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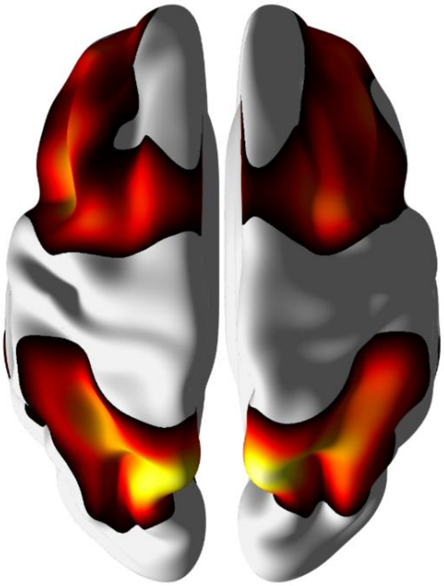
Cognitive fatigue in young, middle-aged, and older people: behavioral and functional neuroimaging investigations



Jessica Gilsoul

A thesis submitted in partial fulfillment of the requirements
for the award of the degree of

Doctor in Psychological Sciences

2019 - 2020

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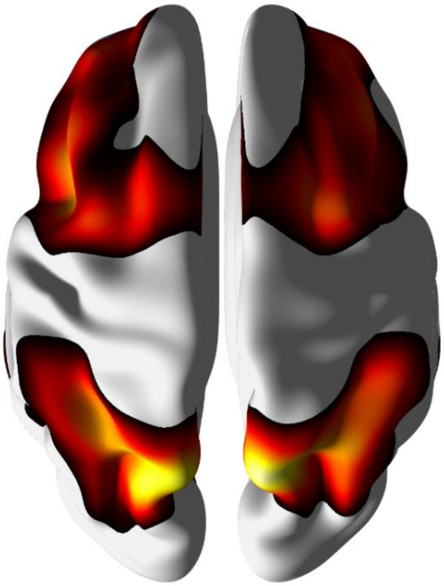

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To my parents.

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“There is no fatigue as long as a purpose itself is not fatigued”
Raymond B. Cattell, 1941

“Since it was difficult to obtain volunteers for such studies – or because of researchers’ distrust in any but their own motivation to stay the course – these were usually conducted on the researchers themselves.”
G. Robert J. Hockey, 2013

Table of Content

List of Abbreviations **21**

List of Figures **27**

List of Boxes **29**

Preface **33**

Theoretical Introduction **43**

- **Chapter 1: Definitions and Models of Cognitive Fatigue** **45**
  - Cognitive versus Physical Fatigue 45
  - Several Definitions of Cognitive Fatigue 47
  - Initial Models of Cognitive Fatigue 55
  - Motivation, Costs/Benefits Calculation, and Goal Selection 63
  - Fatigue, Dopamine, and the Reward System 81
  - Models of Pathological Fatigue 89
  - Confounding Variables of Cognitive Fatigue 95
  - Intermediate Summary 97
- **Chapter 2: Empirical Studies in Young People** **99**
  - Time-on-Task and Probe Approaches 99
  - Time-on-Task Approach 102
  - Probe Approach 112
  - Subjective Cognitive Fatigue 118
- **Chapter 3: Models of Cognitive and Cerebral Aging** **121**
  - Cognitive Modifications in Normal Aging 121
  - Cerebral Reserve, Cognitive Reserve, and Compensation Hypotheses 124
  - Brain Resources, Genetics, and Dopamine 137
  - Selective Engagement of Cognitive Resources 140
- **Chapter 4: Empirical Studies in Older and Middle-aged People** **143**
  - Empirical Studies in Older People 143
  - Empirical Studies in Middle-aged People 149
  - Intermediate Summary 153

Experimental Part 155

  Objectives and Hypotheses 157

General Discussion 167

    Principle Results from Study 1 and Study 2 170

    How to Explain our Results with Cognitive Fatigue Models 171

    Future Perspectives for Study 1 and Study 2 175

    Principle Results from Study 3 179

    How to Explain our Results with Cognitive Fatigue Models 179

    Future Perspectives for Study 3 183

    Conclusions 185

List of References 188

List of Publications 263

  Articles 263

  Posters and Oral Communications as First Author 264

  Posters and Oral Communications as Co-Author 266

Appendix 269

  Appendix 1 271

  Do Attentional Capacities and Processing Speed Mediate the Effect of Age on Executive Functioning? 271

List of Abbreviations

AAL: automated anatomical labeling

ACC: anterior cingulate cortex

AD: Alzheimer’s disease

AI: anterior insula

ALFF: amplitude of low-frequency fluctuation

ANS: autonomic nervous system

ANT: Attention Network Task

ART: Attention Restoration Theory

ASL: arterial spin labeling

ATMT: Advanced Trail Making Test

B: buffer neutral

BCR: benefit-cost ratio

BCRs: benefit-cost ratios

BFI: Brief Fatigue Inventory

BFS: Brugmann Fatigue Scale

BG: basal ganglia

BLA: basolateral amygdala

BOLD: blood oxygen level-dependent

BRC: brain reserve capacity

BSDT: Blocked Symbol Decoding Task

C: congruent

CBF: cerebral blood flow

CCM: Compensatory Control Model

cECG: capacitive electrocardiography

CEN: central executive network

CES-DS: Center for Epidemiologic Studies Depression Scale

CF: cognitive fatigue

CFQ: Chalder Fatigue Scale

CFS: Chronic Fatigue Syndrome

CNV: contingent negative variation

COGED: COGnitive Effort Discounting

COMT: catechol-O-methyltransferase

CR: correct responses

CRUNCH: Compensation-Related Utilization of Neural Circuits Hypothesis

CVRT: coefficient of variation of reaction time

DA: dopamine

dACC: dorsal anterior cingulate cortex

DARTEL: diffeomorphic anatomical registration through exponentiated lie algebra

DBH: dopamine beta-hydroxylase

DLPFC: dorsolateral prefrontal cortex

DMN: default mode network

DMPFC: dorsomedial prefrontal cortex

DTI: diffusion tensor imaging

ECG: electrocardiography

ECN: executive control network

EEG: electroencephalography or electroencephalographic

EFs: executive functions

ELSA: Early to Late Shift in Aging

EN: executive network

EPI: echo-planar imaging

erfc: complementary error function

ERN: error-related negativity

ERP: event-related potential

ERPs: event-related potentials

ESS: Epworth Sleepiness Scale

EVC: expected value of control

FA: flip angle

FIS: Fatigue Impact Scale

fMRI: functional magnetic resonance imaging

fNIRS: functional near-infrared spectroscopy

FoV: field of view

FSMC: Fatigue Scale for Motor and Cognitive functions

FWE: family-wise error

FWHM: full-width at half maximum

GRAPPA: GeneRalized Autocalibrating Partial Parallel Acquisition

HAROLD: Hemispheric Asymmetry Reduction in Older Adults

HR: heart rate

HRV: heart rate variability

I: incongruent

IC: insular cortex

IIV: intra-individual variability

IMI: Intrinsic Motivation Inventory

IR: incorrect responses

ISI: inter-stimulus interval

KSS: Karolinska Sleepiness Scale

LC-NE: locus coeruleus-central norepinephrine

LF/HF: low frequency/high frequency

LogL: log-likelihood

M: mean

Mattis-DRS: Mattis-Dementia Rating Scale

MEG: magnetoencephalography or magnetoencephalographic

MFG: middle frontal gyrus

MFI: Multidimensional Fatigue Inventory

MFIS: Modified Fatigue Impact Scale

min.: minutes

MNI: Montreal Neurological Institute

MPFC: medial prefrontal cortex

MPRAGE: Magnetization-Prepared RApid Gradient Echo

MRI: magnetic resonance imaging

ms: milliseconds

MS: Multiple Sclerosis

N: neutral

NAc: accumbens nucleus

Ne: negativity

NR: non-responses

OFC: orbitofrontal cortex

PAS: Posterior-Anterior Shift

PASA: Posterior-Anterior Shift in Aging

PCC: posterior cingulate cortex

PD: Parkinson’s disease

PDF: probability density function

Pe: error-related positivity

PET: positron emission tomography

PFC: prefrontal cortex

PFS: Pittsburgh Fatigability Scale

PI: posterior insula

PM: premotor cortex

POMS: Profile of Mood States

POMS-SF: Profile of Mood States-Short Form

PPC: posterior parietal cortex

PSQI: Pittsburgh Sleep Quality Index

PVT: Psychomotor Vigilance Task

rFIC: right fronto-insular cortex

rMSSD: root mean square of successive differences

RSA: respiratory sinus arrhythmia

RSME: Rating Scale Mental Effort

RT: reaction time

RTs: reaction times

RU: relative utility

s.: seconds

SART: Sustained Attention to Response Task

SD: standard deviation

SES: socioeconomic status

SITUTs: stimulus-independent and task-unrelated thoughts

SMA: supplementary motor area

SN: salience network

SNc: substantia nigra pars compacta

SNP: single nucleotide polymorphism

SNPs: single nucleotide polymorphisms

SNR: signal-to-noise ratio

Somat: somatosensory cortex

SRTT: Serial Reaction Time Task

STAC: Scaffolding Theory of Aging and Cognition

STAC-r: Scaffolding Theory of Aging and Cognition-revised

STD: stimulus time duration

TBRS: Time-based Resource-sharing

TE: echo time

TI: inversion time

TLDB: Time Load Dual Back

TMS: transcranial magnetic stimulation

TMT: Trail Making Test

TOI: time of interest

TOL: Tower of London

TP: total spectral power

TPI: time of presentation

TR: repetition time

VAS: visual analogue scales

VLPFC: ventrolateral prefrontal cortex

VOC: value of computation

VP: ventral pallidum

VS: ventral striatum

VTA: ventral tegmental area

WCST: Wisconsin Card Sorting Test

WM: working memory

List of Figures

Figure 1. Arai’s (1912) Data.

