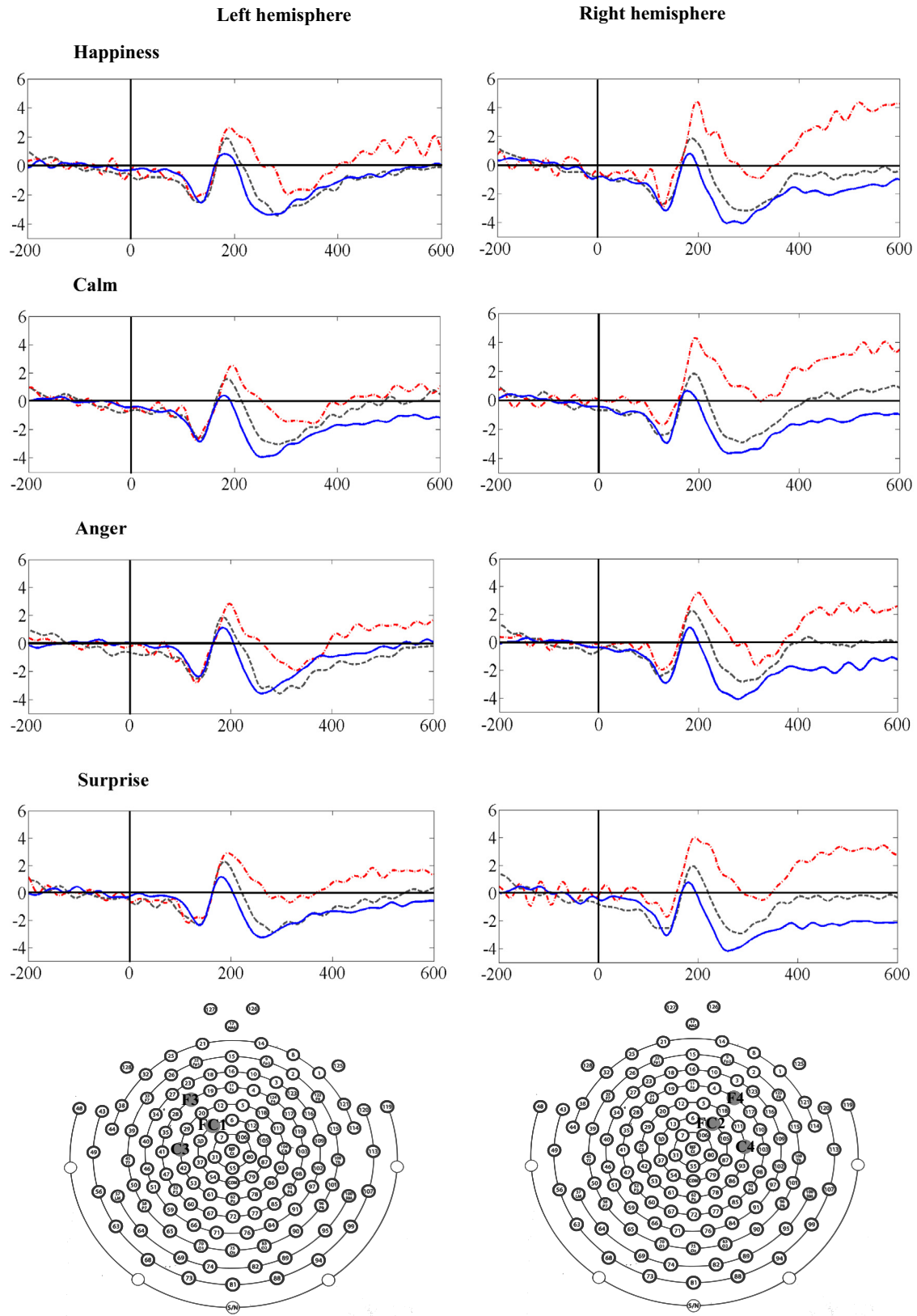


Fig. 2. ERP of the N250 component for each group (averaged across C3, F3, FC1 for the left hemisphere and across C4, F4, FC2 for the right hemisphere). Solid lines (blue) = younger adults, broken lines (black) = middle-aged adults, broken and dotted lines (red) = older adults. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

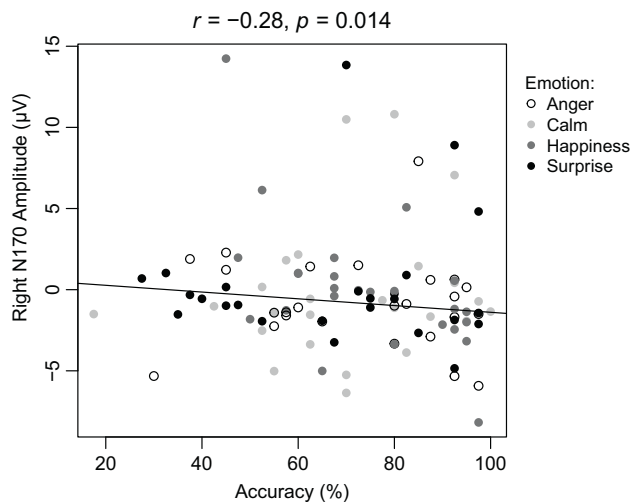


Fig. 3. Association between the mean amplitudes at the right hemisphere of N170 component and behavioral performance in the emotion identification task.

In the present study, P100 modulation in younger and older adults was predicted by performance in a test assessing executive functioning (INECO), and it is well-documented that the prefrontal cortex plays an essential role to explain executive performance in this task (Armitage, 1946; Cavaco et al., 2013a; Moreira et al., 2014; Torralva et al., 2009). Furthermore, P100 modulation in younger and middle-aged adults was also predicted by performance in AVLT, a test that evaluates learning and memory. Thus, executive functioning predicted P100 modulation in the younger and older adults groups, which may reflect a higher effort in these groups.

5. Conclusions

In sum, our data show an emotion effect in the identification of facial expressions consistent with previous reports (Leppänen et al., 2003; Wells et al., 2016). Furthermore, the present study reveals an increased N170 amplitude in the group of older adults, which may be a manifestation of a compensatory function that would explain the equivalent performance in emotion identification. These findings support prior research showing overactivation accompanied by age-equivalent performance (Reuter-Lorenz and Cappell, 2008). The present results also seem to evidence deficits in facial feature decoding abilities in older adults. However, they do not affect the performance when identifying emotional expressions. These findings may help future research to clarify the behavioral and neural processes involved on processing of facial affect identification in neurodegenerative conditions.

Note

Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development. Please contact Nim Tottenham at tot0006@tc.umn.edu for more information concerning the stimulus set. Permission to use the NimStim set in the present research was obtained from Dr. Nim Tottenham.

Acknowledgements

This research was supported by a Grant from the Fundação BIAL. Carina Fernandes was supported by a doctoral fellowship from the Fundação para a Ciência e a Tecnologia (Carina Fernandes – SFRH/BD/112101/2015). We would like to acknowledge to Pro-

grama de Estudos Universitários para Seniores (PEUS) and to Associação de Aposentados Pensionistas e Reformados (APRE) for their help in participant recruitment. We also thank Nim Tottenham for the stimuli used in the emotion identification task.

Conflict of interest

None of the authors have potential conflicts of interest to be disclosed.

References

- Almeida PR, Ferreira-Santos F, Chaves PL, Paiva TO, Barbosa F, Marques-Teixeira J. Perceived arousal of facial expressions of emotion modulates the N170, regardless of emotional category: time domain and time-frequency dynamics. *Int J Psychophysiol* 2016;99:48–56. <https://doi.org/10.1016/j.ijpsycho.2015.11.017>.
- Almeida PR, Ferreira-Santos F, Vieira JB, Moreira PS, Barbosa F, Marques-Teixeira J. Dissociable effects of psychopathic traits on cortical and subcortical visual pathways during facial emotion processing: an ERP study on the N170. *Psychophysiology* 2014;51:645–57. <https://doi.org/10.1111/psyp.12209>.
- Armitage SG. An analysis of certain psychological tests used for the evaluation of brain injury. *Psychol Monogr* 1946;60:i-48. <https://doi.org/10.1037/h0093567>.
- Bentin S, Allison T, Puce A, Perez E, McCarthy G. Electrophysiological studies of face perception in humans. *J Cogn Neurosci* 1996;8:551–65. <https://doi.org/10.1162/jocn.1996.8.6.551>.
- Boake C, Édouard Claparède and the Auditory Verbal Learning Test. *J Clin Exp Neuropsychol* 2000;22:286–92. [https://doi.org/10.1076/1380-3395\(200004\)22:2:1-1:FT286](https://doi.org/10.1076/1380-3395(200004)22:2:1-1:FT286).
- Bradley MM, Lang PJ. Measuring emotion: the Self-Assessment Manikin (SAM) and the semantic differential. *J Exp Psychiatry Behav Ther* 1994;25:49–59. [https://doi.org/10.1016/0005-7916\(94\)90063-9](https://doi.org/10.1016/0005-7916(94)90063-9).
- Calder A, Keane J, Manley T, Sprengelmeyer R, Scott S, Nimmo-Smith I, et al. Facial expression recognition across the adult life span. *Neuropsychologia* 2003;41:195–202. [https://doi.org/10.1016/S0028-3932\(02\)00149-5](https://doi.org/10.1016/S0028-3932(02)00149-5).
- Canavarro MC. Inventário de sintomas psicopatológicos – BSI. In: Simões MR, Gonçalves M, Almeida LS, editors. *Testes e provas psicológicas em Portugal* 1999;vol. II. Braga: SHO/APPORT; 1999. p. 87–109.
- Carstensen LL, Gross JJ, Fung HH. The social context of emotional experience. *Annu Rev Gerontol Geriatr* 1997;17:325–52.
- Carstensen LL, Isaacowitz DM, Charles ST. Taking time seriously: a theory of socioemotional selectivity. *Am Psychol* 1999;54:165–81. <https://doi.org/10.1037/0003-066X.54.3.165>.
- Cavaco S, Gonçalves A, Pinto C, Almeida E, Gomes F, Moreira I, et al. Trail Making Test: regression-based norms for the Portuguese population. *Arch Clin Neuropsychol* 2013a;28:189–98. <https://doi.org/10.1093/arclin/acs115>.
- Cavaco S, Gonçalves A, Pinto C, Almeida E, Gomes F, Moreira I, et al. Semantic fluency and phonemic fluency: regression-based norms for the Portuguese population. *Arch Clin Neuropsychol* 2013b;28:262–71. <https://doi.org/10.1093/arclin/act001>.
- Cavaco S, Gonçalves A, Pinto C, Almeida E, Gomes F, Moreira I, et al. Auditory Verbal Learning Test in a large nonclinical Portuguese population. *Appl Neuropsychol: Adult* 2015;22:321–31. <https://doi.org/10.1080/23279095.2014.927767>.
- Chung MS, Thomson DM. Development of face recognition. *Br J Psychol* 1995;86:55–87. <https://doi.org/10.1111/j.2044-8295.1995.tb02546.x>.
- Delorme A, Makeig S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods* 2004;134:9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>.
- Derogatis LR. BSI: Brief Symptom Inventory. 3rd ed. Minneapolis: National Computers Systems; 1993.
- Eimer M. The face-sensitive N170 component of the event-related brain potential. In: Calder A, Rhodes G, Johnson MH, Haxby JV, editors. *The Oxford handbook of face perception*. Oxford: Oxford University Press; 2011. p. 329–44.
- Ferreira-Santos F. Modulation of event-related potentials by facial expressions of emotion in infants (at 9, 16, and 24 months) and adults: contributions for the understanding of the ontogenesis of emotional face processing (Doctoral dissertation); 2013. Retrieved from: <<http://hdl.handle.net/10216/68002>>.
- Freitas S, Simões M, Santana I. Montreal Cognitive Assessment (MoCA): Pontos de corte no Défice Cognitivo Ligeiro, Doença de Alzheimer, Demência Frontotemporal e Demência Vascular. *Sinapse* 2014;1:18–30.
- Gao L, Xu J, Zhang B, Zhao L, Harel A, Bentin S. Aging effects on early-stage face perception: an ERP study. *Psychophysiology* 2009;46:970–83. <https://doi.org/10.1111/j.1469-8986.2009.00853.x>.
- García-Rodríguez B, Fusari A, Rodríguez B, Hernández JMZ, Ellgring H. Differential patterns of implicit emotional processing in Alzheimer's disease and healthy aging. *J Alzheimers Dis* 2009;18:541–51. <https://doi.org/10.3233/JAD-2009-1161>.
- Gazzaley A, Sheridan MA, Cooney JW, D'Esposito M. Age-related deficits in component processes of working memory. *Neuropsychology* 2007;21:532–9. <https://doi.org/10.1037/0894-4105.21.5.532>.
- Gross JJ, Richards JM, John OP. Emotion regulation in everyday life. In: Snyder DK, Simpson JA, Hughes JN, editors. *Emotion regulation in couples and families:*

- pathways to dysfunction and health. Washington, DC: American Psychological Association. p. 13–35.
- Halgren E, Raji T, Marinkovic K, Jousmaki V, Hari R. Cognitive response profile of the human fusiform face area as determined by MEG. *Cereb Cortex* 2000;10:69–81. <https://doi.org/10.1093/cercor/10.1.69>.
- Hilimire MR, Mienaltowski A, Blanchard-Fields F, Corballis PM. Age-related differences in event-related potentials for early visual processing of emotional faces. *Soc Cogn Affect Neurosci* 2014;9:969–76. <https://doi.org/10.1093/scan/nst071>.
- Hinojosa JA, Mercado F, Carretié L. N170 sensitivity to facial expression: a meta-analysis. *Neurosci Biobehav Rev* 2015;55:498–509. <https://doi.org/10.1016/j.neubiorev.2015.06.002>.
- Kirita T, Endo M. Happy face advantage in recognizing facial expressions. *Acta Psychol* 1995;89:149–63. [https://doi.org/10.1016/0001-6918\(94\)00021-8](https://doi.org/10.1016/0001-6918(94)00021-8).
- Komes J, Schweinberger SR, Wiese H. Preserved fine-tuning of face perception and memory: evidence from the own-race bias in high- and low-performing older adults. *Front Aging Neurosci* 2014;6:1–10. <https://doi.org/10.3389/fnagi.2014.00060>.
- Labouvie-Vief G. Dynamic integration: affect, cognition, and the self in adulthood. *Curr Dir Psychol Sci* 2003;12:201–6. <https://doi.org/10.1046/j.0963-7214.2003.01262.x>.
- Lambrecht L, Kreifelts B, Wildgruber D. Age-related decrease in recognition of emotional facial and prosodic expressions. *Emotion* 2012;12:529–39. <https://doi.org/10.1037/a0026827>.
- Leigland LA, Schulz LE, Janowsky JS. Age related changes in emotional memory. *Neurobiol Aging* 2004;25:1117–24. <https://doi.org/10.1016/j.neurobiolaging.2003.10.015>.
- Leppänen J, Tenhunen M, Hietanen J. Faster choice-reaction times to positive than to negative facial expressions: the role of cognitive and motor processes. *J Psychophysiol* 2003;17:113–23. <https://doi.org/10.1027//0269-8803.17.3.113>.
- Liao X, Wang K, Lin K, Chan RCK, Zhang X. Neural temporal dynamics of facial emotion processing: age effects and relationship to cognitive function. *Front Psychol* 2017;8:1–10. <https://doi.org/10.3389/fpsyg.2017.01110>.
- Luck SJ. An introduction to the event-related potential technique. 2nd ed. Cambridge, MA: MIT Press; 2014.
- Mather M, Carstensen LL. Aging and motivated cognition: the positivity effect in attention and memory. *Trends Cogn Sci* 2005;9:496–502. <https://doi.org/10.1016/j.tics.2005.08.005>.
- Mather M, Knight M. Goal-directed memory: the role of cognitive control in older adults' emotional memory. *Psychol Aging* 2005;20:554–70. <https://doi.org/10.1037/0882-7974.20.4.554>.
- Moreira HS, Lima CF, Vicente SG. Examining Executive Dysfunction with the Institute of Cognitive Neurology (INECO) Frontal Screening (IFS): normative values from a healthy sample and clinical utility in Alzheimer's disease. *J Alzheimers Dis* 2014;42:261–73. <https://doi.org/10.3233/JAD-132348>.
- Murphy NA, Isaacowitz DM. Age effects and gaze patterns in recognising emotional expressions: an in-depth look at gaze measures and covariates. *Cogn Emot* 2010;24:436–52. <https://doi.org/10.1080/02699930802664623>.
- Nasreddine ZS, Phillips NA, Bédirian V, Charbonneau S, Whitehead V, Collin I, et al. The Montreal Cognitive Assessment, MoCA: a brief screening tool for mild cognitive impairment. *J Am Geriatr Soc* 2005;53:695–9. <https://doi.org/10.1111/j.1532-5415.2005.53221.x>.
- Orgeta V. Effects of age and task difficulty on recognition of facial affect. *The J Gerontol B Psychol Sci Soc Sci* 2010;65:323–7. <https://doi.org/10.1093/geronb/gbq007>.
- Pais-Ribeiro J, Silva I, Ferreira T, Martins A, Meneses R, Baltar M. Validation study of a Portuguese version of the Hospital Anxiety and Depression Scale. *Psychol Health Med* 2007;12:225–37. <https://doi.org/10.1080/13548500500524088>.
- Park DC, Smith AD, Lautenschlager G, Earles JL, Frieske D, Zwahr M. Mediators of long-term memory performance across the life span. *Psychol Aging* 1996;11:621–37. <https://doi.org/10.1037/0882-7974.11.4.621>.
- Phillips LH, MacLean RDJ, Allen R. Aging and the perception and understanding of emotions: Neuropsychological and Sociocognitive Perspectives. *J Gerontol Ser B: Psychol Sci Social Sci* 2002;57:526–30. <https://doi.org/10.1093/geronb/57.6.P526>.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. nlme: Linear and nonlinear mixed effects models. R package version 3.1-131; 2017. Retrieved from <<https://cran.r-project.org/package=nlme>>.
- Pourtois G, Grandjean D, Sander D, Vuilleumier P. Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cereb Cortex* 2004;14:619–33. <https://doi.org/10.1093/cercor/bbh023>.
- R Core Team. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing; 2017. Retrieved from <<https://www.r-project.org/>>.
- Reuter-Lorenz PA, Cappell KA. Neurocognitive aging and the compensation hypothesis. *Curr Dir Psychol Sci* 2008;17:177–82.
- Ruffman T, Henry JD, Livingstone V, Phillips LH. A meta-analytic review of emotion recognition and aging: implications for neuropsychological models of aging. *Neurosci Biobehav Rev* 2008;32:863–81. <https://doi.org/10.1016/j.neubiorev.2008.01.001>.
- Salthouse TA. When does age-related cognitive decline begin? *Neurobiol Aging* 2009;30:507–14. <https://doi.org/10.1016/j.neurobiolaging.2008.09.023>.
- Snaith RP, Zigmond AP. The hospital anxiety and depression scale manual. Windsor: NFER-Nelson; 1994.
- Strauss E, Sherman EM, Spreen O. A compendium of neuropsychological tests: administration, norms, and commentary. 3rd ed. New York: Oxford University Press; 2006.
- Streit M, Ioannides AA, Liu L, Wölwer W, Dammers J, Gross J, et al. Neurophysiological correlates of the recognition of facial expressions of emotion as revealed by magnetoencephalography. *Brain Res* 1999;7:481–91. [https://doi.org/10.1016/S0926-6410\(98\)00048-2](https://doi.org/10.1016/S0926-6410(98)00048-2).
- Suzuki T, Akiyama H. Cognitive aging explains age-related differences in face-based recognition of basic emotions except for anger and disgust. *Aging Neuropsychol Cogn* 2013;20:253–70. <https://doi.org/10.1080/13825585.2012.692761>.
- Torralva T, Roca M, Gleichgerricht E, LoPez P, Manes F. INECO Frontal Screening (IFS): a brief, sensitive, and specific tool to assess executive functions in dementia. *J Int Neuropsychol Soc* 2009;15:777–86. <https://doi.org/10.1017/S1355617709990415>.
- Tottenham N, Tanaka J, Leon AC, McCarry T, Nurse M, Hare TA, et al. The NimStim set of facial expressions: judgments from untrained research participants. *Psychiatry Res* 2009;168:242–9. <https://doi.org/10.1016/j.psychres.2008.05.006>.
- Wechsler D. WMS – III. Escala de memória de Wechsler. Lisboa: CEGOC/TEA; 2008.
- Wells LJ, Gillespie SM, Rotshtein P. Identification of emotional facial expressions: effects of expression, intensity, and sex on eye gaze. *PLoS One* 2016;11:1–20. <https://doi.org/10.1371/journal.pone.0168307>.
- Wynn JK, Lee J, Horan WP, Green MF. Using event related potentials to explore stages of facial affect recognition deficits in schizophrenia. *Schizophr Bull* 2008;34:679–87. <https://doi.org/10.1093/schbul/sbn047>.

2.2 AGE-RELATED DECLINE IN EMOTIONAL PERSPECTIVE-TAKING: ITS EFFECT ON THE LATE POSITIVE POTENTIAL



Age-related decline in emotional perspective-taking: Its effect on the late positive potential

Carina Fernandes^{1,2,3} · A. R. Gonçalves¹ · R. Pasion¹ · F. Ferreira-Santos¹ · F. Barbosa¹ · I. P. Martins³ · J. Marques-Teixeira¹

© Psychonomic Society, Inc. 2018

Abstract

Aging is associated with changes in cognitive and affective functioning, which likely shape older adults' social cognition. As the neural and psychological mechanisms underlying age differences in social abilities remain poorly understood, the present study aims to extend the research in this field. To this purpose, younger ($n = 30$; $M_{age} = 26.6$), middle-aged ($n = 30$; $M_{age} = 48.4$), and older adults ($n = 29$; $M_{age} = 64.5$) performed a task designed to assess affective perspective-taking, during an EEG recording. In this task, participants decided whether a target facial expression of emotion (FEE) was congruent or incongruent with that of a masked intervener of a previous scenario, which portrayed a neutral or an emotional scene. Older adults showed worse performance in comparison to the other groups. Regarding electrophysiological results, while younger and middle-aged adults showed higher late positive potentials (LPPs) after FEEs congruent with previous scenarios than after incongruent FEEs, older adults had similar amplitudes after both. This insensitivity of older adults' LPPs in differentiating congruent from incongruent emotional context-target FEE may be related to their difficulty in generating information about others' inner states and using that information in social interactions.

Keywords Aging · Emotional processing · Perspective-taking · N170 · Late positive potentials

Emotional perspective-taking is an important source of human empathy and is considered an indispensable element in the fully developed, mature Theory of Mind (ToM; Decety & Jackson, 2004). It is defined as the ability to take the perspective of another person, and determines the success of social interactions (Derntl et al., 2009). Through perspective-taking, one is able to infer, understand, and foresee others' mental and emotional states – ToM – as well as to share and to respond appropriately to such states – empathy.

Electronic supplementary material The online version of this article (<https://doi.org/10.3758/s13415-018-00648-1>) contains supplementary material, which is available to authorized users.

✉ Carina Fernandes
carinafernandes@fpce.up.pt

¹ Laboratory of Neuropsychophysiology, Faculty of Psychology and Education Sciences, University of Porto, Porto, Portugal

² Faculty of Medicine, University of Porto, Porto, Portugal

³ Language Research Laboratory, Institute of Molecular Medicine, Faculty of Medicine, University of Lisbon, Lisboa, Portugal

Investigations on perspective-taking abilities during aging have been mainly conducted with the perspective-taking subscale of the Interpersonal Reactivity Index (IRI; Davis, 1983). While one study showed that older adults reported better perspective-taking than younger adults but worse than middle-aged adults (O'Brien, Konrath, Grühn, & Hagen, 2012), another study revealed that this ability seems not to change with aging (Yi et al., 2017). However, considering that aging appears to affect ToM abilities (Henry, Phillips, Ruffman, & Bailey, 2013; Moran, 2013), it is important to understand the neural and psychological mechanisms underlying such age-related differences. According to a meta-analysis, younger adults outperform older adults in all types of ToM tasks (Henry et al., 2013). However, studies that included matched control tasks showed that age-related deficits are similar in both ToM and non-ToM conditions, being unclear whether group differences are specific to ToM or secondary to age-related cognitive decline (Henry et al., 2013). A comprehensive review suggested that older adults' performance in tasks using visual stimuli are relatively independent of cognitive deficits, while performance in tasks using verbal stories are more dependent on cognitive abilities, such as working

memory, processing speed, and executive function (Moran, 2013).

Neuroimaging studies suggested that older adults compensate impairments in domain-specific ToM by using domain-general processing skills (Moran, 2013). For instance, while younger and older adults activated the right inferior frontal gyrus (IFG) during a ToM task, an area associated with facial visual encoding (Kelley et al., 1998), older adults also had higher activation of the left IFG (Castelli et al., 2010), an area typically associated with verbal memory (Kelley et al., 1998). Other studies also found that older adults had reduced activation of brain areas associated with ToM, such as the anterior cingulate cortex (Castelli et al., 2010), medial prefrontal cortex, and temporoparietal junction (Moran, Jolly, & Mitchell, 2012).

Functional MRI studies have allowed localizing several regions implicated in perspective-taking processes (e.g., David et al., 2008; Jackson, Meltzoff, & Decety, 2006). However, considering the poor temporal resolution of fMRI, tracking the temporal nature of these processes is crucial to understand neuroimaging and behavioral results better. Studies using event-related potentials (ERPs), which have very precise temporal resolution, are well suited to this function (Liu, Sabbagh, Gehring, & Wellman, 2004). However, to the best of our knowledge, older adults were not included in any of the previous studies examining brain potentials related to ToM (Bowman, Liu, Meltzoff, & Wellman, 2012; Liu et al., 2004; Liu, Meltzoff, & Wellman, 2009; Meinhardt, Sodian, Thoermer, Döhl, & Sommer, 2011; Sabbagh & Taylor, 2000; Wang et al., 2010), or to perspective-taking abilities (Decety, Yang, & Cheng, 2010; Li & Han, 2010; McCleery, Surtees, Graham, Richards, & Apperly, 2011).

In an attempt to fill this gap, we examine age-related differences in behavioral and neural responses to a perspective-taking task, which assesses participants' ability in inferring emotional states of others. To this purpose, we adapted a task previously used in an fMRI study (Derntl et al., 2009), in which participants observe scenarios showing two persons involved in social interactions, portraying emotional and neutral scenes. One person in each scenario is masked, and participants must infer his/her affective mental state. Then, a target facial expression of emotion (FEE) is displayed, and participants have to decide if the emotion presented is congruent or incongruent with the emotion inferred during the scenario. In half of the trials the FEEs are congruent with the affective state of the person with the masked expression (congruent condition), whereas in the other half they are not (incongruent condition). This experimental design was based on previous studies that assessed contextual congruency (Diéguez-Risco, Aguado, Albert, & Hinojosa, 2013), defined here as the matching between a target emotion portrayed in a facial expression and the emotion portrayed by the previous scenario.

Different to previous studies, an accurate decision in our task requires an accurate inference of the emotional state of the masked intervener. That is, participants have to accurately infer the emotion of a masked actor in a given scenario, compare it to the emotion presented in a target FEE, and decide whether the inferred and visualized emotions were congruent or incongruent. Thus, with this experimental manipulation, we investigate perspective-taking abilities through the behavioral performance, while we assess how these abilities modulate two ERP components that are typically influenced by the affective and evaluative congruency: the N170 and the late positive potential (LPP).

The N170 is an occipitotemporal negative deflection that usually appears at ~170 ms after stimulus onset (Rossion & Jacques, 2008). This component appears to reflect the earliest stage of facial structure encoding (Bentin, Allison, Puce, Perez, & McCarthy, 1996), but is also sensitive to the emotional content (Almeida et al., 2016; Hinojosa, Mercado, & Carretié, 2015). Regarding contextual effects, N170 amplitude is usually larger in congruent trials, at least when pictures are used as contextual stimuli (Hietanen & Astikainen, 2013; Righart & de Gelder, 2006; Righart & de Gelder, 2008a, 2008b). This component appears not to be affected by aging (Gao et al., 2009). While one study showed reduced lateralization (typically evidenced to the right hemisphere), interpreted as compensation for age-related decline (Komes, Schweinberger, & Wiese, 2014), another study showed that older adults had an increased N170 for negative faces and a similar N170 for positive faces (Liao, Wang, Lin, Chan, & Zhang, 2017). Indeed, a study from our group showed that younger, middle-aged, and older adults had similar performances in an emotional identification task, which was accompanied by an increased N170 amplitude in the older group (Gonçalves et al., 2018b).

The LPP is a centro-parietal positive deflection that usually appears between 300 and 700 ms after the stimulus onset (Herring, Taylor, White, & Crites, 2011). This component reflects facilitated attention to emotional stimuli, and its amplitude is greater after emotionally arousing compared to neutral pictures (Foti & Hajcak, 2008). In studies such as ours, which manipulated congruency between a prime and a target, the LPP indexes the processing of affective or evaluative congruency, and its amplitude is larger to incongruent targets compared to congruent ones (Morioka et al., 2016). This component is also modulated by cognitive appraisal and motivated attention (Weinberg & Hajcak, 2010), helping scenes (Cowell & Decety, 2015), and morally good actions (Yoder & Decety, 2014). Previous studies showed reduced LPP amplitude in older adults during the presentation of unpleasant stimuli, and augmented amplitude during pleasant scenes (Kisley, Wood, & Burrows, 2007; Wood & Kisley, 2006). However, another study showed reduced LPP for older adults in all emotional scenes, regardless of content (Renfroe, Bradley,

Sege, & Bowers, 2016). A study from our group found that, in comparison with younger adults, older adults showed a reduced LPP during the visualization of scenarios displaying harmful action, which participants had to evaluate as intentional or accidental (Pasion et al., 2018).

In our experiment, we used visual stimuli to assess perspective-taking independently of general cognition (Moran, 2013). However, to confirm this assumption, neurocognitive measures were collected, and the scores were correlated with behavioral and electrophysiological results. Based on previous findings about the effects of aging on ToM, we predicted poorer performance of older adults in our perspective-taking task. Regarding electrophysiological results, we predicted the influence of perspective-taking processes on early and later stages of the affective and evaluative processing, indexed by a modulation of N170 and LPP components. The N170 should be enhanced in congruent trials (Hietanen & Astikainen, 2013; Righart & de Gelder, 2006; Righart & de Gelder, 2008a, 2008b), while the LPP should be enhanced in incongruent trials (Diéguez-Risco et al., 2013; Dozolme, Brunet-Gouet, Passerieux, & Amorim, 2015; Herring et al., 2011). As we expected a decreased perspective-taking in the older group, we hypothesized that these ERP modulations would be absent in this group.

Method

Participants

One hundred and eighty-three participants were recruited from the local community and assigned to three age groups: younger adults (age range: 20–35 years), middle-aged adults (age range: 40–55 years), and older adults (age range: 60–75 years). We excluded participants with scores lower than 22 ($n = 6$) in the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005; Portuguese norms by Freitas, Simões, & Santana, 2014), as well as participants who reported uncorrected visual impairments ($n = 3$), use of psychotropic medication ($n = 15$), history of brain injury, alcohol or drug abuse, and neurological or psychiatric diagnosis ($n = 25$). Besides the participants excluded, 45 participants dropped out of the study before the electrophysiological assessment, leading to a final sample composed of 30 younger (15 female; $\text{Age} = 26.6$, $SD = 4.05$, $\text{Meducation} = 16.3$, $SD = 4.05$), 30 middle-aged (14 female; $\text{Age} = 48.4$, $SD = 5.50$, $\text{Meducation} = 15.4$, $SD = 4.81$), and 29 older (18 female; $\text{Age} = 64.5$, $SD = 4.10$, $\text{Meducation} = 14.1$, $SD = 4.84$) adults. All participants were Caucasian and the groups were statistically matched for years of formal education, $F(2,88) = 1.96$, $p = .148$, sex, $\chi^2(2, N = 89) = 0.92$, $p = .631$, and handedness, $\chi^2(2, N = 89) = 2.77$, $p = .250$.

A formal sample size calculation was not performed due to the exploratory nature of this investigation and the lack of information regarding the effects of perspective-taking abilities in the ERP components of interest. However, prior to conducting the study, we targeted a sample size of 30 for each age group, somewhat higher than in previous studies using ERP methodologies applied to perspective-taking or ToM tasks (Bowman et al., 2012; Decety et al., 2010; Li & Han, 2010; Liu et al., 2004; Liu et al., 2009; Meinhardt et al., 2011; McCleery et al., 2011; Wang et al., 2010). The current study was part of a larger research project (Fernandes et al., 2018; Gonçalves et al., 2018b; Pasion et al., 2018), which was approved by the local Ethics Committee. Participants provided written informed consent in accordance with the Declaration of Helsinki and were compensated with a fixed amount of 20€ (as a gift card) for their time.

Instruments and tasks

Neuropsychological measures The MoCA was used as a screening instrument since it was specifically developed for the assessment of milder forms of cognitive impairment (Freitas et al., 2014). According to a validation study performed with the Portuguese population, this instrument has an optimal cutoff point of 22 for mild cognitive impairment (Freitas et al., 2014). In addition, we also assessed: (a) executive functioning through the Trail Making Test (TMT = Part B - Part A; Armitage, 1946; Portuguese norms by Cavaco et al., 2013b) and the Institute of Cognitive Neurology Frontal Screening (IFS; Torralva, Roca, Gleichgerricht, Lopez, & Manes, 2009; Portuguese norms by Moreira, Lima, & Vicente, 2014); (b) visuospatial short-term memory through the Corsi Block-Tapping Task (Wechsler, 2008); (c) non-motor processing speed and language production through the Semantic and Phonemic Fluency tests (Strauss, Sherman, & Spreen, 2006; Portuguese norms by Cavaco et al., 2013a); and (d) learning, immediate and episodic memory through the Auditory Verbal Learning Test (AVLT; Boake, 2000; Portuguese norms by Cavaco et al., 2015). Finally, anxiety and depression were evaluated by the Hospital Anxiety and Depression Scale (HADS; Snaith & Zigmond, 1994; Portuguese norms by Pais-Ribeiro et al., 2007), and psychopathological symptoms were assessed through the Brief Symptom Inventory (BSI; Derogatis, 1982/1993; Portuguese norms by Canavaro, 1999).

Emotional perspective-taking task This task was adapted from a previous fMRI study that assessed perspective-taking (Dentl et al., 2009). In order to assess this ability during an ERP experiment, we adapted the protocol used by Dentl et al. (2009) according to experimental designs that were previously used in studies of contextual congruency (Diéguez-Risco

et al., 2013; Dozolme et al., 2015; Herring et al., 2011; Hietanen & Astikainen, 2013; Righart & de Gelder, 2006; Righart & de Gelder, 2008a, 2008b). In the present study, contextual congruency is defined by the matching between a target FEE and the emotion portrayed by a masked face in a previous scenario. To judge accurately the contextual congruency, participants had to evoke perspective-taking abilities: first, they had to see the scenario and analyze it from the other's point of view; then they had to judge whether a FEE displayed afterward was congruent or not with the expected emotion of the masked person.

To this purpose, participants viewed 360 pictures depicting scenes of two persons (Caucasians) involved in social interactions. In each scenario, the face of one of the actors was masked, and participants were asked to infer her/his emotional expression (see Fig. 1 for an example). The scenarios portrayed emotional (anger, fear, disgust, sadness, happiness) and neutral scenes. After the scenario, a target FEE was displayed, and participants had to decide if it was congruent or incongruent with the inferred FFE of the masked character, based on their perspective-taking abilities. Participants were instructed to respond only when the response slide was displayed (to avoid preparatory response potentials to overlap with the ERP components of interest) using two response buttons held in the right and left hand. Half of the sample used the left button to respond "yes" and the right button to "no," while the other half used the opposite response scheme. The structure of each trial is depicted in Fig. 1.

The original set of stimuli (Derntl et al., 2009) included ten scenarios for each emotional condition, and each one was repeated six times. In the congruent conditions, the FEE was randomly selected from all alternative actors with the congruent emotion. In the incongruent conditions, the FEE was randomly selected from all the incongruent alternatives. This led to 30 congruent trials (in which the target FEE was congruent with the emotion portrayed in the scenario) and 30 incongruent trials (in which the target FEE was incongruent with the emotion portrayed in the scenario) for each emotional condition. The FEEs were selected from the NimStim Face Stimulus Set (Tottenham et al., 2009), and displayed adult Caucasians with closed mouth and direct eye contact. For each emotional condition, we selected the five most accurately identified facial expressions according to the original study (Tottenham et al., 2009), resulting in 30 female and 30 male facial stimuli.

The task was programmed and delivered in E-Prime 2.0 (2011, Psychology Software Tools, Inc., Sharpsburg, PA, USA), and was composed of two experimental blocks of 180 trials, with a pause between them. The stimuli were presented on a 17-in. screen with $6.67^\circ \times 8.55^\circ$ visual angle and a refresh rate of 60 Hz.

Procedures

Participants were tested individually in two experimental sessions to avoid fatigue effects. The first session included the neuropsychological assessment and the second included the electrophysiological experiment. During the first session, participants gave the informed consent and completed a semi-structured interview followed by the MoCA. The remaining tests and self-report measures were administered afterward, in a random order between participants. The AVLT was applied in the second session to avoid the interference of other words listed during the neuropsychological assessment in the subtests of the AVLT. During the second session, participants sat inside an EEG chamber, with ~115 cm between them and the screen where the experimental task was displayed. After the placement of the EEG cap, participants read the instructions and completed six practice trials. Whenever possible, data collection sessions were conducted in the middle of the morning or afternoon, and the participants from the three groups were equally distributed in this schedule.

EEG recording and processing

The electroencephalographic (EEG) data were recorded through the NetStation V4.5.2 (2008, Electrical Geodesics Inc., Eugene, OR, USA – EGI), using a 128-electrode Hydrocel Geodesic Sensor Net, connected to a Net Amps 300 amplifier. Impedances were kept below 50 kOhm for all electrodes (since this is a high impedance system). The EEG data were recorded with a sampling rate of 500 Hz, filtered with a notch filter of 50 Hz and referenced to the Cz.

During the pre-processing, conducted in version 11 of the EEGLAB (Delorme & Makeig, 2004), a MATLAB toolbox (2010, The Mathworks Inc., Natick, MA, USA), the continuous EEG signal was downsampled to 250 Hz and bandpass filtered (0.2–30 Hz). The EEG signal underwent Independent Components Analysis, and eyeblink, saccade, and heart rate artifacts were corrected, by subtracting the respective Independent Component activity from the data. Channels with artifacts were interpolated (maximum of 10% of the sensors) using the spherical spline interpolation method (Perrin, Pernier, Bertrand, & Echallier, 1989). At this point, the EEG signal was re-referenced to the average of all electrodes and segmented into epochs (-200 to 800 ms) time-locked to the onset of the target FEE. All segments were visually inspected and epochs containing alpha activity, electrode drifts, and cardiac, muscle, and ocular artifacts were rejected. Trials in which participants gave incorrect responses were also excluded, resulting in a significantly different number of valid trials between groups, $F(2, 86) = 7.30, p = .001$.¹ All epochs were

¹ As a consequence, the statistical analyses performed on the ERP results were repeated using the number of valid trials as covariant.