Figure 2. The Process Model of Ego-Depletion.

Figure 3. Three Phases of the Work Decrement Function.

Figure 4. First Version of the Compensatory Control Model (CCM) of Performance Regulation.

Figure 5. Second Version of the Compensatory Control Model.

Figure 6. Third Version of the Compensatory Control Model.

Figure 7. Proposed Systems in the Brain Underlying Motivational Fatigue.

Figure 8. Mental Effort as Opportunity Cost.

Figure 9. Two Alternative Formulations for the Positive Valuation of Effort.

Figure 10. Inverted U-Shaped Relationship between Working Memory Performance and Cerebral Dopamine Levels.

Figure 11. The Three Main Dopaminergic Pathways.

Figure 12. Cognitive Fatigue as Costs and Benefits Calculation.

Figure 13. A Neurocomputational Model of Effort.

Figure 14. Dual Regulation System of Fatigue.

Figure 15. Perceived Effort as a Lack of Sensory Attenuation.

Figure 16: Wang et al. (2016)’s Data.

Figure 17. Persson et al. (2007)’s Data.

Figure 18. Patterns of Activation and Performance Levels Predicted by the CRUNCH.

Figure 19. Hemispheric Asymmetry Reduction in Older Adults.

Figure 20. A Model of Age-Related Compensation.

Figure 21. The Scaffolding Theory of Aging and Cognition (STAC).

Figure 22. A Conceptual Model of the Scaffolding Theory of Aging and Cognition-revised (STAC-r).

Figure 23. The Resource Modulation Hypothesis.

Figure 24. Age and Genetic Effects on the Inverted U-Shaped Curve Linking Dopamine and Performance.

Figure 25. Selective Engagement of Cognitive Resources.

Figure 26. Normal Probability Density Function of Cognitive Scores for Younger, Middle-aged, and Older Adults.

Figure 27. Probability Density Function (Φ(x)) of the Ex-Gaussian Function.

List of Boxes

Box 1. Fatigue and Boredom

Box 2. Sustained Attention and Vigilance

Box 3. Demand, Effort, Motivation, and Effort Discounting

Box 4. Cognitive Control Account

Box 5. Limbic System and Limbic Loop

Box 6. What is Middle Age?

Box 7. Presentation of Different Networks

Preface

In our modern societies, humans are constantly cognitively solicited until a relatively advanced age. This continuous cognitive stimulation can obviously be experienced at work but it can also more insidiously come from overcrowded environments, social networks, or constant advertisement on the internet, which eventually bury people in an uninterrupted flow of information. Cognitive fatigue has progressively become one of the most prevalent causes of accidents in everyday life (Dinges, 1995; Shen et al., 2008) but also in the workplace (McCormick et al., 2012). If cognitive fatigue can be considered a normal and adaptive response to long-lasting tasks (Boksem & Tops, 2008), it can also lead to tragic consequences in certain professions. For example, studies have already found evidence of attention drops in airplane pilots (Bartlett, 1943) or large speed variation in car or train drivers under cognitive fatigue (Brown, 1994; Campagne et al., 2004; Kecklund & Akerstedt, 1993; Torsvall & Akerstedt, 1987). This phenomenon is also striking in emergency services like in firefighters (Aisbett & Nichols, 2007; Aisbett et al., 2012; Ferguson et al., 2016) and in intensive care unit physicians (Maltese et al., 2016). When continuously exposed to cognitive fatigue, some individuals can unfortunately develop the so-called burnout condition (Maslach et al., 2001) with its inherent costs for the public health care system but also for the employer (Ricci et al., 2007), in addition to the burden for the individual.

Cognitive fatigue can be observed in various domains: Blain et al. (2016) showed that daylong intense cognitive work tends to enhance impulsivity in economic decisions. Likewise, cognitive fatigue has been shown to impair economic decisions, preferences, strategies (Mullette-Gillman et al., 2015), emotion regulation (Grillon et al., 2015), as well as cognitive flexibility in university students (Plukaard et al., 2015). In the sport domain, cognitive fatigue has also been found to alter soccer-specific decision-making (Smith et al., 2016), intermittent running performance (Smith et al., 2015) as well as table tennis performance (Le Mansec et al., 2018).

In more severe cases, cognitive fatigue can further develop into a permanent condition, such as Chronic Fatigue Syndrome (CFS; Tanaka & Watanabe, 2010). Cognitive fatigue is also frequently reported in psychological conditions such as depression (Demyttenaere et al., 2005; Lavidor et al., 2002) and neurological illnesses such as Parkinson's disease (PD), Multiple Sclerosis (MS), traumatic brain injury, stroke, myasthenia gravis, amyotrophic lateral sclerosis, or postpolio syndrome (Chaudhuri & Behan, 2000; Kluger et al., 2013). Obviously, given the potentially tragic consequences of cognitive fatigue, studies are needed to better understand this phenomenon.

On the other hand, medical progress has radically increased life expectancy in the last decades, reaching the age of 81.44 in Belgium (in 2017). At the same time, people have been progressively required to work until a more advanced age although diminished cognitive functioning efficiency has been found in older age (Collette & Salmon, 2014; Crawford et al., 2000; Salthouse et al., 2003; West, 1996, 2000). Therefore, it seems crucial to become aware of how cognitive fatigue manifests in advancing age. Surprisingly, very few studies have investigated cognitive fatigue, behaviorally or at the cerebral level, in aging populations.

In addition to older age, the middle-aged population also seems particularly at risk for cognitive fatigue. Indeed, midlife has sometimes been considered as the most challenging life period due to the presence of many cognitive requirements (children to care for, work, social life, everyday duties). However, middle-aged people have scarcely been the focus of interest in the literature, probably because of the difficulty reaching this busy population. In an attempt to understand cognitive fatigue at different life stages, studies presented in this Thesis work have systematically focused on three age groups: young, middle-aged, and older people.

The first chapter of this Thesis work starts by presenting definitions and models of cognitive fatigue, from those emphasizing energy depletion as the consequence of long-lasting work to those integrating notions that more particularly focus on the voluntarily controlled effort (e.g., executive function, costs/benefits or effort/reward calculation, opportunity cost) invested by the individual into a cognitive activity. For the sake of completeness, this chapter ends by the presentation of some pathological fatigue models.

The second chapter describes studies investigating cognitive fatigue in young people. This chapter makes the distinction between experimental protocols based on the *Time-on-Task approach* (i.e., performing a unique long-lasting task) and those based on the *Probe approach* (i.e., performing two consecutive tasks in order to test transfer fatigue effects from the first to the second). The presentation of studies also distinguishes between objective (behavioral, electrophysiologic, neuroimaging, connectivity, motivation-related) and subjective (self-reported scales) assessment of cognitive fatigue.

The third chapter is dedicated to the presentation of models of cognitive and cerebral aging. It starts by describing cognitive functions that are known to decline with age as well as potential mediators (i.e., processing speed and inhibition) of age-related declines. It presents the well-recognized patterns of cognitive reserve (Stern, 2002, 2009) as well as cerebral compensation postulated in the PASA, ELSA, CRUNCH, and HAROLD hypotheses. It also presents models that more largely integrate factors potentially influencing cognitive aging (Dennis & Cabeza, 2013; STAC; STAC-R) as well as the hypothesis of the declining dopaminergic system. This chapter ends by describing cognitive efficiency in the middle-aged population.

The last introductory chapter is dedicated to the presentation of studies about cognitive fatigue in older as well as in middle-aged population.

Regarding the experimental part of the Thesis, the first study was based on a Time-on-Task approach in which a 160-minute Stroop task was continuously administrated to young, middle-aged, and older people in order to test performance decrement (increase in extreme reaction times (RTs)) as a function of both the time spent on task and age.

The second study was based on the same protocol as the first one, except that rest breaks were given every 40 minutes. This study allowed us to test whether periodically interrupting the task with short breaks (5 minutes) might relieve cognitive fatigue and allow people to maintain performance. The extent to which the three age groups benefit from breaks was also investigated.

The third study used a Probe approach in which a fatigue condition (i.e., a long-lasting Stroop task) or a control condition (i.e., watching videos) was directly followed by an N-Back task during functional magnetic resonance imaging (fMRI) acquisition. This procedure allowed us to test whether cerebral activity is differentially modulated by a fatigue state as a function of age.

This work ends by a general discussion of the results of the three studies and proposes future lines of investigation in this research field.

We hope our results will contribute to advance knowledge about cognitive fatigue in aging and will be the starting point of many other studies afterwards. We already thank all readers for their interest and wish them a compelling reading.

Préface

Dans nos sociétés modernes, les êtres humains sont constamment sollicités cognitivement, et ce jusqu’à un âge relativement avancé. Cette stimulation cognitive continue peut être vécue au travail mais peut également provenir de façon insidieuse de nos environnements surchargés, des réseaux sociaux, ou des publicités constantes sur Internet, plongeant finalement les individus dans un flot ininterrompu d’information. La fatigue cognitive est progressivement devenue l’une des plus importantes causes d’accidents dans la vie quotidienne (Dinges, 1995; Shen et al., 2008) mais également dans le milieu du travail (McCormick et al., 2012). Si la fatigue cognitive peut être considérée comme une réponse normale et adaptée face à des tâches de longue durée (Boksem & Tops, 2008), elle peut également mener à des conséquences tragiques dans certaines professions. Par exemple, des études ont montré des chutes d’attention chez les pilotes d’avion (Bartlett, 1943) ou de grande variation de vitesse chez des conducteurs de voitures ou de train cognitivement fatigués (Brown, 1994; Campagne et al., 2004; Kecklund & Akerstedt, 1993; Torsvall & Akerstedt, 1987). Ce phénomène est également évident dans les services d’urgence tels que chez les pompiers (Aisbett & Nichols, 2007; Aisbett et al., 2012; Ferguson et al., 2016) et les médecins attelés aux unités de soins intensifs (Maltese et al., 2016). À force d’être confrontés de façon continue à la fatigue cognitive, certains individus peuvent malheureusement développer une condition dite de *burnout* (Maslach et al., 2001), engendrant des coûts tant au niveau du système de soins de santé publique qu’au niveau des employeurs (Ricci et al., 2007).

La fatigue cognitive est présente dans des domaines variés : Blain et al. (2006) ont montré qu’un travail cognitif intense durant toute la journée tend à augmenter l’impulsivité dans les prises de décision économiques. De la même façon, il a été montré que la fatigue cognitive dégrade les prises de décisions, les préférences, et les stratégies économiques (Mullette-Gillman et al., 2015), la régulation des émotions (Grillon et al., 2015), ainsi que la flexibilité cognitive chez des étudiants universitaires (Plukaard et al., 2015). Dans le domaine du sport, on a également montré que la fatigue cognitive altère les décisions footballistiques (Smith et al., 2016), la performance lors de courses intermittentes (Smith et al., 2015), ainsi que les performances au tennis de table (Le Mansec et al., 2018).

Dans les cas les plus importants, la fatigue cognitive peut devenir une condition permanente comme chez les patients avec le Syndrome de Fatigue Chronique (CFS; Tanaka

& Watanabe, 2010). La fatigue cognitive est également fréquemment rapportée dans des conditions psychologiques telles que la dépression (Demyttenaere et al., 2005; Lavidor et al., 2002) et dans les maladies neurologiques telles que la maladie de Parkinson, la sclérose en plaques, les accidents traumatiques crâniens, les accidents vasculaires cérébraux, la myasthénie, la sclérose latérale amyotrophique, ou le syndrome postpolio (Chaudhuri & Behan, 2000; Kluger et al., 2013). Etant donné les conséquences tragiques de la fatigue cognitive, la nécessité de réaliser des études permettant de mieux comprendre ce phénomène est évidente.

Par ailleurs, les progrès médicaux de ces dernières décennies ont radicalement augmenté l'espérance de vie, atteignant l'âge de 81.44 ans (en 2017) en Belgique. Parallèlement, l'on a progressivement demandé aux individus de travailler jusqu'à un âge avancé, alors que des diminutions de l'efficacité du fonctionnement cognitif ont été montrées à un âge plus élevé (Collette & Salmon, 2014; Crawford et al., 2000; Salthouse et al., 2003; West, 1996, 2000). Par conséquent, prendre conscience de la manifestation de la fatigue cognitive dans les âges plus avancés semble crucial. De façon surprenante, très peu d'études ont investigué la fatigue cognitive, aussi bien du point de vue comportemental que cérébral, dans les populations vieillissantes.

Outre l'âge élevé, l'âge moyen semble également constituer une population particulièrement à risque de souffrir de fatigue cognitive. En effet, l'âge moyen a parfois été considéré comme la période de vie la plus difficile vu les nombreuses exigences l'accompagnant (prendre soins des enfants, travailler, avoir une vie sociale, gérer les tâches du quotidien). Cependant, les individus d'âge moyen ont rarement été le centre d'intérêt des recherches scientifique, probablement à cause de la difficulté à accéder à cette population.

Le premier chapitre de ce travail de Thèse commence par la présentation de définitions et modèles de la fatigue cognitive, allant de ceux soulignant la déplétion d'énergie comme étant la conséquence d'un travail de longue durée jusqu'à ceux intégrant des notions se focalisant plus particulièrement sur l'effort contrôlé et volontaire (ex. : les modèles faisant intervenir les fonctions exécutives, le calcul coûts/bénéfices ou effort/récompense, les coûts d'opportunité) investi par l'individu dans une activité cognitive. Par souci d'exhaustivité, ce chapitre se termine par la présentation de certains modèles portant sur la fatigue pathologique.

Le deuxième chapitre décrit un ensemble d'études ayant investigué la fatigue cognitive chez les individus jeunes. Ce chapitre fait la distinction entre les protocoles expérimentaux basés sur l'approche *Time-on-Task* (c.-à-d. réaliser une tâche unique de longue durée) et ceux basés sur l'approche *Probe* (c.-à.-d. réaliser deux tâches consécutives dans le but de tester si l'effet de fatigue de la première tâche est transférable à la seconde tâche). La présentation des études fait également la distinction entre les mesures objectives (comportementales, électrophysiologiques, de neuroimagerie, de connectivité, liées à la motivation) et subjectives (échelles auto-rapportées) de la fatigue cognitive.

Le troisième chapitre est dédié à la présentation des modèles du vieillissement cognitif et cérébral. Il débute par la présentation des fonctions cognitives connues pour décliner avec l'âge ainsi que les médiateurs potentiels (c.-à-d. vitesse de traitement et inhibition) de ces déclins liés à l'âge. Ce chapitre présente les patterns bien connus de réserve cognitive (Stern, 2002, 2009) ainsi que de compensation cérébrale postulée dans les hypothèses PASA, ELSA, CRUNCH, et HAROLD. Il présente également des modèles qui intègrent plus largement les facteurs potentiels pouvant influencer le vieillissement cognitif (Dennis & Cabeza, 2013; STAC; STAC-R) ainsi que l'hypothèse du déclin du système dopaminergique. Ce chapitre se termine par la description de l'efficience cognitive dans la population d'âge moyen.

Le dernier chapitre d'introduction est dédié à la présentation d'études portant sur la fatigue cognitive chez les personnes plus âgées ainsi que dans la population d'âge moyen.

Concernant la partie expérimentale de la Thèse, la première étude était basée sur l'approche Time-on-Task dans laquelle une tâche Stroop de 160 minutes a été administrée de façon continue à des personnes jeunes, d'âge moyen, et plus âgées afin de tester les diminutions de performances (augmentation des temps de réaction extrêmes (RTs)) en fonction du temps passé sur la tâche et de l'âge.

La deuxième étude était basée sur le même protocole que la première, à l'exception de l'introduction de pauses de repos toutes les 40 minutes. Cette étude nous a permis de tester si le fait d'interrompre périodiquement la tâche avec des pauses courtes (5 minutes) peut soulager la fatigue cognitive et permettre aux individus de maintenir la performance, mais également de tester si les trois groupes d'âge bénéficient des pauses de la même façon.

La troisième étude a utilisé une approche Probe dans laquelle une condition fatigante (c.-à-d. une tâche Stroop de longue durée) ou une condition contrôle (c.-à-d. visionnage de vidéos) était directement suivie par une tâche N-Back durant une acquisition d'imagerie par résonance magnétique fonctionnelle (fMRI). Cette procédure nous a permis de tester si l'activité cérébrale était modulée de façon différente par un état de fatigue en fonction de l'âge.

Ce travail se termine par une discussion générale des résultats des trois études et propose de futures lignes d'investigation dans ce domaine de recherche.

Nous espérons que ces résultats contribueront à faire avancer les connaissances sur la fatigue cognitive dans le vieillissement et seront le point de départ d'autres études par la suite. Nous remercions déjà tous les lecteurs pour leur intérêt et leur souhaitons une agréable lecture.