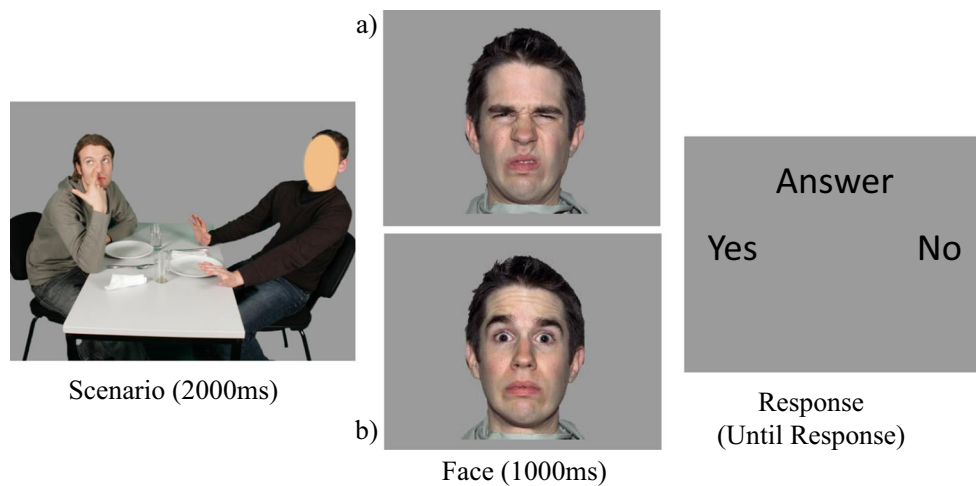


Fig. 1 Schematic representation of a trial of the perspective-taking task. In this example, the scenario was a picture portraying a “disgust” scene. The scenario was followed by an interstimulus interval (displaying a “+” in the center of the screen for 250 ms) and by a facial expression of

emotion (FEE) congruent (a) or incongruent (b) with the emotion that was portrayed. The FEE was followed by an interstimulus interval (500 ms) and by the response slide. The next trial started after an intertrial interval (500 ms)

baseline-corrected (200 ms pre-stimulus) and averaged by *congruency* (congruent, incongruent) and *emotion* (anger, fear, disgust, sadness, happiness, neutral).

Based on previous studies and visual inspection of grand-average waveforms and topographical maps, three time-windows and three regions of interest (ROIs)² were selected for statistical analysis (Fig. 2). For the N170 component, its higher amplitude occurs bilaterally at occipitotemporal regions, specifically at P7/P8 and PO7/PO8, being more pronounced at the inferior locations as P9/P10 and PO9/PO10 (Rossion & Jacques, 2008). The visual inspection of our topographical maps showed a negative maximum over these regions, leading us to select a ROI including these and a cluster of surrounding electrodes, in order to increase the signal-to-noise ratio (Musial, Baker, Gerstein, King, & Keating, 2002; Zeman, Till, Livingston, Tanaka, & Driessen, 2007). Thus, the N170 peak amplitudes were calculated between 150 and 250 ms after FEE onset, at right (electrodes 83, 84, 89, 90 [PO8], 91, 95 [P10], 96 [P8]) and left (70, 66, 69, 65 [PO7], 64 [P9], 58 [P7], 59) ROIs. Similarly, previous studies evidenced that the LPP reaches its largest amplitude over centro-parietal sites such as CPz and Pz (Herring et al., 2011). As our topographical maps are consistent with this evidence (see below), we measured the mean LPP amplitudes at the centro-parietal ROI (54, 55 [CPz], 61, 62 [Pz], 78, 79). As the LPP shows a temporally broad distribution (e.g., Diéguez-Risco et al., 2015), we divided its corresponding time-window into an early (LPPe; 300–500 ms after FEE onset) and late component (LPPi; 500–700 ms).

² Electrode notation included in the ROIs correspond to the 128-channel Geodesic Sensor Net (EGI). Electrodes described in brackets are their 10-10 International System Equivalents.

Statistical analysis

The results of the neuropsychological tests were compared through independent one-way ANOVAs, using *group* (younger, middle-aged, older adults) as a between-participants factor. Perspective-taking results were obtained from the accuracy rates (percentage of correct responses in relation to the total number of trials), computed by participant and condition. To investigate the effects of emotion, congruency, and group on perspective-taking results, we performed a mixed ANOVA, with

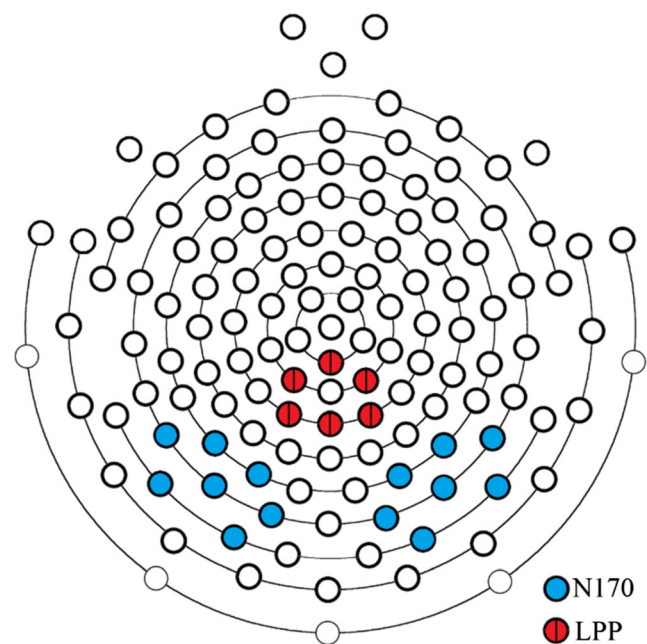


Fig. 2 Electrode locations in the 128-channel HydroCel Geodesic Sensor Net (EGI) where event-related-potential components were measured

emotion (anger, fear, disgust, sadness, happiness, neutral) and *congruency* (congruent, incongruent) as within-participants factors, and *group* (younger, middle-aged, older adults) as between-participants factor. The same model was used for reaction times.

Regarding electrophysiological results, the N170 was analyzed in a mixed ANOVA, with *hemisphere* (left, right), *congruency*, and *emotion* as within-participants factors, and *group* as between-participants factor. The LPPs were analyzed in a mixed ANOVA, with *congruency* and *emotion* as within-participants factors, and *group* as between-participants factor. Exploratory analyses using gender as an additional between-participants factor were performed for the perspective-taking and electrophysiological results (described in the Online Supplementary Material).

To test whether group differences were correlated with age-related differences in cognitive abilities, age-specific Pearson's correlations were computed between neurocognitive scores in which groups differed significantly and perspective-taking and ERP results (averaged by *congruency*). Significant correlations were explored through linear regression models, conducted by group, in which the neurocognitive scores were entered as main predictors of perspective-taking and electrophysiological results.

The threshold for statistical significance was set at $\alpha = .05$, and the p -values reported for all analyses are from two-tailed tests. Statistical analysis was performed using SPSS 24 (IBM Corp., Armonk, NY, USA). Violations of sphericity were corrected via the Greenhouse-Geisser method, and post-hoc pairwise comparisons were corrected for multiple comparisons using the Sidak procedure.

Results

Neuropsychological results

The groups did not differ in Semantic and Phonemic Fluency, anxiety, depression nor in psychopathological symptomatology. Significant differences emerged in MoCA, IFS, Corsi Block-Tapping Task, TMT, Learning, Delayed Recall and Delayed Recognition subtests of the AVLT. Younger adults outperformed older adults in all of these neuropsychological tests, while middle-aged adults outperformed older adults in MoCA, TMT, Corsi Block-Tapping Task, Learning and Delayed Recall subtests of the AVLT. Descriptive statistics and one-way ANOVA results are presented in Table 1 of the Online Supplementary Material.

Emotional perspective-taking task

Behavioral results

For accuracy, we found a main effect of *group*, $F(2, 86) = 27.3$, $p < .001$, $\eta^2_p = .388$, revealing that older adults were

significantly less accurate than younger ($p < .001$) and middle-aged adults ($p < .001$). Middle-aged adults were marginally less accurate than younger adults ($p = .054$). We found a main effect of *emotion*, $F(5, 430) = 102$, $p < .001$, $\eta^2_p = .542$, $\varepsilon = .980$, revealing accuracy rates significantly higher following scenarios portraying happiness ($p < .001$), sadness, and neutral scenes, without significant differences between the latter ($p > .998$). Scenarios portraying anger, disgust, and fear elicited similar accuracy rates (all $p > .988$). We also found a main effect of *congruency*, $F(1, 86) = 9.77$, $p = .002$, $\eta^2_p = .102$, revealing higher accuracy rates in congruent than in incongruent trials ($p = .002$). The *congruency*group* interaction was non-significant, ($F < 1$), but we found a significant *emotion*congruency* interaction, $F(5, 430) = 18.9$, $p < .001$, $\eta^2_p = .180$, along with a significant *emotion*congruency*group* interaction, $F(10, 430) = 2.69$, $p = .003$, $\eta^2_p = .059$. Post-hoc comparisons (represented in Fig. 3) revealed that the three groups obtained similar results in congruent condition portraying happiness (all $p > .534$), but younger adults outperformed older adults in the remaining congruent and incongruent conditions (all $p < .033$). Younger and middle-aged adults had similar performances in all congruent and incongruent conditions (all $p > .091$), except for incongruent condition portraying disgust ($p = .011$), in which younger adults had higher accuracy rates. Middle-aged adults outperformed older adults in all incongruent conditions (all $p < .024$), except for the incongruent condition portraying disgust ($p = .074$). Regarding congruent conditions, middle-aged adults outperformed older adults in conditions portraying disgust, neutrality, and sadness (all $p < .022$), having similar performance in conditions portraying anger, fear, and happiness (all $p > .186$). Descriptive statistics of perspective-taking results are presented in Table 2 of the Online Supplementary Material.

Regarding reaction times, we obtained a main effect of *group*, $F(2, 86) = 3.43$, $p < .001$, $\eta^2_p = .177$, revealing faster responses for younger ($p = .007$) and middle-aged adults ($p < .001$) than for older adults. We also found a main effect of *emotion*, $F(5, 430) = 3.43$, $p = .020$, $\eta^2_p = .038$, $\varepsilon = .597$, revealing faster responses in scenarios portraying happiness than in the remaining scenarios (all $p < .027$), with the exception of trials portraying disgust ($p = .322$). We found a marginal main effect of *congruency*, $F(1, 86) = 3.23$, $p = .076$, $\eta^2_p = .036$, but no significant interactions emerged (all $F < 1$). Descriptive statistics of reaction times are presented in Table 3 of the Online Supplementary Material.

The results of the Pearson's correlations are presented in Table 4 of the Online Supplementary Material. According to the linear regression models (Table 5 of the Online Supplementary Material), the scores of the IFS were significant predictors of the results obtained in the congruent conditions for younger adults, while the scores of the Learning

subtest of the AVLTL were significant predictors of the results obtained in the congruent conditions for older adults. The scores of the IFS were significant predictors of the results obtained in the incongruent conditions for older adults.

Electrophysiological results³

The statistical analysis of the N170 showed a significant main effect of *group*, $F(2, 86) = 13.2$, $p < .001$, $\eta^2_p = .236$, revealing N170 amplitudes that were significantly lower for younger than for middle-aged ($p = .017$) and older adults ($p < .001$). Middle-aged adults had N170 amplitudes marginally lower than older adults ($p = .065$). We found a main effect of *hemisphere* $F(1, 86) = 9.67$, $p = .003$, $\eta^2_p = .101$, revealing N170 amplitudes significantly higher at the right than at the left hemisphere. The main effect of *emotion* was marginally significant, $F(5, 430) = 2.00$, $p = .078$, $\eta^2_p = .023$, but the main effect of *congruency* was not significant ($F < 1$). We found a significant *emotion*congruency* interaction, $F(5, 430) = 4.54$, $p < .001$, $\eta^2_p = .050$, along with a significant *emotion*congruency*hemisphere*group* interaction, $F(10, 430) = 2.19$, $p = .017$, $\eta^2_p = .048$. No other significant interactions emerged (all $F < 1.79$, $p > .060$). Since our aim was to explore age differences in the processing of FEEs congruent and incongruent with previous scenarios, we explored this three-way interaction through three repeated measures ANOVAs, conducted by group (Fig. 4). Results of younger and middle-aged adults showed marginally significant *emotion*congruency* interactions,

respectively $F(5, 145) = 2.66$, $p = .050$, $\eta^2_p = .084$, $\varepsilon = .720$ and $F(5, 140) = 2.15$, $p = .069$, $\eta^2_p = .112$. In older adults this interaction was significant, $F(5, 140) = 3.52$, $p = .011$, $\eta^2_p = .112$, $\varepsilon = .887$, revealing N170 amplitudes significantly higher for incongruent than for congruent conditions portraying fear ($p = .007$). Descriptive statistics of N170 amplitudes are presented in Table 6 of the Online Supplementary Material.

Statistical analysis of the LPPE showed a main effect of *group*, $F(2, 86) = 3.79$, $p = .027$, $\eta^2_p = .081$, revealing that younger adults had amplitudes significantly higher than middle-aged adults ($p = .042$), but marginally higher than older adults ($p = .083$). A main effect of *congruency* emerged, $F(1, 86) = 29.5$, $p < .001$, $\eta^2_p = .255$, revealing higher amplitudes for congruent than for incongruent conditions. However, we did not find a main effect of *emotion*, $F(5, 430) = 2.38$, $p = .232$, $\eta^2_p = .016$, $\varepsilon = .947$. The *emotion*congruency*group* was not significant, $F(10, 430) = 1.03$, $p = .421$, $\eta^2_p = .023$, but we found a significant *congruency*group* interaction, $F(2, 86) = 5.24$, $p = .007$, $\eta^2_p = .109$. Pairwise comparisons (Fig. 5) revealed that congruent and incongruent conditions elicited similar LPPE amplitudes for older adults ($p = .313$), but younger ($p < .001$) and middle-aged adults ($p = .006$) showed LPPE amplitudes significantly higher for congruent than for incongruent conditions.

Regarding the LPPI, we found a main effect of *group*, $F(2, 86) = 3.27$, $p = .046$, $\eta^2_p = .071$, revealing that younger adults had amplitudes marginally higher than older adults ($p = .072$). We did not find a main effect of *emotion*, $F(5, 430) = 1.37$,

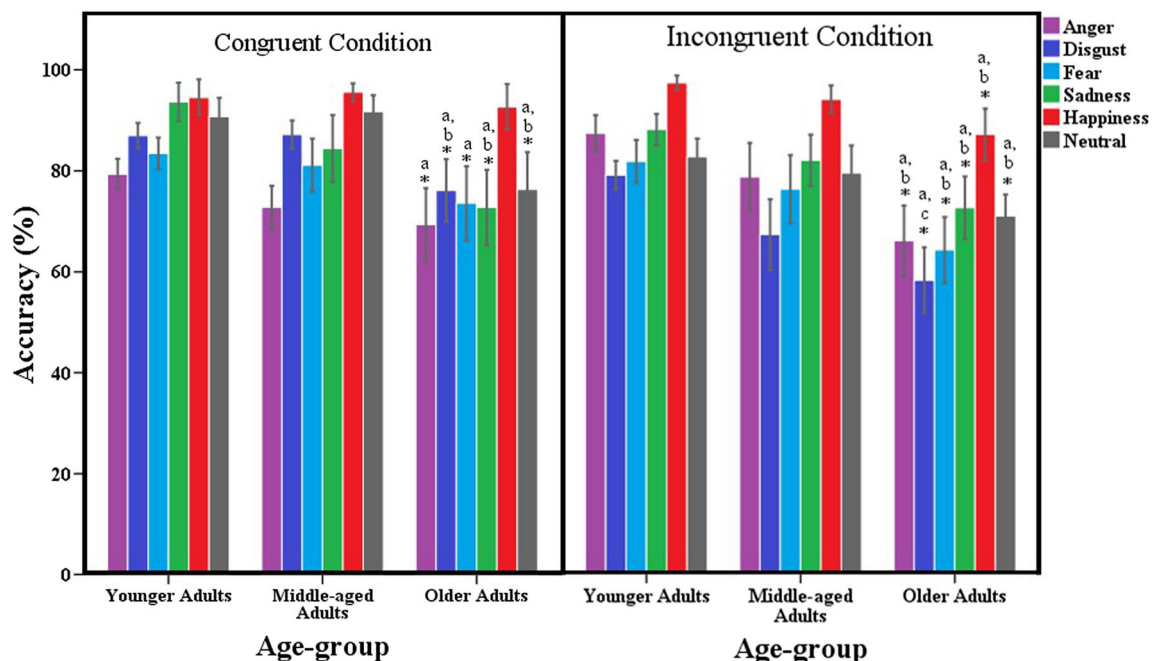


Fig. 3 Average rates of accuracy (%) for each emotional and congruence condition. Asterisks and letters represent significant differences (a) between younger and older adults; (b) between middle-aged and older

adults; and (c) between younger and middle-aged adults. Error bars indicate 95% confidence intervals

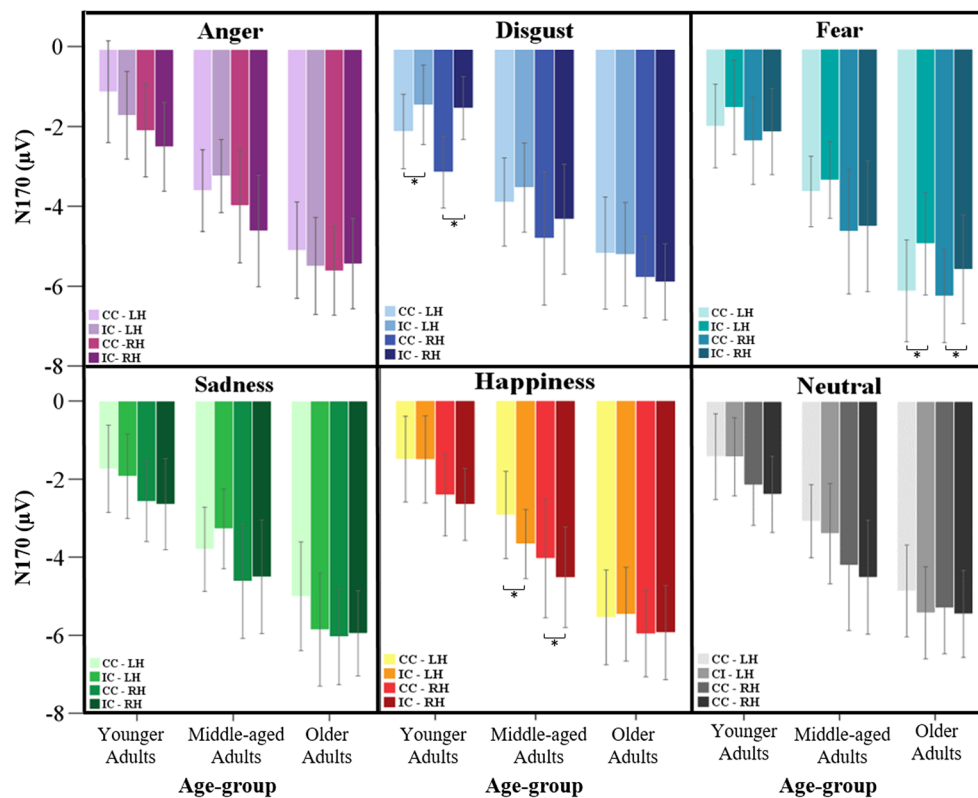


Fig. 4 Means of the N170 amplitudes (μV) evoked by each emotional and congruence condition. Asterisks represent significant differences and error bars indicate 95% confidence intervals. *CC* congruent condition, *IC* incongruent condition, *LH* left hemisphere, *RH* right hemisphere

$p = .236$, $\eta^2_p = .016$, $\varepsilon = .829$, but we found a significant main effect of *congruency*, $F(1, 86) = 33.4$, $p < .001$, $\eta^2_p = .279$, revealing higher amplitudes for congruent than for incongruent conditions. The *emotion*congruency*group* interaction was not significant, $F(10, 430) = 1.17$, $p = .312$, $\eta^2_p = .026$, but we found a significant *congruency*group* interaction, $F(2, 86) = 6.91$, $p = .002$, $\eta^2_p = .138$. Pairwise comparisons (Fig. 5) revealed that congruent and incongruent conditions elicited

similar LPPi amplitudes for older adults ($p = .674$), but younger ($p < .001$) and middle-aged adults ($p < .001$) showed LPPi amplitudes significantly higher for congruent than for incongruent conditions. The LPPs are plotted in Fig. 6, and descriptive statistics are presented in Table 7 of the Online Supplementary Material.

For younger adults, the N170 amplitudes elicited by incongruent trials in the left hemisphere were positively correlated

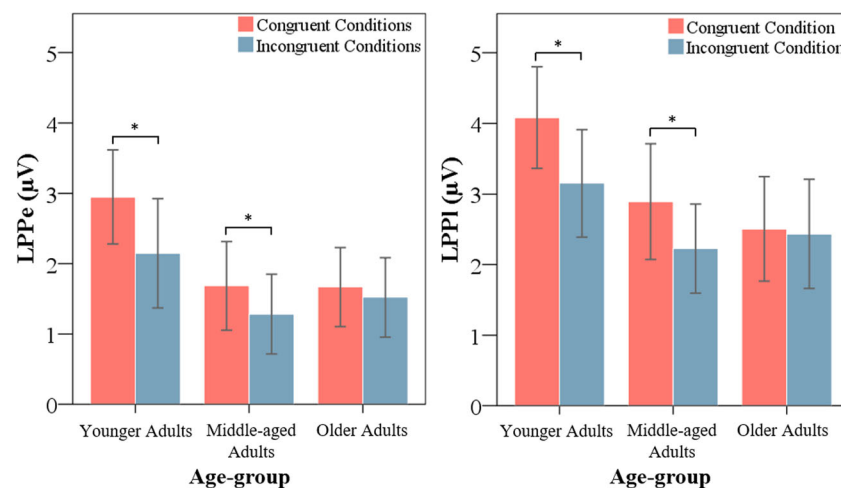


Fig. 5 Means of the LPPe and LPPi amplitudes (μV) evoked by congruent and incongruent conditions. Asterisks represent significant differences and error bars indicate 95% confidence intervals. *Note:*

Since we did not find a main effect of *emotion*, all emotional conditions were averaged by *congruency*

with the scores of the Delayed Recognition subtest of the AVLT (Table 8 of the Online Supplementary Material). The LPpe amplitudes elicited by congruent trials were positively correlated with the scores of the Learning subtest of the AVLT for younger adults, while the LPpe amplitudes elicited by incongruent trials were negatively correlated with the scores of the TMT for older adults. The LPpi amplitudes elicited by both congruent and incongruent trials were positively correlated with the scores of the Learning subtest of the AVLT for middle-aged adults, and negatively correlated with the scores of the Delayed Recognition subtest of the AVLT for older adults.

Discussion

Aging seems to affect ToM, but its effect on emotional perspective-taking is less well studied. Few studies have focused on the neural mechanisms underlying emotional perspective-taking, and the rare ones that investigated this ability with ERP methodology did not include older adults. Considering this gap, we adapted a perspective-taking task previously used in an fMRI study in order to build a context-target congruency task that could elicit two ERPs that were shown to be modulated by the affective and evaluative congruency: the N170 and LPP. Our aim was to examine how perspective-taking abilities – assessed in the present study as the accuracy in inferring the emotion of a masked actor of a given scenario, and decide its congruency with a target facial expression of emotion – could modulate the neural responses to congruent and incongruent context-target trials, in different age groups.

Considering previous results found in ToM, we formulated two main predictions. We expected poorer performance of older adults in comparison to middle-aged and younger adults (Henry et al., 2013), independent of neurocognitive performance (Moran, 2013). We also predicted the influence of perspective-taking on earlier and later stages of affective processing, indexed by a modulation in the N170 and LPP components. The N170 should be enhanced in congruent trials (Hietanen & Astikainen, 2013; Righart & de Gelder, 2006, 2008a, 2008b), while the LPP should be enhanced in incongruent trials (Diéguez-Risco et al., 2013; Dozolme, Brunet-Gouet, Passerieux, & Amorim, 2015; Herring et al., 2011). As we expected a decreased perspective-taking in the older group, we predicted an absence of these ERP modulations in this group.

The behavioral results were according to our hypothesis. Younger adults outperformed older adults in all conditions, except in congruent trials portraying happiness, in which groups had similar performances. This finding may be explained by the aging positivity effect (Mather & Carstensen, 2005), which postulates that older adults allocate more

attention and memorize positive better than negative emotional stimuli (Nashiro, Sakaki, & Mather, 2012). Our results did not completely support this effect, since older adults had a similar instead of greater accuracy in trials portraying happiness. However, the positivity effect may be manifested by a preserved ability to infer happiness during aging, contrary to what happens in neutral and negative emotions. The worse performance of older adults in the remaining conditions is in accordance with previous findings. For instance, two meta-analyses showed that an age-related decline in emotional recognition is the predominant pattern across all emotions, with increased difficulties for anger, fear, and sadness (Gonçalves et al., 2018a; Ruffman, Henry, Livingstone, & Phillips, 2008). Middle-aged adults also outperformed older adults, but in fewer conditions than younger adults did.

Interestingly, the results obtained in the congruent trials were significantly predicted by better executive functioning for younger adults, being predicted by better working memory for older adults. The results obtained in incongruent trials were also predicted by better executive function, but only for older adults. This was an unexpected finding if we consider results obtained in ToM tasks. According to a comprehensive review (Moran, 2013), older adults' performance in ToM tasks using visual stimuli are relatively independent of cognitive abilities, while tasks using verbal stories are more dependent on neurocognition. However, the complexity of our task may account for the increased impact of cognitive abilities on perspective-taking performance. Visual stimuli used previously in ToM tasks usually did not require the interpretation of stories (e.g., see the “reading the mind in the eyes” task by Baron-Cohen, Golan, Ashwin, Ashwin, & Robertson, 1997). Contrarily, tasks using verbal stimuli (e.g., see “strange stories” by Happé, 1994), may be more demanding on cognitive abilities, since they comprise situations where people say things that are not literally interpretable. In these stories, to understand the speaker's intention, participants may have to sidestep the literal meaning of the sentence and infer the speaker's mental state. Similarly, in our task, participants may have had to forfeit their own perspective for an accurate response, which may explain the role of executive functioning in behavioral performance. Moreover, an accurate answer was also dependent on the ability to maintain in working memory the emotion inferred during the visualization of the scenario, which was then compared with the emotion displayed by the target FEE. Thus, as the performance was predicted by better results in executive functions, our results suggest that the involvement of cognitive abilities in empathic tasks may be dependent on the complexity of the task, particularly on the demands of inhibitory control.

Regarding electrophysiological results, we found significantly more negative N170 amplitudes at the right hemisphere, which is a systematic finding (e.g., Rossion & Jacques, 2008). Interestingly, N170 amplitudes of older

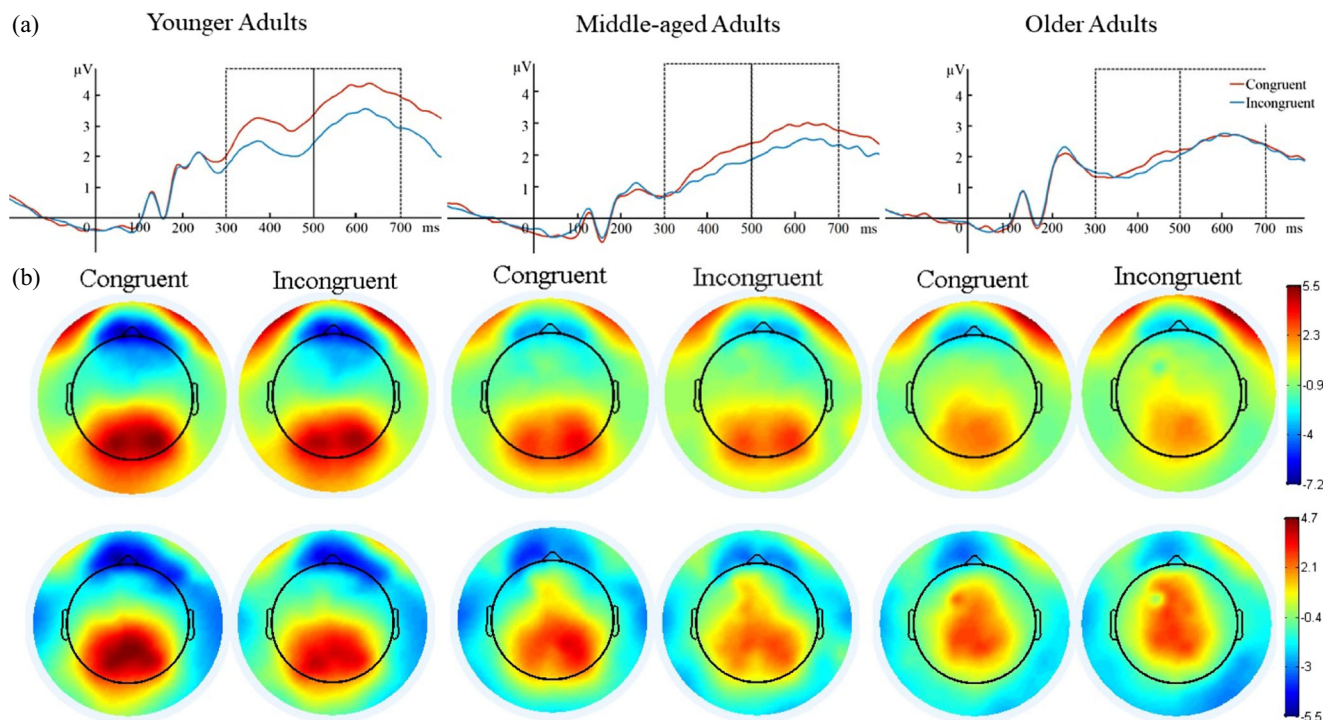


Fig. 6 (a) Grand-average of LPPe (300–500 ms) and LPPi (500–700 ms) for younger, middle-aged, and older adults obtained in the centro-parietal region of interest. (b) Topographical maps for event-related potentials

elicited by congruent and incongruent conditions at 300–500 ms (above) and 500–700 ms (below). Note: Since we did not find a main effect of emotion, all emotional conditions were averaged by congruency

adults were significantly higher than those of younger adults and marginally higher than those of middle-aged adults. This is consistent with the results of a previous study conducted by our group, in which we examined age-related differences in emotion identification abilities (Gonçalves et al., 2018b). In this study, such results occur simultaneously with an equivalent performance in emotion identification, which is consistent with the compensation hypothesis (Cabeza, 2002; Reuter-Lorenz & Cappell, 2008). According to this hypothesis, additional neural activity serves a beneficial, compensatory function during aging, without which performance decline would occur. Taken together, these findings suggest that older adults may have a preserved ability to encode facial structure and emotion, supported by increased neural resources employed during this function.

The main effect of emotion was marginally significant, which can be explained by a lack of instructions to identify the emotion displayed by the target FEE. A previous study only found a N170 modulated by emotion in a task demanding emotional discrimination, in comparison with a task demanding sex discrimination (Wronka & Walentowska, 2011). This component was not modulated by the congruency between the emotional contexts and the target's FEE, which was unexpected considering that previous studies that used pictures as contexts found a systematically higher N170 in congruent trials (Hietanen & Astikainen, 2013; Righart & de Gelder, 2006,

2008a, 2008b). Nonetheless, this modulation is less consistent in tasks using sentences as contexts. Two previous studies did not find a congruency modulation in N170 (Diéguez-Risco et al., 2013; Dozolme et al., 2015), while one study showed a higher N170 in incongruent trials (Diéguez-Risco et al., 2015). Once again, it is possible that our results are closer to those obtained with verbal stimuli; an equivalent demand in interpretation would result only in the modulation of later ERP components.

Taking previous findings into account, the results concerning the emotion by congruency interaction are difficult to interpret. Righart and de Gelder (2006, 2008a, 2008b) found larger N170 amplitudes after fearful faces congruent with fearful scenarios, and Hietanen and Astikainen (2013) reported equivalent results in sad and happy conditions. However, Diéguez-Risco et al. (2015) found larger N170s for anger and happiness incongruent conditions, and we found similar results, but only for older adults and in the fear condition. These discrepant results may arise from differences in the task demands. While previous studies required the emotional identification displayed by the target FEE, here (as in our study) study participants had to judge the congruency between the target FEE and the preceding context. Thus, an enhanced N170 after incongruent trials could reflect the influence of deliberative processes that would involve the interaction of face-processing systems with previous knowledge about the emotional reactions that are expected in different situations.

According to this interpretation, perceptual processing would be increased for stimuli involving a violation of expectations, since their emotional meaning is inconsistent with the context (Diéguez-Risco et al., 2015). This interpretation sounds plausible, but does not fully explain why this result was found only for older adults and in such a specific emotional category. Such a discrepancy highlights that further work is needed to clarify the influence of different contextual stimuli in N170 modulation.

The results obtained in the LPPs were consistent between the early and late time-windows, showing higher amplitudes in congruent than in incongruent trials. The direction of this effect is unexpected, since previous studies using context-target congruency tasks found larger LPPs after incongruent FEE, in conditions involving both implicit (Diéguez-Risco et al., 2013; Morioka et al., 2016) and explicit processing of congruency (Diéguez-Risco et al., 2015). Higher LPP amplitudes elicited by incongruent trials are systematically reported in the priming literature, namely in tasks requiring an evaluative congruity between primes and facial (Herring et al., 2011; Werheid, Alpay, Jentzsch, & Sommer, 2005) or verbal targets (Zhang, Li, Gold, & Jiang, 2010). This effect is interpreted as a spreading activation of affective priming (Hietanen & Astikainen, 2013), in which an affective context activates the associated affective evaluation, facilitating the processing of affectively congruent stimuli (Hietanen & Astikainen, 2013). For instance, in evaluative priming paradigms, a prime word such as “champion” activates pleasant concepts in memory, which produce a quicker response to target-congruent words (e.g., “saint”) compared to the target-incongruent words (e.g., “killer”). In such tasks, incongruent targets would evoke larger LPPs, reflecting a more demanding retrieval required to evaluate congruency.

As we found an opposite pattern of activation, it is possible that our task could have evoked other neural processes than the ones underlying the priming effects reported by previous studies (Diéguez-Risco et al., 2013, 2015; Morioka et al., 2016). For instance, Diéguez-Risco et al. (2013, 2015) used happy- or anger-inducing sentences that might have worked as primes during the processing of FEE. Similarly, in Morioka and colleagues’ study (2016), stimuli were sentences describing moderately affective events relevant to participants. On the contrary, we instructed participants to attend the scenes, infer the mental state of the masked interveners, and decide if the FEE displayed after the scene matched the one previously inferred. As the LPP is also modulated by the explicit recognition of stimuli, being larger to recognized stimuli in comparison to new (Danker et al., 2008; Münte, Urbach, Duzel & Kutas, 2000), the increased amplitudes to congruent stimuli may reflect the recognition of the masked person’s emotion in those displayed by the target FEE. In fact, this recruitment of

memory resources to perform the perspective-taking task explains the unexpected influence of executive functioning in the behavioral results.

According to our hypothesis, older adults did not show the LPP modulation found in younger and middle-aged adults. That is, while younger and middle-aged adults showed higher LPP amplitudes after FEEs congruent with previous scenarios than after incongruent FEEs, older adults had similar amplitudes after both. It is worth noting that this insensitivity of older adults’ LPP to the congruency of the trials is not explained by an age-related decline in face encoding, bearing in mind the results obtained with the N170 amplitudes (Gonçalves et al., 2018b). Moreover, this was observed independent of the accuracy, since only correct trials were considered on the analysis of the ERPs. Thereby, this result may be interpreted as a difficulty of older adults in inferring accurate emotional states during the visualization of the scenarios. Thus, while younger and middle-aged adults are able to infer the appropriate actor’s emotional state during the observation of the scenario, which they maintain in working memory and then compare with the emotion displayed in the target FEE, older adults only reach the correct response after observing the target FEE, which may act as a clue. This may underlie older adults’ difficulties in using the facial expression of others to understand their inner states and take their emotional perspective, as well as to understand the relation between their mental states and the ongoing social events.

Considering that previous studies suggest there are differences in empathy between males and females (e.g., Christov-Moore et al., 2014), we preformed an exploratory analysis comparing behavioral and electrophysiological results of males and females. Despite the fact that we did not find gender differences (Supplementary Material), a recent review showed quantitative gender differences in the basic networks involved in affective and cognitive forms of empathy, as well as qualitative differences in how emotional information is integrated to support decision-making processes (Christov-Moore et al., 2014). Thereby, our contrasting results unveil the need for further research in this field, and using designs with greater statistical power and considering convergent tasks may improve and help to uncover the nature of gender differences in empathy.

Our results bring important contributions to the state of the art in the research field of aging and perspective-taking. Aging is typically associated with impairments in ToM, which can lead to difficulties in social functioning (Moran, 2013). As emotional perspective-taking is an indispensable element in the fully developed ToM (Decety & Jackson, 2004), research on this ability may help to better understand older adults’ difficulties during social interactions. Moreover, study of the modulation of ERPs by perspective-taking may unveil the

time course of the processing of the information regarding contexts and the eliciting emotions, as well as the stage of this processing in which older adults' difficulties emerged.

Interestingly, middle-aged adults appear to be at an intermediate level between younger and older adults, at least behaviorally. They had better results than older adults, but in fewer conditions than younger adults did. The lack of previous studies with a similar group design makes these results more difficult to interpret. The existing literature typically compares younger and older adults, but introducing middle-aged adults allows better analysis of the development of perspective-taking abilities across adulthood.

Acknowledgements This research was supported by a Grant from the BIAL Foundation. Carina Fernandes was supported by a doctoral fellowship from the Fundação para a Ciência e a Tecnologia (SFRH/BD/112101/2015). We thank Brigit Derntl for her permission to use the stimuli displayed as scenarios in the emotional perspective-taking task, and Nim Tottenham for her permission to use the face stimuli displayed as target FEE. Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development. Please contact Dr. Nim Tottenham for more information concerning the stimulus set (nlt7@columbia.edu; <http://danlab7.wixsite.com/nimstim>). We also thank Programa de Estudos Universitários para Seniores and Associação de Aposentados Pensionistas e Reformados for their help in participant recruitment.