Theoretical Introduction

Chapter 1: Definitions and Models of Cognitive Fatigue

"Cognitive fatigue" or "mental fatigue" has become a frequently used expression but is yet not that simple to define. As readers will appreciate, definitions vary from an author to the other. Most of the time, authors have linked cognitive fatigue to objective decrements in performance in the task at hand. Cognitive fatigue has also been proposed to result from different causes such as energy depletion, sustained demands, workload/overload, boredom/underload, effort, or demotivation. Otherwise, some relationships exist between cognitive and physical fatigue, certain studies showing that one kind of fatigue is likely to influence the other (Mehta & Parasuraman, 2014; Van Cutsem et al., 2017). However, given this Thesis work is not focused on physical fatigue, the Introduction will start by a brief distinction between these two types of fatigue and only focus on cognitive fatigue afterwards.

As above-mentioned, there exist many different definitions of cognitive fatigue and it is not straightforward to *choose* or to isolate a consensual definition. Therefore, before presenting the most influencing models of cognitive fatigue, it is important to present the different aspects but also the different categories of cognitive fatigue. For example, some authors have considered fatigue as an adaptive emotion (Boksem & Tops, 2008; Hockey, 2013) or have pointed out that some related feelings are very close and sometimes confounded with the feeling of fatigue (Hockey, 2013; Kuppuswamy, 2017). We also present the well-recognized distinction between Active *versus* Passive cognitive fatigue. Finally, we present the objective (i.e., performance-related) *versus* subjective (feeling-related) aspects of cognitive fatigue. Through the Introduction, the reader will also find some Boxes highlighting, defining, or contrasting some key concepts presented in the main text.

Cognitive versus Physical Fatigue

Some authors claim that cognitive and physical fatigue have to be considered as a unique concept and have proposed a common definition integrating the two aspects. For example, the Japanese Society of Fatigue Science defines fatigue as follows:

> A decline in the ability and efficiency of mental and/or physical activities that is caused by excessive mental or physical activities or disease. Fatigue is often

> accompanied by a peculiar sense of discomfort, a desire to rest, and a decline in motivation, referred to as fatigue sensation. (Kitani, 2011)

Similarly, Kuppuswamy (2017) proposed that fatigue is an inference on the first place and must be considered as a single construct which does not distinguish between the mental or the physical aspect.

Contrary to this unitary view, other authors make the distinction between the cognitive and physical aspects that have been referred as central and peripheral fatigues (Chaudhuri & Behan, 2000). While peripheral fatigue refers to neuromuscular and muscular failure, central fatigue relates to the reduction in attention, in self-motivation, as well as in efficiency of mental workload in the absence of cognitive failure or motor weakness (Chaudhuri & Behan, 2000, 2004). It has also been proposed that cognitive fatigue would be partly responsible for physical fatigue (Mehta & Parasuraman, 2014; Van Cutsem et al., 2017) but further studies are needed to confirm this link (McMorris et al., 2018).

Otherwise, different tools are used to assess these two types of fatigues. Physical fatigue is often targeted by muscle evaluation while cognitive fatigue is measured by cognitive tasks. From a clinical point of view, myopathic weakness is considered a reliable index of peripheral fatigue. Likewise, performing a series of strong muscle contractions has been shown to induce a shortening of the muscle group during several minutes (Chaudhuri & Behan, 2004). Studies assessing neuromuscular fatigue also often require participants to perform handgrip strength exercises (Mehta & Parasuraman, 2014; Shortz et al., 2015; Shortz & Metha, 2017, Terentjeviene et al., 2018). By contrast, measures of cognitive fatigue target mental operations that do not require muscle contractions. For example, cognitive fatigue studies typically require participants to perform a mental task (e.g., arithmetic problems, visual attention task, switching task, inhibition task) during several minutes or even several hours.

Several Definitions of Cognitive Fatigue

Defining cognitive fatigue is not straightforward and the main issues are presumably the relationships between cognitive fatigue and some intrinsically related notions such as motivational aspects or boredom (Lorist, 2008). Indeed, it appears that our everyday use of different expressions such as “I’m tired”, “ I’m feeling sleepy”, or “I’m bored” have progressively triggered a certain conceptual blurring in the scientific community, so that depending on the authors, definitions emphasize more or less one aspect or another. The following lines present some definitions belonging to different authors. Trejo et al. (2005, p.1) defined cognitive fatigue as “the unwillingness of alert, motivated subjects to continue performance of mental work”, this state being independent from sleepiness, motivating, learning, or physical fatigue. According to Lorist et al. (2005, p. 199), “mental fatigue refers to the effects that people experience following and during the course of prolonged periods of demanding cognitive activity, requiring sustained mental efficiency.” Holtzer et al. (2011, p.8) defined cognitive fatigue “as an executive failure to monitor performance over acute but sustained cognitive effort, which results in decline and more variable performance than the individual’s optimal ability.” In his thesis, Borragán also proposed to define cognitive fatigue as being:

> The temporary decrease in mental resources developing over time on sustained cognitive demands/effort. The onset of cognitive fatigue is gradual and depends on each individual’s capacity. Its presence often comes with an increased subjective feeling of mental exhaustion and a usual failure to maintain optimized behavioral performance in a context where the level of motivation remains stable. (2016, p.25, unpublished thesis)

Cognitive Fatigue as an Adaptive Emotion

Some authors also consider fatigue as an evolutionary adaptive emotion. For example, Hockey (2013) defined fatigue as “as an emotion, having an adaptive, goal-directing function and a central role in the system responsible for maintaining motivational priorities.” Similarly, van der Linden (2011) proposed that “fatigue might be considered as a *stop emotion*” (p. 153, italics original). Kurzban et al. (2013) also agreed that “subjective experience can be understood computationally as motivating the organism to behave adaptively” (Lazarus, 1993;

Tooby et al., 2008). In this sense, fatigue would have a metacognitive function leading to the interruption of the current task goal and allowing other goals to be considered instead. Also considering cognitive fatigue as an adaptive response, Boksem and Tops (2008, p. 126) proposed that "mental fatigue refers to the feeling that people may experience after or during prolonged periods of cognitive activity." These feelings may involve tiredness, exhaustion, an aversion to continue the current task, and a decrease in the level of commitment to the task at hand (Holding, 1983; Hockey, 1997; Meijman, 2000). In addition, Boksem and Tops also proposed that mental fatigue can be associated with impaired cognitive and behavioral performance. This latter proposal will be fully supported by experimental studies I will present in **Chapter 2** (see for example Boksem et al., 2005; Lorist et al., 2005; van der Linden & Eling, 2006).

Some authors have also claimed that fatigue takes place in different steps. Trejo et al. (2007) described cognitive fatigue as manifesting in three stages: 1) a brief state in which alertness is high; 2) a longer state of normal alertness; 3) a final state associated with the real state of fatigue at the end of the task. Hockey (2013) also proposed a very interesting view of the process of fatigue and postulated that this phenomenon appears as soon as the task begins with two main stages to be distinguished. Firstly, there is an early-onset inhibitory response to task engagement[1]. This very early fatigue is experienced as a vague sense of cognitive discomfort and is characterized by rapid subtle disruption of performances. This phenomenon mostly appears at the very beginning in response to task in which rapid and homogenous stimuli are experienced. Secondly, there is a later fatigue, which Hockey referred to as "strain". This represents an effort-driven process triggered by the conflict opposing wanting to maintain the current task goal and performances *versus* the will to disengage. In this step, the individual experiences feelings of effort, stress and, in turn, aversion to pursue the task. This distinction between early-onset and later strain will be explained later in this chapter in the *Three phases of the work decrement function* (**Figure 3**).

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[1] In this context, "inhibitory response" does not refer to the classical executive inhibition function (e.g., the ability to inhibit dominant response). Rather, Hockey (2013, p.71) uses these terms to refer to the phenomenon of habituation consisting in a reduced response to repeated event patterns that are found not to be of value to the individual.

Cognitive Fatigue and Related Feelings

As abovementioned, fatigue is difficult to define because of related feelings. Boredom is the phenomenon the most argued against fatigue by *fatigue dementors*, particularly in the case of fatigue induced by a long-lasting task. These two related concepts are compared in **Box 1**. Besides boredom, fatigue may also appear in combination with anxiety, depression, or apathy. According to Hockey (2013), if it is useful to distinguish fatigue from anxiety, he also recognized that these two feelings often occur in parallel to form the classic strain pattern associated with an effortful response to demanding work (Hockey et al., 1996). In the Compensatory Control Model (CCM; Hockey, 1997) that will be developed further in this chapter, anxiety is the response to a perceived threat which occurs when demands are unexpectedly high. Anxiety is also considered as the precursor of fatigue in such situations, but only when sustained effort is recruited to meet these demands. According to Kuppuswamy (2017), fatigue, apathy and depression are defined by a significant reduction in self-initiated voluntary action which calls on two systems: the motivational system to self-initiate, and the executive (sensorimotor) system that delivers voluntary action. Given the sensorimotor system is rather preserved in fatigue, apathy and depression, she proposes that these three feelings rely on the motivational system which also comprises two subsystems: the directional and the activational systems. While the directional system determines the choice of directing one particular behavior towards or away from a stimulus, the activational system informs action (Salamone et al., 2016). In apathy and depression, patients are not interested in performing actions while they are able to do it. By contrast, in fatigue, individuals are still willing to act but feel unable to perform. Based on this distinction, Kuppuswamy proposed that apathy and depression are primarily caused by dysfunction of the directional system while she defined fatigue as “a percept arising primarily from alterations within the activational systems that inform voluntary action” (Kuppuswamy, 2017, p.2241).

Box 1. Fatigue and Boredom

Are performance decrements during a fatigue-inducing task really attributable to cognitive fatigue or rather to task disengagement due to boredom? The distinction between these two feelings has raised debate among researchers for a while. As soon as in 1937, Myers differentiated between mental fatigue and boredom but recognized that these two feelings may affect performance in a similar way. Specifically, he defined boredom as "the outcome of a failure to find interests which can maintain spontaneous or voluntary attention" (p. 298), while fatigue was "a general impotence to concentrate attention and to act purposefully, intelligently and creatively" (p. 299). Barmack (1937) proposed that boredom developed in task situations under low intrinsic motivation, and represents a state of conflict between remaining in the situation and wanting to get away from it. This state of conflict was assumed to be partially relieved by a state of disengagement or withdrawal.

"Overload Triggers Fatigue, Underload Triggers Boredom"

Some other authors distinguished between fatigue and boredom by opposing their respective assumed causes: overload *versus* underload. Welford (1968) suggested that fatigue occurs as a consequence of information overload (i.e., a level of arousal which is too high), and considered decrements as the consequence of increased "neural noise" under the sustained stimulation of demanding tasks. By contrast, he proposed that boredom was caused by underload (i.e., a level of arousal which is too low), brought about by inadequate environmental stimulation. In a similar vein, O'Hanlon (1981) has suggested that boredom is a response to repetitive or monotonous situations. Finally, Bartley and Chute (1947) also related boredom to monotony of the environment and fatigue to the perception of inadequacy to manage the task. This distinction finds echo in a more recent proposal distinguishing between different types of fatigue: active *versus* passive fatigue.

Mental Workload and the Active versus Passive Fatigue Hypothesis

A factor that is likely to influence cognitive fatigue is the intensity of the work or activity, which is known as workload. Initial theories of mental workload were derived from the *energy depletion hypothesis*[2] according to which human cognition has a limited resource

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[2] This hypothesis will be entered into more details in the section "Initial Models of Cognitive Fatigue".

supply that is depleted after a period of work (Hockey, 2013). It was thus primarily assumed that performance decrements during mental activities were due to excessive demands (i.e., high workload) that outweighed the limited information processing capacity. In agreement with this view, some studies have shown that performances decrease to a larger extent in a high workload condition as compared to a low workload condition (Borragán et al, 2017; Schmidtke, 1976). However, this unilateral hypothesis has been challenged by authors that differentiate between different types of cognitive fatigue.

In this regard, Hancock and Desmond (2000) distinguished between active *versus* passive fatigue. According to these authors, active fatigue can be induced by tasks in which sustained and prolonged demands involve continuous perceptual or motor adjustment (e.g., driving in high-density traffic). By contrast, passive fatigue would be triggered by vigilance tasks (see **Box 2**) requiring a monitoring system with few adjustments (e.g., driving on a roadway with little traffic and using automated system). Such a lack of demands for long-lasting periods induces a state of inactivity. This linkage between vigilance and underload is not new. Indeed, some authors (Manly et al. 1999; Robertson et al., 1997; Stuss et al. 1995) already stated that vigilance decrement is due to attentional withdrawal of the supervisory attentional system because of underarousal caused by insufficient workload. Related to this proposal, Pattyn et al. (2008) found that performing a vigilance task was associated with a lack of variation of sympathetic activation – classically linked to overload – as well as an increase of parasympathetic activation – classically linked to underload. These results pointed towards task disengagement and thus, to the underload hypothesis to explain vigilance decrements.

As introduced in **Box 1**, it has also been proposed that cognitive fatigue may result from either cognitive overload (active task-related fatigue) or cognitive underload (passive task-related fatigue) triggered by monotony (May & Baldwin, 2009). This proposal echoes the Yerkes-Dodson law (Yerkes & Dodson, 1908) according to which the function linking performances to arousal level follows an inverted U-shaped curve, meaning that underarousal but also overarousal are detrimental for performance. Similarly, cognitive fatigue may be triggered not only by very demanding (i.e., high workload) but also by very unchallenging (i.e. low workload) tasks (Matthews & Desmond, 2002; Saxby et al., 2007). For example, Shigihara et al. (2013) showed that participants in their experiment became slower as a function of the time spent on the task (30 minutes) in the low-demanding (0-Back) but not in the high-demanding (2-Back) condition. In parallel with this slowdown in processing speed for the 0-Back condition, the authors also found that the feeling of sleepiness increased after performing the 0-Back but not after the 2-Back condition. It was concluded that the 0-Back, because of its easiness and inherent boredom, triggered a cognitive underload state (May & Baldwin, 2009), which in turn, led to a withdrawal of the attentional system and to impaired performance.

Box 2. Sustained Attention and Vigilance

Sustained attention and vigilance refer to different tonic attentional states that are erroneously interchangeably used in the literature. These states are triggered as a function of the rate of information to be processed (Borragán et al., 2016, unpublished thesis).

Vigilance is induced by monotonous context in which stimuli are unpredictable and infrequent. This type of manipulation leaves the cognitive system in an under-arousal activation or underload state in which attention fluctuates. In van Zomeren and Brouwer’s (1994) model of attention, vigilance (which the authors called alertness) refers to the ability to quickly react to a recurrent stimulus that is presented at irregular intervals. This attentional process is classically assessed by the Psychomotor Vigilance Task (PVT; Dinges & Powell, 1985) or the Mackworth’s Clock test (1948).

Sustained attention is induced by continuous and rapid flow of information to be processed. According to van Zomeren and Brouwer (1994), sustained attention characterizes one’s abilities to maintain an attentional investment during relatively long periods in order to react to frequent stimulations. In this condition, the cognitive system is in high arousal or overload state.

Based on these definitions, it has been proposed that cognitive overload is more linked to sustained attention while cognitive underload is more related to vigilance, task monotony, and boredom (Hancock & Desmond, 2000).

Objective versus Subjective Fatigue

If establishing a definitive definition of cognitive fatigue remains to be done, a consensus seems to exist on a particular aspect. Indeed, there is a general agreement according to which cognitive fatigue can be divided into two distinguishable aspects: objective fatigue (or fatigability) is used to describe declines in task performances – such as response times or accuracy – while subjective fatigue (or perceived fatigue) refers to the feeling of a deteriorated ability to engage in mental activities (Bailey et al., 2007; Gergelyfi et al., 2015; Lorist, 2008).

Regarding objective impairments, cognitive fatigue has been associated with declines in executive functions such as response inhibition (Kato et al., 2009), task switching (Lorist et al., 2009), working memory updating (Hopstaken et al., 2015a, 2015b; Hopstaken, 2016), perseveration (van der Linden et al., 2003), as well as action monitoring (Boksem et al., 2006; Lorist et al., 2005). It is also associated with diminished attentional capacities such as sustained attention (Dorrian et al., 2007; Lim et al., 2010), divided attention (van der Linden & Eling, 2006), and psychomotor vigilance (Gui et al., 2015; Lim et al., 2010). Cognitive fatigue is also more likely to impact goal-directed attention, as manifested by reduced top-down control, increased distractibility, and difficulties ignoring irrelevant stimuli (Boksem et al., 2005). Likewise, cognitive fatigue has also been found to impact goal-directed planning and preparation (Lorist et al., 2000; Lorist, 2008, van der Linden et al., 2003). By contrast, automatic bottom-up processes seem to better resist cognitive fatigue (Langner et al., 2010). As above-mentioned, these cognitive fatigue-related impairments will be presented in more details in **Chapter 2** that is dedicated to experimental studies in the young population.

Regarding subjective feelings of fatigue, these may include the sensation of weariness, increasing sense of effort, mismatch between expended effort and actual performance, or exhaustion (Kluger et al., 2013) but sometimes also an aversion in pursuing the current activity or task (Hockey, 1997; Holding, 1983; Lorist et al., 2000). Subjective feelings can be assessed by subjective scales indexing how people feel at a particular time point of the experiment. In this regard, the Karolinska Sleepiness Scale (KSS; Akerstedt & Gillberg, 1990; Kaida et al., 2006) is recommended to assess sleepiness and simply consists in a 9-point scale to fill according to one’s immediate feeling of alertness. Similarly to the KSS, the Stanford Sleepiness Scale (SSS; Hoddes et al., 1972) can also be used to assess the degree of alertness and progressive steps in sleepiness at different time points over the course of an experiment.