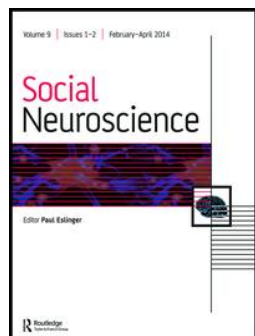
References

- Almeida, P. R., Ferreira-Santos, F., Chaves, P. L., Paiva, T. O., Barbosa, F., & Marques-Teixeira, J. (2016). Perceived arousal of facial expressions of emotion modulates the N170, regardless of emotional category: Time domain and time–frequency dynamics. *International Journal of Psychophysiology*, 99, 48–56. <https://doi.org/10.1016/j.ijpsycho.2015.11.017>
- Armitage, S. G. (1946). An analysis of certain psychological tests used for the evaluation of brain injury. *Psychology Monographs*, 60(1), 1–48. <https://doi.org/10.1037/h0093567>
- Baron-Cohen, S., Jolliffe, T., Mortimore, C., & Robertson, M. (1997). Another advanced test of theory of mind: Evidence from very high functioning adults with autism or Asperger syndrome. *Journal of Child Psychology and Psychiatry*, 38, 813–822. <https://doi.org/10.1111/j.1469-7610.1997.tb01599.x>
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8(6), 551–565. <https://doi.org/10.1162/jocn.1996.8.6.551>
- Boake, C. (2000). Édouard Claparède and the Auditory Verbal Learning Test. *Journal of Clinical and Experimental Neuropsychology*, 22(2), 286–292. [https://doi.org/10.1076/1380-3395\(200004\)22:2;1-I;FT286](https://doi.org/10.1076/1380-3395(200004)22:2;1-I;FT286)
- Bowman, L. C., Liu, D., Meltzoff, A. N., & Wellman, H. M. (2012). Neural correlates of belief-and desire-reasoning in 7-and 8-year-old children: an event-related potential study. *Developmental Science*, 15(5), 618–632. <https://doi.org/10.1111/j.1467-7687.2012.01158.x>
- Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: the HAROLD Model. *Psychology and Aging*, 17(1), 85–100.
- Canavarro, M. C. (1999). Inventário de sintomas psicopatológicos - BSI. Em M. G. M. R. Simões, *Testes e Provas Psicológicas em Portugal (Vol. II)* (pp. 87–109). Braga: SHO/APPORT.
- Castelli, I., Baglio, F., Blasi, V. A., Falini, A., Liverta-Sempio, O., & Marchetti, A. (2010). Effects of aging on mindreading ability through the eyes: an fMRI study. *Neuropsychologia*, 48(9), 2586–2594. <https://doi.org/10.1016/j.neuropsychologia.2010.05.005>
- Cavaco, S., Gonçalves, A., Pinto, C., Almeida, E., Gomes, F., Moreira, I., ... Teixeira-Pinto, A. (2013a). Semantic fluency and phonemic fluency: regression-based norms for the Portuguese population. *Archives of Clinical Neuropsychology*, 28(3), 262–271. <https://doi.org/10.1093/arclin/act001>
- Cavaco, S., Gonçalves, A., Pinto, C., Almeida, E., Gomes, F., Moreira, I., ... Teixeira-Pinto, A. (2013b). Trail Making Test: Regression-based norms for the Portuguese population. *Archives of Clinical Neuropsychology*, 28(2), 189–198. <https://doi.org/10.1093/arclin/acs>
- Cavaco, S., Gonçalves, A., Pinto, C., Almeida, E., Gomes, F., Moreira, I., ... Teixeira-Pinto, A. (2015). Auditory Verbal Learning Test in a large nonclinical Portuguese population. *Applied Neuropsychology: Adult*, 22(5), 321–331. <https://doi.org/10.1080/23279095.2014.927767>
- Christov-Moore, L., Simpson, E. A., Coudé, G., Grigaityte, K., Iacoboni, M., & Ferrari, P. F. (2014). Empathy: gender effects in brain and behavior. *Neuroscience & Biobehavioral Reviews*, 46, 604–627.
- Cowell, J. M., & Decety, J. (2015). Precursors to morality in development as a complex interplay between neural, socioenvironmental, and behavioral facets. *Proceedings of the National Academy of Sciences*, 112(41), 12657–12662. <https://doi.org/10.1073/pnas.1508832112>
- Danker, J. F., Hwang, G. M., Gauthier, L., Geller, A., Kahana, M. J., & Sekuler, R. (2008). Characterizing the ERP Old–New effect in a short-term memory task. *Psychophysiology*, 45, 784–793. <https://doi.org/10.1111/j.1469-8986.2008.00672.x>
- David, N., Aumann, C., Santos, N. S., Bewernick, B. H., Eickhoff, S. B., Newen, A., ... & Vogeley, K. (2008). Differential involvement of the posterior temporal cortex in mentalizing but not perspective taking. *Social Cognitive and Affective Neuroscience*, 3(3), 279–289. <https://doi.org/10.1093/scan/nsn023>
- Davis, M. H. (1983). Measuring individual differences in empathy: Evidence for a multidimensional approach. *Journal of Personality and Social Psychology*, 44(1), 113. <https://doi.org/10.1037/0022-3514.44.1.113>
- Decety, J., & Jackson, P. L. (2004). The functional architecture of human empathy. *Behavioral and Cognitive Neuroscience Reviews*, 3(2), 71–100.
- Decety, J., Yang, C. Y., & Cheng, Y. (2010). Physicians down-regulate their pain empathy response: an event-related brain potential study. *Neuroimage*, 50(4), 1676–1682. <https://doi.org/10.1016/j.neuroimage.2010.01.025>
- Delorme, A., & Makeig, S. (2004). An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Derntl, B., Finkelmeyer, A., Toygar, T. K., Hülsmann, A., Schneider, F., Falkenberg, D. I., & Habel, U. (2009). Generalized deficit in all core components of empathy in schizophrenia. *Schizophrenia Research*, 108(1), 197–206. <https://doi.org/10.1016/j.schres.2008.11.009>
- Derogatis, L. R. (1982/1993). *BSI: Brief Symptom Inventory (3rd ed.)*. Minneapolis: National Computers Systems.
- Diéguez-Risco, T., Aguado, L., Albert, J., & Hinojosa, J. A. (2013). Faces in context: modulation of expression processing by situational information. *Social Neuroscience*, 8(6), 601–620. <https://doi.org/10.1080/17470919.2013.834842>
- Diéguez-Risco, T., Aguado, L., Albert, J., & Hinojosa, J. A. (2015). Judging emotional congruency: Explicit attention to situational context modulates processing of facial expressions of emotion.

- Biological Psychology*, 112, 27–38. <https://doi.org/10.1016/j.biopsycho.2015.09.012>
- Dozolme, D., Brunet-Gouet, E., Passerieux, C., & Amorim, M. (2015). Neuroelectric correlates of pragmatic emotional incongruence processing: empathy matters. *PLOS One*, 10(6), e0129770. <https://doi.org/10.1371/journal.pone.0129770>
- Fernandes, C., Pasion, R., Gonçalves, A. R., Ferreira-Santos, F., Barbosa, F., Martins, I. P., & Marques-Teixeira, J. (2018). Age differences in neural correlates of feedback processing after economic decisions under risk. *Neurobiology of aging*, 65, 51–59.
- Foti, D., & Hajcak, G. (2008). Deconstructing reappraisal: Descriptions preceding arousing pictures modulate the subsequent neural response. *Journal of Cognitive Neuroscience*, 20(6), 977–988. <https://doi.org/10.1162/jocn.2008.20066>
- Freitas, S., Simões, M. R., & Santana, I. (2014). Montreal Cognitive Assessment (MoCA): Pontos de corte no Déficit Cognitivo Ligeiro, Doença de Alzheimer, Demência Frontotemporal e Demência Vascular. *Sinapse*, 14, 18–30.
- Gao, L., Xu, J., Zhang, B., Zhao, L., Harel, A., & Bentin, S. (2009). Aging effects on early-stage face perception: An ERP study. *Psychophysiology*, 46(5), 970–983. <https://doi.org/10.1111/j.1469-8986.2009.00853.x>
- Gonçalves, A. R., Fernandes, C., Pasion, R., Ferreira-Santos, F., Barbosa, F., & Marques-Teixeira, J. (2018a). Effects of age on the identification of emotions in facial expressions: a meta-analysis. *PeerJ*, 6, e5278.
- Gonçalves, A. R., Fernandes, C., Pasion, R., Ferreira-Santos, F., Barbosa, F., & Marques-Teixeira, J. (2018b). Emotion identification and aging: Behavioral and neural age-related changes. *Clinical Neurophysiology*, 129(5), 1020–1029. <https://doi.org/10.1016/j.clinph.2018.02.128>
- Happé, F. G. (1994). An advanced test of theory of mind: Understanding of story characters' thoughts and feelings by able autistic, mentally handicapped, and normal children and adults. *Journal of Autism and Developmental Disorders*, 24, 129–154.
- Henry, J. D., Phillips, L. H., Ruffman, T., & Bailey, P. E. (2013). A meta-analytic review of age differences in theory of mind. *Psychology and Aging*, 28(3), 826–839. <https://doi.org/10.1037/a0030677>
- Herring, D. R., Taylor, J. H., White, K. R., & Crites, S. L. (2011). Electrophysiological responses to evaluative priming: the LPP is sensitive to incongruity. *Emotion*, 11(4), 794–806. <https://doi.org/10.1037/a0022804>
- Hietanen, J. K., & Astikainen, P. (2013). N170 response to facial expressions is modulated by the affective congruency between the emotional expression and preceding affective picture. *Biological Psychology*, 92(2), 114–124. <https://doi.org/10.1016/j.biopsycho.2012.10.005>
- Hinojosa, J. A., Mercado, F., & Carretié, L. (2015). N170 sensitivity to facial expression: A meta-analysis. *Neuroscience & Biobehavioral Reviews*, 55, 498–509. <https://doi.org/10.1016/j.neubiorev.2015.06.002>
- Jackson, P. L., Meltzoff, A. N., & Decety, J. (2006). Neural circuits involved in imitation and perspective-taking. *Neuroimage*, 31(1), 429–439. <https://doi.org/10.1016/j.neuroimage.2005.11.026>
- Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., ... Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron*, 20(5), 927–936. [https://doi.org/10.1016/S0896-6273\(00\)80474-2](https://doi.org/10.1016/S0896-6273(00)80474-2)
- Kisley, M. A., Wood, S., & Burrows, C. L. (2007). Looking at the sunny side of life: Age-related change in an event-related potential measure of the negativity bias. *Psychological Science*, 18(9), 838–843.
- Komes, J., Schweinberger, S. R., & Wiese, H. (2014). Preserved fine-tuning of face perception and memory: evidence from the own-race bias in high- and low-performing older adults. *Frontiers in Aging Neuroscience*, 6, 60. <https://doi.org/10.3389/fnagi.2014.00060>
- Li, W., & Han, S. (2010). Perspective taking modulates event-related potentials to perceived pain. *Neuroscience Letters*, 469(3), 328–332. <https://doi.org/10.1016/j.neulet.2009.12.021>
- Liao, X., Wang, K., Lin, K., Chan, R. C., & Zhang, X. (2017). Neural temporal dynamics of facial emotion processing: age effects and relationship to cognitive function. *Frontiers in Psychology*, 8, 1110. <https://doi.org/10.3389/fpsyg.2017.01110>
- Liu, D., Meltzoff, A. N., & Wellman, H. M. (2009). Neural Correlates of Belief-and Desire-Reasoning. *Child Development*, 80(4), 1163–1171. <https://doi.org/10.1111/j.1467-8624.2009.01323.x>
- Liu, D., Sabbagh, M. A., Gehring, W. J., & Wellman, H. M. (2004). Decoupling beliefs from reality in the brain: an ERP study of theory of mind. *NeuroReport*, 15, 991–995. <https://doi.org/10.1097/01.wnr.0000123388.87650.06>
- Mather, M., & Carstensen, L. L. (2005). Aging and motivated cognition: The positivity effect in attention and memory. *Trends in Cognitive Sciences*, 9(10) 496–502. <https://doi.org/10.1016/j.tics.2005.08.005>
- McCleery, J. P., Surtees, A. D., Graham, K. A., Richards, J. E., & Apperly, I. A. (2011). The neural and cognitive time course of theory of mind. *Journal of Neuroscience*, 31(36), 12849–12854. <https://doi.org/10.1523/JNEUROSCI.1392-11.2011>
- Meinhardt, J., Sodian, B., Thoermer, C., Döhnel, K., & Sommer, M. (2011). True-and false-belief reasoning in children and adults: An event-related potential study of theory of mind. *Developmental Cognitive Neuroscience*, 1(1), 67–76. <https://doi.org/10.1016/j.dcn.2010.08.001>
- Moran, J. M. (2013). Lifespan development: The effects of typical aging on theory of mind. *Behavioural Brain Research*, 237, 32–40. <https://doi.org/10.1016/j.bbr.2012.09.020>
- Moran, J. M., Jolly, E., & Mitchell, J. P. (2012). Social-cognitive deficits in normal aging. *Journal of Neuroscience*, 32(16), 5553–5561.
- Moreira, H. S., Lima, C. F., & Vicente, S. G. (2014). Examining Executive Dysfunction with the Institute of Cognitive Neurology (INECO) Frontal Screening (IFS): normative values from a healthy sample and clinical utility in Alzheimer's disease. *Journal of Alzheimer's Disease*, 42(1), 261–273. <https://doi.org/10.3233/JAD-132348>
- Morioka, S., Osumi, M., Shiotani, M., Nobusako, M., Maeoka, H., Okada, Y., ... Matsuo, A. (2016). Incongruence between Verbal and Non-Verbal Information Enhances the Late Positive Potential. *PloS One*, 11, 1–11. <https://doi.org/10.1371/journal.pone.0164633>
- Münté, T. F., Urbach, T. P., Duzel, E., & Kutas, M. (2000). Event-related brain potentials in the study of human cognition and neuropsychology. In F. Boller, G. J., & G. Rizzolatti, *Handbook of Neuropsychology*, Vol. 1, 2nd edition (pp. 1–97). Netherlands: Elsevier Science Publishers.
- Musial, P. G., Baker, S. N., Gerstein, G. L., King, E. A., & Keating, J. G. (2002). Signal-to-noise ratio improvement in multiple electrode recording. *Journal of neuroscience methods*, 115(1), 29–43. [https://doi.org/10.1016/S0165-0270\(01\)00516-7](https://doi.org/10.1016/S0165-0270(01)00516-7)
- Nashiro, K., Sakaki, M., & Mather, M. (2012). Age differences in brain activity during emotion processing: Reflections of age-related decline or increased emotion regulation? *Gerontology*, 58(2), 156–163. <https://doi.org/10.1159/000328465>
- Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S. V., Whitehead, I., Collin, I., ... Chertkow, H. (2005). The Montreal Cognitive Assessment, MoCA: a brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, 53(4), 695–699. <https://doi.org/10.1111/j.1532-5415.2005.53221.x>
- O'Brien, E., Konrath, S. H., Gröhn, D., & Hagen, A. L. (2012). Empathic concern and perspective taking: Linear and quadratic effects of age across the adult life span. *Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, 68(2), 168–175. <https://doi.org/10.1093/geronb/gbs055>
- Pais-Ribeiro, J., Silva, I., Ferreira, T., Martins, A., Meneses, R., & Baltar, M. (2007). Validation study of a Portuguese version of the Hospital Anxiety and Depression Scale. *Psychology*,

- Health & Medicine*, 12(2), 225–237. <https://doi.org/10.1080/13548500500524088>
- Pasion, R., Fernandes, C., Gonçalves, A. R., Ferreira-Santos, F., Páscoa, R., Barbosa, F., & Marques-Teixeira, J. (2018). The effect of aging on the (mis) perception of intentionality—an ERP study. *Social Neuroscience* <https://doi.org/10.1080/17470919.2018.1430614>
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and clinical neurophysiology*, 72(2), 184–187. [https://doi.org/10.1016/0013-4694\(89\)90180-6](https://doi.org/10.1016/0013-4694(89)90180-6)
- Renfroe, J. B., Bradley, M. M., Sege, C. T., & Bowers, D. (2016). Emotional modulation of the late positive potential during picture free viewing in older and young adults. *PLoS One*, 11(9), e0162323. <https://doi.org/10.1371/journal.pone.0162323>
- Reuter-Lorenz, P. A., & Cappel, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, 17(3), 177–182.
- Righart, R., & de Gelder, B. (2006). Context influences early perceptual analysis offaces an electrophysiological study. *Cerebral Cortex*, 16(9), 1249–1257. <https://doi.org/10.1093/cercor/bhj066>
- Righart, R., & de Gelder, B. (2008a). Rapid influence of emotional scenes on encoding of facial expressions: an ERP study. *Social, Cognitive and Affective Neuroscience*, 3(3), 270–278. <https://doi.org/10.1093/scan/nsn021>
- Righart, R., & de Gelder, B. (2008b). Recognition of facial expressions is influenced by emotional scene gist. *Cognitive, Affective, and Behavioral Neuroscience*, 8(3), 264–272. <https://doi.org/10.3758/CABN.8.3.264>
- Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage*, 39(4), 1959–1979. <https://doi.org/10.1016/j.neuroimage.2007.10.011>
- Ruffman, T., Henry, J. D., Livingstone, V., & Phillips, L. H. (2008). A meta-analytic review of emotion recognition and aging: Implications for neuropsychological models of aging. *Neuroscience & Biobehavioral Reviews*, 32(4), 863–881. <https://doi.org/10.1016/j.neubiorev.2008.01.001>
- Sabbagh, M. A., & Taylor, M. (2000). Neural correlates of theory-of-mind reasoning: an event-related potential study. *Psychological Science*, 11(1), 46–50.
- Snaith, R. P., & Zigmond, A. P. (1994). *The Hospital Anxiety and Depression Scale Manual*. Windsor: NFER-Nelson.
- Strauss, E., Sherman, E. M., & Spreen, O. (2006). *A compendium of neuropsychological tests: Administration, norms, and commentary* (3rd). New York: Oxford University Press.
- Torralva, T., Roca, M., Gleichgerrcht, E., Lopez, P., & Manes, F. (2009). INECO Frontal Screening (IFS): A brief, sensitive, and specific tool to assess executive functions in dementia. *Journal of the International Neuropsychological Society*, 15(5), 777–786. <https://doi.org/10.1017/S1355617709990415>
- Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., ... Nelson, C. (2009). The NimStim set of facial expressions: judgments from untrained research participants. *Psychiatry Research*, 168(3), 242–249. <https://doi.org/10.1016/j.psychres.2008.05.006>
- Wang, Y. W., Lin, C. D., Yuan, B., Huang, L., Zhang, W. X., & Shen, D. L. (2010). Person perception precedes theory of mind: an event related potential analysis. *Neuroscience*, 170(1), 238–246. <https://doi.org/10.1016/j.neuroscience.2010.06.055>
- Wechsler, D. (2008). WMS - III. Escala de memória de Wechsler. Lisboa: CEGOC-TEA.
- Weinberg, A., & Hajcak, G. (2010). Beyond good and evil: The time-course of neural activity elicited by specific picture content. *Emotion*, 10(6), 767.
- Werheid, K., Alpay, G., Jentsch, I., & Sommer, W. (2005). Priming emotional facial expressions as evidenced by event-related brain potentials. *International Journal of Psychophysiology*, 55(2), 209–219. <https://doi.org/10.1016/j.ijpsycho.2004.07.006>
- Wood, S., & Kisley, M. A. (2006). The negativity bias is eliminated in older adults: age-related reduction in event-related brain potentials associated with evaluative categorization. *Psychology and Aging*, 21(4), 815. <https://doi.org/10.1037/0882-7974.21.4.815>
- Wronka, E., & Walentowska, W. (2011). Attention modulates emotional expression processing. *Psychophysiology*, 48(8), 1047–1056. <https://doi.org/10.1111/j.1469-8986.2011.01180.x>
- Yi, D., Chu, K., Ko, H., Lee, Y., Byun, M. S., Lee, J. H., & Lee, D. Y. (2017). Changes in perspective taking ability in aging process are dependent on gender and alzheimer-related cognitive decline. *Alzheimer's & Dementia: The Journal of the Alzheimer's Association*, 13(7), P369. <https://doi.org/10.1016/j.jalz.2017.06.319>
- Yoder, K. J., & Decety, J. (2014). Spatiotemporal neural dynamics of moral judgment: a high-density ERP study. *Neuropsychologia*, 60, 39–45. <https://doi.org/10.1016/j.neuropsychologia.2014.05.022>
- Zeman, P. M., Till, B. C., Livingston, N. J., Tanaka, J. W., & Driessen, P. F. (2007). Independent component analysis and clustering improve signal-to-noise ratio for statistical analysis of event-related potentials. *Clinical Neurophysiology*, 118(12), 2591–2604. <https://doi.org/10.1016/j.clinph.2007.09.001>
- Zhang, Q., Li, X., Gold, B. T., & Jiang, Y. (2010). Neural correlates of cross-domain affective priming. *Brain Research*, 1329, 142–151. <https://doi.org/10.1016/j.brainres.2010.03.021>

2.3 THE EFFECT OF AGING ON THE (MIS)PERCEPTION OF INTENTIONALITY - AN ERP STUDY



The effect of aging on the (mis)perception of intentionality - an ERP study

R. Pasion, C. Fernandes, A. R. Gonçalves, F. Ferreira-Santos, R. Páscoa, F. Barbosa & J. Marques-Teixeira

To cite this article: R. Pasion, C. Fernandes, A. R. Gonçalves, F. Ferreira-Santos, R. Páscoa, F. Barbosa & J. Marques-Teixeira (2018): The effect of aging on the (mis)perception of intentionality - an ERP study, *Social Neuroscience*

To link to this article: <https://doi.org/10.1080/17470919.2018.1430614>



Accepted author version posted online: 18 Jan 2018.
Published online: 23 Jan 2018.



Submit your article to this journal [↗](#)



Article views: 3



View related articles [↗](#)



View Crossmark data [↗](#)

ARTICLE



The effect of aging on the (mis)perception of intentionality - an ERP study

R. Pasion^a, C. Fernandes^{a,b,c}, A. R. Gonçalves^a, F. Ferreira-Santos^{ib,a}, R. Páscoa^d, F. Barbosa^{ib,a} and J. Marques-Teixeira^a

^aLaboratory of Neuropsychophysiology, Faculty of Psychology and Education Sciences, University of Porto, Porto, Portugal; ^bFaculty of Medicine, University of Porto, Porto, Portugal; ^cLanguage Research Laboratory, Institute of Molecular Medicine, Faculty of Medicine, University of Lisbon, Lisbon, Portugal; ^dREQUIMTE/LAQV - Departamento de Ciências Químicas, Laboratório de Química Aplicada, Faculdade de Farmácia, Universidade do Porto, Porto, Portugal

ABSTRACT

Despite the accumulated knowledge on moral decision-making in the early stages of development, empirical evidence is still limited in the old-aged adults. The current study contributes to unveil the neural correlates of judgments of moral transgressions as a function of aging, by examining the temporal dynamics of neural activation elicited by intentional and accidental harmful actions in three groups of healthy participants: young adults (18–35), adults (40–55), and older adults (60–75). Older adults were slower and less accurate in rating intentionality, compared to the younger groups. In ERP analysis, the older group showed increased P2 amplitude, which was predicted by poorer performance on neuropsychological tests. Reduced amplitudes were found on critical ERP components to moral cognition (N2 and LPP), namely while processing intentional harmful scenarios. Older adults seem to allocate more attentional resources (P2) to the task, probably to compensate the age-related decline in executive functioning, while younger groups show a pronounced negativity while detecting harm (N2) and increased neural activation to encode the intentions behind the acts (LPP).

ARTICLE HISTORY

Received 30 May 2017
 Revised 18 December 2017
 Published online 25 January 2018

KEYWORDS

P2; N2; LPP; aging; moral

Moral decision-making is a fundamental component of social cognition that frames the identification, evaluation, and judgment of others' social behavior considering whether these actions are morally acceptable or not, good or bad, harmful or harmless, competitive or cooperative, antisocial or prosocial, intentional or accidental (Decety & Cacioppo, 2012; Hamlin, 2013).

Moral decision-making is of great biological importance (Decety & Cacioppo, 2012; Hamlin, 2013), and developmental studies document that nascent moral evaluations (Hamlin, 2013) and sense of fairness (Schmidt & Sommerville, 2011) may be observed very early in life.

Despite the accumulated knowledge during the first years of life, a comprehensive understanding of moral decision-making in later life is still limited (Moran, 2013; Rosen, Brand, & Kalbe, 2016).

From this standpoint, the theory of mind (ToM; Premack & Woodruff, 1978) – the ability to infer mental states of others and recognize that these may differ from our own – may provide some insights (Rosen et al., 2016). The ToM offers a comprehensive framework to explain how humans perceive interactions, since behavior and mental states are fundamentally

linked (Malle & Guglielmo, 2012). Specifically, ToM modulates the evaluation of intentional and accidental moral transgressions (Killen, Mulvey, Richardson, Jampol, & Woodward, 2011). In aging, meta-analytic data evidences that older adults perform poorly than younger adults on ToM tasks (Henry, Phillips, Ruffman, & Bailey, 2013). Considering that moral decision-making is a second-order ToM ability, and that the deficits are expected to be first detected in complex tasks (vs. first order ToM-based abilities) we might infer that moral judgment is impaired in older adults (Moran, 2013). Confirming this assumption, a longitudinal study revealed that moral perspective declined over a 4-year period on older adults (Pratt, Diessner, Pratt, Hunsberger, & Pancer, 1996).

Functional changes in affective processing provide an alternative framework to explain impairments in moral decision-making in elderly. Older adults tend to approach positive stimuli and avoid negative information (the “positivity bias”; Mather et al., 2004). In the moral domain, older adults' judgments of trustworthiness are associated with both happy and angry facial representations, while in younger adults only happy representations account for trustworthiness (Éthier-

Majcher, Joubert, & Gosselin, 2013). During the rating of the permissibility of moral transgressions, older adults place more emphasis in outcomes than in negative intentions compared to younger individuals, suggesting that older adults are less likely to consider the negative intentions of a moral agent (Moran, Jolly, & Mitchell, 2012). The shift toward positive social information may also be observed in the recruitment of brain regions. The sub-rating of negative intentions by older adults correlates with BOLD response signal decrease in the dorsomedial prefrontal cortex (Moran et al., 2012). Moreover, when forming negative impressions of face-behavior pairs, increased activity in dorsal and ventromedial prefrontal cortex and posterior cingulate cortex was evidenced in younger adults, while in older adults these areas were activated during positive impressions (Cassidy, Leshikar, Shih, Aizenman, & Gutchess, 2013).

In summary, age-related changes in ToM (Henry et al., 2013) and affective processing (Cassidy et al., 2013; Éthier-Majcher et al., 2013; Moran et al., 2012) point towards deficits in moral-decision making in later life.

However, before establishing robust conclusions more data directly assessing moral evaluations of others' behavior is needed. The current study contributes to unveil the neural correlates of judgments of moral transgressions as a function of aging, by examining the temporal dynamics of neural activation elicited by the perception of intentional vs. accidental harm in three groups of healthy participants: young adults (18–35), adults (40–55), and older adults (60–75).

Previous studies reported that intentional harm is easier to detect and is considered wronger than accidental harm (Decety & Cacioppo, 2012). A network of brain regions involved in the evaluation of intentional harmful actions was identified, confirming the brain capability to discriminate intentional from accidental harm. The perception of intentional harmful behavior induced increased pupil dilation and was associated with increased activity in the amygdala, periaqueductal gray, insula, ventromedial prefrontal cortex, and the right temporo-parietal junction (Decety & Cacioppo, 2012; Decety, Michalska, & Kinzler, 2012). Young, Cushman, Hauser, and Saxe (2007) proposed that the right temporo-parietal junction is particularly sensitive to attempted harm compared to accidental harm, while accidental harm is associated with activity in the anterior cingulate cortex and dorsolateral prefrontal cortex (Young et al., 2007).

However, the low temporal resolution of neuroimaging techniques and the limitations of source localization analysis constrains the time-course tracking of

processes involved in moral judgment. Electroencephalography (EEG) may shed new light on mechanisms of moral cognition (Wagner, Chaves, & Wolff, 2017). The EEG high-temporal resolution allows for describing the attentional, cognitive, and affective mechanisms immediately following the morally relevant stimulus. Specifically, Event-Related Potential (ERP) technique allows examining the time-course of moral processing at different sub-stages: from early processing of emotional salience and late cognitive referral to moral rules. Event-related potentials are, therefore, critical to advance our knowledge in the neuroscience of morality (Yoder & Decety, 2014).

The visual P2 is an early component that peaks about 200 after stimulus onset. P2 is a neural correlate of attention allocation, reflecting a top-down mechanism of selective attention to stimulus and subsequent categorization, classification and evaluation (Johannes, Münte, Heinze, & Mangun, 1995).

Several studies suggest that P2 is not sensitive to aging, but both no age-related changes in P2 amplitude (e.g., Getzmann, Golob, & Wascher, 2016; Getzmann, Jasny, & Falkenstein, 2017; Getzmann, Wascher, & Falkenstein, 2015a; Iragui, Kutas, Mitchiner, & Hillyard, 1993; Polich, 1997; Wood & Kisley, 2006), and P2 enhancement with increased age (e.g., Anderer, Semlitsch, & Saletu, 1996; Fabiani, Low, Wee, Sable, & Gratton, 2006; West & Alain, 2000) are well documented in the literature (Crowley & Colrain, 2004; see also Czigler, Csibra, & Csontos, 1992). Despite the increased allocation of attentional resources, there is an uniform slowing (Birren & Fisher, 1995) of neural transmission with advancing age that may be observed from early stages of information processing (Anderer et al., 1996), as confirmed by studies assessing P2 latency (e.g., Anderer et al., 1996; Getzmann et al., 2015a; Getzmann et al., 2016; Iragui et al., 1993).

The P2 is frequently preceded by the N2 component, a negative deflection that peaks between 200 and 350 ms post-stimulus and is highly relevant to understand social cognition and moral decision-making (Petras, Ten Oever, & Jansma, 2015; Wagner et al., 2017). The N2 captures conflict detection, expectancy violation (Folstein & Van Petten, 2008), and the affective evaluation of negative outcomes (Cui, Ma, & Luo, 2016; Lahat, Helwig, & Zelazo, 2013). These processes are frequently demanded by moral decision-making (Petras et al., 2015). Petras et al. (2015) found an increased conflict (i.e., augmented N2 amplitude) to conduct harmful actions in function of proximity, suggesting more moral engagement when the target is closer. Larger N2 amplitudes are reported during the processing of moral violations (vs. conventional

violations), indicating that N2 signals the negative consequences for others (Lahat et al., 2013). In this line, N2 is sensitive to others' physical pain, and is considered an affective component of empathy for pain (Cui et al., 2016). Yoder and Decety (2014) also propose that N2 may distinguish pleasant and rewarding scenarios, given that N2 amplitude is augmented in good social interactions compared to antisocial interactions.

Studies on aging evidenced a negative association in N2 amplitude with increased age (Getzmann et al., 2017, 2015a; Iragui et al., 1993), with several studies reporting the inexistence of the expected N2 peak morphology in older adults (Getzmann, Falkenstein, & Wascher, 2015b; Getzmann et al., 2016; Wascher, Falkenstein, & Wild-Wall, 2011). Also in accordance with the slowing hypotheses (Birren & Fisher, 1995), N2 increased latencies are reported in elderly (e.g., Anderer et al., 1996; Getzmann et al., 2017; Polich, 1997).

Previous research has proposed the distinction between early components (< 300 ms), associated with automatic processes as emotional saliency, and later components (>300 ms), which may reflect more elaborative processes such as continued processing and encoding, cognitive appraisal and affective-motivated attention (Weinberg & Hajcak, 2010). Specifically, a long latency P3-like wave (Cacioppo, Crites, Gardner, & Berntson, 1994) – the late positive potential (LPP) – indexes a finer-grained distinction of emotional stimulus (Weinberg & Hajcak, 2010), and is considered a critical process to moral cognition as N2 (Wagner et al., 2017). LPP increased amplitude seems to be modulated by helping scenes (Cowell & Decety, 2015), morally good actions (Yoder & Decety, 2014), and moral disgust pictures (Zhang, Guo, Zhang, Lou, & Ding, 2015). Studies from emotional processing evidence reduced LPP amplitude in older adults during the presentation of unpleasant stimuli (Wood & Kisley, 2006; Kisley, Wood, & Burrows, 2007; Mathieu et al., 2014) and augmented amplitude in pleasant scenes (Rehmert & Kisley, 2013), confirming the existence of a positivity bias (Mather et al., 2004). Another study documented, however, that LPP attenuation in the later life is extended to all emotional scenes, regardless of content (Renfroe, Bradley, Sege, & Bowers, 2016).

Despite the accumulated evidence in the last years on the P2, N2 and LPP components, none of the above-mentioned studies analyzed the modulation of the main components in older adults under judgments of moral transgressions. From the available knowledge, we expect less accuracy of older adults when

rating accidental and intentional harm compared to younger adults (H1), which may be associated with blunted and delayed N2 and LPP amplitudes to harmful scenes (H2).

Method

Participants

Theoretical backgrounds and methodological constraints were considered to divide the age groups. Several studies documented that the human prefrontal brain does not reach maturity until at least the 20s and may not be fully developed until halfway through the third decade of life (e.g., Giedd, 2004; Petanjek et al., 2011; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999). As the prefrontal functioning has prompted interest to moral judgment, an age range of 20–35 was defined to the younger group. Research on neuropsychology also establishes 55 years old as an approximate age above which relevant functional changes occur in the human brain (e.g., Denburg, Recknor, Bechara, & Tranel, 2006). For this reason, we decided to limit our middle-aged group within the 40–55 age range. The 15-years interval is uniform and allows maintaining a 5-year interval between groups. The 60–75 age range included, therefore, the older group. Moreover, as our study was integrated within a larger protocol, the inclusion of participants older than 75 would not be advisable (e.g., increased sensory and motor alterations, fatigue, etc.).

A sample of 58 younger (age range 20–35), 68 middle-aged (age range 40–55 years) and 57 older adults (age range 60–75 years) was recruited from the community. The following inclusion criteria were applied: (1) nationality (Portuguese); (2) more than four years of formal education; (3) normal or corrected-to-normal vision; (4) psychotropic medication-free at the time of screening; (5) no self-reported neurological or psychiatric disorders; (6) and no history of brain injuries or substance abuse. A score above the suggested cut-off score of the Montreal Cognitive Assessment (Nasreddine et al., 2005) for mild cognitive impairment (≥ 22 ; Freitas, Simões, & Santana, 2014) was also required.

Participants were excluded from the analysis by comparing the individual ERP morphology in relation to the grand average. Two independent raters, revealing almost perfect agreement, conducted the visual inspection of ERP morphology (CF and RP, $k = 0.91$). Disagreements were resolved by consensus.

The final sample was composed by 26 younger adults, 23 middle-aged adults, and 25 older adults

Table 1. Means (and SD) values of socio-demographic, neuropsychological, and behavioral data for younger adults, middle-aged adults, and older adults.

	Younger adults	Middle-aged adults	Older adults
Socio-demographic data			
<i>n</i>	26	23	25
Gender (<i>n</i> female)	13	10	14
Age (years)	26.8 (4.15)	48.3 (5.61)	64.1 (3.91)
Years of Education	16.2 (2.37)	14.6 (4.28)	14.0 (5.16)
Neuropsychological data			
MoCA	27.8 (1.52)	27.0 (2.16)	25.4 (1.98)
IFS	24.5 (2.39)	24.7 (3.34)	22.6 (3.11)
Corsi Blocks	17.9 (3.01)	17.5 (3.62)	15.2 (3.42)
TMT	35.3 (18.3)	41.0 (21.2)	60.2 (26.6)
AVLT	95.0 (9.52)	89.7 (12.8)	79.0 (13.8)
Phonemic Fluency	39.0 (8.89)	36.8 (12.7)	35.9 (11.9)
Semantic Fluency	20.9 (4.45)	20.0 (6.23)	18.7 (5.21)
HADS (depression)	2.81 (2.28)	4.17 (3.68)	3.56 (2.42)
HADS (anxiety)	6.12 (3.37)	5.70 (3.80)	4.48 (3.10)
BSI	28.5 (21.0)	30.7 (22.8)	22.2 (14.6)
Behavioral data			
Accuracy Accidental	28.0 (1.66)	24.1 (7.43)	21.1 (10.0)
Accuracy Intentional	28.5 (2.10)	27.8 (2.48)	26.7 (2.90)
RT Accidental (ms)	608 (190)	665 (213)	855 (279)
RT Intentional (ms)	515 (144)	603 (188)	836 (309)

MOCA: Montreal Cognitive Assessment; IFS: Institute of Cognitive Neurology Frontal Screening; TMT: Trail Making Test; AVLT: Auditory Verbal Learning Test; HADS: Hospital Anxiety and Depression Scale; BSI: Brief Symptom Inventory.

($M_{age} = 64.1$, $DP_{age} = 3.91$). Socio-demographic data is presented in Table 1. Groups were matched for gender, $\chi^2(2, N = 74) = 0.75$, $p = .687$, and years of education, $F(2,73) = 2.04$, $p = .138$.

Measures and stimuli

Self-report measures

Anxiety and depression traits were measured by the Hospital Anxiety and Depression Scale (HADS; Snaith & Zigmond, 1994; adapted by Pais-Ribeiro et al., 2007), and psychopathological symptomatology by the Brief Symptom Inventory (BSI; Derogatis, 1982/1993; adapted by Canavarro, 1999).

Neuropsychological measures

Executive functioning was assessed using the Trail Making Test (TMT; Armitage, 1946; normative data by Cavaco et al., 2013a), and the INECO Frontal Screening (IFS; Torralva, Roca, Gleichgerricht, LoPez, & Manes, 2009; adapted by Moreira, Lima, & Vicente, 2014). Semantic Fluency and Phonemic Fluency tests were used to assess non-motor processing speed, language production and executive functions (Strauss, Sherman, & Spreen, 2006; adapted by Cavaco et al., 2013b). Short-term memory was assessed by the Corsi Block-Tapping Task (Wechsler, 2008), while verbal, immediate and episodic declarative memory were tested using the Auditory Verbal Learning Test (AVLT; Boake, 2000; adapted by Cavaco et al., 2015).

Stimuli

Dynamic visual stimuli representing moral transgressions were adapted from Decety and Cacioppo (2012) Intention Inference Task (Decety et al., 2012) and built on E-Prime V2.0 (2.0, Psychology Software Tools, Inc., Sharpsburg, PA, USA). From the 47 scenarios that composed the original set of stimuli (Decety et al., 2012), we included in our task the 15 scenarios on each condition (intentional and accidental harm) that obtained higher accuracy rates in a previous validation study.

During the task, participants watched three-frame color video clips (2 blocks; 30 clips of accidental actions and 30 clips of intentional actions), randomly presented in the center of a monitor screen. The first frame (T1; 1000 ms) presents the visual scenario and provides the first cues on intention; the second frame (T2; 1000 ms) displays an individual hurting another intentionally or accidentally; and the third frame (T3; 1000 ms) confirms the intentionality of the action. The clips showed situations with distinct degrees of intensity, portraying people from multiple race, ethnic, and age groups. Importantly, faces showing emotional reactions were not visible to the participants. A fixation cross (500 ms) preceded T1 and T3, while T1 and T2 were presented successively to suggest motion. Between T2 and T3, a response panel was displayed and the participants were asked to judge whether the transgression was either intentional or accidental using two response buttons held in the right and left hand. Half of the sample used the left button to accidental and the

right button to intentional, while the other half used the opposite response pattern. KR-20 values ranged from .71 (intentional) to .90 (accidental), revealing acceptable to good internal consistency in moral scenarios.

Procedure

This study was approved by the local Research Ethics Committee and was conducted in accordance with the Declaration of Helsinki. All participants gave informed consent and all mandatory laboratory health and safety procedures have been complied. All the participants were tested individually in two sessions to avoid fatigue effects. In the screening session, a semi-structured interview and the MoCA were conducted to assess inclusion criteria. All the neuropsychological tests and self-report measures were then administered in a random order between participants. Participants meeting the inclusion criteria were invited to participate on a second session, in which the experimental task was performed simultaneously to EEG recording. The AVLIT was administered in this session to avoid the possible interference of word lists from other tests with the later evocation and recognition of words from the AVLIT. This session was part of a larger research protocol with 240 minutes of duration approximately (including breaks), requiring all experimental tasks to be randomized. After the placement of the EEG cap, participants read the instructions and completed a practice block. Participants received 20€ (gift card).

EEG recording and pre-processing

EEG data was recorded on the acquisition software NetStation V4.5.2 (2008, Electrical Geodesics Inc., Eugene, OR, USA – EGI) using a 128-electrode Hydrocel Geodesic Sensor Net with a Net Amps 300 amplifier (EGI). Impedances were kept below 50 kOhm for all electrodes (high-input impedance system). Data were recorded with a sampling rate of 500 Hz, a 50Hz notch filter and the electrodes were referenced to the vertex (Cz).

The EEG raw data were pre-processed in the EEGLAB (version 11; Delorme & Makeig, 2004), a MATLAB toolbox (2010, The Mathworks Inc., Natick, MA, USA). Continuous EEG recordings were down-sampled to 250 Hz and the signal was re-referenced to the electrodes placed in the left and right mastoids. EEG recordings were then band-pass filtered (0.2–30 Hz), bad channels were interpolated (up to a maximum of 10% of the sensors), and submitted to an Independent Components Analysis (ICA) decomposition. Eye blinks, saccades, and cardiac activity were corrected by subtracting the respective independent

component activity from the data. Pre- and post-subtraction EEG traces were visually inspected to ensure that signals were not altered outside the time windows of the artifacts. Epoching was performed based on previous studies using this task (Decety et al., 2012; Yoder & Decety, 2014), but T1 was also considered to better capture the neural-temporal dynamics of judgments on moral transgressions. Continuous EEG data was, therefore, segmented into correct trials epochs of 1000 ms (–200 ms) time-locked to T1 and T2 stimuli onset. All segments were subjected to visual inspection and manual artifact rejection. No differences were found between groups for the number of excluded epochs ($F < 1$). Finally, all epochs were baseline corrected (200 ms pre-stimulus) and averaged by condition (intentional harm, accidental harm) and time (T1, T2) for each participant. By visual inspection of the grand average, the P2 [T1: 130–230; T2: 50–150], N2 [T1: 230 – 330; T2: 100–300], and LPP [T1: 350–600; T1: 350–600] mean amplitudes were extracted as the average of the 200 voltage-samples around the peak amplitude in the defined time-window for the Fz, Cz, and Pz electrode sites.

Statistical analysis

Outliers were excluded from behavioral and electrophysiological data analyses based on extreme values obtained from standardized Z-Scores (> 3.0 or < -3.0) and detected in the ANOVA models conducted to test for group differences. The number of cases excluded varied between analysis, with a maximum number of 3 cases excluded by group.

Mixed Repeated Measures ANOVAs were computed for behavioral data (accuracy in ratings and reaction time) with *Condition* (accidental, intentional) as within-subject factor, and *Group* (younger adults, middle-aged, older adults) as between-subject factors. The analysis of behavioral data was performed in accordance with the original analysis of the task (Decety & Cacioppo, 2012). Accuracy and reaction times were assessed in the main effect of *Condition*. *Group* differences were examined in the *Condition*Group* interaction.

To further explore intentional-accidental harm differences in processing, ERP component amplitudes were analyzed considering the main effects of *Time* and *Condition* and *Time*Condition* interaction. This data was retrieved from the Repeated Measures ANOVA conducted to analyze group differences. *Time* (T1, T2), *Condition* (accidental, intentional), and *Electrode* (Fz, Cz, Pz) were entered in this model as within-subject factors, and *Group* (younger, middle-aged, older adults) as between-subject factor. *Group*Time*Condition*Electrode*

was the main interaction of interest to isolate group differences relative to time, condition, and electrode. Greenhouse-Geisser correction was used to control for violations of the sphericity assumption.

One-way ANOVAs were further computed to analyze group differences in neuropsychological performance and self-report measures. To test the influence of cognitive decline in ERPs modulation, a Linear Regression Model was computed given the shared variance across tests (all $r > .295$, except for the non-significant association between TMT and Corsi Blocks). Scores of cognitive tests in which differences between groups were detected, were entered as main predictors of P2, N2 and LPP modulation (independent models). Only electrode sites where group differences were significant were considered to the analysis.

All data was analyzed with criteria $\alpha = .05$ for significance. Bonferroni corrections were used in post-hoc tests to account for multiple comparisons.

Results

Behavioral data

Table 1 presents the behavioral data (accuracy and reaction times).

A main effect of *Condition* was found to ratings of moral transgressions, $F(1, 70) = 11.7$, $p = .001$, $\eta^2_p = .144$. The perception of intentional harm was associated with higher accuracy ($p = .001$). Pairwise comparisons of the *Group*Condition* interaction, $F(2, 70) = 2.38$, $p = .100$, $\eta^2_p = .064$, showed that the older group was

less accurate in rating accidental ($p = .007$) and intentional harmful actions ($p = .041$) than the younger group (Table 1).

Considering reaction times, $F(1, 71) = 8.73$, $p = .004$, $\eta^2_p = .109$. intentional harm was faster to detect than accidental harm ($p = .004$). For the *Group*Condition* interaction, $F(2, 71) = 1.21$, $p = .305$, $\eta^2_p = .033$, younger ($p = .001$) and middle-aged adults ($p = .017$) were faster than older adults in responding to accidental scenarios. The same differences between younger ($p < .001$) and middle-aged groups ($p = .002$) and older adults were found in intentional frames (Table 1).

Electrophysiology

Figure 1 illustrates the grand-average of P2, N2 and LPP components. Table 2 displays P2, N2, and LPP mean amplitudes and latencies.

P2 amplitude

The main effect of *Time* was significant for P2 amplitude, $F(1, 66) = 6.81$, $p = .011$, $\eta^2_p = .064$, despite non-significance of *Condition*, $F(1, 66) = 1.51$, $p = .224$, $\eta^2_p = .022$, and *Time*Condition*, $F(1, 68) = 1.09$, $p = .301$, $\eta^2_p = .016$. P2 was reduced in T2, compared to T1 ($p = .011$), particularly in the intentional condition ($p = .008$). In the accidental condition, the differences between T1 and T2 were marginal ($p = .062$).

Post-Hoc decompositions on the *Group*Time*Condition*Electrode* interaction ($F < 1$) revealed that in both

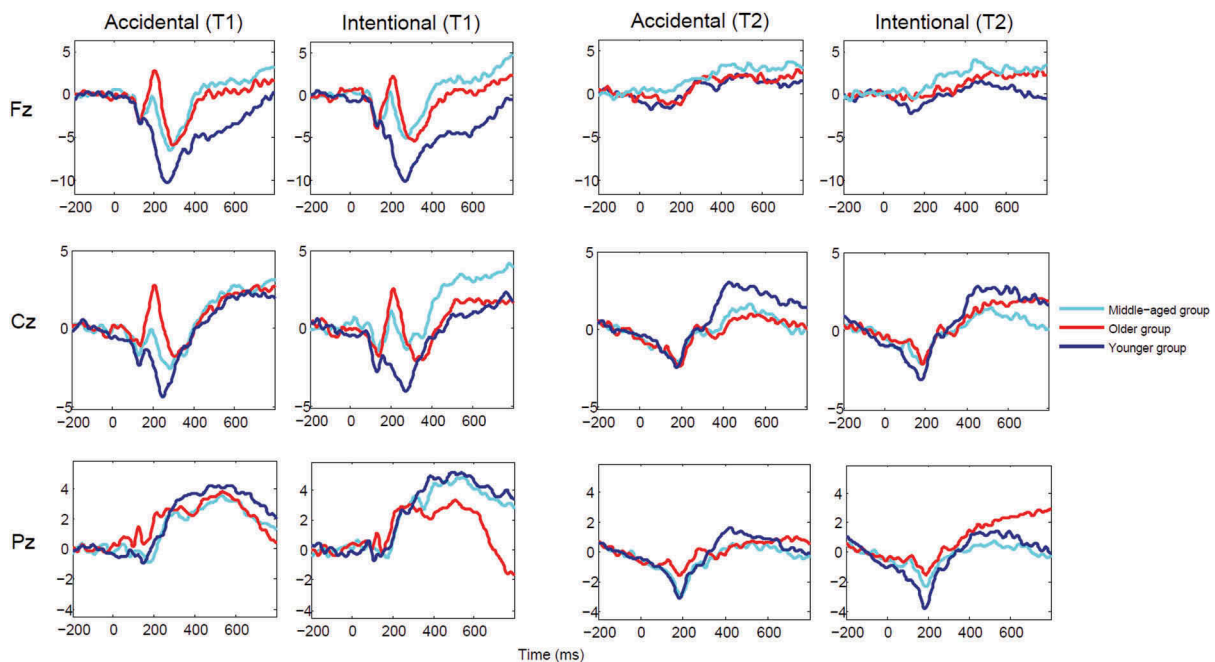


Figure 1. Grandaverages at Fz, Cz and Pz.

Table 2. Means (and SD) values for P2 and N2 amplitudes and latencies (in μV).

	Amplitude						Latency					
	P2 (T1)	P2 (T2)	N2 (T1)	N2 (T2)	LPP (T1)	LPP (T2)	P2 (T1)	P2 (T2)	N2 (T1)	N2 (T2)	LPP (T1)	LPP (T2)
Younger adults												
Accidental	Fz -3.98 (3.81)	0.43 (2.18)	-8.52 (4.26)	0.94 (2.51)	-3.10 (5.77)	2.57 (3.29)	162.8 (21.1)	103.4 (30.4)	271.8 (28.1)	207.2 (68.0)	524.1 (72.7)	487.9 (76.7)
	Cz -1.05 (2.53)	-1.27 (1.18)	-1.10 (4.43)	-1.60 (1.58)	3.25 (3.73)	1.13 (2.51)	184.9 (33.1)	84.8 (34.5)	259.5 (30.8)	204.9 (56.8)	550.2 (55.6)	486.0 (76.1)
	Pz 0.55 (2.18)	-1.29 (0.98)	1.79 (4.31)	-1.74 (1.44)	4.51 (3.50)	0.89 (1.96)	196.8 (35.4)	95.5 (35.38)	259.5 (34.9)	192.0 (48.6)	518.5 (77.4)	477.7 (62.1)
Intentional	Fz -3.79 (3.09)	0.07 (2.12)	-7.80 (5.32)	0.78 (2.55)	-3.99 (5.96)	2.72 (3.34)	159.2 (21.1)	90.3 (31.4)	276.0 (29.4)	172.8 (55.5)	531.4 (70.8)	445.8 (82.1)
	Cz -0.64 (2.71)	-2.10 (1.79)	-0.42 (4.73)	-2.36 (2.05)	4.15 (4.39)	1.33 (1.96)	195.4 (33.3)	83.1 (30.2)	269.5 (27.6)	192.9 (42.9)	532.1 (61.3)	487.7 (63.6)
	Pz 0.59 (2.69)	-1.89 (1.57)	2.28 (4.55)	-2.34 (1.92)	5.58 (4.33)	0.84 (1.92)	206.5 (32.9)	92.9 (29.9)	268.6 (34.9)	189.7 (41.5)	518.0 (63.8)	481.7 (66.1)
Middle-aged adults												
Accidental	Fz -2.13 (3.45)	-0.96 (2.41)	-5.90 (5.30)	-0.12 (3.12)	0.86 (5.43)	1.41 (3.94)	184.6 (25.4)	96.6 (29.7)	288.3 (26.5)	182.3 (53.3)	524.1 (72.7)	487.9 (76.7)
	Cz 0.25 (2.08)	-1.52 (1.14)	0.07 (3.07)	-1.53 (1.79)	3.12 (3.48)	0.77 (2.09)	195.9 (28.7)	99.4 (34.8)	270.5 (31.8)	184.3 (46.5)	550.2 (55.6)	486.0 (76.1)
	Pz 0.07 (1.85)	-1.18 (1.38)	1.11 (2.94)	-1.54 (1.62)	3.17 (3.17)	0.74 (1.84)	194.9 (35.5)	96.4 (34.0)	264.8 (32.5)	193.9 (43.9)	518.5 (77.4)	477.7 (62.1)
Intentional	Fz -2.37 (3.00)	-1.50 (1.80)	-5.46 (4.37)	-0.95 (2.14)	0.27 (4.89)	0.21 (2.88)	198.0 (21.8)	109.3 (33.4)	278.0 (30.7)	172.5 (54.1)	531.4 (70.8)	445.8 (82.1)
	Cz -0.02 (2.23)	-1.87 (1.69)	0.12 (4.14)	-1.83 (1.93)	3.10 (3.63)	-0.13 (2.14)	198.5 (28.9)	93.7 (31.4)	278.2 (26.2)	183.1 (42.0)	532.1 (61.3)	487.7 (63.6)
	Pz 0.11 (1.56)	-1.31 (1.41)	1.67 (3.40)	-1.81 (2.36)	3.91 (3.35)	-0.30 (1.87)	207.9 (29.0)	104.8 (30.6)	280.8 (34.7)	187.5 (41.8)	518.0 (63.8)	481.7 (66.1)
Older adults												
Accidental	Fz 0.88 (3.30)	-0.45 (2.60)	-3.83 (4.66)	-0.01 (3.45)	1.36 (5.07)	1.91 (3.76)	203.9 (23.0)	97.7 (36.2)	301.0 (24.9)	171.0 (48.7)	521.5 (66.2)	467.4 (78.2)
	Cz 1.32 (2.41)	-0.76 (1.24)	-0.07 (2.97)	-1.06 (1.90)	1.13 (2.99)	0.62 (2.05)	193.4 (29.3)	95.3 (29.9)	286.0 (37.0)	195.2 (50.6)	523.9 (77.6)	502.5 (75.1)
	Pz 1.15 (2.48)	-0.86 (1.18)	1.36 (2.52)	-1.15 (1.55)	2.06 (2.19)	0.21 (2.39)	184.9 (32.2)	101.8 (31.9)	282.0 (37.2)	204.6 (45.1)	516.7 (82.6)	504.4 (69.6)
Intentional	Fz -0.05 (3.37)	-0.69 (2.48)	-3.52 (4.17)	-0.55 (3.53)	0.83 (3.80)	0.65 (2.97)	203.6 (27.3)	101.0 (35.3)	299.4 (28.1)	192.0 (60.9)	518.0 (70.1)	490.8 (58.4)
	Cz 1.17 (2.26)	-0.43 (1.59)	0.65 (2.80)	-0.70 (2.10)	2.05 (2.62)	0.96 (1.71)	199.9 (29.8)	107.9 (32.6)	283.0 (40.0)	201.8 (32.3)	528.1 (69.2)	503.3 (65.9)
	Pz 1.52 (2.46)	-0.70 (1.86)	2.45 (3.00)	-0.78 (1.62)	3.19 (2.91)	0.54 (1.90)	195.3 (34.0)	103.1 (33.9)	277.2 (37.5)	200.3 (34.5)	529.8 (71.5)	490.0 (69.8)

accidental and intentional conditions P2 (T1-locked) amplitude was higher on older adults compared to younger adults at Fz (both $p < .001$). Also, older adults exhibited increased P2 (T1-locked) amplitude on both accidental and intentional conditions at Fz (both $p < .012$) compared to middle-aged adults. This pattern of findings was found at Cz ($p = .006$), but only between younger and older adults in the accidental condition, while in the intentional harm the difference was in the threshold of significance ($p = 0.55$). In the intentional condition, middle-aged adults also showed reduced P2 amplitude compared to older adults at Cz ($p = 0.34$) and Pz ($p = 0.46$). P2 (T2-locked) amplitude was found to be increased in older adults in the intentional condition, compared to young adults ($p = .002$) and middle-aged adults ($p = .030$) at Cz.

P2 latency

The visual inspection of grand-averages resulted in distinct time-windows at T1 and T2 to isolate P2 modulation. The statistical analyses confirmed the effect of *Time*, $F(1, 71) = 827.1$, $p < .001$, $\eta^2_p = .921$, and *Condition*, $F(1, 71) = 4.89$, $p = .030$, $\eta^2_p = .064$. P2 latency was reduced in T2 compared to T1 for both intentional and accidental conditions (all $p < .001$).

Considering the Group*Time*Condition*Electrode interaction, $F < 1$, pairwise comparisons showed that during the processing of accidental stimuli, P2 (T1-locked) peak latency was increased at Fz in older adults compared to younger ($p < .001$) and middle-aged adults ($p = .015$), while in the intentional stimuli delayed peak latency on older adults only reached significance in relation to younger group ($p < .001$). Also, delayed latency (T1-locked) was found in middle-aged adults compared to the younger group at Fz on both accidental ($p = .005$) and intentional conditions ($p < .001$). A significant difference between older and younger adults was detected at Cz for P2 latency (T2-locked), indicating that augmented P2 latency for older adults ($p = .018$).

N2 amplitude

No significant effects of *Time* ($F < 1$), *Condition* ($F < 1$), nor Time*Condition, $F(1, 68) = 3.94$, $p = .051$, $\eta^2_p = .055$, were observed for N2 amplitude. No significant differences emerged on the Post-Hoc decomposition for the Time*Condition interaction (all $p > .084$).

From the Group*Time*Condition*Electrode interaction ($F < 1$), Bonferroni tests evidenced that N2 (T1-locked) amplitude was reduced on older adults compared to the younger group on both accidental ($p = .002$) and intentional conditions ($p = .009$) at Fz. In response to the second frame, N2 amplitude (T2-locked) was only found

to be decreased in older adults in the intentional condition, compared to the younger group at Cz ($p = .003$) and Pz ($p = .018$). This pattern of findings was also found to middle-aged adults at Cz ($p = .048$).

N2 latency

In line with previous results, an effect of *Time*, $F(1, 71) = 516.3$, $p < .001$, $\eta^2_p = .879$, but no effect of *Condition* ($F < 1$) was found to latency. N2 latency was reduced in T2, compared to T1 ($p < .001$).

Bonferroni comparisons considering the Group*Time*Condition*Electrode interaction, $F(4, 142) = 1.28$, $p = .283$, $\eta^2_p = .035$, $\epsilon = .810$, showed that during the processing of accidental stimuli, N2 (T1-locked) latency was increased in older adults compared to younger adults at Fz ($p = .001$) and Cz ($p = .018$). In the intentional stimuli delayed peak latency on older adults reached significance in relation to younger ($p = .017$) and middle-aged groups ($p = .042$) at Fz. No differences were detected between groups (all $p > .084$) in N2 (T2-locked).

LPP amplitude

Condition main effect was not significant ($F < 1$). An effect of *Time* was observed, $F(1, 67) = 5.02$, $p = .028$, $\eta^2_p = .070$, indicating that LPP amplitude was higher in T1 than T2 ($p = .028$). Despite the non-significant interaction Time*Condition, $F(1, 67) = 2.61$, $p = .111$, $\eta^2_p = .038$, the LPP reduction in T2 was specific to intentional scenarios ($p = .007$). From the post-hoc analysis on Group*Time*Condition*Electrode ($F < 1$), younger adults exhibited reduced LPP amplitude compared to middle-aged ($p = .045$) and older adults ($p = .018$) at Fz, relative to T1 and accidental condition. Interestingly, at Pz, in the same frame (T1) and condition (accidental), younger adults showed increased LPP amplitude compared to older adults ($p = .019$). This pattern of findings is also observed in the intentional condition at T1. Reduced LPP amplitudes are reported for younger adults compared to the middle-aged ($p = .014$) and older groups ($p = .004$) at Fz, while at Pz the younger group tend to exhibit increased LPP amplitudes compared to older adults ($p = .075$). In T2, the differences were restricted to the intentional condition. Younger adults exhibited enhanced LPP amplitude at Fz compared to middle-aged ($p = .022$) and older adults ($p = .072$). The differences between younger and middle-aged adults were also observed at Cz ($p = .036$).

LPP latency

A main effect emerged on *Time*, $F(1, 71) = 33.6$, $p < .001$, $\eta^2_p = .321$, despite no effect of *Condition* ($F < 1$). LPP

latency was reduced in T2 compared to T1 for both scenarios (all $p < .001$).

Considering the Group*Time*Condition*Electrode interaction, $F(4, 142) = 2.64$, $p = .047$, $\eta^2_p = .321$, $\epsilon = .868$, no group differences in LPP latency across time, conditions and electrodes were detected (all $p > .119$).

Neuropsychology and erps

No differences were found between groups in *Semantic Fluency*, $F(2,72) = 1.12$, $p = .334$, *Phonemic Fluency*, $F < 1$, *anxiety*, $F(2,73) = 1.55$, $p = .219$, *depression*, $F(2,73) = 1.44$, $p = .244$, and *psychopathological symptomatology*, $F(2,73) = 1.24$, $p = .296$. However, group differences were observed on *IFS*, $F(2,73) = 3.80$, $p = .027$, *Corsi blocks*, $F(2,73) = 4.79$, $p = .011$, *TMT*, $F(2,73) = 8.57$, $p < .001$, *AVLT*, $F(2,70) = 10.8$, $p < .001$. Older adults were outperformed in all neuropsychological tests compared to the younger groups (see Table 1).

Only the Regression Model conducted for the older group in P2 intentional condition at Fz was significant, $F(3, 23) = 4.94$, $p = .010$. *TMT* ($\beta = .656$, $p = .002$) and *IFS* ($\beta = -.446$, $p = .037$) were significant predictors of augmented P2 amplitude in the intentional condition.

Discussion

The current study was designed to assess the behavioral and neuropsychophysiological correlates of moral decision-making over lifespan.

In line with Decety and Cacioppo (2012), intentional harmful actions were faster and easier to detect. However, and confirming H1, older adults were less accurate in distinguishing intentional from accidental harmful actions compared to younger and middle-aged groups, suggesting a lower ability to distinguish the intentionality of moral transgressions in the elderly. Their rating was also associated with higher reaction times, providing support for the slowing motor response hypothesis (Bashore, Osman, & Heffley, 1989).

Previous studies further documented the brain capability to discriminate the intentionality of behavior in moral transgressions (Decety & Cacioppo, 2012; Decety et al., 2012; Moran, Jolly, & Mitchell, 2012; Yoder & Decety, 2014; Young et al., 2007). The first studies on the Intention Inference Task were focused on T2 and found that the perception of intentional harmful actions was associated with increased pupil size and activity in the amygdala, periaqueductal gray, insula, ventromedial prefrontal cortex, and right temporo-

parietal junction (Decety & Cacioppo, 2012; Decety et al., 2012).

In our study, T1 and T2 were both used to understand the sequential processing of harmful actions in the Intention Inference Task. There was no main effect of condition in P2 N2 and LPP, indicating that components modulation was comparable across conditions. The components, therefore, were not able to discriminate between intentional and accidental actions in both T1 and T2 across electrodes. Taking behavioral and electrophysiological data together, it seems that the processes contributing for the differentiation between intentional and accidental actions at the behavioral level may not be detected at ERP analysis, and may be explained in a greater extent by brain microstates, functional connectivity, and brain activation of specific regions of interest (Decety & Cacioppo, 2012; Decety et al., 2012). Nevertheless, some specificities may be found in these components while processing T1 and T2 stimuli. First, P2 and LPP amplitudes were reduced at T2, suggesting that the allocation of attentional resources was demanded to a greater extent by the perception of the initial frame. The initial frame constitutes the relevant cue to the moral transgression, demanding a general alerting system and increased motivated attention. Second, and supporting the simplification of visual processing, the latency of N2, P2, and LPP components was detected in an earlier time-window in T2. Finally, a frontocentral distribution of N2 was observed at T1, while a centroparietal topography was found at T2.

Group differences further help to understand P2, N2 and LPP modulation under judgments of moral transgressions. Consistently with the classic literature, the older group exhibited increased frontal-central P2 amplitude compared to younger and middle-aged adults (e.g., Anderer et al., 1996; Getzmann, et al., 2015a; Getzmann et al., 2016; West & Alain, 2000; Iragui et al., 1993). In T2, P2 enhancement was restricted to intentional conditions. The research in P2 points to the existence of a progressive age-related deficit to withdraw attentional resources from stimuli, particularly in frontal sites that overlie brain regions most affected by aging (Crowley & Colrain, 2004).

The current sample of older adults exhibited a significant disadvantage in several neuropsychological tests (TMT, IFS, AVLT, Corsi Blocks) compared to the younger groups. Interestingly, the frontal P2 wave (T1-locked) in the intentional condition was predicted by low performance in tests assessing executive functioning (TMT and IFS), and it is well-documented that the prefrontal cortex plays an essential role to explain executive performance in these tasks (Armitage, 1946;

Cavaco, et al., 2013a; Moreira et al., 2014; Torralva et al., 2009).

From this pattern of findings, we propose that the increased allocation of attentional resources to the task, as reflected by the enhanced P2 amplitude in older adults, may constitute a compensatory mechanism of frontal executive deficits in later life.

The increased attention to visual stimuli in older adults would be expected to facilitate subsequent processes of categorization, classification, evaluation and recall (Crowley & Colrain, 2004), but the low accuracy of older adults in rating accidental and intentional scenarios suggests that components modulation at N2 and LPP time-windows may be more relevant processes. Importantly, both N2 and LPP components are thought to be the critical processes to moral cognition (Wagner et al., 2017).

Nevertheless, it should be acknowledged that intentional and accidental harmful actions were not discriminated by N2 amplitude. Since both accidental and intentional actions have the same outcome – harm – it raises the possibility that the consequences of harmful actions explain in a greater extent N2 amplitude, than perceived intentions. Interestingly, these results are consistent with N2 research tradition in social cognition and moral laden scenarios, in which N2 is considered a neural correlate of moral engagement and empathy for pain to physical harm (Cui et al., 2016; Lahat et al., 2013; Petras et al., 2015)

The N2 amplitude in later life seems to be characterized by a slight negative deflection relative to the P2 positivity (Getzmann et al., 2015b), while younger adults show a pronounced N2 amplitude (e.g., Getzmann et al., 2015b, 2016, 2017, 2015a; Iragui et al., 1993). Our results support the validity of this assumption when considering social cognition and moral judgment processes. Confirming H2, N2 amplitude was reduced in older adults compared to the younger group in T1 and, noteworthy, blunted N2 amplitude in older adults was restricted to intentional scenarios in T2.

The differential modulation of P2 and N2 across groups seems to reflect distinct temporal dynamics in moral judgment. Specifically, older adults seem to allocate more attentional resources than the younger group (P2), while the younger group signals the harm in a greater extent than older adults (N2). A distinct LPP topographical distribution across lifespan provides further evidence for differential neural dynamics in moral judgment.

At T1, LPP amplitude was reduced in younger adults compared to older and middle-aged groups at Fz. In line with P2 results, older adults seem to allocate more

frontal attentional resources to the stimuli. In an opposite pattern, and confirming H2, younger adults evidenced higher LPP amplitude than older adults at Pz. At T2, LPP increased amplitude was observed in younger adults and was uniquely related with intentional transgressions. LPP amplitude at intentional harmful scenarios (T2-locked) was significantly and marginally reduced in middle-aged and older adults, respectively. Interestingly, the main findings are in accordance with N2 modulation and previous proposals that aging affects emotional processing, as captured by LPP modulation (Renfroe et al., 2016). This effect is particularly observed during unpleasant scenes (Wood & Kisley, 2006; Kisley et al., 2007; Mathieu et al., 2014) as the used moral laden scenarios. The early-N2 and late-PP processing of harmful intentional actions does not seem to be compensated, therefore, by the increased attentional allocation at P2 time-window.

The ERP latencies may also provide information about slowing in brain processes that cannot be assessed from the single examination of age-related slowing reaction times during task performance (Birren & Fisher, 1995). In the current study, and consistent with previous studies (e.g., Anderer et al., 1996; Getzmann et al., 2017; Polich, 1997), delayed latency was observed in older adults compared to younger and middle-aged groups for both P2 and N2 (T1-time locked). The delay in P2 and N2 latency in the older group evidence age-related deficits in processing speed.

The main findings further provide empirical evidence for the Moran's (2013) proposal that we might expect to detect impairments in ToM second-order processes (i.e., moral decision-making) in older adults, given the first-order deficits in less complex ToM task (Henry et al., 2013). The lack of differentiation between intentions detected in the current study and Moran et al. (2012) supports the older adults' difficulty to interpret others' behavior.

In light of the positivity bias (Mather et al., 2004), results from P2 component are challenging. Our data suggests that older adults did not avoid negative information as they allocated more attentional resources to harmful scenarios. However, compelling evidence may also be retrieved from N2 and LPP components. Younger and middle-aged adults seem to be more responsive to negative stimuli than older adults in the early-N2 component, a time-window conceptualized as the affective-empathic response to negative outcomes (Cui et al., 2016; Lahat et al., 2013; Petras et al., 2015; Yoder & Decety, 2014), and in the late-PP component, that reflects continued encoding, cognitive appraisal, saliency processing,

and affective-motivated attention (Weinberg & Hajcak, 2010).

As Cassidy et al. (2013) previously described, the age-shift toward negative stimuli may protect older adults from an excessive focus in health, cognitive and physical decline concomitant with age, but may also compromise social functioning (e.g., fraud susceptibility).

One important caveat of the current study is the lack of positive interactions in Decety and Cacioppo (2012) Intention Inference Task to test directly the positive bias hypothesis. Although accidental harm scenarios are somewhat less negative than intentional harm interactions, the outcome is similar. The inclusion of positive interactions (e.g., cooperative behavior) in the stimuli set would be highly relevant to provide a more comprehensive approach to the condition effects. We recommend to retrieve these stimuli from Yoder and Decety (2014). Objects may also be included as targets of intentional and accidental harm to provide a more neutral term of comparison (Decety et al., 2012), and were not considered in the present study due to time restraints and predictable fatigue effects from the larger protocol in which this task was incorporated. A measure of empathy should also be included to explore the mediating role of empathy in N2 modulation and processing of harmful intentions over lifespan. Another important direction for future studies is to include a Likert scale of perceived harm after each response to test directly if the degree of harm modulates the N2 amplitude.

Despite the above limitations, our study brings important contributions to the current state of art on the aging effects on social cognition and moral decision-making. In this research field, the results are abundant for younger samples and using neuroimaging techniques, but limited for older adults and ERPs (Decety & Cacioppo, 2012; Moran et al., 2012; Rosen et al., 2016). Our findings highlighted that older and younger groups show differential strategies to evaluate scenarios of moral transgressions. Older adults seem to allocate more attentional resources (P2) to the task, probably to compensate the age-related functional decline in executive functioning, while younger groups show a pronounced negativity in detecting harm emotional-saliency (N2) and increased motivated-attention to encode the intentions behind the acts (LPP).

Acknowledgements

This work was supported by the Fundação BIAL; under a special Grant “The aging social brain”; Carina Fernandes is supported by a doctoral fellowship from the Fundação para a Ciência e a Tecnologia under grant SFRH/BD/112101/2015.

We would also like to acknowledge to Programa de Estudos Universitários para Seniores (PEUS) and to Associação de Aposentados Pensionistas e Reformados (APRE) for their help in participant recruitment.

This work was funded by the Fundação BIAL; under a special grant “The aging social brain” awarded to João Marques-Teixeira; Carina Fernandes is supported by a doctoral fellowship from the Fundação para a Ciência e a Tecnologia under grant SFRH/BD/112101/2015

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Fundação Bial [The Aging Social Brain];

ORCID

F. Ferreira-Santos  <http://orcid.org/0000-0002-2656-5291>

F. Barbosa  <http://orcid.org/0000-0002-2656-5291>

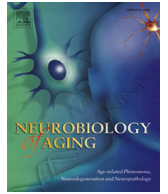
References

- Anderer, P., Semlitsch, H. V., & Saletu, B. (1996). Multichannel auditory event-related brain potentials: Effects of normal aging on the scalp distribution of N1, P2, N2 and P300 latencies and amplitudes. *Electroencephalography and Clinical Neurophysiology*, 99(5), 458–472.
- Armitage, S. G. (1946). An analysis of certain psychological tests used for the evaluation of brain injury. *Psychological Monographs*, 60, i–48.
- Bashore, T. R., Osman, A., & Heffley, E. F. III. (1989). Mental slowing in elderly persons: A cognitive psychophysiological analysis. *Psychology and Aging*, 4(2), 235–244. doi: 10.1037/0882-7974.4.2.235
- Birren, J. E., & Fisher, L. M. (1995). Aging and speed of behavior: Possible consequences for psychological functioning. *Annual Review of Psychology*, 46(1), 329–353.
- Boake, C. (2000). Édouard Claparède and the auditory verbal learning test. *Journal of Clinical and Experimental Neuropsychology*, 22, 286–292.
- Cacioppo, J. T., Crites, S. L., Gardner, W. L., & Berntson, G. G. (1994). Bioelectrical echoes from evaluative categorizations: I. A late positive brain potential that varies as a function of trait negativity and extremity. *Journal of Personality and Social Psychology*, 67(1), 115.
- Canavarro, M. C. (1999). Inventário de sintomas psicopatológicos - BSI. In M. R. Simões, M. Gonçalves, & L. S. Almeida (eds.), *Testes e provas psicológicas em Portugal* (Vol. II, pp. 87–109). Braga: SHO/APPORT.
- Cassidy, B. S., Leshikar, E. D., Shih, J. Y., Aizenman, A., & Gutchess, A. H. (2013). Valence-based age differences in medial prefrontal activity during impression formation. *Social Neuroscience*, 8(5), 462–473.
- Cavaco, S., Gonçalves, A., Pinto, C., Almeida, E., Gomes, F., Moreira, I., ... Teixeira-Pinto, A. (2013a). Trail Making Test:

- Regression-based norms for the Portuguese population. *Archives of Clinical Neuropsychology*, 28, 189–198.
- Cavaco, S., Gonçalves, A., Pinto, C., Almeida, E., Gomes, F., Moreira, I., ... Teixeira-Pinto, A. (2013b). Semantic fluency and phonemic fluency: Regression-based norms for the Portuguese population. *Archives of Clinical Neuropsychology*, 28, 262–271.
- Cavaco, S., Gonçalves, A., Pinto, C., Almeida, E., Gomes, F., Moreira, I., ... Teixeira-Pinto, A. (2015). Auditory verbal learning test in a large nonclinical Portuguese population. *Applied Neuropsychology: Adult*, 22, 321–331.
- Cowell, J. M., & Decety, J. (2015). The neuroscience of implicit moral evaluation and its relation to generosity in early childhood. *Current Biology*, 25(1), 93–97.
- Crowley, K. E., & Colrain, I. M. (2004). A review of the evidence for P2 being an independent component process: Age, sleep and modality. *Clinical Neurophysiology*, 115(4), 732–744.
- Cui, F., Ma, N., & Luo, Y. J. (2016). Moral judgment modulates neural responses to the perception of other's pain: An ERP study. *Scientific Reports*, 6. doi:10.1038/srep20851
- Czigler, I., Csibra, G., & Csontos, A. (1992). Age and inter-stimulus interval effects on event-related potentials to frequent and infrequent auditory stimuli. *Biological Psychology*, 33(2), 195–206.
- Decety, J., & Cacioppo, S. (2012). The speed of morality: A high-density electrical neuroimaging study. *Journal of Neurophysiology*, 108(11), 3068–3072.
- Decety, J., Michalska, K. J., & Kinzler, K. D. (2012). The contribution of emotion and cognition to moral sensitivity: A neurodevelopmental study. *Cerebral Cortex*, 22(1), 209–220.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21.
- Denburg, N. L., Recknor, E. C., Bechara, A., & Tranel, D. (2006). Psychophysiological anticipation of positive outcomes promotes advantageous decision-making in normal older persons. *International Journal of Psychophysiology*, 61(1), 19–25.
- Derogatis, L. R. (1982/1993). *BSI: Brief Symptom Inventory* (3rd ed.). Minneapolis: National Computers Systems.
- Éthier-Majcher, C., Joubert, S., & Gosselin, F. (2013). Reverse correlating trustworthy faces in young and older adults. *Frontiers in Psychology*, 4. doi:10.3389/fpsyg.2013.00592
- Fabiani, M., Low, K. A., Wee, E., Sable, J. J., & Gratton, G. (2006). Reduced suppression or labile memory? Mechanisms of inefficient filtering of irrelevant information in older adults. *Journal of Cognitive Neuroscience*, 18(4), 637–650.
- Folstein, J. R., & Van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: A review. *Psychophysiology*, 45(1), 152–170.
- Freitas, S., Simões, M., & Santana, I. (2014). Montreal Cognitive Assessment (MoCA): Pontos de corte no défice cognitivo ligeiro, doença de alzheimer, demência frontotemporal e demência vascular. *Sinapse*, 1(14), 18–30.
- Getzmann, S., Falkenstein, M., & Wascher, E. (2015b). ERP correlates of auditory goal-directed behavior of younger and older adults in a dynamic speech perception task. *Behavioural Brain Research*, 278, 435–445.
- Getzmann, S., Golob, E. J., & Wascher, E. (2016). Focused and divided attention in a simulated cocktail-party situation: ERP evidence from younger and older adults. *Neurobiology of Aging*, 41, 138–149.
- Getzmann, S., Jasny, J., & Falkenstein, M. (2017). Switching of auditory attention in “cocktail-party” listening: ERP evidence of cueing effects in younger and older adults. *Brain and Cognition*, 111, 1–12.
- Getzmann, S., Wascher, E., & Falkenstein, M. (2015a). What does successful speech-in-noise perception in aging depend on? Electrophysiological correlates of high and low performance in older adults. *Neuropsychologia*, 70, 43–57.
- Giedd, J. N. (2004). Structural magnetic resonance imaging of the adolescent brain. *Annals of the New York Academy of Sciences*, 1021(1), 77–85.
- Hamlin, J. K. (2013). Moral judgment and action in preverbal infants and toddlers evidence for an innate moral core. *Current Directions in Psychological Science*, 22(3), 186–193.
- Henry, J. D., Phillips, L. H., Ruffman, T., & Bailey, P. E. (2013). A meta-analytic review of age differences in theory of mind. *Psychology and Aging*, 28(3), 826–839.
- Iragui, V. J., Kutas, M., Mitchiner, M. R., & Hillyard, S. A. (1993). Effects of aging on event-related brain potentials and reaction times in an auditory oddball task. *Psychophysiology*, 30(1), 10–22.
- Johannes, S., Münte, T. F., Heinze, H. J., & Mangun, G. R. (1995). Luminance and spatial attention effects on early visual processing. *Cognitive Brain Research*, 2(3), 189–205.
- Killen, M., Mulvey, K. L., Richardson, C., Jampol, N., & Woodward, A. (2011). The accidental transgressor: Morally-relevant theory of mind. *Cognition*, 119(2), 197–215. doi: 10.1016/j.cognition.2011.01.006
- Kisley, M. A., Wood, S., & Burrows, C. L. (2007). Looking at the sunny side of life: Age-related change in an event-related potential measure of the negativity bias. *Psychological Science*, 18(9), 838–843.
- Lahat, A., Helwig, C. C., & Zelazo, P. D. (2013). An event-related potential study of adolescents' and young adults' judgments of moral and social conventional violations. *Child Development*, 84(3), 955–969.
- Malle, B. F., & Guglielmo, S. 2012. Are intentionality judgments fundamentally moral. In Langdon & Mackenzie eds., *Emotions, imagination, and moral reasoning* (pp. 275–293). New York: Psychology Press. ISBN: 978-1-84872-900-1
- Mather, M., Canli, T., English, T., Whitfield, S., Wais, P., Ochsner, K., ... Carstensen, L. L. (2004). Amygdala responses to emotionally valenced stimuli in older and younger adults. *Psychological Science*, 15(4), 259–263.
- Mathieu, N. G., Gentaz, E., Harquel, S., Vercueil, L., Chauvin, A., Bonnet, S., & Campagne, A. (2014). Brain processing of emotional scenes in aging: Effect of arousal and affective context. *PLoS One*, 9(6), e99523.
- Moran, J. M. (2013). Lifespan development: The effects of typical aging on theory of mind. *Behavioural Brain Research*, 237, 32–40.
- Moran, J. M., Jolly, E., & Mitchell, J. P. (2012). Social-cognitive deficits in normal aging. *Journal of Neuroscience*, 32(16), 5553–5561.
- Moreira, H. S., Lima, C. F., & Vicente, S. G. (2014). Examining executive dysfunction with the institute of cognitive neurology (INECO) frontal screening (IFS): Normative values from a healthy sample and clinical utility in Alzheimer's disease. *Journal of Alzheimer's Disease*, 42, 261–273.
- Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., ... Chertkow, H. (2005). The

- montreal cognitive assessment, MoCA: A brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, 53, 695–699.
- Pais-Ribeiro, J., Silva, I., Ferreira, T., Martins, A., Meneses, R., & Baltar, M. (2007). Validation study of a Portuguese version of the hospital anxiety and depression scale. *Psychology, Health & Medicine*, 12, 225–237.
- Petanjek, Z., Judaš, M., Šimić, G., Rašin, M. R., Uylings, H. B., Rakic, P., & Kostović, I. (2011). Extraordinary neoteny of synaptic spines in the human prefrontal cortex. *Proceedings of the National Academy of Sciences*, 108(32), 13281–13286.
- Petrus, K., Ten Oever, S., & Jansma, B. M. (2015). The effect of distance on moral engagement: Event related potentials and alpha power are sensitive to perspective in a virtual shooting task. *Frontiers in Psychology*, 6. doi:10.3389/fpsyg.2015.02008
- Polich, J. (1997). EEG and ERP assessment of normal aging. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, 104(3), 244–256.
- Pratt, M. W., Diessner, R., Pratt, A., Hunsberger, B., & Pancer, S. M. (1996). Moral and social reasoning and perspective taking in later life: A longitudinal study. *Psychology and Aging*, 11(1), 66.
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, 1(04), 515–526.
- Rehmer, A. E., & Kisley, M. A. (2013). Can older adults resist the positivity effect in neural responding? The impact of verbal framing on event-related brain potentials elicited by emotional images. *Emotion*, 13(5), 949.
- Renfroe, J. B., Bradley, M. M., Sege, C. T., & Bowers, D. (2016). Emotional modulation of the late positive potential during picture free viewing in older and young adults. *PloS One*, 11(9), e0162323.
- Rosen, J. B., Brand, M., & Kalbe, E. (2016). Empathy mediates the effects of age and sex on altruistic moral decision making. *Frontiers in Behavioral Neuroscience*, 10. doi:10.3389/fnbeh.2016.00067
- Schmidt, M. F., & Sommerville, J. A. (2011). Fairness expectations and altruistic sharing in 15-month-old human infants. *PloS One*, 6(10), e23223.
- Snaith, R. P., & Zigmond, A. P. (1994). *The hospital anxiety and depression scale manual*. Windsor: NFER-Nelson.
- Sowell, E. R., Thompson, P. M., Holmes, C. J., Jernigan, T. L., & Toga, A. W. (1999). In vivo evidence for post-adolescent brain maturation in frontal and striatal regions. *Nature Neuroscience*, 2(10), 859–861.
- Strauss, E., Sherman, E. M., & Spreen, O. (2006). *A compendium of neuropsychological tests: Administration, norms, and commentary* (3rd ed. ed.). New York: Oxford University Press.
- Torralva, T., Roca, M., Gleichgerricht, E., LoPez, P., & Manes, F. (2009). INECO Frontal Screening (IFS): A brief, sensitive, and specific tool to assess executive functions in dementia. *Journal of the International Neuropsychological Society*, 15, 777–786.
- Wagner, N. F., Chaves, P., & Wolff, A. (2017). Discovering the neural nature of moral cognition? Empirical, theoretical, and practical challenges in bioethical research with electroencephalography (EEG). *Journal of Bioethical Inquiry*, 14(2), 1–15.
- Wascher, E., Falkenstein, M., & Wild-Wall, N. (2011). Age related strategic differences in processing irrelevant information. *Neuroscience Letters*, 487(1), 66–69.
- Wechsler, D. (2008). *WMS - III. Escala de memória de Wechsler*. Lisboa: CEGOCETA.
- Weinberg, A., & Hajcak, G. (2010). Beyond good and evil: The time-course of neural activity elicited by specific picture content. *Emotion*, 10(6), 767.
- West, R., & Alain, C. (2000). Age-related decline in inhibitory control contributes to the increased Stroop effect observed in older adults. *Psychophysiology*, 37(2), 179–189.
- Wood, S., & Kisley, M. A. (2006). The negativity bias is eliminated in older adults: Age-related reduction in event-related brain potentials associated with evaluative categorization. *Psychology and Aging*, 21(4), 815.
- Yoder, K. J., & Decety, J. (2014). Spatiotemporal neural dynamics of moral judgment: A high-density ERP study. *Neuropsychologia*, 60, 39–45.
- Young, L., Cushman, F., Hauser, M., & Saxe, R. (2007). The neural basis of the interaction between theory of mind and moral judgment. *Proceedings of the National Academy of Sciences*, 104(20), 8235–8240.
- Zhang, X., Guo, Q., Zhang, Y., Lou, L., & Ding, D. (2015). Different timing features in brain processing of core and moral disgust pictures: An event-related potentials study. *PloS One*, 10(5), e0128531.