Also often employed in research studies, visual analogue scales (VAS) are used to assess current moods and consist in pair of words (e.g., Fresh/Exhausted; Motivated/Demotivated; Relaxed/Stressed; Low Effort/Many Effort) placed to the left and to the right sides of an horizontal line with a cursor to move towards the corresponding adjective (for example, see Lee et al., 1991 for VAS for Fatigue; Borg, 1998 for VAS for Exertion; see for example Tanaka et al., 2014a for VAS for Sleepiness). More related to effort assessment, the Rating Scale Mental Effort (RSME; Zijlstra, 1993) is a unidimensional mental workload assessment procedure that is built upon the notion of effort exerted over a task. People are required to rate different current aspects of mental fatigue (e.g., difficulty keeping attention on the task, difficulty exerting further effort in the task) on seven vertical lines, within the interval 0 to 150 (from "not at all" to "extremely"). The fatigue subscale of the Profile of Mood States questionnaire (POMS; McNair et al., 1971) consists of seven adjectives used to describe fatigue (i.e. worn-out, listless, fatigue, exhausted, sluggish, weary and bushed) that have to be answered on a 5-point scale.

Besides these *momentary* scales assessing fatigue at a particular time (e.g., before or after an experimental task), there also exist questionnaires measuring self-reported cognitive fatigue experienced in daily life activities. As the reader will appreciate, most of these subjective fatigue scales have primary been developed and validated for pathological populations. For example, the Fibro Fatigue Scale (Zachrisson et al., 2002) is a 12-item scale used in fibromyalgia and CFS patients. Likewise, the Chalder Fatigue Scale (CFQ-11; Chalder et al., 1993) was initially developed to assess chronic fatigue symptoms within clinical populations but was revised and is now more widely used to measure the severity of tiredness. Likewise, many scales have been built to assess severity and impact of fatigue in cancer patients, such as the Multidimensional Fatigue Inventory (MFI; Smets et al. 1995) and the Brief Fatigue Inventory (BFI; Mendoza et al., 1999). Several scales have also been developed in the context of MS condition, such as the Fatigue Scale for Motor and Cognitive functions (FSMC; Penner et al., 2009) particularly relevant to assess cognitive and motor fatigue in MS patients or the Fatigue Impact Scale (FIS and MFIS; Fisk et al., 1994) that comprises a physical, a cognitive, and a psychosocial subscale.

As previously mentioned, most of these scales were designed as tools for evaluating fatigue in patients with particular conditions. These scales thus provide good reliability and validity in clinical populations. However, they may have a limited sensitivity in the evaluation of "normal fatigue" experienced by healthy individuals and that is not associated with significant functional impairments. Regarding scales more often used in healthy population, the Epworth Sleepiness Scale (ESS; Johns, 1991) assesses daytime sleepiness and comprises eight items related to daily live activities for which the participant has to estimate on a 4-point (from 0 to 3) scale his or her probability of dozing off or falling asleep while engaged in these different activities. Sharing a similar conceptual background with the ESS, the Brugmann Fatigue Scale (BFS; Mairesse et al., 2017) has been proposed to assess mental and physical fatigue but it focuses specifically on rest propensity. This scale comprises eight items (four related to mental fatigue and four related to physical fatigue) for which participants had to determine their need to rest after having been engaged in the proposed activity.

Finally, the Pittsburgh Fatigability Scale (PFS; Glynn et al., 2015) has been developed to assess perceived fatigability in older people. It is a 10-item scale in which participants are asked to rate the imagined fatigue level, from a score of 0 (no fatigue) to 5 (extreme fatigue), that would arise from implication in activities of specific duration and intensity. The scale comprises both a physical and a mental fatigability subscore.

However, it is important to underline that objective and subjective cognitive fatigue would rather be independent processes that are not systematically correlated (DeLuca, 2005). Indeed, performance decrements can appear in the absence of subjective feelings and vice versa. According to Hockey (2013), the subjective feeling of fatigue should even be considered as the primary marker of the state of fatigue, before performance decrement which is not always found in experimental studies.

Initial Models of Cognitive Fatigue

In his notorious book entitled "The Psychology of Fatigue", Robert Hockey (2013) retraces the history of cognitive fatigue, from its first dominant views as an energy failure – the so-called energy depletion hypothesis – inherited from the late nineteenth century's industrialization context, to the incorporation of more recent concepts, leading to a more comprehensive picture of cognitive fatigue that encompasses motivational control mechanisms regulating current goal evaluation and the deployment of effort. Therefore, I will base the following lines on Hockey's proposal of fatigue history, starting with the energy depletion hypothesis and the principle of homogeneity. I will also present the ego-depletion framework in its first conception as well as in its more evaluated view, followed by the three stages of the Compensatory Control Model (Hockey, 1997, 2011, 2013). Afterwards, I will present the most influential models of cognitive fatigue stressing the voluntary control of the individual which assesses the costs and rewards of maintaining a particular behavior, I will also illustrate models presenting mental effort as opportunity costs as well as models linking cognitive fatigue to the dopaminergic influence on prefrontal and subcortical regions. Finally, I will present models trying to predict how acute fatigue may transform into chronic or pathological fatigue.

The Energy Depletion Hypothesis

From an historical point of view, the second half of the nineteenth century is characterized by the Industrial Revolution, which strongly emphasized the concept of energy as a central purpose in machine functioning but also as the cause of limited production. In such a work context, the relationship *work* → *energy depletion* describing machine functioning progressively expanded to mental and physical activities of human beings (Rabinbach, 1990). Therefore, some factory-based expressions – "I'm depleted", "I lack energy", "I'm exhausted", or "I have no fuel" – started to characterize human fatigue. This general view according to which fatigue is due to work performing was referred to by Hockey (2013) as the *work-fatigue hypothesis*. Regarding the research field, most paradigms were designed following the working-derived idea of people performing a task during a long-lasting period without break, which has progressively made popular the pursuit of performance decrement as the proof of fatigue.

Two mains topics animated the historical context of the study of fatigue: the time course of fatigue as well as the generality – or transfer – of fatigue to other activities. These issues led to the development of two still currently used approaches: the *continuous work approach* (Bills, 1937; Robinson, 1923) allowing the assessment of decrements in the long-lasting fatiguing task itself as a function of the time spent on a task (what we classically call Time-on-Task), and the *probe approach* allowing the assessment of decrements induced by a primary task – referred to as the loading task – on a separate probe task which is often administered before and after the fatiguing task (Hockey, 2013). The comparison of these two approaches will be entered more into details in **Chapter 2**.

However, whether the continuous work approach or the probe approach was adopted, the common feature of the fatiguing task was generally its long duration and the characterization of fatigue was always the performance decrements. For example, in an attempt to mathematically represent the development of fatigue – performance decrease – as a function of the time spent on a task, researchers such as Emil Kraepelin (1902) tried to model what they called the *work curve*. As a consequence, fatigue was primarily regarded as being characterized by *performance decrements* with only few interest allocated to its subjective dimension. After Kraepelin, one of the most recognized investigation of the work curve was that of Arai (1912), which administered to herself challenging arithmetic problems during uninterrupted 12-hour periods. Even if the results have been somewhat challenged by general practice effects (i.e., improvements) over the four days as well as questions about the time of day effect, her study showed decrements as indexed by increases in time spent to solve a problem with Time-on-Task (see **Figure 1).**

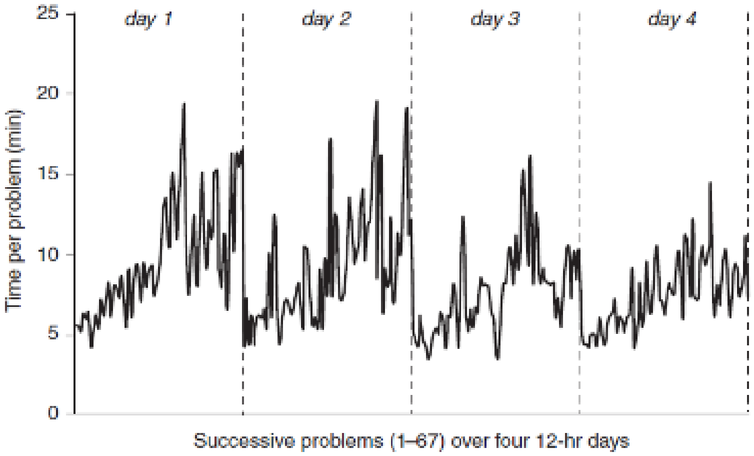

Figure 1. Arai's (1912) Data. This graph shows the time taken for mental arithmetic problems over 12-hour days. From The Psychology of Fatigue: Work, Effort, and Control (Hockey; 2013). Reproduced with permission of the Licensor through PLSclear. Copyright.