2.4 AGE DIFFERENCES IN NEURAL CORRELATES OF FEEDBACK PROCESSING AFTER ECONOMIC DECISIONS UNDER RISK



Age differences in neural correlates of feedback processing after economic decisions under risk



Carina Fernandes^{a,b,c,*}, Rita Pasion^a, Ana R. Gonçalves^a, Fernando Ferreira-Santos^a,
Fernando Barbosa^a, Isabel P. Martins^c, João Marques-Teixeira^a

^a Laboratory of Neuropsychophysiology, Faculty of Psychology and Education Sciences, University of Porto, Porto, Portugal

^b Faculty of Medicine, University of Porto, Porto, Portugal

^c Language Research Laboratory, Institute of Molecular Medicine, Faculty of Medicine, University of Lisbon, Lisbon, Portugal

ARTICLE INFO

Article history:

Received 21 September 2017

Received in revised form 4 January 2018

Accepted 7 January 2018

Available online 17 January 2018

Keywords:

Decision-making

Risk

Feedback processing

Feedback-related negativity

P3

ABSTRACT

This study examines age-related differences in behavioral responses to risk and in the neurophysiological correlates of feedback processing. Our sample was composed of younger, middle-aged, and older adults, who were asked to decide between 2 risky options, in the gain and loss domains, during an EEG recording. Results evidenced group-related differences in early and later stages of feedback processing, indexed by differences in the feedback-related negativity (FRN) and P3 amplitudes. Specifically, in the loss domain, younger adults showed higher FRN amplitudes after non-losses than after losses, whereas middle-aged and older adults had similar FRN amplitudes after both. In the gain domain, younger and middle-aged adults had higher P3 amplitudes after gains than after non-gains, whereas older adults had similar P3 amplitudes after both. Behaviorally, older adults had higher rates of risky decisions than younger adults in the loss domain, a result that was correlated with poorer performance in memory and executive functions. Our results suggest age-related differences in the outcome-related expectations, as well as in the affective relevance attributed to the outcomes, which may underlie the group differences found in risk-aversion.

© 2018 Elsevier Inc. All rights reserved.

Aging affects economic decision-making, which has several negative implications (Mata et al., 2011). Older adults represent a significant proportion of the global population, who face economic challenges daily and have limited time to overcome disadvantageous decisions.

The neural mechanisms underlying age-related differences in decision-making are still scarcely known, and the research in this field is hampered by the evidence that the risk preferences of the older adults vary substantially within tasks (Mata et al., 2011). For instance, older adults can be simultaneously more risk-averse and risk-seeking than younger controls, preferring a sure smaller gain over a chance to win higher rewards, but also preferring the chance of losing higher rewards rather than having certain smaller losses (Mather et al., 2012). These findings are in accordance with the prospect theory, which postulates that individuals are risk-averse for gains and risk-seeking for losses (Kahneman and Tversky, 1979), but contrast with recent findings of higher risk-seeking of older adults also in the gain domain (Pachur et al., 2016).

Aging appears to preserve gain anticipation, while reducing the anticipation of losses (Samanez-Larkin and Knutson, 2015). Moreover, older adults report less negative arousal during the anticipation of losses (Samanez-Larkin et al., 2007), show less negative and more positive emotions than younger adults after losses (Bruine de Bruin et al., 2017), and do not exhibit loss aversion (Pachur et al., 2016). This set of evidence suggests that older adults may underestimate the losses, a finding that may be explained by the positivity effect (Mather and Carstensen, 2005), according to which older adults favor the processing of positive information in detriment of negative material (Mather and Carstensen, 2005).

In this study, we investigated age differences in risk-aversion, using a task designed to overcome methodological limitations found in decision-making tasks previously used with older adults, which may have contributed to heterogeneous results (Pachur et al., 2016). Most of the tasks require a decision between a risky option and a sure gain/loss, and the interpretations of these approaches may have confounded age differences in risk-aversion with age differences in cognitive abilities. Accepting a sure gain or rejecting a sure loss is cognitively less demanding than to calculate the most rewarding option (Burks et al., 2009), being the most likely decision when cognitive resources decline (Pachur et al., 2016). To overcome this issue, each trial of our task involves 2 risky options. Moreover,

* Corresponding author at: Laboratório de Neuropsicofisiologia, Faculdade de Psicologia e de Ciências da Educação, Universidade do Porto, R. Alfredo Allen, 4200-135 Porto, Portugal. Tel.: +351 226 079 700; fax: +351 916 410 584.

E-mail address: carinafernandes@fpce.up.pt (C. Fernandes).

to limit the demands of abstraction and numeracy abilities, the probabilities of each option were visually represented by a ratio of colored/black balls (instead of a percentage), since the cognitive complexity of the stimuli may also affect older adults' decisions (Pachur et al., 2016).

In addition to the behavioral results, we also aimed to analyze the neural mechanisms underlying age-related differences in feedback processing, using an event-related potentials (ERPs) methodology. We examined ERPs evoked by favorable and unfavorable feedbacks, delivered in the gain and loss domain. The ERPs have a high temporal resolution, allowing the analysis of neural phenomena specifically locked to feedback processing. Owing to this, processes associated with the response preparation or outcome anticipation are unlikely to affect the features of feedback-related components. Thus, the results of this analysis may contribute to a new interpretation of previous findings.

We analyzed the feedback-related negativity (FRN) and the P3 components, which play a crucial role in the feedback processing (Martín, 2012). The FRN is generated in the anterior cingulate cortex (Holroyd and Coles, 2002), being measured over the frontal-central region at ~250 ms after the feedback onset (Martín, 2012). According to the reward prediction error hypothesis (Miltner et al., 1997), the FRN is consistently larger for negative than for positive feedbacks, a valence dependency confirmed using monetary and non-monetary feedbacks (Martín, 2012).

The P3 has widespread sources, being measured over the centroparietal region at ~300–600 ms after the feedback onset (Martín, 2012). According to the context-updating hypothesis (Donchin and Coles, 1988), the P3 indexes the brain activity underlying the revision of a mental model of a task induced by a stimulus. If a stimulus delivers information that is inconsistent with the mental model, it will be updated and the P3 amplitude will be proportional to the amount of cognitive resources used during the updating (Martín, 2012). Outcomes associated with higher levels of arousal or task-relevance elicit larger P3 amplitudes, reflecting increased allocation of attention (Nieuwenhuis, 2011). Thus, while the FRN appears to be sensitive to expectancy violations, the P3 appears to be sensitive to the arousing nature of the feedback.

Previous studies using reinforcement learning tasks (Eppinger et al., 2008; Ferdinand and Kray, 2013) consistently found the FRN reduced for older adults, despite this result being less consistent in economic decision-making tasks. In the latter, while 2 experiments found similar FRN amplitudes for younger and older adults (Di Rosa et al., 2017; Kardos et al., 2017), one study found reduced FRN amplitudes for older adults (West et al., 2014). The P3 amplitude also appears to be reduced for older adults, since this is a robust finding in both learning (e.g., Ferdinand and Kray, 2013) and economic tasks (Di Rosa et al., 2017; Kardos et al., 2017). Based on this research, we predicted reduced FRN and P3 amplitudes for the older group. Moreover, based on research on age-by-valence interactions in memory and attention tasks (Mather and Carstensen, 2005), we also predicted a positivity effect in older adults' feedback processing that would be reflected in an attenuation of the FRN and P3 components only after unfavorable feedbacks.

Neurocognitive measures were collected to explore whether patterns of decision would be associated with age-related changes in cognition, and we predicted a correlation between the performance on cognitive and decision-making tasks (e.g., Henninger et al., 2010). Our study included a sample of younger, middle-aged, and older participants, to overcome a limitation of previous experimental designs, which typically compared younger with older adults (Mata et al., 2011). Considering that risk preferences change considerably from youth to adulthood and less afterward (Daly and Wilson, 1997), contrasting younger with older adults prevents the study of risk behavior across adult development and

increases the chance of finding significant differences (Mata et al., 2011). However, a study found that older adults were more risk-averse than younger and middle-aged adults (Tymula et al., 2013), leading us to hypothesize significant differences between the older and the other groups.

1. Method

1.1. Participants

One hundred and eighty-three participants were recruited from the local community. Participants were included if they had more than 4 years of formal education and excluded if they (1) had uncorrected visual impairments ($n = 3$); (2) had a score inferior to 22 points ($n = 6$)—cutoff for mild cognitive impairment—in the Montreal Cognitive Assessment (MoCA; Freitas et al., 2014; Nasreddine et al., 2005); use psychotropic medications ($n = 15$); and had history of brain injury, neurological, or psychiatric diagnosis ($n = 25$). Forty-six participants dropped out the study after the neuropsychological assessment. Thus, the final sample was composed of 30 younger (15 females; $M_{age} = 26.6$, $SD = 4.05$, age range = 20–35 years), 29 middle-aged (16 females; $M_{age} = 48.3$, $SD = 5.59$, age range = 40–55 years), and 29 older adults (18 females; $M_{age} = 64.5$, $SD = 4.10$, age range = 60–75 years). The groups were statistically matched for years of education [$F(2, 85) = 2.10$, $p = 0.132$].

Data from 2 older adults were not included in the ERP analysis because of a computer error in saving the EEG data. Three participants (1 older adult and 2 younger adults) were excluded from the ERP analysis because of the absence of the expected ERP morphology, considering the morphology of the grand-average.

The present study was part of a larger research project and was approved by the local Research Ethics Committee. Participants provided written informed consent and were compensated with a fixed amount of €20 (gift card) for their time.

1.2. Instruments and tasks

1.2.1. Neuropsychological measures

The MoCA was used as a measure of neurocognitive screening. The Trail Making Test (TMT = Part B – Part A; Armitage, 1946; Cavaco et al., 2013a,b) and the Institute of Cognitive Neurology Frontal Screening (IFS; Moreira et al., 2014; Torralva et al., 2009) assessed executive functioning. The Corsi block-tapping task (Wechsler, 2008) assessed visuospatial short-term memory, and the Auditory Verbal Learning Test (AVLT; Boake, 2000; Cavaco et al., 2015) assessed learning, immediate, and episodic memory. The semantic and phonemic fluency tests (Cavaco et al., 2013a,b; Strauss et al., 2006) assessed nonmotor processing speed and language production. The Hospital Anxiety and Depression Scale (Pais-Ribeiro et al., 2007; Snaith and Zigmond, 1994) assessed anxiety and depression, and the Brief Symptom Inventory (Canavarro, 1999; Derogatis, 1982/1993) assessed psychopathological symptoms.

1.2.2. Decision-making task

The experimental task was presented in E-Prime 2.0 (2011, Psychology Software Tools, Inc., Sharpsburg, PA, USA), and it was designed to assess decision-making under risk, during a simultaneous EEG recording. The task was composed of 120 trials presented randomly, one half related to the gain domain (in which participants could get a positive or a zero-value outcome) and the remaining half related to the loss domain (in which participants could get a negative or a zero-value outcome). As depicted in Fig. 1, each trial comprised a choice phase followed by a feedback phase.

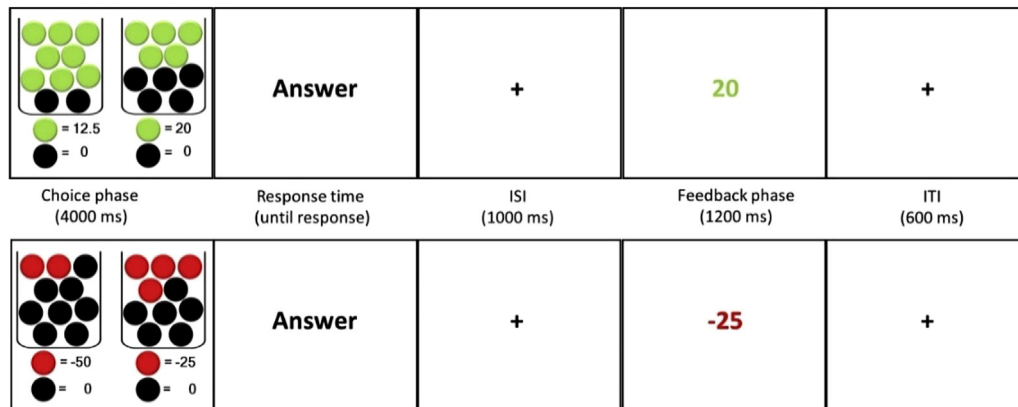


Fig. 1. Schematic representations of a trial in the gain domain (top) and in the loss domain (bottom) in the decision-making task. Abbreviations: ISI, interstimulus interval; ITI, intertrial interval.

In the choice phase, 2 jars were displayed, containing different ratios of black and green balls (gain domain) or black and red balls (loss domain). Participants were instructed to select a jar at each trial and were informed that the computer would select a random ball from the chosen jar. They were also informed that they would neither gain nor lose anything if a black ball was drawn. However, if a colored ball was selected, the amount won or lost would depend on the chosen jar, as presented below the jar (Fig. 1). Participants pressed the button held in their right hand to choose the jar displayed on the right side of the screen or in their left hand to choose the jar displayed on the left side. The number of points collected was presented in the feedback phase, and participants were instructed to try to win as many points as possible.

Thus, for each jar, participants knew the number of points they could win/lose, as well as the probability of winning/losing, determined by the number of colored balls. Four different jars were created and paired together, forming 6 different pairs of jars to each domain (Table 1). All jars had the same expected value ($EV = 10$ for gains and $EV = -10$ for losses). Larger gains had lower probabilities of occurring (e.g., see the Jar 1 of Table 1), whereas smaller gains had higher probabilities (Jar 2). Symmetrically, larger losses had lower probabilities (Jar 1), whereas smaller losses had higher probabilities (Jar 2). Thereby, in the gain domain, the choice for Jar 1 was considered the riskier decision in comparison with Jar 2 because gains were less probable. In the loss domain, the choice for Jar 1 was considered the safer decision because losses were less probable. The position of the jars on the screen was counter-balanced during the task.

During the feedback phase, the outcome was shown. There were 4 feedback conditions: gains and non-gains (gain domain), as well as losses and non-losses (loss domain). Gains and non-losses represented favorable feedbacks within their contexts, whereas non-gains and losses represented unfavorable feedbacks.

Unbeknownst to participants, the outcomes were manipulated to guarantee that all participants viewed 30 trials of each feedback condition, allowing an adequate signal-to-noise ratio for the ERPs analysis. Participants were asked about their strategy in a final

questionnaire, to guarantee that they believed that the outcome was dependent on the probabilities.

1.3. Procedures

1.3.1. Neuropsychological assessment

Participants were tested individually in 2 experimental sessions. The first session aimed to confirm the inclusion criteria and to collect sociodemographic and neurocognitive data. The MoCA was applied first, and the remaining tests were applied in a randomized order. The AVLT was applied in the second session to avoid the interference of the words listed during the neuropsychological assessment in the delayed recall and recognition subtests of the AVLT.

Participants who fulfilled the inclusion criteria were recruited for the second session in which the experimental task was performed inside an EEG chamber. After the placement of the EEG cap, participants sat comfortably at 115 cm from a 19" screen, read the instructions, and completed 6 practice trials.

1.3.2. EEG recording and processing

The EEG data were recorded using a 128-electrode HydroCel Geodesic Sensor Net, with a Net Amps 300 amplifier (Electrical Geodesics Inc., Eugene, Oregon, USA) and a digitizing rate of 500 Hz. Impedances were kept below 50 k Ω for all electrodes (as this is a high input impedance system). The electrodes were referenced to Cz during recording and re-referenced offline to the average of the electrodes placed in the left and right mastoids. The EEG data were preprocessed in EEGLAB (version 11; Delorme and Makeig, 2004). The data were downsampled to 250 Hz and band-pass filtered at 0.1–30 Hz. Bad channels were interpolated (up to a maximum of 10% of the sensors), and data were decomposed through Independent Components Analysis. Eye-blink, saccade, and heart rate artifacts were corrected by subtracting the respective component activity from the data. The EEG records were segmented into epochs ranging from –200 to 1000 ms, time-locked to the feedback onset. All segments were visually inspected, and the remaining

Table 1
Probabilities (P) and magnitudes (M) of points in each pair of jars

		Gain domain						Loss domain					
Jar 1	P	0.2	0.2	0.2	0.4	0.4	0.5	0.2	0.2	0.2	0.4	0.4	0.5
	M	50	50	50	25	25	20	–50	–50	–50	–25	–25	–20
Jar 2	P	0.4	0.5	0.8	0.5	0.8	12.5	0.4	0.5	0.8	0.5	0.8	0.8
	M	25	20	12.5	20	0.8	12.5	–25	–20	–12.5	–20	–12.5	–12.5

artificial epochs were rejected. All epochs were baseline corrected (200 ms pre-stimulus) and averaged by condition (gains, non-gains, losses, and non-losses). A repeated-measures analysis of variance (ANOVA) was performed on the number of valid trials to test whether the signal-to-noise ratio differed across groups and conditions (all $p > 0.059$).

Two feedback-locked ERP components were analyzed for each participant. As the latency of the components varied between groups, the time windows of each component were defined based on the grand average of each group (for a similar procedure, see Eppinger et al., 2008; Ferdinand and Kray, 2013). The FRN was measured at FCz, and it was quantified as the mean amplitude in the time window of 260–360 ms after feedback onset in the younger group, 270–370 ms in the middle-aged group, and 300–400 ms in the older group. The FRN is typically represented by a difference wave, calculated by subtracting the ERP elicited by the positive feedback from the ERP elicited by the negative feedback (e.g., Eppinger et al., 2008). However, because the previous studies that assessed the aging effects in the FRN amplitudes during decision-making tasks analyzed the waveforms obtained in each feedback condition (Di Rosa et al., 2017; Kardos et al., 2017; West et al., 2014), we adopted the same procedure to allow the comparison of results. Regarding the P3 component, it was measured at Pz, and it was quantified as the mean amplitude in the time window of the 300–500 ms in the younger group, 350–550 ms in the middle-aged group, and 400–600 in the older group.

1.3.3. Statistical analysis

The results of the neuropsychological tests were compared through independent one-way ANOVAs, using *group* (younger, middle-aged, older adults) as a between-subjects factor. To analyze decision-making data, the rates of risk-averse decisions (percentage of safe decisions in relation to the total number of decisions) were computed for each participant and for each domain. The effects of domain and age on the rates of risk-averse decisions were investigated through a mixed-factors ANOVA, with *group* as a between-subjects factor and *domain* (gains, losses) as a within-subjects factor. The same model was used to analyze reaction times. The effects of age, domain, and feedback on the FRN and P3 amplitudes were analyzed in a mixed-factors ANOVA, with *group* as a between-subjects factor and *domain* (gains, losses) and *feedback* (favorable, unfavorable) as within-subjects factors. Pearson's r was computed to explore the correlations between age, risk-averse decisions, neurocognitive scores, and ERP results. Significant correlations were explored through linear regression models.

The threshold for statistical significance was set at $\alpha = 0.05$ for all analyses. Violations of sphericity were corrected via the Greenhouse-Geisser method. Significant ANOVA main effects were quantified using Sidak-corrected post hoc comparisons. Statistical analysis was performed using SPSS 24 (IBM Corp., Armonk, NY, USA).

2. Results

2.1. Behavioral results

The results of the neuropsychological tests are presented in [Supplementary Material \(Table 1\)](#). Regarding risk-averse decisions ([Fig. 2](#)), we found a main effect of *group* [$F(2, 85) = 5.08, p = 0.008, \eta_p^2 = 0.107$], revealing that older adults were significantly more risk-seeking than younger adults ($p = 0.008$) and marginally more risk-seeking than middle-aged adults ($p = 0.085$). We did not find a main effect of *domain* [$F(1, 85) = 1.017, p = 0.316, \eta_p^2 = 0.012$], but we found a significant *domain* $\times$ *group* interaction [$F(2, 85) = 4.60, p = 0.013, \eta_p^2 = 0.098$]. In the loss domain, younger adults were

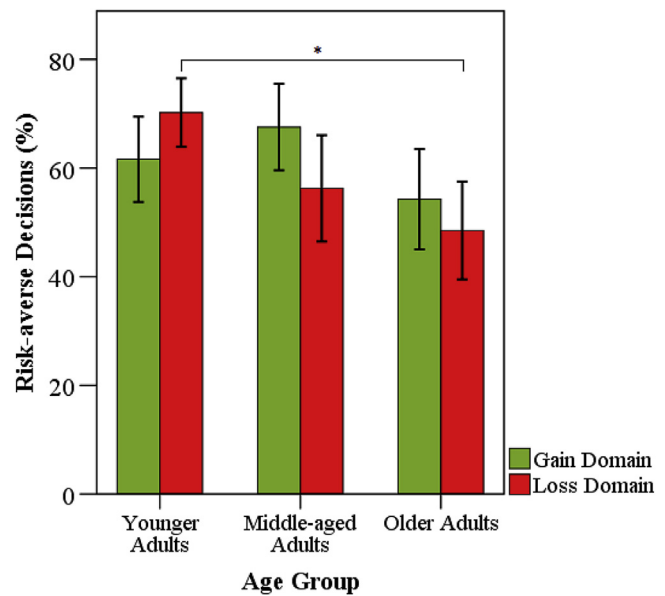


Fig. 2. Average rates of risk-averse decisions (%) for the 3 groups in the gain and loss domains. Error bars indicate 95% confidence intervals. Descriptive statistics are presented in [Supplementary Material \(Table 2\)](#). The asterisks represent significant differences.

significantly more risk-averse than older adults ($p < 0.001$) and marginally more risk-averse than middle-aged adults ($p = 0.055$). In the gain domain, middle-aged adults were marginally more risk-averse than older adults ($p = 0.073$). Regarding reaction times, we did not find a main effect of *group* [$F(2, 85) = 2.10, p = 0.129, \eta_p^2 = 0.047$], but we found a main effect of *domain* [$F(1, 85) = 33.7$,

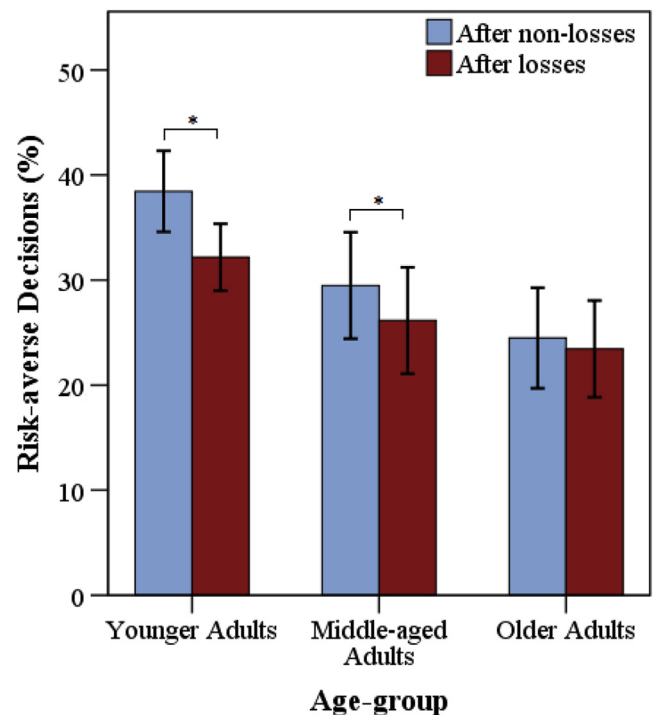


Fig. 3. Average rates of risk-averse decisions (%) after non-losses and losses for the 3 groups. Error bars indicate 95% confidence intervals. The asterisks represent significant differences.

$p < 0.001$, $\eta_p^2 = 0.284$], revealing faster responses in the gain than in the loss domain. The interaction $group \times domain$ was nonsignificant ($F < 1$).

Considering that groups differed significantly in the loss domain, we did a further analysis to explore if the type of outcome received in this domain influenced differently the subsequent decisions of each group. For this purpose, we computed a new variable (outcome) with 2 conditions: the rate of risk-averse decisions after non-losses and the rate of risk-averse decisions after losses. A mixed-factors ANOVA was conducted, with *group* as a between-subjects factor and *outcome* as a within-subjects factor. We found a main effect of *group* [$F(2, 85) = 7.93$, $p = 0.001$, $\eta_p^2 = 0.157$], revealing that younger adults were significantly more risk-averse than older ($p = 0.001$) and middle-aged adults ($p = 0.034$). We also found a main effect of *outcome* [$F(1, 85) = 18.3$, $p < 0.001$, $\eta_p^2 = 0.177$], revealing higher rates of risk-averse decisions after non-losses than after losses. A significant *outcome* $\times$ *group* interaction emerged [$F(2, 85) = 3.37$, $p = 0.039$, $\eta_p^2 = 0.073$], revealing that younger ($p < 0.001$) and middle-aged adults ($p = 0.024$) had higher rates of risk-averse decisions after non-losses than after losses (Fig. 3), but older adults had similar rates of risk-averse decisions after both conditions ($p = 0.476$).

The results of the correlations are presented in [Supplementary Material \(Table 3\)](#). The rates of risk-averse decisions in the loss domain were positively correlated with the scores of the IFS, Corsi blocks-tapping task, and learning subtest of the AVLT and negatively correlated with age and TMT scores. According to the linear regression models (presented in [Table 4](#) of the [Supplementary Material](#)), none of these variables were significant predictors of risk-averse decisions.

2.2. Electrophysiological results

Regarding the FRN amplitudes (Fig. 4), we did not find a main effect of *group* ($F < 1$) or a main effect of *domain* ($F < 1$), but a main effect of *feedback* emerged [$F(1, 80) = 26.3$, $p < 0.001$, $\eta_p^2 = 0.248$], revealing that unfavorable feedback (non-gains and losses) elicited lower amplitudes than favorable feedback (gains and non-losses). We found a significant *domain* $\times$ *feedback* $\times$ *group* interaction [$F(2, 80) = 3.84$, $p = 0.026$, $\eta_p^2 = 0.088$]. According to post hoc comparisons, in the loss domain, favorable feedback elicited significantly lower amplitudes than unfavorable feedback for

younger adults ($p < 0.001$), but this difference was nonsignificant for middle-aged ($p = 0.189$) and older adults ($p = 0.998$). In the gain domain, unfavorable feedback elicited significantly lower amplitudes than favorable feedback for all groups (all $p < 0.001$). The *domain* $\times$ *group* and *feedback* $\times$ *group* interactions were nonsignificant (both $F < 1$).

The FRN amplitude elicited by favorable feedback received in the gain domain was positively correlated with the IFS and Corsi blocks-tapping task scores and negatively correlated with the TMT scores. However, according to the linear regression model, none of these scores were significant predictors of the FRN amplitude. The FRN amplitude elicited by unfavorable feedback received in the loss domain was also negatively correlated with TMT scores, but no further significant correlation emerged in this domain.

The analysis of the P3 component (Fig. 4) did not reveal a main effect of *group* [$F(2, 80) = 1.05$, $p = 0.356$, $\eta_p^2 = 0.026$], but a main effect of *domain* emerged [$F(1, 80) = 7.41$, $p = 0.008$, $\eta_p^2 = 0.085$], revealing higher amplitudes for the loss in comparison with the gain domain. We did not find a main effect of *feedback* [$F(1, 80) = 2.36$, $p = 0.129$, $\eta_p^2 = 0.029$], but we found a significant *domain* $\times$ *feedback* interaction [$F(2, 80) = 4.76$, $p = 0.032$, $\eta_p^2 = 0.056$], along with a significant *domain* $\times$ *feedback* $\times$ *group* interaction [$F(2, 80) = 4.06$, $p = 0.021$, $\eta_p^2 = 0.092$]. Post hoc comparisons showed significant differences in the gain domain, in which favorable feedback elicited higher amplitudes than unfavorable feedback for younger ($p = 0.001$) and middle-aged adults ($p = 0.012$), but not for older adults ($p = 0.225$). The *domain* $\times$ *group* and *feedback* $\times$ *group* interactions were nonsignificant (both $F < 2.36$; both $p > 0.167$).

The P3 amplitudes elicited by favorable feedback received in the gain domain and by unfavorable feedback received in the loss domain were negatively correlated with risk-averse decisions in the gain domain. According to the linear regression model, the P3 amplitude elicited by favorable feedback received in the gain domain was the only predictor of risk-averse decisions. Regarding the neurocognitive results, the P3 amplitudes elicited by favorable feedback received in the gain domain, as well as by both types of feedback received in the loss domain, were positively correlated with the IFS and Corsi blocks-tapping task scores and negatively correlated with the TMT scores.

Three independent linear regression models were computed, in which the neurocognitive results entered as main predictors of the P3 amplitudes evoked by the 3 feedback conditions. The TMT score

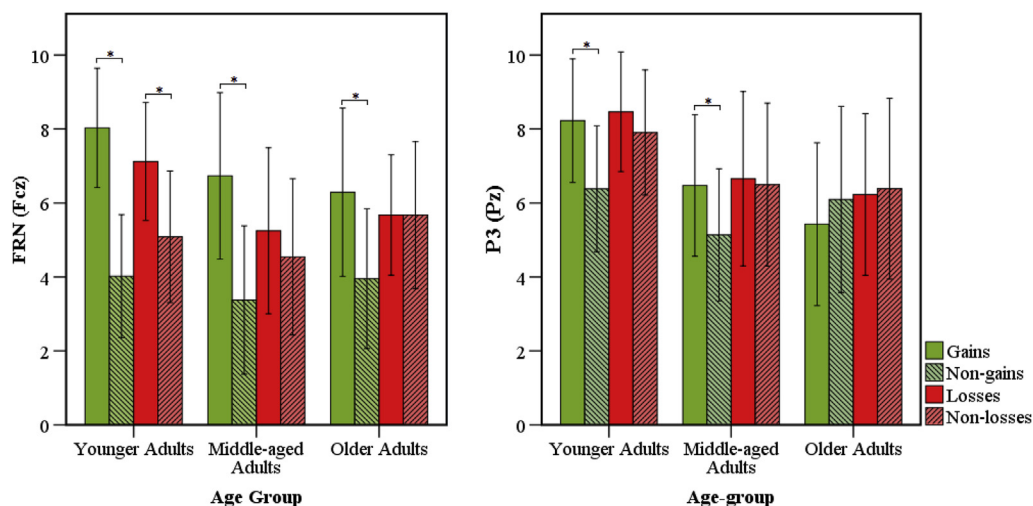


Fig. 4. Means of the FRN and P3 amplitudes (μV) evoked by gains and non-gains (gain domain), as well as losses and non-losses (loss domain). Gains and non-losses are favorable feedbacks, whereas non-gains and losses are unfavorable feedbacks. Error bars indicate 95% confidence intervals. Abbreviations: FRN, feedback-related negativity. The asterisks represent significant differences.

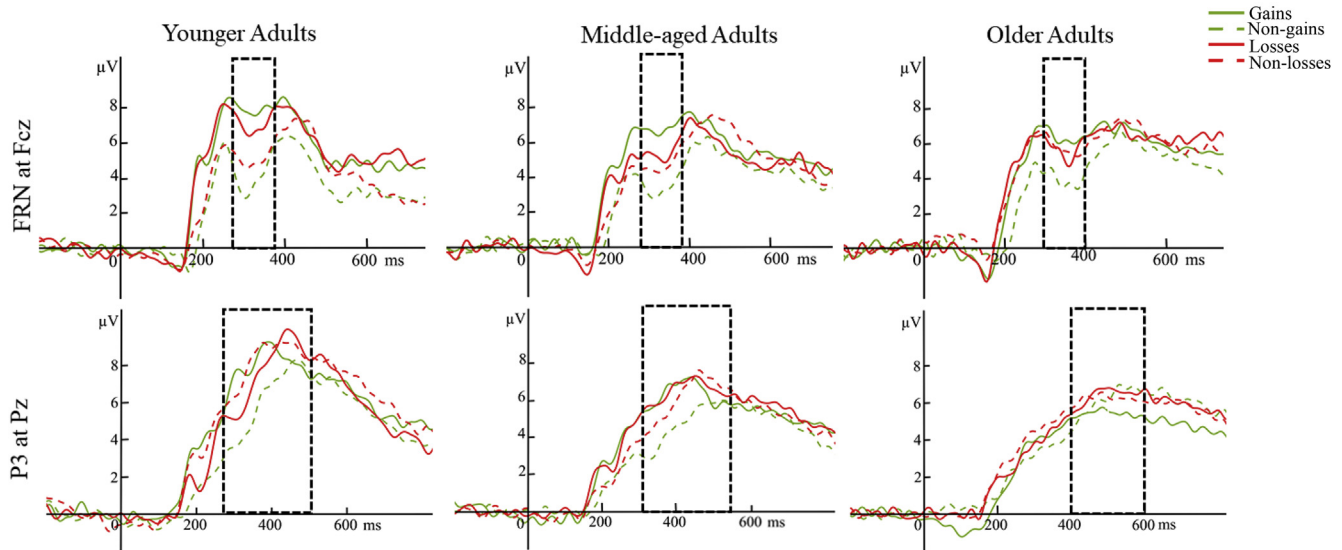


Fig. 5. Grand-average of the FRN (top) and P3 (bottom) amplitudes for younger, middle-aged, and older adult during the feedback phase. The marked areas depict the time windows during which the ERPs were measured. The green lines represent gain domain, whereas the red lines represent loss domain. The broken lines represent the zero-value outcomes, whereas the solid lines represent negative or positive outcomes. Descriptive statistics of the ERP results are presented in [Supplementary Material \(Table 5\)](#). Abbreviations: ERP, event-related potential; FRN, feedback-related negativity. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

was a significant predictor of the P3 amplitude elicited by unfavorable feedback received in the loss domain. The FRN and P3 components are plotted in [Fig. 5](#).

3. Discussion

In this study, we examined age-related differences in risk-aversion and neurophysiological correlates of feedback processing, in groups of younger, middle-aged, and older participants. Risk-aversion was examined through trials involving 2 risky options, with stimuli designed to reduce demands of abstraction and numeracy abilities. Behaviorally, the groups did not differ in the gain domain, but older participants were more risk-seeking than younger participants in the loss domain. The analysis of the neurophysiological data showed group-related differences in early and later stages of feedback processing, indexed by differences in the FRN and P3 amplitudes.

3.1. Behavioral results

In the gain domain, both groups had similar rates of risk-averse decisions, preferring smaller gains associated with higher probabilities of winning rather than larger gains with lower probabilities of occurring. However, in the loss domain, older adults were more risk-seeking than younger adults, preferring smaller losses associated with higher probabilities of losing, while younger adults preferred larger, but less probable losses.

The results obtained in the older group are in agreement with the assumptions of the prospect theory, according to which individuals are risk-averse in the gain domain and risk-seeking in the loss domain. This tendency reflects an underestimation of probable in comparison to certain outcomes (the certainty effect), which leads individuals to prefer smaller certain gains rather than possible larger gains, but also possible larger losses rather than smaller certain losses ([Kahneman and Tversky, 1979](#)). However, considering that our task required decisions between 2 risky options and not between certain and possible gains/losses, our results may be better explained by the age-related differences in loss aversion. This

hypothesis is also supported by the results of a previous study that used a similar task, in which older adults did not exhibit loss aversion ([Pachur et al., 2016](#)). Regarding our results, when we analyzed group differences in the decisions taken in this domain, we found that younger and middle-aged adults had higher rates of risk-averse decisions after non-losses than after losses, while older adults preserved their risk preferences independently of the previous feedback.

Despite these age-related differences, a meta-analytic study ([Mata et al., 2011](#)) showed that younger and older adults had similar risk-aversion in the majority of the tasks evaluating decision-making under risk. Group-related differences emerged in decisions under uncertainty, in which older adults were more risk-averse than younger adults when learning led to risk-seeking behavior but were more risk-seeking when learning led to risk-avoidance behavior. Moreover, this study did not find clear age-related differences as a function of gain/loss domain ([Mata et al., 2011](#)). However, a more recent study found that older adults were more risk-seeking than younger adults for losses but more risk-averse for gains in decisions between sure and probable gains/losses ([Mather et al., 2012](#)). Other experiment using gambles with 2 risky options found higher rates of risky decisions in older adults only in the gain domain ([Pachur et al., 2016](#)).

Interestingly, the middle-aged group appears to be in an intermediate level between the younger and older groups. This group was marginally more risk-seeking than younger adults in the loss domain but also marginally more risk-averse than older adults in the gain domain. This evidence contrasts with the results of a previous study ([Tymula et al., 2013](#)) that used a task in which participants decided between a certain and a probable gain/loss. In this study, older adults were more risk-averse than younger and middle-aged adults, who did not differ from each other. However, besides differences in the gambles, the age of the older adults included in both studies may explain these contrasting results. While our older group included participants with ages between 60 and 75 years, the older group of Tymula et al.'s study included participants with ages between 65 and 90 years.

An unanswered question is whether changes in decision-making reflect a consequence of aging or an effect of age-related decline in cognitive abilities. We found a correlation between better performance on executive functions and memory and higher levels of risk-averse decisions in the loss domain, but cognitive results were not predictors of decision-making, contrasting with previous results (Henninger et al., 2010). Nevertheless, our experiment was designed to reduce demands of abstraction and numeracy abilities, leading to a less cognitively demanding task. Moreover, 2 of the tasks used in the study by Henninger et al. (2010) assessed decisions under uncertainty. Under this context, the probabilities and magnitudes of the outcomes are unknown and must be learned throughout experience, which is cognitively more demanding.

3.2. Electrophysiological results: FRN amplitudes

The results regarding the FRN component showed that aging did not affect early stages of the feedback processing, when the feedback was received in the gain domain. In this domain, all groups had a more negative FRN for unfavorable (non-gains) than for favorable feedbacks (gains). This result is in accordance with the reward prediction error hypothesis (Miltner et al., 1997), which postulates that the FRN is consistently larger for negative than for positive feedbacks. According to the reinforcement-learning theory (Holroyd and Coles, 2002), the increased FRN amplitude elicited by negative outcomes results from the decreasing dopaminergic activity after events that are worse than expected, which allows the adaptation of the motor system control according to the feedback contingencies (Holroyd and Coles, 2002).

In the loss domain, younger adults had a higher FRN after favorable (non-losses) than after unfavorable feedbacks (losses), whereas middle-aged and older adults had similar FRN amplitudes after both types of feedback. This result may suggest that the loss domain elicits positive instead of negative reward prediction errors and possibly explains the behavioral results that we obtained in the loss domain. We found that younger adults had higher rates of risk-averse decisions after non-losses than after losses, which we interpreted as a performance adjustment. This performance adjustment was not observed in the older group, who had similar FRN amplitudes after non-losses and losses. However, middle-aged adults evidenced this performance adjustment, despite having had similar FRN amplitudes after both types of feedback, leading us to propose that this group is in an intermediate level. That is, they are closer to younger adults in the behavioral performance and closer to older adults in the neural processing of the feedback.

Regarding group comparisons, our results stand in contrast with different aspects of previous findings. Di Rosa et al. (2017) found similar FRN amplitudes for younger and older adults after gains and losses received during the Iowa gambling task. Indeed, we did not find significant domain-by-group or valence-by-group interactions, but group differences emerged in a significant domain-by-valence-by-group interaction. Closer to our findings are the results of the Kardos et al.'s study (Kardos et al., 2017) that used a 2-choice single-outcome task that delivered 4 types of feedback: large and small losses, as well as large and small gains. Their results showed that younger adults had a significantly more negative FRN after losses than after gains, whereas older adults had similar FRN amplitudes after both conditions. One study using a blackjack game found an attenuated FRN in older adults after busts, wins, and losses (West et al., 2014).

Taken together, both ours and previous results (Kardos et al., 2017; West et al., 2014) suggest that aging may alter outcome-related expectations. However, since middle-aged and older

adults had a similar pattern of FRN results, this feature may be a nonspecific pattern of aging, starting during the adult development.

3.3. Electrophysiological results: P3 amplitudes

The results obtained with the P3 component showed that aging did not alter the later stages of the feedback processing, when the feedback was received in the loss domain. In this domain, all groups had similar P3 amplitudes after favorable (non-losses) and unfavorable (losses) feedback. The lack of an outcome valence effect in the loss domain was previously found in a study in which participants received feedbacks of gains, non-gains, losses, and non-losses (Zheng et al., 2017). According to the authors' interpretation, it could reflect an increased relevance attributed to the gain versus the loss domain (Zheng et al., 2017), a plausible hypothesis considering that the P3 modulation may change depending on the task goal and, particularly, depending on the arousing levels of the stimuli (Martín, 2012). For instance, previous studies have found large P3 amplitudes both after negative and positive stimuli, provided that they were matched according to subjective ratings of arousal (e.g., Keil et al., 2002). In both tasks, as participants were instructed to win as many points as possible, feedbacks received in the loss domain could evoke similar levels of arousal, contrary to what happens in the gain domain, where gains are more arousing than non-gains.

Group differences emerged in the gain domain, in which younger and middle-aged adults had higher P3 amplitudes after gains than after non-gains, whereas older adults had similar P3 amplitudes in both conditions. Importantly, the P3 elicited by gains was negatively correlated with risk-averse decisions in the gain domain, which did not differ between groups. Considering that risk-taking behavior might be interpreted as the best strategy in the gain domain, the increased P3 in the younger and middle-aged groups after gains may have decreased their risk-aversion, mediating the lack of behavioral differences found between groups.

The results obtained in the P3 amplitudes also contrast with different aspects of previous results. While West et al. (2014) found similar P3 amplitudes for younger and older adults, Di Rosa et al. (2017) found lower P3 amplitudes for older adults after losses, and Kardos et al. (2017) found reduced P3 amplitudes for older adults after losses and gains (Kardos et al., 2017). None of these results are in accordance with ours, which might be driven by differences in the contexts of the tasks. While our task assessed decision-making under risk, in which the magnitudes and probabilities of the outcomes were known for each option, all the referenced tasks assessed decision-making under uncertainty, in which the probabilities were unknown.

The P3 amplitude is highly modulated by the subjective probability of the eliciting stimuli (Nieuwenhuis, 2011), being larger for stimuli with lower probabilities (e.g., Bellebaum and Daum, 2008). According to the context-updating hypothesis (Donchin and Coles, 1988), receiving improbable outcomes signals the need to update the current mental model, and the P3 amplitude reflects the amount of cognitive resources allocated to this updating (Martín, 2012). However, beyond the probability, arousing stimuli, either positive or negative, elicit larger P3 amplitudes (Nieuwenhuis, 2011). In our task, even in those trials in which participants received the less probable feedback, they had previously known this low probability. Thereby, while the P3 amplitudes found in the previous studies are more likely to be modulated by its probability, the P3 amplitudes found in our study are more likely to be modulated by the arousing level of the feedback.

According to this interpretation, the arousal modulation of P3 amplitudes may also underlie the age-related differences observed in the gain domain. We found higher P3 amplitudes after gains than after non-gains for younger and middle-aged adults, but not for older adults. This result may suggest age-related differences in the affective relevance attributed to the outcomes or, in an alternative interpretation, age-related difficulties in adapting the processing priorities to the task goals.

4. Conclusion

Aging appears to alter early and later stages of feedback processing, indexed by differences in the FRN and P3 amplitudes. In the FRN time window, aging did not affect the processing of feedback received in the gain domain, but in the loss domain, middle-aged and older adults were insensitive to the feedback valence while younger adults had a higher FRN after non-losses than after losses. As the FRN appears to reflect the decrease of the dopaminergic activity (Holroyd and Coles, 2002) after unexpected outcomes (Oliveira et al., 2007), to allow an adjustment of the response strategy (Holroyd and Coles, 2002), these results suggest that aging may change the outcome-related expectations, which may reduce the reward prediction error and the consequent behavioral adjustment. In the P3 time window, aging did not affect the processing of feedback received in the loss domain. However, in the gain domain, older adults were insensitive to the feedback valence, while younger and middle-aged adults had higher P3 amplitudes after gains than after non-gains. As P3 amplitudes are modulated by the arousing nature of the feedback (Nieuwenhuis, 2011), possibly defined by the task goals (Martín, 2012), our results may suggest age-related differences in the affective relevance attributed to the outcomes or, in an alternative interpretation, age-related difficulties in adapting the processing priorities according to the task goals.

Behaviorally, we found that all groups were risk-averse in the gain domain, but in the loss domain, older adults were more risk-seeking than younger adults. We interpreted these results as age-related differences in loss aversion, which were previously evidenced in a similar task (Pachur et al., 2016).

Interestingly, middle-aged adults appear to be in an intermediate level between younger and older adults. Specifically, their FRN results were closer to those of the older adults, but their P3 results were closer to those of the younger adults. Behaviorally, their results were closer to those of the younger adults in the gain domain and closer to those of the older adults in decisions in the loss domain.

Finally, we did not find evidence of a positivity bias of the older group regarding feedback processing. Instead, positive and negative feedbacks appear to have the same meaning to older adults, evidenced by the FRN component in the loss domain and by the P3 in the gain domain. Further studies must confirm whether this pattern of neural and behavioral responses persists in other risk tasks and in tasks assessing decision-making under uncertainty, since decision-making has been demonstrated to be a heterogeneous process during aging.

Disclosure statement

The authors have no conflicts of interest to disclose.

Acknowledgements

The authors thank Programa de Estudos Universitários para Seniores and Associação de Aposentados Pensionistas e Reformados for their help in participant recruitment. This research was

supported by a grant from the Fundação BIAL. CF was supported by a doctoral fellowship from the Fundação para a Ciência e a Tecnologia (SFRH/BD/112101/2015).

Appendix A. Supplementary data

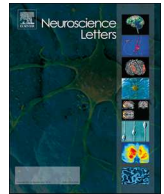
Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.neurobiolaging.2018.01.003>.

References

- Armitage, S.G., 1946. An analysis of certain psychological tests used for the evaluation of brain injury. *Psychol. Monogr.* 60, i–48.
- Bellebaum, C., Daum, I., 2008. Learning-related changes in reward expectancy are reflected in the feedback-related negativity. *Eur. J. Neurosci.* 27, 1823–1835.
- Boake, C., 2000. Édouard Claparède and the Auditory Verbal Learning Test. *J. Clin. Exp. Neuropsychol.* 22, 286–292.
- Bruine de Bruin, W., van Putten, M., van Emden, R., Strough, J., 2017. Age differences in emotional responses to monetary losses and gains. *Psychol. Aging*.
- Burks, S.V., Carpenter, J.P., Goette, L., Rustichini, A., 2009. Cognitive skills affect economic preferences, strategic behavior, and job attachment. *Proc. Natl. Acad. Sci. U. S. A.* 106, 7745–7750.
- Canavaro, M.C., 1999. Inventário de sintomas psicopatológicos - BSI. In: Simões, M.R., Gonçalves, M., Almeida, L.S. (Eds.), *Testes e provas psicológicas em Portugal*. SHO/APPORT, Braga, pp. 87–109.
- Cavaco, S., Gonçalves, A., Pinto, C., Almeida, E., Gomes, F., Moreira, I., Fernandes, J., Teixeira-Pinto, A., 2013a. Semantic fluency and phonemic fluency: regression-based norms for the Portuguese population. *Arch. Clin. Neuropsychol.* 28, 262–271.
- Cavaco, S., Gonçalves, A., Pinto, C., Almeida, E., Gomes, F., Moreira, I., Fernandes, J., Teixeira-Pinto, A., 2013b. Trail Making Test: regression-based norms for the Portuguese population. *Arch. Clin. Neuropsychol.* 28, 189–198.
- Cavaco, S., Gonçalves, A., Pinto, C., Almeida, E., Gomes, F., Moreira, I., Fernandes, J., Teixeira-Pinto, A., 2015. Auditory Verbal learning test in a large nonclinical Portuguese population. *Appl. Neuropsychol. Adult* 22, 321–331.
- Daly, M., Wilson, M., 1997. Crime and conflict: homicide in evolutionary psychological perspective. *Crime and Justice* 22, 51–100.
- Delorme, A., Makeig, S., 2004. An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134, 9–21.
- Derogatis, L.R., 1982/1993. BSI: Brief Symptom Inventory, third ed. National Computers Systems, Minneapolis.
- Di Rosa, E., Mapelli, D., Arcara, G., Amodio, P., Tamburin, S., Schiff, S., 2017. Aging and risky decision-making: new ERP evidence from the Iowa gambling task. *Neurosci. Lett.* 640, 93–98.
- Donchin, E., Coles, M.G., 1988. Is the P300 component a manifestation of context updating? *Behav. Brain Sci.* 11, 357–374.
- Eppinger, B., Kray, J., Mock, B., Mecklinger, A., 2008. Better or worse than expected? Aging, learning, and the ERN. *Neuropsychologia* 46, 521–539.
- Ferdinand, N.K., Kray, J., 2013. Age-related changes in processing positive and negative feedback: is there a positivity effect for older adults? *Biol. Psychol.* 94, 235–241.
- Freitas, S., Simões, M.R., Santana, I., 2014. Montreal cognitive assessment (MoCA): pontos de corte no défice cognitivo ligeiro, doença de Alzheimer, demência frontotemporal e demência vascular. *Sinapse* 14, 18–30.
- Henninger, D.E., Madden, D.J., Huettel, S.A., 2010. Processing speed and memory mediate age-related differences in decision making. *Psychol. Aging* 25, 262–270.
- Holroyd, C.B., Coles, M.G., 2002. The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychol. Rev.* 109, 679–709.
- Kahneman, D., Tversky, A., 1979. Prospect theory: an analysis of decision under risk. *Econometrica* 47, 263–291.
- Kardos, Z., Tóth, B., Boha, R., File, B., Molnár, M., 2017. Age-dependent characteristics of feedback evaluation related to monetary gains and losses. *Int. J. Psychophysiol.* 122, 42–49.
- Keil, A., Bradley, M.M., Hauk, O., Rockstroh, B., Elbert, T., Lang, P.J., 2002. Large-scale neural correlates of affective picture processing. *Psychophysiology* 39, 641–649.
- Nieuwenhuis, S., 2011. Learning, the P3, and the locus coeruleus-norepinephrine system. In: Mars, R., Sallet, J., Rushworth, M.F., Yeung, N. (Eds.), *Neural Basis of Motivational and Cognitive Control*. MIT Press, Cambridge, pp. 209–222.
- Martín, S.R., 2012. Event-related potential studies of outcome processing and feedback-guided learning. *Front. Hum. Neurosci.* 6, 1–17.
- Mata, R., Josef, A.K., Samanez-Larkin, G.R., Hertwig, R., 2011. Age differences in risky choice: a meta-analysis. *Ann. N. Y. Acad. Sci.* 1235, 18–29.
- Mather, M., Carstensen, L.L., 2005. Aging and motivated cognition: the positivity effect in attention and memory. *Trends Cogn. Sci.* 9, 496–502.

- Mather, M., Mazar, N., Gorlick, M.A., Lighthall, N.R., Burgeno, J., Schoeke, A., Ariely, D., 2012. Risk preferences and aging: the “certainty effect” in older adults’ decision making. *Psychol. Aging* 27, 801–816.
- Miltner, W.H., Braun, C.H., Coles, M.G., 1997. Event-related brain potentials following incorrect feedback in a time-estimation task: evidence for a “generic” neural system for error detection. *J. Cogn. Neurosci.* 9, 788–798.
- Moreira, H.S., Lima, C.F., Vicente, S.G., 2014. Examining executive dysfunction with the Institute of Cognitive Neurology (INECO) Frontal Screening (IFS): normative values from a healthy sample and clinical utility in Alzheimer’s disease. *J. Alzheimers Dis.* 42, 261–273.
- Nasreddine, Z.S., Phillips, N.A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., Cummings, J.L., Chertkow, H., 2005. The Montreal Cognitive Assessment, MoCA: a brief screening tool for mild cognitive impairment. *J. Am. Geriatr. Soc.* 53, 695–699.
- Oliveira, F.T., McDonald, J.J., Goodman, D., 2007. Performance monitoring in the anterior cingulate is not all error related: expectancy deviation and the representation of action-outcome associations. *J. Cogn. Neurosci.* 19, 1994–2004.
- Pachur, T., Mata, R., Hertwig, R., 2016. Who dares, who errs? Disentangling cognitive and motivational roots of age differences in decisions under risk. *Psychol. Sci.* 28, 1–15.
- Pais-Ribeiro, J., Silva, I., Ferreira, T., Martins, A., Meneses, R., Baltar, M., 2007. Validation study of a Portuguese version of the hospital anxiety and depression scale. *Psychol. Health Med.* 12, 225–237.
- Samanez-Larkin, G.R., Knutson, B., 2015. Decision making in the ageing brain: changes in affective and motivational circuits. *Nat. Rev. Neurosci.* 16, 278–289.
- Samanez-Larkin, G.R., Gibbs, S.E., Khanna, K., Nielsen, L., Carstensen, L.L., Knutson, B., 2007. Anticipation of monetary gain but not loss in healthy older adults. *Nat. Neurosci.* 10, 787–791.
- Snaith, R.P., Zigmond, A.P., 1994. The Hospital Anxiety and Depression Scale Manual. NFER-Nelson, Windsor.
- Strauss, E., Sherman, E.M., Spreen, O., 2006. A Compendium of Neuropsychological Tests: Administration, Norms, and Commentary, third ed. Oxford University Press, New York.
- Torralva, T., Roca, M., Gleichgerricht, E., Lopez, P., Manes, F., 2009. INECO Frontal Screening (IFS): a brief, sensitive, and specific tool to assess executive functions in dementia. *J. Int. Neuropsychol. Soc.* 2009, 777–786.
- Tymula, A., Belmaker, L.A., Ruderman, L., Glimcher, P.W., Levy, I., 2013. Like cognitive function, decision making across the life span shows profound age-related changes. *Proc. Natl. Acad. Sci. U. S. A.* 110, 17143–17148.
- Wechsler, D., 2008. Escala de memória de Wechsler. CEGOC-TEA, Lisboa.
- West, R., Tiernan, B.N., Kieffaber, P.D., Bailey, K., Anderson, S., 2014. The effects of age on the neural correlates of feedback processing in a naturalistic gambling game. *Psychophysiology* 51, 734–745.
- Zheng, Y., Li, Q., Zhang, Y., Li, Q., Shen, H., Gao, Q., Zhou, S., 2017. Reward processing in gain versus loss context: an ERP study. *Psychophysiology* 54, 1–14.

2.5 AGE-RELATED CHANGES IN SOCIAL DECISION-MAKING: AN ELECTROPHYSIOLOGICAL ANALYSIS OF UNFAIRNESS EVALUATION IN THE ULTIMATUM GAME



Research article

Age-related changes in social decision-making: An electrophysiological analysis of unfairness evaluation in the Ultimatum Game

Fernandes C.^{a,b,c,*}, Gonçalves A.R.^a, Pasion R.^a, Ferreira-Santos F.^a, Barbosa F.^a, Martins I.P.^c, Marques-Teixeira J.^a

^a Laboratory of Neuropsychophysiology, Faculty of Psychology and Education Sciences, University of Porto, Portugal

^b Faculty of Medicine, University of Porto, Portugal

^c Language Research Laboratory, Institute of Molecular Medicine, Faculty of Medicine, University of Lisbon, Portugal

ARTICLE INFO

Keywords:

Aging
Ultimatum game
Decision-making
ERPs
MFN

ABSTRACT

This study examines age-related differences in behavioral and neural responses to unfairness. Our sample was composed of younger, middle-aged, and older adults, who performed the Ultimatum Game in the proposer role, and in the respondent role during an EEG recording. We administered neurocognitive tests to identify whether patterns in decision-making are associated with age-related changes in cognition. Despite the worse performance in measures of executive functioning, older adults had the best economic strategy by accepting more unfair offers than younger and middle-aged adults. Regarding electrophysiological results, while younger adults showed higher medial frontal negativity (MFN) amplitudes after unfair than after fair offers, middle-aged and older adults had similar amplitudes after both conditions. Our results suggest that aging may be accompanied by an insensitivity to unfairness, which may underlie their higher rates of unfair offers acceptance.

Older adults face significant economic challenges daily, and poor decision-making may have severe consequences considering their limited time and resources to overcome negative choices [1]. However, the mechanisms underlying age-related changes in decision-making are still unknown, and research on this field is hampered by evidence that risk preferences vary substantially within tasks [2].

In this study, we investigated age-related differences in social economic decision-making through the performance in the Ultimatum Game (UG) [3]. We analyzed the Medial Frontal Negativity (MFN) induced by fair and unfair offers, which was proposed as an index of unfairness sensitivity [4].

The UG involves two players: the proposer (splits amounts of money) and the responder (accepts/rejects proposer's offers). If the responder accepts the offer, the stake is divided as proposed, but if s/he rejects the offer, both players get nothing. From an economic standpoint, the rational solution for the proposer is to offer the smallest possible amount, and for the responder is to accept it [5]. Previous studies evidenced that older adults were significantly less likely to accept unfair offers [1,6,7], and expected to receive higher offers [6]. Younger and older adults revealed a similar pattern of neural activation after fair offers, but older adults showed a greater activation in the left dorsolateral prefrontal cortex and left inferior parietal region, as well as

a lower activation in anterior insula after unfair offers [6]. In another study, younger and older participants played both roles on the UG, with younger and older partners. As proposers, older adults made higher offers, regardless of their partners' age. As responders, older adults accepted more unfair offers than younger adults, but both groups reported higher anger rates in response to unfair offers from younger proposers [8].

In summary, compared to younger adults, older adults tend to reject more unfair offers (except data from one study). However, despite being the most disadvantageous strategy, unfair offers (< 40% of the stake) tend to be rejected half the times [9], what is interpreted as an altruistic punishment of proposers' fairness violation [10]. In this sense, it is possible that a greater sensitivity to unfairness, rather than a poorer economic judgment, drives this behavior in elderly. According to this hypothesis, older adults are more punitive than younger adults during moral violations [11], and less likely to adjust their evaluations to situational goals [12].

The analysis of the MFN may play a crucial role in disentangling the neural mechanisms behind results reached with the UG. It was recently proposed as an index of unfairness sensitivity, being larger for unfair than for fair offers [4,13,14]. This component belongs to a family of event-related potentials (ERPs) generated in the anterior cingulate

* Corresponding author at: Faculdade de Psicologia e Ciências da Educação, Universidade do Porto, R. Alfredo Allen, 4200-135, Porto, Portugal.

E-mail address: carinafernandes@fpce.up.pt (C. Fernandes).

<https://doi.org/10.1016/j.neulet.2018.10.061>

Received 15 September 2018; Received in revised form 27 October 2018; Accepted 30 October 2018

Available online 01 November 2018

0304-3940/© 2018 Elsevier B.V. All rights reserved.

cortex (ACC) [15], that are elicited both after errors [16] or feedbacks (feedback-related negativity; FRN) [17]. According to the reward prediction error hypothesis [17], these components are consistently larger for negative than for positive results and, according to the reinforcement-learning theory, this reflects a decreased dopaminergic activity, required to adapt the motor system control according to the feedback contingencies [18].

This study investigates aging effects in the MFN, which may unveil the neural mechanisms underlying evaluations of fair and unfair offers across the lifespan. According to behavioral evidence, we expect higher sensitivity to unfairness from older adults, indexed by higher rejection rates of unfair offers. Higher MFN amplitude for older adults is expected to explain these differences. Regarding the proposer role, we expect higher offers from the older group. Measures of cognitive function were collected to explore whether age-related patterns in decision are associated with or independent of age-related changes in cognition.

1. Method

1.1. Participants

The sample was composed of 30 younger (20–35 years), 30 middle-aged (40–55 years) and 29 older adults (60–75 years; Table 1 of Supplementary Material). The inclusion criteria were normal or corrected-to-normal vision, a score ≥ 22 in the Montreal Cognitive Assessment (MoCA) [19,20], no history of brain injury, neurological or psychiatric diagnosis, neither current use of psychotropic medication.

Data from one middle-aged and two older adults were not included in the electrophysiological analysis due to an error in saving data. Data from one younger, one middle-aged and two older adults were not included in the electrophysiological analysis for having less than 20 valid trials in each condition [21].

1.2. Neuropsychological measures

The MoCA was used as neurocognitive screening. Executive functioning was assessed through the Trail Making Test (TMT) [22,23] and INECO Frontal Screening [24,25]. The visuospatial short-term memory was assessed through the Corsi Block-Tapping Task [26]. The language production was assessed through Fluency tests [27,28]. Anxiety and depression were evaluated by the Hospital Anxiety and Depression Scale [29,30], and the Brief Symptom Inventory [31,32] evaluated psychopathological symptoms. The Auditory Verbal Learning Test [33,34] assessed immediate and episodic memory.

1.3. Experimental task

Participants played as respondents in series of one-shot UG, during simultaneous EEG recording. Participants were instructed that they would see offers and photos from previous participants and had to accept or reject each offer. Photos of other players were selected from the Radboud Faces Database [35] and were from Caucasians displaying closed mouth, direct eye contact, and neutral facial expression. After the proposer's photo, the stake was displayed and followed by the offer.

Participants responded during the response slide, using two buttons held in the right and left hands. Each round ends with a feedback slide (Fig. 1).

Participants played 84 rounds (42 unfair, 42 fair). There were two possible offered amounts (5 and 15), and the stake size varied (fair stakes: 10, 11, 12.5, 30, 33, 37.5; unfair stakes: 15, 20, 25, 45, 60, 75) [36]. Each stake was repeated 14 times. The task was programmed in E-Prime 2.0 (2011, Psychology Software Tools Inc., Pennsylvania, USA).

1.4. Procedures

The study was approved by the local Ethics Committee. Participants provided informed consent and were compensated with 20€ (gift card) for their time. The current study was part of a larger research project.

Participants were tested in two experimental sessions. The first section aimed to confirm the inclusion/exclusion criteria and to collect neurocognitive data. Participants who fulfilled the inclusion criteria were recruited for the second session, in which the experimental task was performed. Participants were informed that the offers were made by previous players and that their offers would be presented to the following participants [5,36].

After the placement of the EEG cap, participants sat at 115 cm from a 17" screen and completed four practice and 84 experimental trials presented randomly. Afterward, participants made their offers (proponent role) and rated the fairness of each offer received, using a Likert scale (1 = very unfair; 7 = very fair).

1.5. EEG recording and processing

The EEG data were recorded using a 128-electrode Hydrocel Geodesic Net with a Net Amps 300 amplifier (Electrical Geodesics Inc., Eugene, EUA), with a digitizing rate of 500 Hz. Impedances were kept below 50kOhm. The electrodes were referenced to the Cz during recording and re-referenced offline to the average of the electrodes placed in the left and right mastoids. EEG data were pre-processed in EEGLAB 14. The signal was band-pass filtered (0.1–30 Hz), bad channels were interpolated (maximum of 10% of the sensors), and data were submitted to an Independent Components Analysis decomposition. Eye blinks, saccades and heart rate were corrected by subtracting the respective independent component activity from the data. The signal was segmented into epochs (–200 to 800 ms) time-locked to the stake and offer onsets. All segments were inspected and the remaining artifacts were rejected. Groups had a similar number of valid trials ($p = .242$). All epochs were baseline corrected (–200 ms) and averaged by condition (unfair, fair).

The MFN is typically time-locked to the offer onset. However, according to the inspection of our waveforms, this event failed to elicit this component. Otherwise, a waveform with the MFN morphology emerged time-locked to the stake (Fig. 2). This is not surprising considering that the amounts offered in both fair and unfair conditions were the same (5 and 15) and the fairness of the gamble was defined by the magnitude of the stake.

The MFN typically reaches its maximum at 320 ms after the stimuli onset, on multiple frontal electrodes [4]. To define our electrodes of

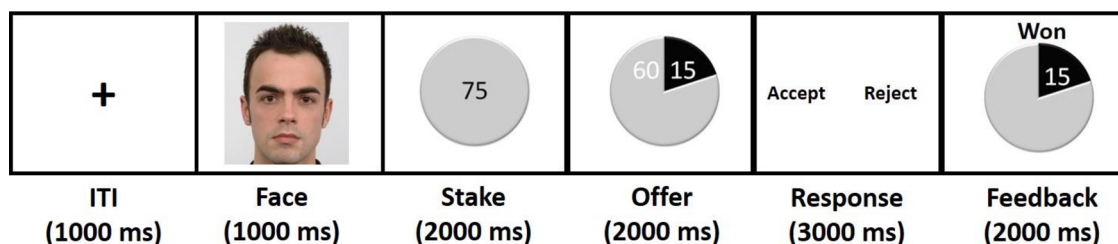


Fig. 1. Depiction of one round of the UG (dark-gray portion = respondent; light-gray portion = proposer).

interest, we evaluated the MFN component (unfair wave minus fair wave) on the left (F3, FC3), right (F4, FC4) and medial (Fz, FCz) frontal regions. As the mean amplitude of the MFN was higher at different electrodes and latencies according to the groups (FCz at 320 ms for younger, FC3 at 320 ms for middle-aged, and FC4 at 350 ms for older adults), we based our analysis on these electrodes. This component was quantified as the mean amplitude in the time-window of 290–350 ms for younger, 290–350 ms for middle-aged, and 320–380 ms for older adults.

The MFN is typically represented by a difference wave [4]. However, previous studies that assessed aging effects in the FRN during decision-making tasks analyzed the waveforms obtained in each condition [37,38]. Accordingly, we adopted the same procedure to allow the discussion of our results in light of these studies.

1.6. Statistical analysis

The neuropsychological results were compared with independent One-Way ANOVAs, using *group* (young, middle-aged, older adults) as between-subjects factor. To the respondent role, the acceptance rates of fair and unfair offers were calculated for each participant. To investigate the effects of offer type and age on the acceptance rates and reaction times, we performed a mixed factors ANOVA, with *offer* (fair, unfair) as within-subjects factor and *group* as between-subjects factor.

To investigate the effects of age on perceived fairness, we performed a mixed factors ANOVA, with *offer* as within-subjects factor and *group* as between-subjects factor. To analyze the effects of age on the proposer role, the amount offered (%) was tested in a One-Way ANOVA, using *group* as between-subjects factor.

The ERPs elicited by fair and unfair offers were analyzed in a mixed factors ANOVA, with *group* as between-subjects factor, and *offer* and *electrode* (FCz, FC4, FC3) as within-subjects factors. The correlations between neurocognitive, behavioral and electrophysiological results were explored through Spearman Correlations [39].

The threshold for statistical significance was set at $\alpha = .05$ for all

analyses. Statistical analysis was performed using SPSS 24 (SPSS Inc., Chicago, IL, USA). Significant ANOVA main effects were quantified using Sidak-corrected post-hoc comparisons.

2. Results

2.1. Behavioral results

Descriptive statistics for the neurocognitive results are presented in Table 1 of Supplementary Material. We did not find a main effect of *group* in the respondent role, $F(186) = 1.820$, $p = .168$, $\eta_p^2 = .041$, but we obtained a main effect of *offer*, $F(186) = 182.9$, $p < .001$, $\eta_p^2 = .680$, with fair offers being accepted more often ($M = 83.2$, $SD = 18.7$) than unfair offers ($M = 36.7$, $SD = 35.1$). We found a significant *offer*group* interaction, $F(286) = 5.07$, $p = .008$, $\eta_p^2 = .105$, showing that older adults accepted more often unfair offers than younger adults ($p = .029$). The acceptance rates of unfair offers were positively correlated with worse results of the TMT ($r_s = .313$, $p = .003$).

Regarding reaction times, we found a marginally significant main effect of *offer*, $F(186) = 2.97$, $p = .088$, $\eta_p^2 = .033$, but the interaction *offer*group* was non-significant ($F < 1$).

Regarding the perceived fairness, we did not find a main effect of *group*, $F(184) = .748$, $p = .477$, $\eta_p^2 = .017$, but we found a main effect of *offer*, with fair offers being rated as more fair than unfair offers, $F(184) = 893.6$, $p < .001$, $\eta_p^2 = .914$. The interactions *group*offer* was non-significant, $F(284) = 1.02$, $p = .367$, $\eta_p^2 = .024$. The amount offered in the proposer role was similar between groups, ($F < 1$). Descriptive statistics for the acceptance rates, fairness ratings and amounts offered are presented in Table 2 of Supplementary Material.

2.2. Electrophysiological results

The ERPs evoked by fair and unfair offers are plotted in Fig. 2. We found a main effect of *group*, $F(279) = 4.03$, $p = .022$, $\eta_p^2 = .092$, revealing that older adults had amplitudes significantly more negative

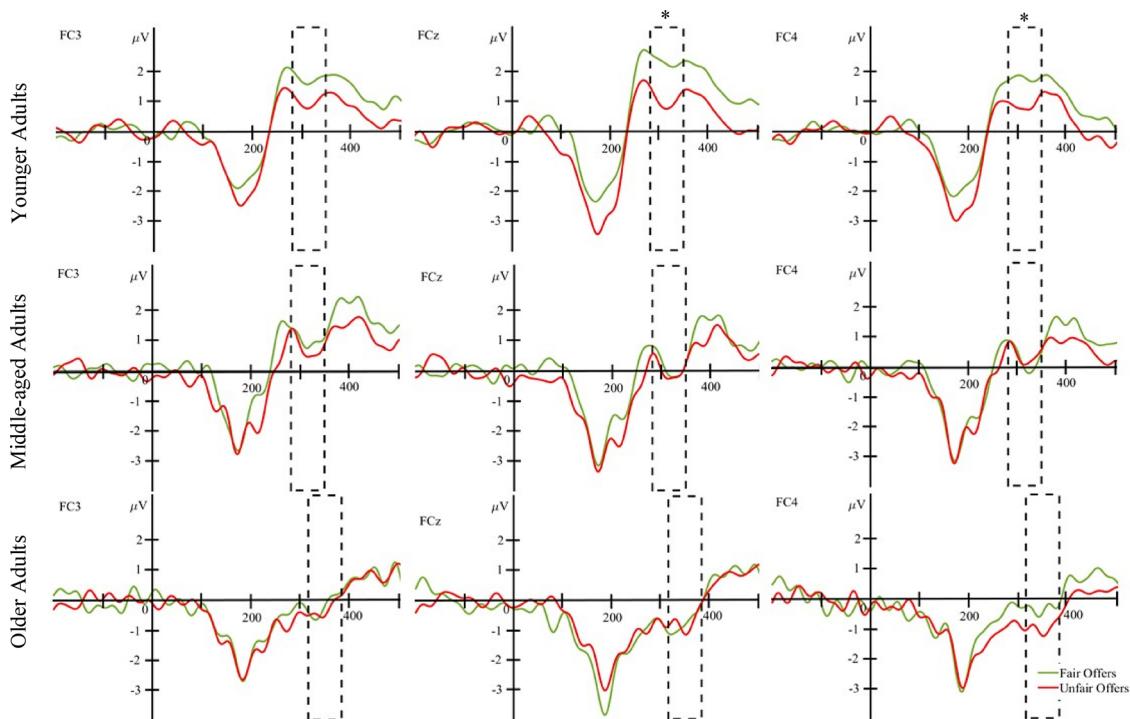


Fig. 2. The green line represents the ERP elicited by fair offers, and the red line represents the ERP elicited by unfair offers. The marked areas depict the time-windows during which the ERPs were measured. Note: *significant differences between conditions (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

than younger adults ($p = .018$). We did not find a main effect of *electrode*, $F(279) = 2.33$, $p = .114$, $\eta_p^2 = .029$, $\varepsilon = 0.79$, but we found a marginally significant main effect of *offer*, $F(279) = 3.23$, $p = .076$, $\eta_p^2 = .039$, revealing that unfair offers elicited amplitudes marginally more negative than fair offers. The interactions *group*electrode*, *group*condition* and *offer*electrode* did not approach significance (all $F < 1.80$; all $p > .132$). However, we found a marginally significant *offer*electrode*group* interaction, $F(4158) = 2.35$, $p = 0.56$, $\eta_p^2 = .056$. This interaction is explained by significant differences between fair and unfair offers only for younger adults at FCz ($p = .007$) and FC4 ($p = .033$), in which unfair offers elicited amplitudes significantly more negative than fair offers. Descriptive statistics of the ERPs are presented in Table 3 of Supplementary Material.

The correlations between the ERPs evoked by fair and unfair offers, the acceptance rates, the fairness ratings and the amount offered in the proposer role were non-significant (all $p > .113$).

3. Discussion

This study aimed to clarify if distinct patterns of decision between younger, middle-aged and older adults in the UG could be explained by different sensitivity to unfairness or by different economic preference. For this purpose, we explored age-related differences in the MFN, which is proposed as an index of unfairness sensitivity.

According to previous studies, we expected higher rates of unfair offers rejection from older adults, which we expected to be explained by a higher sensitivity to unfairness, indexed by higher MFN amplitudes [4,13,14]. We also expected higher offers from older adults.

From an economic standpoint, older adults adopted a more advantageous economic solution [5], accepting more unfair offers than younger adults. This result contrasts with our hypothesis and with previous studies [1,6,7], being in accordance with one study [8]. Experimental differences may explain these contrasting results. For instance, Beadle and colleagues [1] used a naturalistic design of the UG, in which participants played against fixed and real opponents. In their study, although older adults had rejected more unfair offers, they completed the UG with higher payoff than younger adults. This finding reveals that the optimal strategy varies across experimental designs and, in a naturalistic design, where the rejection of unfair offers leads to the increase of proposer's subsequent offers, older responders showed a better strategy, not revealed in non-naturalist designs. Other experimental differences arise from the amount offered during the gambles. In Bailey and colleagues' study [8], as in ours, the amounts offered in both fair and unfair conditions were the same, and the fairness of the gamble was defined by the magnitude of the stake. In previous studies, the stakes had the same magnitude and offers could be fair and slightly, moderately and very unfair. These findings reinforce that decision-making strategies are highly heterogeneous during aging and older adults' economic preferences vary substantially within tasks [2].

Based on these unexpected findings, we explored reaction times to test if older adults' higher acceptance of unfair offers could be attributed to longer reaction times. Longer deliberation has been associated with less prosocial but economically more advantageous choices [40]. Thereby, older adults' decisions could reflect lower impulsivity in the conflict between losing money and accepting unfair offers, or higher cognitive effort to override negative emotional responses to unfairness. However, the reaction times were similar between groups, and the acceptance rates of unfair offers were correlated with worse performance in executive functioning.

Regarding the proposer role, in contrast with Bailey and colleagues' results [8] and with our prediction, all groups offered similar amounts of money. We expected that older adults would give higher amounts of money for being more empathetic than younger and middle-aged adults. Empathy was not manipulated in our tasks, but Beadle and colleagues suggest that it may play a critical role in social decision-making tasks [41].

Regarding the electrophysiological results, we found amplitudes significantly more negative for older than for younger adults. However, while younger adults showed higher amplitudes after unfair than after fair offers, middle-aged and older adults had similar amplitudes after both conditions. This evidence arose from a marginally significant *offer*electrode*group* interaction, but is in line with FRN results, and may explain older adults' higher rates of unfair offers acceptance.

One study found that younger adults had FRN amplitudes more negative after losses than after gains, while older adults had similar amplitudes after both conditions [37]. More interestingly, one study from our group conducted with the same sample, found that middle-aged and older adults had similar FRN amplitudes after losses and non-losses losses, while younger adults showed higher amplitudes after non-losses than after losses [38]. Taken together, these results suggest that middle-aged adults may be at an intermediate level between younger and older adults. Their MFN/FRN were closer to those of the older adults, but their behavioral results were closer to those of the younger adults [38].

The MFN appears to reflect drops in the activity of the mesencephalic dopaminergic neurons after unexpected outcomes, which require an adjustment of the response strategy [18]. These and previous results [37,38] suggest that aging may alter outcome-related expectations, which would affect the reward prediction error and the consequent behavioral adjustment. This interpretation is in accordance with a similar activity of older adults' ACC during the processing of positive and negative feedback [42], and with the decline in the dopaminergic function found during aging [43]. Since middle-aged and older adults had similar MFN results, these features may be a nonspecific pattern of aging, starting during the adult development.