The Principle of Homogeneity

Robinson and Bills (1926) further claimed that performance decrements in long-lasting tasks were primarily due to the homogeneity of the task. This principle of homogeneity states that fatigue will be induced by highly repetitive task while tasks that possess varying features are less likely to suffer from Time-on-Task or to transfer to other tasks. In agreement with this principle, other researchers found evidence of performance decrement in homogeneous long-lasting tasks as compared to varying tasks (Noll, 1932; Poffenberger, 1927). Likewise, complex monitoring tasks have been shown to be less prone to performance decrement (Adams et al., 1961) because they are complex, varying, and not monotonous. More recently, Ackerman and Kanfer (2009) also administered their participants long-lasting batteries made of many different types of tests and did not find any performance decrement as a function of the session length.

If there was a slowdown in the fatigue literature during the second half of the 20th century, the scientific interest emerged for vigilance tasks. In 1943, Mackworth was interested in signal detection decrements undergone by radar operators on anti-submarine patrols (Hockey, 2013). In that context, Mackworth (1948) decided to build the well-recognized Mackworth Clock-Test. It consists very simply in a pointer traveling the face of a clock at regular steps separated by 1 second interval. However, at random intervals, the pointer travels the usual distance twice (i.e., "double jump"). The instruction given to the participant is to press a key as accurately and quickly as possible when he detects a double jump. As a measure of the time spent on the task (more than 2 hours), vigilance was found to decrease as attested by diminished number of correctly detected targets (hits) and increased mean of reaction times. However, the very reason behind performance decrement in vigilance tasks has been discussed. While some authors relate decrements in vigilance task to homogeneity triggering underarousal and disengagement (Deese, 1955; Welford, 1968) as supported by the passive fatigue hypothesis (Hancock & Desmond, 2000; May & Baldwin, 2009), other have hypothesized that vigilance rather implies a certain level of mental effort (Grier et al., 2003; Warm, Parasuraman & Matthews, 2008).

According to Hockey (2013), what is common between the work performance and the vigilance literature is that performance decrements can be explained by two common processes. The first one is called *habituation* and can be defined as an inhibitory response to repeated events with a low value for the individual. This process can be related to the principle of homogeneity above-mentioned. The second one is the *effortful control* of alertness which involves executive functions to maintain orientation to the task goal (top-down control) and reduces the habituation effect. However, even in the presence of top-down control of attention, processing long-lasting, rapid, and very homogenous stimuli may still reduce the maintenance of task goal and reorient attention towards higher valued stimuli.

The Ego-Depletion Framework

We also find reminiscence of the "energetic" view in the first theories of the ego-depletion framework. Indeed, the well-recognized theory in the field was that proposed by Roy Baumeister and his followers: the *resource model of self-control*. According to this model, self-control – the fact of engaging in controlled, willing action – will consume a limited inner resource or energy capacity (Baumeister & Heatherton, 1996; Baumeister et al., 1994;

Baumeister & Tierney, 2011; Muraven & Baumeister, 2000). Once the resource is empty, one becomes what is usually called *ego-depleted* and subsequent self-control attempts are compromised. To echo the probe approach mentioned earlier, the ego-depletion framework has commonly used a sequential task paradigm to show that exerting self-control at Time 1 (e.g., inhibiting the temptation to eat cookies) weakens self-control capacity (e.g., performing mental challenges) at Time 2 (Baumeister et al., 1998; Inzlicht & Schmeichel, 2012).

Some authors have tried to specify the nature of the inner resource and linked it to blood glucose levels. It was showed that engaging in self-control consumed glucose, leading to an ego-depleted state (Gailliot et al., 2007) but also that ingesting glucose counteracted the ego-depletion effect (e.g., Masicampo & Baumeister, 2008). Baumeister also claimed that glucose was the basis of "willpower" and that exerting self-control, which depletes the inner resource, weakens willpower. Likewise, it was also suggested that sustaining performance in a Time-on-Task paradigm consumed energy, diminishing the supply of lactate (Killeen et al., 2016). Such findings of consumptions in blood glucose were also found in task requiring high effort such as that involving incongruent trial processing in a Stroop task (Fairclough & Houston, 2004).

However, initial interpretations in terms of energy loss has been questioned. Indeed, it was shown that the difference in glucose consumption by the brain between low demanding as compared to high demanding tasks were relatively small and never led to energy depletion (Gibson, 2007; Raichle & Mintun, 2006). According to Hockey (2011), if glucose oxidation is inherent to brain functioning, there is no direct evidence that fatigue is triggered by glucose depletion. Indeed, some studies did not find evidence of increased glucose oxidation during long-lasting demanding tasks (Marcora et al., 2009).

Interestingly, Muraven and Slessareva (2003) showed that motivation was able to counteract the ego-depletion effect at Time 2, challenging the concept of a finite resource capacity. Therefore, the ego-depletion framework got away from the energy depletion hypothesis to go towards the integration of motivational aspects. Inzlicht and Schmeichel (2012) proposed a renewal of the ego-depletion model: *the Process Model of Ego Depletion*. In this model, the authors proposed that exerting self-control at Time 1 will induce a shift in motivational orientation as well as in attentional focus that interact to weaken self-control at Time 2 **(**see **Figure 2**). More precisely, the shift in motivation goes from exerting voluntary control towards more gratifying and rewarding activities for the individual. Likewise, shift in attention goes from cues signaling control towards more rewarding cues.

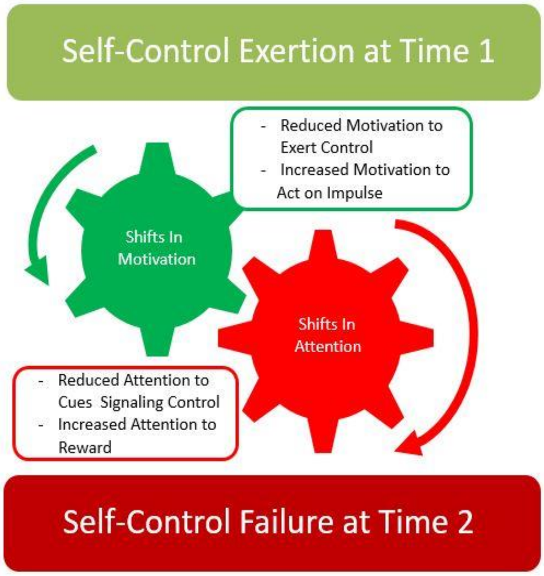

Figure 2. The Process Model of Ego-Depletion. Self-control exertion at Time 1 leads to self-control failure at Time 2 by inducing shifts in motivation away from exerting control and towards self-gratification as well as shifts in attention away from cues signaling control and towards cues of reward. Adapted from Inzlicht and Schmeichel (2012).

As the ego-depletion field questioned the energy depletion hypothesis, Hockey (2013) also strongly argued that the initial view of cognitive fatigue as being due to a loss of energy with work performing (the work-fatigue hypothesis) has dramatically weakened and distracted the research field. According to Hockey, a challenge to the energy depletion hypothesis is its few arguments to explain the relationships between performance decrement – objective cognitive fatigue – and feelings of fatigue – subjective fatigue. If we adopt the energy depletion view, since the individual becomes completely resource depleted after a period of work, he should systematically show performance decrement. However, performance decrement are not systematically detected in fatiguing tasks and objective and subjective fatigues are often uncorrelated (Poffenberger, 1928; Thorndike, 1900).

Hockey (2013) explained this lack of correlation as follows: if there is no deployment of effort, performance will decrease but there is no feeling of fatigue. By contrast, highly motivated individuals will provide controlled effort, leading to the maintenance of task goals and performances but also to increased subjective feelings of fatigue. Therefore, it is not the workload itself that triggers fatigue, but rather the deployment of high efforts to meet task demands (see **Box 3**). In agreement with this view, Earle (2004) found that for a given workload level, feelings of fatigue were higher when large effort strategies were deployed as compared to low effort strategies (see also Earle et al., 2015 for similar conclusions).

However, even if it has been questioned to some extent (see Hockey, 2011, 2013), it is worth mentioning that the energy depletion hypothesis is still up to date and continues to animate the research field. Close to this view, the Attention-Resource Model (Davies & Parasuraman, 1982; Warm et al., 2008) also proposes that sustaining attention control exhausts underlying mental resources (Maclean et al., 2010). Likewise, the *resource depletion account* attributes vigilance decrement to the depletion of resources necessary for task performance (Ariga & Lleras, 2011; Hancock & Warm, 1989; Mackworth, 1948). Interestingly, it has been proposed that the resources necessary to maintain vigilance performance are renewable and are able to self-recover if the system is allowed to rest. According to Finkbeiner et al. (2016), people that criticize the resource theory account do not take into consideration this renewable nature of cognitive resources.