The MFN results add an important interpretation to previous neuroimaging results, which found a lower activation of older adults' anterior insula after unfair offers [4,6]. As this region has been linked to the experience of negative affect, such anger, and disgust [44], their results could link the rejection of unfair offers by older adults to an increased sensitivity to unfairness. However, the slow time course of the BOLD response makes it difficult to distinguish between processes related to the fairness evaluation and processes related to the intention of accept/reject these offers [4]. For instance, insula deactivation may have reflected a negative affect experienced upon receiving unfair offers, but also an aversion to the anticipation of losses resulting from the rejection of unfair offers. In contrast, the higher temporal resolution of ERPs allows the evaluation of processes that are time-locked to offers, and processes such as response preparation or outcome anticipation are unlikely to affect their amplitudes [4].

In conclusion, the present study evidenced that older adults outperformed younger and middle-aged adults, deciding more often for the best economic strategy. Higher rates of unfair offers acceptance may underlie a lack of unfairness sensitivity since older adults had similar ERP amplitudes after fair and unfair offers.

Nevertheless, alternative interpretations must be considered and further tested. For instance, higher acceptance rates of unfair offers may be mediated by the aging positivity effect [43], which postulates that older adults allocate more attention to positive than negative emotional materials. In light of this theory, our results can be interpreted as a lower negative affect attributed to situations typically considered as aversive by younger adults. Moreover, older adults may prioritize social instead of economic rewards, and their need to avoid opponents' loss of money would explain their higher rates of unfair offers acceptance.

Funding

Research supported by Fundação BIAL and Fundação para a Ciência e a Tecnologia (SFRH/BD/112101/2015).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.neulet.2018.10.061>.

References

- [1] J.N. Beadle, S. Paradiso, C. Kovach, L. Polgreen, N.L. Denburg, D. Tranel, Effects of age-related differences in empathy on social economic decision-making, *Int. Psychogeriatr.* 24 (2012) 822–833, <https://doi.org/10.1017/S1041610211002547>.
- [2] R. Mata, A.K. Josef, G.R. Samanez-Larkin, R. Hertwig, Age differences in risky choice: a meta-analysis, *Ann. N. Y. Acad. Sci.* 1235 (2011) 18–29, <https://doi.org/10.1111/j.1749-6632.2011.06200.x>.
- [3] A.G. Sanfey, J.K. Rilling, J.A. Aronson, L.E. Nystrom, J.D. Cohen, The neural basis of economic decision-making in the ultimatum game, *Science* 300 (2003) 1755–1758, <https://doi.org/10.1126/science.1082976>.
- [4] M.A. Boksem, D. De Cremer, Fairness concerns predict medial frontal negativity amplitude in ultimatum bargaining, *Soc. Neurosci.* 5 (2010) 118–128, <https://doi.org/10.1080/17470910903202666>.
- [5] J.B. Vieira, P.R. Almeida, F. Ferreira-Santos, F. Barbosa, J. Marques-Teixeira, A.A. Marsh, Distinct neural activation patterns underlie economic decisions in high and low psychopathy scorers, *Soc. Cogn. Affect. Neurosci.* 9 (2014) 1099–1107, <https://doi.org/10.1093/scan/nst093>.
- [6] K.M. Harlé, A.G. Sanfey, Social economic decision-making across the lifespan: an fMRI investigation, *Neuropsychologia* 50 (2012) 1416–1424, <https://doi.org/10.1016/j.neuropsychologia.2012.02.026>.
- [7] D.R. Roalf, S.H. Mitchell, W.T. Harbaugh, J.S. Janowsky, Risk, reward, and economic decision making in aging, *J. Gerontol. B Psychol. Sci. Soc. Sci.* 67 (2011) 289–298, <https://doi.org/10.1093/geronb/gbr099>.
- [8] P.E. Bailey, T. Ruffman, P.G. Rendell, Age-related differences in social economic decision making: the ultimatum game, *J. Gerontol. B Psychol. Sci. Soc. Sci.* 68 (2013) 356–363, <https://doi.org/10.1093/geronb/gbs073>.
- [9] H. Oosterbeek, S. Randolph, G. Van De Kuilen, Cultural differences in ultimatum game experiments: evidence from a meta-analysis, *Exp. Econ.* 7 (2004) 171–188, <https://doi.org/10.1023/B:EXEC.0000026978.14316.74>.
- [10] E. Fehr, S. Gächter, Altruistic punishment in humans, *Nature* 415 (2002) 137–140, <https://doi.org/10.1038/415137a>.
- [11] M. Maxfield, T. Pyszczynski, J. Greenberg, R. Pepin, H. Davis, The moderating role of executive functioning in older adults' responses to a reminder of mortality, *Psychol. Aging* 27 (2012) 256–263, <https://doi.org/10.1037/a0023902>.
- [12] T.M. Hess, D. Kotter-Grühn, Social knowledge and goal-based influences on social information processing in adulthood, *Psychol. Aging* 26 (2011) 792–802, <https://doi.org/10.1037/a0023775>.
- [13] C. Campanhã, L. Minati, F. Fregni, P.S. Boggio, Responding to unfair offers made by a friend: neuroelectrical activity changes in the anterior medial prefrontal cortex, *J. Neurosci.* 31 (2011) 15569–15574, <https://doi.org/10.1523/JNEUROSCI.1253-11.2011>.
- [14] R. Osinsky, P. Mussel, L. Öhrlein, J. Hewig, A neural signature of the creation of social evaluation, *Soc. Cogn. Affect. Neurosci.* 9 (2013) 731–736, <https://doi.org/10.1093/scan/nst051>.
- [15] W.J. Gehring, A.R. Willoughby, The medial frontal cortex and the rapid processing of monetary gains and losses, *Science* 295 (2002) 2279–2282, <https://doi.org/10.1126/science.1066893>.
- [16] M. Falkenstein, J. Hohnsbein, J. Hoormann, L. Blanke, Effects of errors in choice reaction tasks on the ERP under focussed and divided attention, in: C.H.M. Brunia, A.W.K. Gaillard, A. Kok (Eds.), *Psychophysiological Brain Research*, Tilburg University Press, Netherlands, 1990, pp. 192–195.
- [17] W.H. Miltner, C.H. Braun, M.G. Coles, Event-related brain potentials following incorrect feedback in a time-estimation task: evidence for a “generic” neural system for error detection, *J. Cogn. Neurosci.* 9 (1997) 788–798.
- [18] C.B. Holroyd, M.G. Coles, The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity, *Psychol. Rev.* 109 (2002) 679–709, <https://doi.org/10.1037/0033-295X.109.4.679>.
- [19] S. Freitas, M.R. Simões, I. Santana, Montreal Cognitive Assessment (MoCA): Pontos de corte no Déficit Cognitivo Ligeiro, Doença de Alzheimer, Demência Frontotemporal e Demência Vascular, *Sinapse* 14 (2014) 18–30.
- [20] Z.S. Nasreddine, N.A. Phillips, V. Valérie Bédirian, S.V.W. Charbonneau, I. Collin, J.L. Cummings, H. Chertkow, The Montreal Cognitive Assessment, MoCA: a brief screening tool for mild cognitive impairment, *J. Am. Geriatr. Soc.* 53 (2005) 695–699, <https://doi.org/10.1111/j.1532-5415.2005.53221.x>.
- [21] J. Marco-Pallares, D. Cucurell, T.F. Münte, N. Strien, A. Rodriguez-Fornells, On the number of trials needed for a stable feedback-related negativity, *Psychophysiology* 48 (2011) 852–860.
- [22] S.G. Armitage, An analysis of certain psychological tests used for the evaluation of brain injury, *Psychol. Monogr.* 60 (1946) i–48, <https://doi.org/10.1037/h0093567>.
- [23] S. Cavaco, A. Gonçalves, C. Pinto, E. Almeida, F. Gomes, I. Moreira, J. Fernandes, A. Teixeira-Pinto, Trail making test: regression-based norms for the Portuguese population, *Arch. Clin. Neuropsychol.* 28 (2013) 189–198, <https://doi.org/10.1093/arclin/acs115>.
- [24] H.S. Moreira, C.F. Lima, S.G. Vicente, Examining Executive Dysfunction with the Institute of Cognitive Neurology (INECO) Frontal Screening (IFS): normative values from a healthy sample and clinical utility in Alzheimer's disease, *J. Alzheimers Dis.* 42 (2014) 261–273, <https://doi.org/10.3233/JAD-132348>.
- [25] T. Torralva, M. Roca, E. Gleichgerricht, P. Lopez, F. Manes, INECO Frontal Screening (IFS): a brief, sensitive, and specific tool to assess executive functions in dementia, *J. Int. Neuropsychol. Soc.* 15 (2009) 777–786, <https://doi.org/10.1017/S1355617709990415>.
- [26] D. Wechsler, WMS - III. Escala de memória de Wechsler, CEGOC-TEA, Lisboa, 2008.
- [27] S. Cavaco, A. Gonçalves, C. Pinto, E. Almeida, F. Gomes, I. Moreira, J. Fernandes, A. Teixeira-Pinto, Semantic fluency and phonemic fluency: regression-based norms for the Portuguese population, *Arch. Clin. Neuropsychol.* 28 (2013) 262–271, <https://doi.org/10.1093/arclin/act001>.
- [28] E. Strauss, Sherman E.M., O. Spreen, *A Compendium of Neuropsychological Tests: Administration, Norms, and Commentary*, 3rd ed., Oxford University Press, New York, 2006.
- [29] J. Pais-Ribeiro, I. Silva, T. Ferreira, A. Martins, R. Meneses, M. Baltar, Validation study of a Portuguese version of the hospital anxiety and depression scale, *Psychol. Health Med.* 12 (2007) 225–237, <https://doi.org/10.1080/13548500500524088>.
- [30] R.P. Snaith, A.P. Zigmond, *The Hospital Anxiety and Depression Scale Manual*, NFER-Nelson, Windsor, 1994.
- [31] M.C. Canavarro, Inventário de sintomas psicopatológicos – BSI, in: M.R. Simões, M. Gonçalves, L.S. Almeida (Eds.), *Testes e provas psicológicas em Portugal, SHO/APPORT*, Braga, 1999pp. Vol. II 87–109.
- [32] L.R. Derogatis, BSI: Brief Symptom Inventory, 3rd ed., National Computers Systems, Minneapolis, 1982/1993.
- [33] C. Boake, Édouard claparède and the auditory verbal learning test, *J. Clin. Exp. Neuropsychol.* 22 (2000) 286–292, [https://doi.org/10.1076/1380-3395\(200004\)22:2;1-FT286](https://doi.org/10.1076/1380-3395(200004)22:2;1-FT286).
- [34] S. Cavaco, A. Gonçalves, C. Pinto, E. Almeida, F. Gomes, I. Moreira, J. Fernandes, A. Teixeira-Pinto, Auditory verbal learning test in a large nonclinical Portuguese population, *Appl. Neuropsychol. Adult* 22 (2015) 321–331, <https://doi.org/10.1080/23279095.2014.927767>.
- [35] O. Langner, R. Dotsch, G. Bijlstra, D.H. Wigboldus, S.T. Hawk, A. van Knippenberg, Presentation and validation of the Radboud Faces Database, *Cogn. Emot.* 24 (2010) 1377–1388, <https://doi.org/10.1080/02699930903485076>.
- [36] M.J. Crockett, L. Clark, G. Tabibnia, M.D. Lieberman, T.W. Robbins, Serotonin modulates behavioral reactions to unfairness, *Science* 320 (2008), <https://doi.org/10.1126/science.1155577> 1739–1739.
- [37] Z. Kardos, B. Tóth, R. Boha, B. File, M. Molnár, Age-dependent characteristics of feedback evaluation related to monetary gains and losses, *Int. J. Psychophysiol.* 122 (2017) 42–49, <https://doi.org/10.1016/j.ijpsycho.2016.05.007>.
- [38] C. Fernandes, R. Pasion, A.R. Gonçalves, F. Ferreira-Santos, Barbosa F, I.P. Martins, J. Marques-Teixeira, Age differences in neural correlates of feedback processing after economic decisions under risk, *Neurobiol. Aging* 65 (2018) 51–59, <https://doi.org/10.1016/j.neurobiolaging.2018.01.003>.
- [39] G.A. Rousselet, C.R. Pernet, Improving standards in brain-behavior correlation analyses, *Front. Hum. Neurosci.* 6 (2012) 119, <https://doi.org/10.3389/fnhum.2012.00119>.
- [40] D.G. Rand, J.D. Greene, M.A. Nowak, Spontaneous giving and calculated greed, *Nature* 489 (2012) 427–430, <https://doi.org/10.1038/nature11467>.
- [41] J.N. Beadle, A.H. Sheehan, B. Dahlben, A.H. Gutchess, Aging, empathy, and prosociality, *J. Gerontol. B Psychol. Sci. Soc. Sci.* 70 (2013) 213–222, <https://doi.org/10.1093/geronb/gbt091>.
- [42] K.J. Mathewson, J. Dywan, P.J. Snyder, W.J. Tays, S.J. Segalowitz, Aging and electrocortical response to error feedback during a spatial learning task, *Psychophysiology* 45 (2008) 936–948, <https://doi.org/10.1111/j.1469-8986.2008.00699.x>.
- [43] M. Mather, The affective neuroscience of aging, *Annu. Rev. Psychol.* 67 (2016) 213–238, <https://doi.org/10.1146/annurev-psych-122414-033540>.
- [44] T.F. Denson, W.C. Pedersen, J. Ronquillo, A.S. Nandy, The angry brain: Neural correlates of anger, angry rumination, and aggressive personality, *J. Cogn. Neurosci.* 21 (2018) 734–744, <https://doi.org/10.1162/jocn.2009.21051>.

3. FINAL CONSIDERATIONS

3.1 DISCUSSION

Healthy aging is accompanied by a typical cognitive decline (for a review, see Salthouse, 2009), but also by an increased positive affect (for a review, see Mather, 2016). Considering the role of emotional and cognitive abilities in social cognition and decision-making (Liebherr, Schiebener, Averbek, & Brand, 2017; Penn, Corrigan, Bental, Racenstein, & Newman, 1997), the first evidence would lead to predictions of deficits in social cognition and decision-making during aging, while the later would lead to opposing predictions. These conflicting predictions are, in fact, in agreement with conflicting findings of both impaired (e.g., Castelli et al., 2010) and preserved social cognitive (e.g., Happé, Winner, & Brownell, 1998) and decisional abilities (e.g., Keightley, Winocur, Burianova, Hongwanishkul, & Grady, 2006), highlighting the importance of clarifying the effects of aging on these constructs.

Thereby, the main goal of the present investigation was to examine how social cognitive and decisional abilities, as well as their neural correlates, are altered by aging. Additionally, we aimed to investigate the correlation between these and neurocognitive abilities, bearing in mind that the relationship between social and neurocognition is not yet consensual (Couture, Penn, & Roberts, 2006). In order to increase the consistency in the terminology, to simplify the communication among researchers, and to facilitate inferences across studies, we adopted the framework proposed by the NIMH, which divides social cognition into domains of emotional identification, ToM, and social perception and knowledge (Green et al., 2008). Based on the definitions of each domain, we built three experimental tasks that were performed by a sample of younger, middle-aged and older adults.

Considering that aging also affects economic decision-making (Mata, Josef, Samanez-Larkin, & Hertwig, 2011) and that the neural mechanisms underlying such age-related differences are still scarcely known, we also included two experimental tasks that assessed decisions under risky and in social contexts.

In each task, we assessed the behavioral responses (reaction times, accuracy rates, economic choices) and neural correlates (event-related potentials) induced by social and affective relevant stimuli.

Chapter 2.1 reported the empirical study conducted to examine age-related differences in emotional identification (Gonçalves et al., 2018b). Emotional identification was assessed through a task in which participants identified categorical emotions displayed in facial expressions, rating also their levels of arousal and valence. Regarding neural responses, groups were compared on the processing of facial features and emotional content of the faces, presumably indexed by the N170 and N250 components (Wynn, Lee, Horan, & Green, 2008).

Our results showed an equivalent performance between groups, which was surprising considering a substantial set of literature. For instance, two meta-analysis showed that older adults were less accurate than younger adults at identifying anger, fear, sadness (Gonçalves et al., 2018a; Ruffman, Henry, Livingstone, & Phillips, 2008) and surprise (Gonçalves et al., 2018a), had a comparatively small impairment in identifying happiness (Gonçalves et al., 2018a; Ruffman et al., 2008) and no impairment at identifying disgust (Gonçalves et al., 2018a; Ruffman et al., 2008). Several aspects may explain these previous findings, from age-related differences in the neural function to age-related differences in the face-exploration strategy. For instance, older adults worse performance may be related to a reduced neural specialization of the ventral visual cortex for faces (Park et al., 2004), reduced activity in the fusiform face area (Goh, Suzuki, & Park, 2010; Dennis et al., 2008), and reduced structural integrity of the white matter tracts that pass through the right fusiform gyrus (Thomas et al., 2008). Nonetheless, these neural changes do not explain the specific pattern found for each discrete emotion, which is more compatible with a shift in the strategy of face-exploration (Mather, 2016).

In this matter, several studies showed that older adults were less likely than younger to look at the eyes, more likely to look at the mouth/nose (e.g., Birmingham, Svärd, Kanan, & Fischer, 2018; Circelli, Clark, & Cronin-Golomb, 2013; Firestone, Turk-Browne, & Ryan, 2007; Heisz & Ryan 2011; Murphy & Isaacowitz 2010; Sullivan, Ruffman, & Hutton, 2007; Wong, Cronin-Golomb, & Neargarder, 2005), and less accurate at detecting changes in the eye than in the mouth/nose region of the face (Chaby, Narme, & George, 2011; Slessor, Riby, & Finnerty, 2013). It is worth mentioning that these differences were found for faces, but not for scenes (Circelli et al., 2013).

These differential search strategies may affect the identification of emotional facial expressions, as evidenced in research with younger adults. These studies showed that fear, sadness, and anger are more recognized from the upper half of the face, whereas happiness and disgust are more recognizable from the lower half of the face (Calder, Young, Keane, & Dean, 2000). Surprise did not show a strong top-bottom bias (Calder et al., 2000), which may explain the inconsistent results found for this emotion in both meta-analyses (Gonçalves et al., 2018a; Ruffman et al., 2008). Additionally, one study also found that, among older adults, observing the upper half of the face predicted better identification of anger, fear, and sadness, while looking at the lower half of the face predicted better identification of disgust and happiness. Surprise did not show significant correlations with any of the looking pattern (Wong et al., 2005).

The results of our study are surprising when integrated in the literature (Gonçalves et al., 2018a; Ruffman et al., 2008), but they may be explained by the electrophysiological results. We found that all groups had similar P100 amplitudes, suggestive of similar basic visual processing, but older adults had higher N170 amplitudes than younger adults. This result is consistent with the compensation hypothesis (Cabeza, 2002; Reuter-Lorenz & Cappell, 2008), which suggests that additional neural activity serves a beneficial, compensatory function, without which a performance decline would occur. However, older adults also had lower N250 amplitudes than younger adults, suggesting deficits in facial feature decoding abilities (Wynn et al., 2008). Such age-related underactivation is typically interpreted as a sign of impaired strategies or structural atrophy (Reuter-Lorenz & Cappell, 2008) but, in our study, it was not manifested in a poorer performance. This evidence may suggest that the N170 has a higher contribution to the identification of facial expressions of emotion than N250.

Interestingly, these neurophysiological age-related changes appear to occur gradually across the adult lifespan, since significant differences in Event-related Potential (ERP) components arose only between younger and older adults. Moreover, the emotional identification abilities appear to be independent of the cognitive abilities assessed, since none of the results in the neurocognitive tests were predictors of the performance in our emotion identification task.

Chapter 2.2 reported the empirical study conducted to assess Theory of Mind (ToM; Fernandes et al., 2019b). This task was built to examine perspective-taking abilities, which are considered an indispensable element in the fully developed, mature ToM (Decety & Jackson, 2004). During this task, participants observed scenarios showing the interaction between two persons. One of these persons was masked, and participants must infer his/her affective mental state. Then, a target FEE was displayed, and participants decided if that emotion was congruent or incongruent with the emotion that they inferred. Through this experimental manipulation, we investigated perspective-taking abilities over the accuracy rates, while we assessed how these abilities modulated two ERP components that are typically influenced by the affective and evaluative congruency: the N170 and the Late Positive Potential (LPP, Díezguis-Risco, Aguado, Albert, & Hinojosa, 2013; 2015).

The results obtained with this experimental task showed that older adults had worse behavioral performance than younger and middle-aged adults. The results obtained in the congruent trials (those in which the emotion displayed in the target was congruent with the emotion portrayed in the scenario) were significantly predicted by better executive functioning for younger adults, being predicted by better working memory for older adults. The results obtained in incongruent trials (those in which the emotion displayed in the target was incongruent with the emotion portrayed in the scenario) were predicted by better executive function, but only for older adults.

Consistently with the results reported in chapter 2.1, older adults had N170 amplitudes significantly higher than younger adults, and marginally higher than middle-aged adults. However, this ERP component was not modulated by the congruency between the emotional contexts and the targets FEE. Regarding the LPP, while younger and middle-aged adults showed higher amplitudes after targets congruent with previous scenarios than after incongruent targets, older adults had similar amplitudes after both.

As the LPP is modulated by the explicit recognition of stimuli, being larger to recognized stimuli in comparison to new (Danker et al., 2008; Münte, Urbach, Duzel & Kutas, 2000), we interpreted the increased amplitudes found for younger and middle-aged adults after congruent targets as a recognition of the masked person's emotion in those displayed by the target. Moreover, this recruitment of memory resources to

perform this task is consistent with the influence of executive functioning and working memory in the behavioral results.

According to this interpretation, older adults' results may be understood as a difficulty in inferring accurate emotional states during the visualization of the scenarios. That is, while younger and middle-aged adults were able to infer the appropriate actor's emotional state during the observation of the scenario, which they maintained in working memory and then compared with the emotion displayed in the target, older adults only reached the correct answer after observing the target, which might act as a clue. In other words, younger and middle-aged adults were able to infer the emotions of a masked intervener, a process that modulated the LPP component, with higher amplitudes for targets congruent with those that were inferred. This modulation was absent in older adults, even bearing in mind that the ERPs analysed were those elicited by the correct responses. Such absence may suggest that older adults reached a successful performance by a strategy that was different from those of the other groups. Possibly, older adults reached the correct responses after observing the target, by a process of emotional recognition instead of emotional inference. This interpretation is coherent with the findings of a preserved emotional identification observed in the first study (chapter 2.1; Gonçalves et al., 2018b), but may underlie older adults' difficulties in taking others' emotional perspective, or in understanding the relation between others' mental states and ongoing events.

Chapter 2.3 reported the empirical study conducted to assess social perception (Pasion et al., 2018). In this study, we used a modified version of a standard Intention Inference Task (Decety & Cacioppo, 2012), in which participants observed sets of three-frame video clips. The first frame established the scene; the second displayed an individual hurting another intentionally or accidentally; and the third allowed observers to confirm the intentionality of the action. Participants were asked to judge the intentionality of the harm after the second frame, and we assessed how the social transgressions modulated the P2, N2 and LPP, which appear to reflect respectively selective attention (Johannes, Münte, Heinze, & Mangun, 1995), moral engagement (Cui, Ma, & Luo, 2016; Petras, ten Oever, & Jansma., 2016), and processes involved in moral cognition (Wagner, Chaves, & Wolff, 2017).

Results showed that older adults were less accurate than younger adults in rating the intentionality of the harm, both in intentional or accidental conditions, suggesting an age-related difficulty in evaluating the intentionality of social transgressions. Regarding the electrophysiological results, older adults had higher P2 amplitudes than younger adults for intentional harms, and this finding is consistent with previous literature (e.g., Anderer, Semlitsch, & Saletu, 1996; Getzmann, Golob, & Wascher, 2016; Iragui, Kutas, Mitchiner, & Hillyard, 1993; West & Alain, 2000), and suggestive of a progressive age-related deficit to withdraw attentional resources from stimuli (Crowley & Colrain, 2004).

Interestingly, the increased P2 amplitude found for older adults after the first frame of the intentional condition was predictive of lower performance in tests assessing executive functioning. Based on this result, we hypothesized that the increased allocation of attentional resources to the task, as reflected by the enhanced P2 amplitude in older adults, may constitute a compensatory mechanism of frontal executive deficits in later life. However, contrarily to what we found in our emotional identification task, this augmented recruitment of neural resources was not accompanied by an equivalent performance. Thus, these behavioral results may be rather explained by an older adults' reduction of the N2 and LPP amplitudes. Specifically, regarding the N2 and in comparison with younger adults, older adults had a reduced amplitude in both frames displaying intentional and accidental harms, a result consistent with previous findings (Getzmann, et al., 2016; Getzmann, Jasny, & Falkenstein, 2017; Iragui et al., 1993). Regarding the LPP, younger adults had higher amplitudes than older adults during the second frame showing intentional harm. Thereby, the N2 and LPP results are consistent and in accordance with previous findings of an age-related decline in emotional processing (Renfroe, Bradley, Sege, & Bowers, 2016).

Taken together, the results of this study may suggest distinct neural correlates of intentionality assessment across the lifespan. Specifically, older adults seem to allocate more attention to the scenarios, but younger adults appear to evaluate more effectively the intentions of harmful social transgressions (Pasion et al., 2018).

The worse performance of older adults in this task is not surprising if we consider their worse results in the perspective-taking task (chapter 2.2, Fernandes et al., 2019). In fact, judgments of intentionality of social or moral transgressions are modulated by ToM (Killen, Mulvey, Richardson, Jampol, & Woodward, 2011). That is, while ToM is necessary for basic social interactions, exercising ToM to make social and moral judgments is necessary for more complex social interactions. For instance, several studies suggest that being able to judge someone's culpability for a criminal act requires an understanding of that person's intention during the act (Young, Cushman, Hauser, & Saxe, 2007). Moreover, basic ToM and moral decision-making tasks activate similar neural networks (Moran, Jolly, & Mitchell, 2012), and intact ToM is a persecutor of moral judgments during development (Moran, 2013).

Finally, economic decision-making was assessed through two experiments, presented in chapters 2.4 and 2.5. This domain is not included in the definition of social cognition, but it can be significantly influenced by social cognitive abilities, considering that several economic decisions are made in social contexts. Moreover, the investigation in this field has a significant impact, bearing in mind the increasingly proportion of older adults in the global population. Older adults face significant economic challenges daily, and poor decision-making may have severe consequences at this stage of life due to limited time and resources to overcome from negative choices (Beadle, Sheehan, Dahlben, & Gutches, 2013).

Chapter 2.4 reported the empirical study conducted to examine age-related differences in risk aversion (Fernandes et al., 2018). To this purpose, we built a task composed by a set of gambles that required a decision between two risky options. In addition, we studied the neural mechanisms underlying feedback processing, through the analysis of the Feedback-related Negativity (FRN), an ERP component sensitive to expectancy violations, and the feedback-P3, which is sensitive to the arousing nature of the feedback (San Martín, 2012).

Our results showed that older adults were less risk-averse than younger adults in the loss domain, preferring smaller losses associated with higher probabilities of losing. This decision pattern was correlated with poorer performance in memory and executive functions. A further analysis conducted specifically in the loss domain showed that, while younger and middle-aged adults had higher rates of risk-averse decisions

after non-losses than after losses, older adults preserved their risk preferences independently of the previous feedback. Together with previous findings (Mather et al., 2012; Pachur, Mata, & Hertwig, 2016), these results appear to suggest that aging is accompanied by a reduction in loss aversion.

Regarding electrophysiological results, we found group-related differences in both ERP components analyzed. Specifically, in the loss domain, younger adults showed higher FRN amplitudes after non-losses than after losses, while middle-aged and older adults had similar FRN amplitudes after both. In the gain domain, younger and middle-aged adults had higher feedback-P3 amplitude after gains than after non-gains, while older adults had similar feedback-P3 amplitudes after both.

The FRN appears to reflect a signaling of the basal ganglia to the anterior cingulate cortex (ACC), through phasic drops in the activity of the mesencephalic dopaminergic neurons after unexpected outcomes that require an adjustment of the response strategy (Holroyd & Coles, 2002; Oliveira, McDonald, & Goodman, 2007). Together with previous findings (Kardos, Tóth, Boha, File, & Molnár, 2017; West, Tiernan, Kieffaber, Bailey, & Anderson, 2014), these results suggest that aging alters outcome-related expectations, which would impact the reward prediction error and the consequent behavioral adjustment. This interpretation is in accordance with a similar activity of older adults' ACC in the processing of positive and negative feedback during a learning task (Mathewson, Dywan, Snyder, Tays, & Segalowitz, 2008), as well as with the decline in the dopaminergic function found during aging (Mather, 2016). Moreover, it appears to receive support from our behavioral results. In fact, we found that younger adults had higher rates of risk-averse decisions after non-losses than after losses, which may be interpreted as a performance adjustment that was absent in older adults.

The results obtained in the feedback-P3 contrast with the results of three previous studies (Di Rosa et al., 2017; Kardos et al., 2017; West et al., 2014), which might be driven by methodological differences. That is, while our task assessed decision-making under risk, these studies assessed decision-making under uncertainty, in which the probabilities were unknown. The P3 amplitude is highly modulated by the subjective probability of the eliciting stimuli (Nieuwenhuis, 2011), being larger for less probable stimuli (e.g., Bellebaum & Daum, 2008). However, beyond the probability, other factors modulate the P3 amplitude, such as the arousing level of the stimuli. Thereby, in our

task, feedback-P3 were more likely to be modulated by the arousing level of the feedback than by its probability. As we found higher feedback-P3 amplitudes after gains than after non-gains for younger and middle-aged adults, but not for older adults, this suggests age-related differences in the affective relevance attributed to the outcomes or, in an alternative interpretation, age-related difficulties in adapting the processing priorities to the task goals.

Chapter 2.5 reported the empirical study conducted to assess decision-making in social context (Fernandes et al., 2019a). To this purpose, we examined participants' performance in the Ultimatum Game (UG; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003), in the responder and proposer role. Moreover, we assessed the Medial Frontal Negativity (MFN) during the visualization of fair and unfair offers, since this ERP component was recently proposed as an index of unfairness sensitivity (Boksem & De Cremer, 2010).

From an economic standpoint, our results evidenced that older adults adopted the more advantageous economic solution, accepting more unfair offers than younger and middle-aged adults (Vieira et al., 2014). However, these acceptance rates were positively correlated with worse executive functions. Moreover, in the proposer role, all groups offered similar amounts of money to their counterparts. Regarding the electrophysiological results, while younger adults showed higher amplitudes after unfair than fair offers, middle-aged and older adults had similar amplitudes after both conditions, which is suggestive of an insensitive to unfairness form these groups.

The results obtained for the MFN are in line with the FRN results, and may explain older adults' higher rates of unfair offers acceptance. In fact, both components are belonging to a family of ERPs generated in the ACC (Falkenstein, Hohnsbein, Hoormann & Blanke, 1990; Gehring & Willoughby, 2002), and both suggest that aging may alter outcome-related expectations, the reward prediction error and the consequent behavioral decision-making.

3.2 CONCLUSIONS

The present research evidenced that aging affects some domains of social cognition, preserving others. Specifically, aging appears to preserve emotional identification abilities, which appears to be mediated by an increased (eventually compensatory) neural processing of structural and emotional features of the face. However, aging appears to affect perspective-taking abilities, which are essential to an unimpaired ToM. In our task, even in those trials in which older adults reached an accurate performance, their neural activity pointed to different processing of the socially relevant stimuli, leading us to hypothesize that, while younger and middle-aged adults performed the task using an emotional inference strategy, older adults performed the task using a recognition strategy.

The task that assessed social perception also evidenced that older adults had an impaired performance in judging the intentionality of social transgressions. Such result was reached even with electrophysiological results pointing to an increased allocation of attentional resources to the task. However, older adults showed reduced amplitudes in two ERP components that appear to underlie the evaluation of intentions of harmful transgressions. The results of this task may be mediated by the results obtained in our perspective-taking task, bearing in mind that perspective-taking is necessary to judge the intentionality of a social or moral transgression.

Despite the worse behavioral performance in these tasks, older adults showed a more advantageous strategy in our social economic task. However, such strategy may result from an age-related decline in the neural responses to unfair offers, as shown by a MFN with similar amplitudes after fair and unfair offers. In the same way, older adults showed similar FRN amplitudes after losses and non-losses in a decision-making task under risk, which may also explain lower risk-aversion of this group. This later task also showed that older adults appear to attribute equal affective relevance to gains and non-gains, as shown by similar feedback-P3 amplitudes after both types of feedback.

Interestingly, none of these findings appear to be specific of older adults. In fact, middle-aged adults were in an intermediate level between younger and older adults in all the tasks, both in behavioral as in neural responses to socially relevant cues. This suggests that the effect of aging on social cognition starts earlier in adult development, similarly to what happens to several neurocognitive processes.

With the exception of the emotional identification task, neurocognitive abilities (specifically working memory and executive functioning) were correlated with social cognitive and decisional abilities. This finding is in accordance with previous results showing that neurocognition and social cognition are related, but different constructs.

3.3 FUTURE PERSPECTIVES

Social cognition encompasses the processing of information that is relevant to guide social behavior. However, most information is relevant for social behavior, making social cognition a term that is too general to be useful (Adolphs, 2006). In order to make this construct more measurable, researchers generally divide this domain into several sub-domains, studying these sub-domains separately. When we realize that we are studying such a broad construct, we can conclude that much remains to be done. Particularly, future studies are needed to assess the effects of aging on social cognition, using other types of tasks or focused on other sub-domains. Moreover, within the definition of social cognition, we still lack studies clarifying the hierarchical relationship of its sub-domains. That is, understanding the hierarchical relation of the different sub-domains of social cognition can be important as a therapeutic target in several populations with social cognition deficits.

In this sense, the relation between social cognition and neurocognition is still ambiguous, with researchers in the field being divided into generally polarized opinions. On one side, there are neuroscientists arguing that social information is processed independently from non-social information. On the other, there are those who argue that social cognition is simply cognition, but applied to social stimuli (Adolphs, 2006).

There may be no single answer to this question, but the current perspective is to consider social cognition as a construct that interlinks with neurocognition, often sharing the same neural underpinnings. Yet, it is reasonable to think that it comprises computational mechanisms that are dedicated to guide social behavior, some of these being relatively involuntary, automatic, and relying on neural structures that can be specialized in social cognition (Adolphs, 2006). Thereby, the relationship between social cognition and neurocognition needs to be better understood, and this knowledge may also have important therapeutic implications.

Finally, we have learned from clinical populations that deficits in social cognition have a detrimental impact on social functioning and decision-making (Marques-Teixeira, 2007). Bearing this in mind, the step beyond the characterization of social cognition during aging is to investigate its potential impact on social functionality and daily life abilities. Furthermore, the characterization of social cognition in healthy aging may have a significant impact in characterizing social cognition in pathological aging, which may be useful for the differential diagnosis.

3.4 REFERENCES

- Adolphs, R. (2006). What Is Special about Social Cognition?. In J. T. Cacioppo, P. S. Vlisser, & C. L. Pickett (Eds.), *People thinking about thinking people* (pp. 269-285). Cambridge, Massachusetts: MIT Press.
- Anderer, P., Semlitsch, H. V., & Saletu, B. (1996). Multichannel auditory event-related brain potentials: effects of normal aging on the scalp distribution of N1, P2, N2 and P300 latencies and amplitudes. *Electroencephalography and Clinical Neurophysiology*, 99(5), 458-472. [http://dx.doi.org/10.1016/S0013-4694\(96\)96518-9](http://dx.doi.org/10.1016/S0013-4694(96)96518-9)
- Beadle, J. N., Sheehan, A. H., Dahlben, B., & Gutchess, A. H. (2013). Aging, empathy, and prosociality. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, 70(2), 213-222. <http://dx.doi.org/10.1093/geronb/gbt091>
- Bellebaum, C., & Daum, I. (2008). Learning-related changes in reward expectancy are reflected in the feedback-related negativity. *European Journal of Neuroscience*, 27(7), 1823-1835. <http://dx.doi.org/10.1111/j.1460-9568.2008.06138.x>
- Birmingham, E., Svärd, J., Kanan, C., & Fischer, H. (2018). Exploring emotional expression recognition in aging adults using the Moving Window Technique. *PloS One*, 13(10), e0205341. <http://dx.doi.org/10.1371/journal.pone.0205341>
- Boksem, M. A., & De Cremer, D. (2010). Fairness concerns predict medial frontal negativity amplitude in ultimatum bargaining. *Social Neuroscience*, 5(1), 118-128. <http://dx.doi.org/10.1080/17470910903202666>

- Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: the HAROLD Model. *Psychology and Aging, 17*(1), 85-100. <http://dx.doi.org/10.1037//0882-7974.17.1.85>
- Calder, A. J., Young, A. W., Keane, J., & Dean, M. (2000). Configural information in facial expression perception. *Journal of Experimental Psychology: Human Perception and Performance, 26*(2), 527-551. <http://dx.doi.org/10.1037/0096-1523.26.2.527>
- Castelli, I., Baglio, F., Blasi, V., Alberoni, M., Falini, A., Liverta-Sempio, O., ... & Marchetti, A. (2010). Effects of aging on mindreading ability through the eyes: an fMRI study. *Neuropsychologia, 48*(9), 2586-2594. <http://dx.doi.org/10.1016/j.neuropsychologia.2010.05.005>
- Chaby, L., Narme, P., & George, N. (2011). Older adults' configural processing of faces: Role of second-order information. *Psychology and Aging, 26*(1), 71-79. <http://dx.doi.org/10.1037/a0020873>
- Circelli, K. S., Clark, U. S., & Cronin-Golomb, A. (2013). Visual scanning patterns and executive function in relation to facial emotion recognition in aging. *Aging, Neuropsychology, and Cognition, 20*(2), 148-173. <http://dx.doi.org/10.1080/13825585.2012.675427>
- Couture, S. M., Penn, D. L., & Roberts, D. L. (2006). The functional significance of social cognition in schizophrenia: a review. *Schizophrenia Bulletin, 32*(1), 44-63. <http://dx.doi.org/10.1093/schbul/sbl029>
- Crowley, K. E., & Colrain, I. M. (2004). A review of the evidence for P2 being an independent component process: age, sleep and modality. *Clinical Neurophysiology, 115*(4), 732-744. <http://dx.doi.org/10.1016/j.clinph.2003.11.021>
- Cui, F., Ma, N., & Luo, Y. J. (2016). Moral judgment modulates neural responses to the perception of other's pain: an ERP study. *Scientific Reports, 6*, 1-8.
- Danker, J. F., Hwang, G. M., Gauthier, L., Geller, A., Kahana, M. J., & Sekuler, R. (2008). Characterizing the ERP Old–New effect in a short-term memory task. *Psychophysiology, 45*(5), 784-793. <http://dx.doi.org/10.1111/j.1469-8986.2008.00672.x>

- Decety, J., & Cacioppo, S. (2012). The speed of morality: a high-density electrical neuroimaging study. *Journal of Neurophysiology*, 108(11), 3068-3072.
<http://dx.doi.org/10.1152/jn.00473.2012>
- Decety, J., & Jackson, P. L. (2004). The functional architecture of human empathy. *Behavioral and Cognitive Neuroscience Reviews*, 3(2), 71-100.
<http://dx.doi.org/10.1177/1534582304267187>
- Dennis, N. A., Hayes, S. M., Prince, S. E., Madden, D. J., Huettel, S. A., & Cabeza, R. (2008). Effects of aging on the neural correlates of successful item and source memory encoding. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 34(4), 791-808. <http://dx.doi.org/10.1037/0278-7393.34.4.791>
- Di Rosa, E., Mapelli, D., Arcara, G., Amodio, P., Tamburin, S., & Schiff, S. (2017). Aging and risky decision-making: New ERP evidence from the Iowa Gambling Task. *Neuroscience Letters*, 640, 93-98.
<http://dx.doi.org/10.1016/j.neulet.2017.01.021>
- Diéguez-Risco, T., Aguado, L., Albert, J., & Hinojosa, J. A. (2013). Faces in context: modulation of expression processing by situational information. *Social Neuroscience*, 8(6), 601–620. <http://dx.doi.org/10.1080/17470919.2013.834842>
- Diéguez-Risco, T., Aguado, L., Albert, J., & Hinojosa, J. A. (2015). Judging emotional congruency: Explicit attention to situational context modulates processing of facial expressions of emotion. *Biological Psychology*, 112, 27-38.
<http://dx.doi.org/10.1016/j.biopsycho.2015.09.012>
- Falkenstein, M., Hohnsbein, J., Hoormann, J., & Blanke, L. (1990). Effects of errors in choice reaction tasks on the ERP under focussed and divided attention. In C. H. M. Brunia, A. W. K. Gaillard, & A. Kok (Eds.), *Psychophysiological brain research* (pp. 192-195). Tilburg, The Netherlands: Tilburg University Press.
- Fernandes, C., Gonçalves, A. R., Pasion, R., Ferreira-Santos, F., Barbosa, F., Martins, I. P., & Marques-Teixeira, J. (2019). Age-related changes in social decision-making: An electrophysiological analysis of unfairness evaluation in the Ultimatum Game. *Neuroscience Letters*, 692, 122-126.
<http://dx.doi.org/10.1016/j.neulet.2018.10.061>
- Fernandes, C., Gonçalves, A. R., Pasion, R., Ferreira-Santos, F., Barbosa, F., Martins, I. P., & Marques-Teixeira, J. (2019). Age-related decline in emotional perspective-

- taking: its effect on the Late Positive Potential. *Cognitive, Affective, & Behavioral Neuroscience*, 19, 109-122. <http://dx.doi.org/10.3758/s13415-018-00648-1>
- Fernandes, C., Pasion, R., Gonçalves, A. R., Ferreira-Santos, F., Barbosa, F., Martins, I. P., & Marques-Teixeira, J. (2018). Age differences in neural correlates of feedback processing after economic decisions under risk. *Neurobiology of Aging*, 65, 51-59. <http://dx.doi.org/10.1016/j.neurobiolaging.2018.01.003>
- Firestone, A., Turk-Browne, N. B., & Ryan, J. D. (2007). Age-related deficits in face recognition are related to underlying changes in scanning behavior. *Aging, Neuropsychology, and Cognition*, 14(6), 594-607. <http://dx.doi.org/10.1080/13825580600899717>
- Gehring, W. J., & Willoughby, A. R. (2002). The medial frontal cortex and the rapid processing of monetary gains and losses. *Science*, 295(5563), 2279-2282. <http://dx.doi.org/10.1126/science.1066893>
- Goh, J. O., Suzuki, A., & Park, D. C. (2010). Reduced neural selectivity increases fMRI adaptation with age during face discrimination. *Neuroimage*, 51(1), 336-344. <http://dx.doi.org/10.1016/j.neuroimage.2010.01.107>
- Gonçalves, A. R., Fernandes, C., Pasion, R., Ferreira-Santos, F., Barbosa, F., & Marques-Teixeira, J. (2018a). Effects of age on the identification of emotions in facial expressions: a meta-analysis. *PeerJ*, 6, 1-19. <http://dx.doi.org/10.7717/peerj.5278>
- Gonçalves, A. R., Fernandes, C., Pasion, R., Ferreira-Santos, F., Barbosa, F., & Marques-Teixeira, J. (2018b). Emotion identification and aging: Behavioral and neural age-related changes. *Clinical Neurophysiology*, 129(5), 1020-1029. <http://dx.doi.org/10.1016/j.clinph.2018.02.128>
- Green, M. F., Penn, D. L., Bentall, R., Carpenter, W. T., Gaebel, W., Gur, R. C., ... & Heinssen, R. (2008). Social cognition in schizophrenia: an NIMH workshop on definitions, assessment, and research opportunities. *Schizophrenia Bulletin*, 34(6), 1211-1220. <http://dx.doi.org/10.1093/schbul/sbm145>
- Getzmann, S., Golob, E. J., & Wascher, E. (2016). Focused and divided attention in a simulated cocktail-party situation: ERP evidence from younger and older

- adults. *Neurobiology of Aging*, 41, 138-149.
<http://dx.doi.org/10.1016/j.neurobiolaging.2016.02.018>
- Getzmann, S., Jasny, J., & Falkenstein, M. (2017). Switching of auditory attention in “cocktail-party” listening: ERP evidence of cueing effects in younger and older adults. *Brain and Cognition*, 111, 1-12.
<http://dx.doi.org/10.1016/j.bandc.2016.09.006>
- Happé, F. G., Winner, E., & Brownell, H. (1998). The getting of wisdom: theory of mind in old age. *Developmental Psychology*, 34(2), 358-362.
<http://dx.doi.org/10.1037/0012-1649.34.2.358>
- Heisz, J. J., & Ryan, J. D. (2011). The effects of prior exposure on face processing in younger and older adults. *Frontiers in Aging Neuroscience*, 3, 1-6.
<http://dx.doi.org/10.3389/fnagi.2011.00015>
- Holroyd, C. B., Coles, M. G. (2002). The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychological Reviews*, 109(4), 679-709.
<http://dx.doi.org/10.1111/j.1469-8986.1993.tb03200.x>
- Iragui, V. J., Kutas, M., Mitchiner, M. R., & Hillyard, S. A. (1993). Effects of aging on event-related brain potentials and reaction times in an auditory oddball task. *Psychophysiology*, 30(1), 10-22. . <http://dx.doi.org/10.1111/j.1469-8986.1993.tb03200.x>
- Johannes, S., Münte, T. F., Heinze, H. J., & Mangun, G. R. (1995). Luminance and spatial attention effects on early visual processing. *Cognitive Brain Research*, 2(3), 189-205. [http://dx.doi.org/10.1016/0926-6410\(95\)90008-X](http://dx.doi.org/10.1016/0926-6410(95)90008-X)
- Kardos, Z., Tóth, B., Boha, R., File, B., & Molnár, M. (2017). Age-dependent characteristics of feedback evaluation related to monetary gains and losses. *International Journal of Psychophysiology*, 122(4), 42-49.
<http://dx.doi.org/10.1037/0033-295X.109.4.679>
- Keightley, M. L., Winocur, G., Burianova, H., Hongwanishkul, D., & Grady, C. L. (2006). Age effects on social cognition: faces tell a different story. *Psychology and Aging*, 21(3), 558-572. <http://dx.doi.org/10.1037/0882-7974.21.3.558>

- Killen, M., Mulvey, K. L., Richardson, C., Jampol, N., & Woodward, A. (2011). The accidental transgressor: Morally-relevant theory of mind. *Cognition*, 119(2), 197-215. <http://dx.doi.org/10.1016/j.cognition.2011.01.006>
- Liebherr, M., Schiebener, J., Averbek, H., & Brand, M. (2017). Decision Making under Ambiguity and Objective Risk in Higher Age—A Review on Cognitive and Emotional Contributions. *Frontiers in Psychology*, 8, 1-12. <http://dx.doi.org/10.3389/fpsyg.2017.02128>
- Marques-Teixeira, J. (2007). Neurocognição, cognição social e funcionamento social na esquizofrenia. *Mental Health*, 9(6), 7-10.
- Mata, R., Josef, A. K., Samanez-Larkin, G. R., & Hertwig, R. (2011). Age differences in risky choice: A meta-analysis. *Annals of the New York Academy of Sciences*, 1235(1), 18-29. <http://dx.doi.org/10.1111/j.1749-6632.2011.06200.x>.
- Mather, M. (2016). The affective neuroscience of aging. *Annual Review of Psychology*, 67, 1-26. <http://dx.doi.org/10.1146/annurev-psych-122414-033540>.
- Mather, M., Mazar, N., Gorlick, M. A., Lighthall, N. R., Burgeno, J., Schoeke, A., & Ariely, D. (2012). Risk preferences and aging: The “certainty effect” in older adults' decision making. *Psychology and Aging*, 27(4), 801-816. <http://dx.doi.org/10.1037/a0030174>
- Mathewson, Dywan, J., Snyder, P.J., Tays, W.J., Segalowitz, S.J. (2008). Aging and electrocortical response to error feedback during a spatial learning task. *Psychophysiology*, 45(8), 936-948. <http://dx.doi.org/10.1111/j.1469-8986.2008.00699.x>
- Moran, J. M. (2013). Lifespan development: The effects of typical aging on theory of mind. *Behavioural Brain Research*, 237, 32-40. <http://dx.doi.org/10.1016/j.bbr.2012.09.020>
- Moran, J. M., Jolly, E., & Mitchell, J. P. (2012). Social-cognitive deficits in normal aging. *Journal of Neuroscience*, 32(16), 5553-5561. <http://dx.doi.org/10.1523/JNEUROSCI.5511-11.2012>.
- Münter, T. F., Urbach, T. P., Duzel, E., & Kutas, M. (2000). Event-related brain potentials in the study of human cognition and neuropsychology. In F. Boller, G. J., & G.

- Rizzolatti (Eds.), *Handbook of neuropsychology* (2nd ed., Vol. 1, pp. 1-97). Netherlands: Elsevier Science Publishers.
- Murphy, N. A., & Isaacowitz, D. M. (2010). Age effects and gaze patterns in recognising emotional expressions: An in-depth look at gaze measures and covariates. *Cognition and Emotion*, 24(3), 436-452.
<http://dx.doi.org/10.1080/02699930802664623>
- Nieuwenhuis, S., (2011). Learning, the P3, and the locus coeruleus-norepinephrine system. In R. Mars, J. Sallet, M. F. Rushworth, & N. Yeung, (Eds.), *Neural basis of motivational and cognitive control* (pp. 209-222). Massachusetts, Cambridge: MITPress.
- Oliveira, F. T., McDonald, J. J., & Goodman, D. (2007). Performance monitoring in the anterior cingulate is not all error related: expectancy deviation and the representation of action-outcome associations. *Journal of Cognitive Neuroscience*, 19(12), 1994-2004.
<http://dx.doi.org/10.1162/jocn.2007.19.12.1994>
- Pachur, T., Mata, R., & Hertwig, R. (2017). Who dares, who errs? Disentangling cognitive and motivational roots of age differences in decisions under risk. *Psychological Science*, 28(4), 504-518.
<http://dx.doi.org/10.1177/0956797616687729>
- Park, D. C., Polk, T. A., Park, R., Minear, M., Savage, A., & Smith, M. R. (2004). Aging reduces neural specialization in ventral visual cortex. *Proceedings of the National Academy of Sciences*, 101(35), 13091-13095.
<http://dx.doi.org/10.1073/pnas.0405148101>
- Pasion, R., Fernandes, C., Gonçalves, A. R., Ferreira-Santos, F., Páscoa, R., Barbosa, F., & Marques-Teixeira, J. (2018). The effect of aging on the (mis)perception of intentionality-an ERP study. *Social Neuroscience*, 1-13.
- Penn, D. L., Corrigan, P. W., Bentall, R. P., Racenstein, J., & Newman, L. (1997). Social cognition in schizophrenia. *Psychological Bulletin*, 121(1), 114.
<http://dx.doi.org/10.1038/nrn4005>
- Petrás, K., ten Oever, S., & Jansma, B. M. (2016). The effect of distance on moral engagement: event related potentials and alpha power are sensitive to

- perspective in a virtual shooting task. *Frontiers in Psychology*, 6, 2008.
<http://dx.doi.org/10.3389/fpsyg.2015.02008>
- Renfroe, J. B., Bradley, M. M., Sege, C. T., & Bowers, D. (2016). Emotional modulation of the late positive potential during picture free viewing in older and young adults. *PloS One*, 11(9), e0162323.
<http://dx.doi.org/10.1371/journal.pone.0162323>
- Reuter-Lorenz, P. A., & Cappell, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, 17(3), 177-182. <http://dx.doi.org/10.1111/j.1467-8721.2008.00570.x>
- Ruffman, T., Henry, J. D., Livingstone, V., & Phillips, L. H. (2008). A meta-analytic review of emotion recognition and aging: Implications for neuropsychological models of aging. *Neuroscience & Biobehavioral Reviews*, 32(4), 863-881.
<http://dx.doi.org/10.1016/j.neubiorev.2008.01.001>
- San Martín, R. (2012). Event-related potential studies of outcome processing and feedback-guided learning. *Frontiers in Human Neuroscience*, 6, 304.
<http://dx.doi.org/10.3389/fnhum.2012.00304>
- Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the ultimatum game. *Science*, 300(5626), 1755-1758. <http://dx.doi.org/10.1126/science.1082976>
- Slessor, G., Riby, D. M., & Finnerty, A. N. (2012). Age-related differences in processing face configuration: The importance of the eye region. *Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, 68(2), 228-231.
<http://dx.doi.org/10.1093/geronb/gbs059>
- Salthouse, T. A. (2009). When does age-related cognitive decline begin?. *Neurobiology of Aging*, 30(4), 507-514.
<http://dx.doi.org/10.1016/j.neurobiolaging.2008.09.023>
- Sullivan, S., Ruffman, T., & Hutton, S. B. (2007). Age differences in emotion recognition skills and the visual scanning of emotion faces. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, 62(1), 53-60.
<http://dx.doi.org/10.1093/geronb/62.1.P53>
- Thomas, C., Moya, L., Avidan, G., Humphreys, K., Jung, K. J., Peterson, M. A., & Behrmann, M. (2008). Reduction in white matter connectivity, revealed by

- diffusion tensor imaging, may account for age-related changes in face perception. *Journal of Cognitive Neuroscience*, 20(2), 268-284.
<http://dx.doi.org/10.1162/jocn.2008.20025>
- Vieira, J. B., Almeida, P. R., Ferreira-Santos, F., Barbosa, F., Marques-Teixeira, J., & Marsh, A. A. (2014). Distinct neural activation patterns underlie economic decisions in high and low psychopathy scorers. *Social Cognitive and Affective Neuroscience*, 9(8), 1099-1107. <http://dx.doi.org/10.1093/scan/nst093>
- Wagner, N. F., Chaves, P., & Wolff, A. (2017). Discovering the neural nature of moral cognition? Empirical, theoretical, and practical challenges in bioethical research with electroencephalography (EEG). *Journal of Bioethical Inquiry*, 14(2), 299-313. <http://dx.doi.org/10.1007/s11673-017-9780-2>
- West, R., & Alain, C. (2000). Age-related decline in inhibitory control contributes to the increased Stroop effect observed in older adults. *Psychophysiology*, 37(2), 179-189. <http://dx.doi.org/10.1111/1469-8986.3720179>
- West R., Tiernan, B. N., Kieffaber, P. D., Bailey, K., & Anderson, S. (2014). The effects of age on the neural correlates of feedback processing in a naturalistic gambling game. *Psychophysiology*, 51(8), 734-745.
<http://dx.doi.org/10.1111/psyp.12225>
- Wong, B., Cronin-Golomb, A., & Neargarder, S. (2005). Patterns of visual scanning as predictors of emotion identification in normal aging. *Neuropsychology*, 19(6), 739. <http://dx.doi.org/10.1037/0894-4105.19.6.739>
- Wynn, J. K., Lee, J., Horan, W. P., & Green, M. F. (2008). Using event related potentials to explore stages of facial affect recognition deficits in schizophrenia. *Schizophrenia Bulletin*, 34(4), 679-687.
<http://dx.doi.org/10.1093/schbul/sbn047>
- Young, L., Cushman, F., Hauser, M., & Saxe, R. (2007). The neural basis of the interaction between theory of mind and moral judgment. *Proceedings of the National Academy of Sciences*, 104(20), 8235-8240.
<http://dx.doi.org/10.1073/pnas.0701408104>

APPENDICES

APPENDIX 1

Chapter 2.2 - Supplementary Material

Table 1.

Means (and standard deviations) of the neurocognitive measures for the three age-groups, and one-way ANOVA results for differences between groups.

Measure	Age Group			Group comparisons	
	Younger adults	Middle-aged adults	Older adults	$F(2,88)$	p
MoCA	27.9 (1.53)	26.8 (2.10)	25.6 (1.94)	11.4	.000 ^a
TMT	35.4 (18.0)	40.6 (19.0)	58.5 (25.3)	9.80	.000 ^a
IFS	24.6 (2.54)	24.4 (3.22)	22.7 (3.21)	3.76	.027 ^a
Corsi Block-Tapping Task	17.8 (3.00)	16.9 (3.43)	14.6 (3.72)	6.83	.002 ^a
Semantic Fluency	21.0 (4.31)	20.1 (5.89)	18.5 (4.90)	1.72	.186
Phonemic Fluency	39.0 (8.90)	37.4 (12.5)	35.9 (11.1)	0.52	.596
HADS - Depression	2.90 (2.55)	4.00 (3.52)	3.86 (2.46)	1.23	.296
HADS - Anxiety	5.97 (3.38)	5.90 (3.54)	5.07 (3.73)	0.56	.572
BSI	27.0 (21.1)	28.2 (20.8)	24.1 (16.4)	0.37	.711
AVLT - Learning	54.6 (7.12)	50.1 (8.87)	43.6 (8.77)	12.9	.000 ^a
AVLT - Delayed Recognition	29.5 (1.06)	28.9 (1.44)	28.1 (1.96)	12.5	.000 ^a
AVLT - Delayed Recall	12.0 (2.31)	10.7 (3.29)	8.15 (3.00)	5.46	.006 ^a

Note: Note: significant differences ^abetween younger and older adults; ^bbetween middle-aged and older adults; ^cbetween younger and middle-aged adults. MoCA: Montreal Cognitive Assessment; TMT: Trail Making Test; IFS: Institute of Cognitive Neurology Frontal Screening; HADS: Hospital Anxiety and Depression Scale; BSI: Brief Symptom Inventory; AVLT: Auditory Verbal Learning Test.

Table 2.

Means (and standard deviations) for accuracy rates (%) in the emotional perspective-taking task for the three groups.

	Younger adults	Middle-aged adults	Older adults
Congruent Condition			
Anger	79.3 (8.18)	72.8 (11.4)	69.3 (19.2)
Disgust	87.0 (6.74)	87.2 (7.48)	76.1 (16.3)
Fear	83.4 (8.42)	81.1 (14.1)	73.6 (19.4)
Happiness	94.6 (9.53)	95.6 (4.66)	92.6 (11.8)
Neutral	90.8 (9.93)	91.8 (8.56)	86.4 (15.0)
Sadness	93.7 (10.1)	84.4 (17.8)	72.8 (19.6)
Incongruent Condition			
Anger	87.4 (9.74)	78.8 (18.2)	66.1 (18.4)
Disgust	79.1 (7.68)	67.3 (18.8)	58.3 (17.1)
Fear	81.9 (11.3)	76.3 (18.1)	64.3 (17.2)
Happiness	97.4 (3.88)	94.2 (7.27)	87.2 (13.6)
Neutral	82.8 (9.75)	79.6 (14.7)	71.0 (11.2)
Sadness	88.2 (8.29)	82.1 (13.7)	72.6 (16.4)

Table 3.

Means (and standard deviations) for reaction times (ms) in the emotional perspective-taking task for the three groups.

	Younger adults	Middle-aged adults	Older adults
Congruent Condition			
Anger	858.20 (809.89)	687.09 (229.94)	1106.09 (577.41)
Disgust	877.14 (1030.68)	627.28 (268.37)	903.51 (303.11)
Fear	771.93 (274.26)	696.86 (209.57)	997.94 (379.39)
Happiness	659.55 (279.59)	626.17 (262.73)	882.00 (404.76)
Neutral	722.10 (411.78)	703.13 (324.00)	997.76 (417.52)
Sadness	714.39 (337.05)	690.23 (181.58)	1011.64 (448.04)
Incongruent Condition			
Anger	755.50 (297.33)	668.69 (231.97)	1149.60 (696.75)
Disgust	813.68 (444.61)	757.83 (240.72)	1061.35 (372.98)
Fear	739.48 (318.38)	710.76 (236.92)	1136.12 (501.05)
Happiness	715.93 (417.89)	692.05 (324.11)	965.42 (407.02)
Neutral	861.48 (393.97)	720.22 (221.36)	1051.04 (512.19)
Sadness	770.13 (250.75)	739.02 (237.80)	1032.92 (489.05)

Table 4.

Correlations between neurocognitive results and results of the perspective-taking task, average by congruency and presented by aged-group.

		1.	2.	3.	4.	5.	6.	7.	8.
Young Adults	1. IFS	—							
	2. Corsi Blocks-Tapping Task	.328	—						
	3. AVLT - Learning	.189	.135	—					
	4. AVLT – Delayed Recognition	.173	.377*	.422**	—				
	5. AVLT – Delayed Recall	-.136	-.139	.631**	.509**	—			
	6. TMT	-.323*	-.092	-.228	-.391**	-.137	—		
	7. Congruent Conditions	.393*	.318	-.093	.391*	.010	.123	—	
	8. Incongruent Conditions	-.139	-.186	-.016	-.272	-.020	.299	-.255	—
Middle-aged Adults	1. IFS	—							
	2. Corsi Blocks-Tapping Task	.650**	—						
	3. AVLT - Learning	.118	.144	—					
	4. AVLT – Delayed Recognition	.017	-.064	.612**	—				
	5. AVLT – Delayed Recall	.193	.056	.807**	.543**	—			
	6. TMT	-.249	-.442*	-.033	.174	.161	—		
	7. Congruent Conditions	.523**	.429*	-.009	-.044	.012	-.377*	—	
	8. Incongruent Conditions	.331	.116	.299	.081	.329	-.108	-.053	—
Older Adults	1. IFS	—							
	2. Corsi Blocks-Tapping Task	.323	—						
	3. AVLT - Learning	.171	.420*	—					
	4. AVLT – Delayed Recognition	.124	.242	.617**	—				
	5. AVLT – Delayed Recall	-.095	.381*	.694**	.626**	—			
	6. TMT	-.239	.058	-.102	-.021	.047	—		
	7. Congruent Conditions	.198	.477**	.528**	.345	.186	-.259	—	
	8. Incongruent Conditions	.565**	.381*	.303	-.046	.104	-.078	.066	—

Note: * $p < .05$; ** $p < .01$. Correlations in boldface were explored through Linear Regression Models (Table 5).

Table 5.

Results of the linear regression models performed for the behavioral results. Neurocognitive results entered as predictor of the results of the perspective-taking task, average by congruency.

OUTCOME and predictors	<i>F</i>	<i>AdjR</i> ²	<i>p</i>	<i>β</i>	<i>p</i>
CONGRUENT CONDITIONS - YOUNGER ADULTS	5.11	.227	.013		
IFS				.365	.040
AVLT – Delayed Recognition				.328	.063
CONGRUENT CONDITIONS – MIDDLE-AGED ADULTS	5.45	.235	.010		
IFS				.424	.058
Corsi Blocks-Tapping Task				.153	.480
CONGRUENT CONDITIONS – OLDER ADULTS	6.43	.287	.006		
Corsi Blocks-Tapping Task				.272	.141
AVLT - Learning				.414	.029
INCONGRUENT CONDITIONS – OLDER ADULTS	7.40	.314	.003		
IFS				.493	.006
AVLT - Learning				.222	.192

Note: IFS: Institute of Cognitive Neurology Frontal Screening; AVLT: Auditory Verbal Learning Test.

Table 6.

Means (and standard deviations) for N170 peak amplitudes (μV) evoked by each condition. by age group.

	Younger Adults		Middle-aged Adults		Older Adults	
	Right				Right	
	Left Hemisphere	Hemisphere	Left Hemisphere	Right Hemisphere	Left Hemisphere	Hemisphere
Congruent Condition						
Anger	-1.06 (3.43)	-2.04 (3.12)	-3.55 (2.766)	-3.94 (3.84)	-5.05 (3.19)	-5.57 (2.94)
Disgust	-2.07 (2.52)	-3.10 (2.43)	-3.85 (2.99)	-4.77 (4.50)	-5.14 (3.72)	-5.75 (2.70)
Fear	-1.95 (2.83)	-2.32 (2.96)	-3.60 (2.40)	-4.61 (4.22)	-6.12 (3.38)	-6.24 (3.10)
Happiness	-1.50 (2.96)	-2.42 (2.82)	-2.94 (3.01)	-4.05 (4.07)	-5.56 (3.20)	-5.99 (2.91)
Neutral	-1.41 (2.96)	-2.15 (2.79)	-3.08 (2.52)	-4.21 (4.51)	-4.87 (3.10)	-5.30 (3.11)
Sadness	-1.73 (3.00)	-2.57 (2.76)	-3.80 (2.88)	-4.61 (3.93)	-5.00 (3.66)	-6.04 (3.23)
Incongruent Condition						
Anger	-1.66 (2.95)	-2.45 (3.00)	-3.19 (2.47)	-4.57 (3.75)	-5.45 (3.21)	-5.40 (2.98)
Disgust	-1.40 (2.67)	-1.48 (2.11)	-3.49 (3.02)	-4.28 (3.72)	-5.17 (3.43)	-5.87 (2.51)
Fear	-1.47 (3.19)	-2.09 (2.91)	-3.31 (2.59)	-4.48 (4.43)	-4.92 (3.40)	-5.57 (3.61)
Happiness	-1.51 (3.01)	-2.66 (2.48)	-3.68 (2.37)	-4.54 (3.46)	-5.48 (3.18)	-5.96 (3.19)
Neutral	-1.42 (2.70)	-2.39 (2.63)	-3.40 (3.45)	-4.52 (3.93)	-5.43 (3.12)	-5.46 (2.95)
Sadness	-1.92 (2.90)	-2.64 (3.14)	-3.27 (2.73)	-4.50 (3.89)	-5.85 (3.80)	-5.95 (2.87)

Table 7.

Means (and standard deviations) for LPPs mean amplitudes (μV) evoked by each condition. by age group.

	Younger Adults		Middle-aged Adults		Older Adults	
	LPPe	LPPI	LPPe	LPPI	LPPe	LPPI
Congruent Condition						
Anger	3.09 (2.20)	4.14 (2.21)	1.67 (1.55)	2.92 (2.11)	1.57 (1.64)	2.38 (2.06)
Disgust	3.09 (1.92)	4.26 (2.30)	1.51 (2.01)	2.90 (2.78)	1.91 (1.67)	2.70 (2.55)
Fear	3.20 (1.97)	4.20 (2.00)	1.99 (1.80)	2.91 (2.02)	1.86 (1.79)	2.60 (2.34)
Happiness	2.53 (2.23)	3.84 (2.30)	1.79 (1.89)	3.04 (2.28)	1.80 (1.82)	2.83 (2.13)
Neutral	2.85 (1.78)	4.20 (2.32)	1.67 (2.59)	2.94 (3.17)	1.28 (1.79)	1.98 (2.16)
Sadness	2.93 (2.33)	3.84 (2.37)	1.48 (1.87)	2.64 (2.79)	1.60 (1.98)	2.54 (2.37)
Incongruent Condition						
Anger	1.65 (2.60)	2.85 (2.22)	0.82 (1.68)	1.90 (2.06)	1.30 (1.65)	2.10 (2.16)
Disgust	2.46 (1.96)	3.19 (1.89)	1.17 (1.78)	1.75 (2.22)	1.41 (2.19)	1.84 (2.62)
Fear	2.33 (1.91)	3.58 (1.91)	0.92 (1.40)	1.70 (1.79)	1.28 (1.82)	2.18 (2.44)
Happiness	2.00 (2.52)	3.02 (3.20)	1.41 (2.25)	2.72 (2.59)	1.41 (1.71)	2.86 (2.41)
Neutral	2.33 (3.17)	3.11 (3.79)	1.77 (2.31)	2.81 (2.25)	2.07 (1.32)	3.04 (2.18)
Sadness	2.12 (2.47)	3.16 (2.58)	1.59 (1.54)	2.48 (1.61)	1.65 (2.10)	2.57 (2.48)

Table 8.

Correlations between neurocognitive results and electrophysiological results, average by congruency and presented by aged-group

		1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
Younger Adults	1. IFS	—												
	2. Corsi Blocks-Tapping Task	.328	—											
	3. AVLT - Learning	.189	.135	—										
	4. AVLT – Delayed Recognition	.173	.377*	.422*	—									
	5. AVLT – Delayed Recall	-.136	-.139	.631**	.509**	—								
	6. TMT	-.323	-.092	-.228	-.391*	-.137	—							
	7. N170 – CC – LH	.228	.195	.136	.333	.070	-.106	—						
	8. N170 – IC – LH	.208	.241	.112	.388*	.045	-.045	.950**	—					
	9. N170 – CC – RH	.112	-.036	.009	.013	-.154	-.031	.741**	.726**	—				
	10. N170 – IC – RH	.134	.018	0.040	.017	.017	.034	.704**	.728**	.973**	—			
	11. LPPe – CC	.096	-.016	.383*	.256	.278	.072	.131	.119	.083	.071	—		
	12. LPPe – IC	.203	.144	.340	.256	.220	.024	.178	.148	.100	.129	.906**	—	
	13. LPPI – CC	.080	-.027	.200	.021	.069	.137	-.043	-.074	.009	.001	.804**	.711**	—
	14. LPPI - IC	.083	.020	.281	.089	.203	.083	.039	-.002	.075	.096	.812**	.882**	.871**

Table 8 (Continued).

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
Middle-aged Adults	1. IFS	—											
	2. Corsi Blocks-Tapping Task	.650**	—										
	3. AVLT - Learning	.118	.144	—									
	4. AVLT – Delayed Recognition	.017	-.064	.612**	—								
	5. AVLT – Delayed Recall	.193	.056	.807**	.543**	—							
	6. TMT	-.249	-.442*	-.033	.174	.161	—						
	7. N170 – CC – LH	.283	.171	-.326	-.034	-.260	.171	—					
	8. N170 – IC – LH	.291	.122	-.358	-.056	-.201	.117	.944**	—				
	9. N170 – CC – RH	.212	.251	-.304	-.142	-.242	.075	.822**	.768**	—			
	10. N170 – IC – RH	.270	.269	-.287	-.120	-.194	.087	.797**	.773**	.985**	—		
	11. LPPe – CC	.127	.137	.145	.147	.035	-.172	-.099	-.103	-.310	-.338	—	
	12. LPPe – IC	-.016	.042	-.023	.042	-.016	-.036	-.085	-.053	-.258	-.284	.922**	—
	13. LPPI – CC	.236	.229	.390*	.248	.212	-.307	-.393*	-.397*	-.459*	-.455*	.771**	.615**
	14. LPPI - IC	.141	.190	.365*	.259	.272	-.243	-.371*	-.355	-.450*	-.457*	.758**	.706**

Table 8 (Continued).

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
Older Adults	1. IFS	—											
	2. Corsi Blocks-Tapping Task	.323	—										
	3. AVLT - Learning	.171	.420*	—									
	4. AVLT – Delayed Recognition	.124	.242	.617**	—								
	5. AVLT – Delayed Recall	-.095	.381*	.694**	.626**	—							
	6. TMT	-.239	.058	-.102	-.021	.047	—						
	7. N170 – CC – LH	-.171	.070	.325	.161	.372	.233	—					
	8. N170 – IC – LH	-.176	.067	.331	.182	.331	.185	.973**	—				
	9. N170 – CC – RH	-.267	-.148	.158	.058	.219	.341	.633**	.632**	—			
	10. N170 – IC – RH	-.248	-.181	.210	.104	.281	.292	.696**	.973**		—		
	11. LPPe – CC	.224	.110	-.210	-.224	-.039	-.253	-.105	-.195	-.195	-.242	—	
	12. LPPe – IC	.217	-.063	-.280	-.365	-.196	-.451*	-.176	-.246	-.331	-.356	.859**	—
	13. LPPI – CC	.066	.269	-.265	-.435*	-.106	-.014	-.020	-.097	-.084	-.110	.715**	.614**
	14. LPPI - IC	.088	.086	-.330	-.485*	-.208	-.163	-.149	-.217	-.145	-.175	.694**	.763**

IFS: Institute of Cognitive Neurology Frontal Screening; AVLT: Auditory Verbal Learning Test; TMT: Trail Making Test. CC – Congruent

Condition; IC – Incongruent Condition; LH – Left Hemisphere; RH – Right Hemisphere. *Note:* * $p < .05$; ** $p < .01$

GENDER EFFECTS ON EMOTIONAL PERSPECTIVE-TAKING

Control analyses using sex as an additional between-participants factor did not reveal a significant main effect of sex, nor significant interactions with sex for accuracy rates ($F < 1$). Regarding electrophysiological results, this analysis did not reveal a significant main effect of sex for none of the three ERPs, and the only significant interaction that emerged was emotion*sex for LPPe, $F(5, 415) = 3.50$, $p = .004$, $\eta^2_p = .040$, and LPPI, $F(5, 415) = 2.33$, $p = .042$, $\eta^2_p = .027$. Pairwise comparisons revealed that both interactions were explained by the emotion of disgust, which elicited higher amplitudes for males than for females ($p = .025$ for LPPe and $p = .010$ for LPPI).

APPENDIX 2

Chapter 2.4 - Supplementary Material

Table 1.

Means (and standard deviations) of the neurocognitive measures for the three age-groups, and one-way ANOVA results for differences between groups.

Measures	Age group			Group comparison	
	Younger adults	Middle-aged adults	Older adults	<i>F</i>	<i>p</i>
MoCA	27.9 (1.53)	26.9 (2.10)	25.4 (2.31)	11.2	.000 ^{a,b}
TMT	35.4 (18.0)	41.7 (18.5)	58.5 (25.3)	9.65	.000 ^{a,b}
IFS	24.6 (2.54)	24.5 (3.26)	22.7 (3.21)	3.80	.027 ^a
Corsi Blocks-Tapping Task	17.8 (3.00)	17.0 (3.45)	14.6 (3.72)	6.94	.002 ^{a,b}
Semantic Fluency	21.0 (4.31)	20.1 (6.00)	18.5 (5.00)	1.72	.186
Phonemic Fluency	39.0 (8.90)	37.3 (12.7)	35.9 (11.1)	0.52	.599
HADS Depression	2.90 (2.55)	4.03 (3.57)	3.86 (2.46)	1.32	.273
HADS Anxiety	5.97 (3.38)	5.90 (3.60)	5.07 (3.73)	0.57	.567
BSI	27.0 (21.1)	26.0 (20.1)	22.8 (17.3)	0.38	.686
AVLT - Learning	54.6 (7.12)	52.0 (12.5)	44.0 (9.00)	9.40	.000 ^{a,b}
AVLT - Delayed Recall	12.0 (2.31)	10.8 (3.33)	8.36 (3.14)	11.0	.000 ^{a,b}
AVLT – Delayed Recognition	29.5 (1.10)	29.0 (1.45)	28.2 (2.00)	4.94	.009 ^a

Note: significant differences ^abetween younger and older adults; ^bbetween middle-aged and older adults; ^cbetween younger and middle-aged adults

Table 2.

Means (standard deviations) of risk-averse decisions (%) for the three age-groups in gains and loss domain. Risk-averse decisions in loss domain after non-losses and losses are also presented.

Domain	Age group		
	Younger adults	Middle-aged adults	Older adults
Gains	61.6 (21.0)	67.5 (21.0)	54.3 (24.3)
Losses	70.2 (17.0)	56.3 (25.7)	48.5 (23.7)
After non-losses	38.4 (10.3)	29.5 (13.3)	24.5 (12.6)
After losses	32.2 (8.52)	26.1 (13.1)	23.4 (12.1)

Table 3.

Correlations between age, neurocognitive results, risk-averse decisions, FRN and P3 evoked by both types of conditions

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.
1. Age	—															
2. IFS	-.274**	—														
3. Corsi Blocks	-.418**	.498**	—													
4. AVLT - Learning	-.439**	.243*	.347**	—												
5. AVLT - Recall	-.345**	.122	.239*	.652**	—											
6. AVLT - Recognition	-.470**	.149	.247*	.379**	.634**	—										
7. TMT	.422**	-.357**	-.290**	-.247*	-.177	-.160	—									
8. Decisions - gains domain	-.177	.155	.186	.219*	.206	.089	-.027	—								
9. Decisions - loss domain	-.385**	.232*	.283**	.294**	.183	.064	-.274**	.320**	—							
10. FRN - gains	-.130	.256*	.242*	.044	-.160	-.083	-.242*	-.175	.021	—						
11. FRN - non-gains	.017	.124	.148	-.024	-.283*	-.130	-.123	-.087	.005	.754**	—					
12. FRN - losses	-.122	.170	.211	.101	-.122	-.003	-.288**	-.079	.092	.850**	.749**	—				
13. FRN - non-losses	.058	.145	.142	-.026	-.313**	-.130	-.145	-.243*	-.035	.819**	.820**	.820**	—			
14. P3 - gains	-.200	.244*	.241*	.053	-.118	-.086	-.276*	-.314**	.018	.753**	.648**	.638**	.652**	—		
15. P3 - non-gains	-.012	.168	.208	.011	-.157	-.082	-.150	-.213	-.093	.688**	.791**	.656**	.707**	.830**	—	
16. P3 - losses	-.161	.254*	.242*	.083	-.174	-.124	-.331**	-.228*	.048	.664**	.677**	.745**	.707**	.818**	.789**	—
17. P3 - non-losses	-.121	.233*	.250*	.053	-.148	-.108	-.292**	-.214	.037	.652**	.697**	.637**	.734**	.820**	.832**	.851**

Note: * $p < .05$; ** $p < .01$. Correlations in boldface were explored through Linear Regression Models (Table 4)

Table 4.

Hierarchical Regression Models

OUTCOME and Predictors	<i>F</i>	<i>AdjR</i> ²	<i>p</i>	<i>β</i>	<i>p</i>
RISK-AVERSE DECISIONS IN LOSS DOMAIN	3.90	.143	.003		
Age				-.240	.054
IFS				.062	.604
Corsi Blocks-Tapping Task				.082	.506
TMT				-.098	.395
AVLT – Learning				.121	.289
RISK-AVERSE DECISIONS IN GAIN DOMAIN	4.50	.079	.014		
P3 evoked by gains				-.384	.040
P3 evoked by losses				.086	.643
FRN AMPLITUDES EVOKED BY GAINS	2.940	.066	.038		
IFS				1.09	.279
Corsi Blocks-Tapping Task				.982	.329
TMT				-.123	.224
P3 EVOKED BY GAINS	3.21	.075	.028		
IFS				.111	.386
Corsi Blocks-Tapping Task				.120	.339
TMT				-.191	.108
P3 EVOKED BY NON-LOSSES	.082	3.43	.021		
IFS				.083	.521
Corsi Blocks-Tapping Task				.135	.281
TMT				-.213	.073
P3 EVOKED BY LOSSES	4.13	.103	.009		
IFS				.105	.402
Corsi Blocks-Tapping Task				.101	.412
TMT				-.255	.031

Table 5.

Means (standard deviations) for FRN and P3 amplitudes (μV) evoked by gains and non-gains (gain domain), losses and non-losses (loss domain). Gains and non-losses are favorable outcomes, while non-gains and losses are unfavorable outcomes, within their respective domains. Error bars indicate 95% confidence intervals.

	Age group		
	Younger adults (<i>n</i> = 28)	Middle-aged adults (<i>n</i> = 29)	Older adults (<i>n</i> = 27)
FRN (Fcz)			
Gains	8.03 (4.16)	6.73 (5.91)	6.28 (5.63)
Non-gains	4.01 (4.29)	3.37 (5.27)	3.95 (4.68)
Losses	7.12 (4.11)	5.24 (5.90)	5.67 (4.03)
Non-losses	5.09 (4.59)	4.54 (5.55)	5.67 (4.92)
P3 (Pz)			
Gains	8.26 (4.31)	6.47 (5.03)	5.43 (5.44)
Non-gains	6.38 (4.39)	5.14 (4.70)	6.09 (6.23)
Losses	8.46 (4.17)	6.66 (6.20)	6.22 (5.41)
Non-losses	7.90 (4.36)	6.50 (5.79)	6.38 (6.05)