The Effort-Recovery Model (Meijman & Mulder, 1998), initially created in the context of fatigue at work, proposes that rest breaks allow to counteract increased fatigue associated with high work demands. Rest breaks are assumed to decrease fatigue, improve performance, and restore energy levels that vanished during high work demands by temporarily disengaging the individual from task demands (Meijman & Mulder, 1998). Accordingly, breaks have proven beneficial in many domains. They reduce the risk of accidents in industry (Tucker et al., 2003), improve productivity and job satisfaction (Dababneh et al., 2001; Zacher et al., 2014) as well as employees' daily work engagement (Kühnel et al., 2017). Breaks during school improve test performance (Sievertsen et al. 2016) and well-being (Blasche et al., 2018). Laboratory studies using "breaks paradigms", in which breaks are granted at some time points during the task, have found positive effect of breaks on cognitive performance (Arnau et al., 2017; Chen et al., 2010; Lee et al., 2015; Phipps-Nelson et al., 2010; Ross et al., 2014). Some authors have even resorted to breaks paradigms with the sole aim to support the resource depletion account (Finkbeiner et al., 2016; Ross et al., 2014). For example, Helton and Russell (2015) tested different types of breaks (i.e., rest breaks and breaks implying cognitive activities) and found that rest breaks were the most beneficial, suggesting that a complete break from task-related process enables cognitive resources to recover, which sustains the depletion hypothesis. Without going into details, some authors also propose that not only rest breaks but also other types of breaks such as relaxation or physical activity (Blasche et al., 2018) may be beneficial. The Attention Restoration Theory (ART; Kaplan, 1995; Kaplan & Kaplan, 1989) also proposes that being presented with natural scenes or biological movement is beneficial for attention restoration (Herzog et al., 1997; Kaplan, 1995). Based on this proposal, studies have investigated different types of breaks such as making participants look at a green (natural) *versus* concrete rooftop (Lee et al., 2015) or looking at dog (natural) *versus* robots videos (Finkbeiner et al., 2016).

Moving away from the energy depletion hypothesis, other authors have proposed interpretations of fatigue that emphasized the relevance of the goals for the individual. Bartley and Chute (1947) underlined the importance of taking the attitude and desire towards a task into account. Similarly, Thorndike (1914) claimed that the low intrinsic attractiveness of a task may trigger task disengagement. Therefore, it has progressively become clear that other factors such as the intensity (or workload), the variety, the meaning of the work, or the motivation were also useful in the comprehension of the phenomenon.

In the following sub-sections, I will present some influential models of cognitive fatigue incorporating one or several factors – motivation (see **Box 3**), voluntary control of goal selection, costs/benefits calculation, opportunity costs, effort discounting (see **Box 3**), or the dopaminergic system – that can be involved in the triggering of cognitive fatigue, below and beyond the time course aspect and the energy depletion hypothesis. I will also present an alternative or "outsider" model according to which effort does not necessarily increase the rewarding value of its product but can be considered as rewarding *per se* by certain individuals.

Box 3. Demand, Effort, Motivation, and Effort Discounting

Demand
A property of a stimulus that determines how much mental or physical labor will be required (i.e., level of difficulty or challenge), such as the weight of an object that needs to be pushed. Related to, but distinct from effort, which corresponds to the amount of labor the organism engages in.

Effort
Intensification of either mental or physical activity in the service of meeting some goal (e.g., increasing the force applied to an object). Related to, but distinct from, demand or difficulty, which corresponds to a property of the stimulus not of the organism.

Motivation
A (psychological) force that drives behavior and that consists of a direction (e.g., a goal) and an intensity or amplitude with which this direction is pursued (i.e., effort).

Effort discounting
Decreased liking (or valuation) of objects that are contingent on effort. In other words, the more effort something requires, the less organisms value it.

From Inzlicht et al.'s glossary (2018, p.10)

Motivation, Costs/Benefits Calculation, and Goal Selection

Voluntarily Controlled Effort

As for the ego-depletion framework, the cognitive fatigue literature has begun to encompass other interpretations in term of mental effort. For example, some authors claimed that effort is strategically set up by executive functions (Moray, 1967) and serves to maintain the task at hand under the focus of attention (Kahneman, 1973). Contrary to the “absence of control and awareness” inherent to the energy depletion hypothesis, some authors have underlined the voluntary or controlled aspect of effort. A well-speaking example is the fact that effort is generally provided to a certain extent but never to its maximum. Likewise, a looseness in the deployed effort to perform a low-demanding task that follows a high-demanding task has often been reported (Stark et al., 2000; Young & Stanton, 2002). As mentioned by Hockey (2013), these phenomena were referred to as the "willing to spare capacity" (Kalsbeek, 1968).

Hockey (1997) also underlined the role of controlled mental effort to maintain task goals against distractors. Bartley (1943, p.161) also considered that "the basis of fatigue is conflict and frustration". Bartley and Chute (1947) also considered fatigue as being triggered by conflict between goals. Theories of cognitive control have also underlined the resolution of conflict to select and maintain goal (Botvinick & Braver 2015; Botvinick et al., 2001). All these ideas stress the volitional or willing character of the fatigue feeling, more likely triggered by increased reluctance rather than becoming unable.

Based on these considerations, Hockey (2013) proposed three possible degrees of fatigue as a function of the strategy (**Table 1**). The *acceptance* of interruption leads to performance decrement but minor feelings of fatigue; the manageable *resistance* to interruption allows maintaining good performance at the expense of increased effort and feelings of fatigue; and the *strain* mode leads to slight performance decrement with sustained high effort and high level of fatigue, which may develop into aversion. The three modes are (or are not) associated with after-effects on post-task activities.

Table 1

Possible Patterns of the Fatigue Response to Work Tasks

Mode	Subjective state	Performance decrement	After-effects
Acceptance of interruption	Minor (transient) fatigue	Yes	No
Manageable Resistance to interruption	Increasing effort and fatigue	No	Yes
Strain	Sustained high effort and fatigue; aversive state	Slight	Yes

Note. Adapted from Hockey (2013).

Hockey (2013) also reinterpreted the work curve previously presented as three processes operating in cascade (see **Figure 3**). The first process is *habituation* because a rapid drop in performance – within the first few minutes – is often observed in tasks were rapid and homogenous stimuli are experienced (Chapman & Nolan, 1916; Phillips & King, 1916). The second process was called *strain* – such as the *strain mode* – and represents compensatory effort to counteract the loss of attractiveness induced by the long-lasting task. In this phase, the individual may have to increase its effort to maintain task goals and stabilize its performance. It is this increase in effort that would be responsible for the feeling of fatigue. Finally, *disengagement* – which can be linked to the *acceptance mode* – is an optional phase that may occur if the individual decides to not maintain the task goal anymore because it requires too much effort that are not evaluated as sufficiently rewarding. Interestingly, Hockey also proposed that disengagement does not necessarily means *leaving the task* but it can represent the strategy of an individual that accepts to perform at a lower level in order to reduce the costs associated with effort.

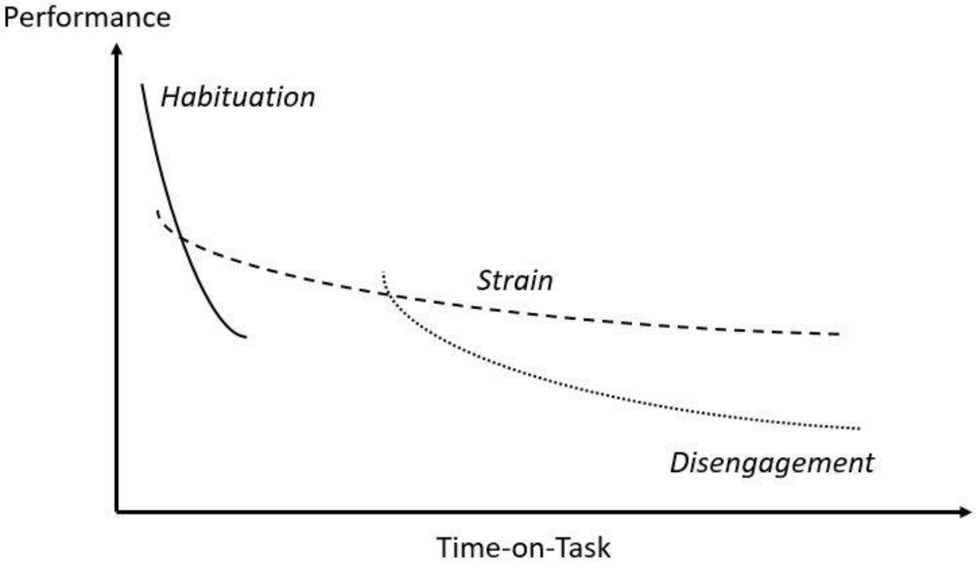

Figure 3. Three Phases of the Work Decrement Function. Adapted from Hockey (2013).

Far from the energy depletion account, Hockey's work (1997, 2011, 2013) has provided the cognitive fatigue literature with a completely different view which relates fatigue to failures in control management of the current goal.

Goals management is thus a central key concept in Hockey's work. Accordingly, he defined goal as "the desired behavior or outcome which any control system is designed to achieve" and considered motivation as the guide of goal-directed behavior, assessing the ratio between costs and benefits of competitor actions. Each goal is therefore pursued according to its rewards and its costs. Obviously, personal and meaningful goals (*want to*) are higher valued with lower perceived costs. If costs increase, the individual will deploy efforts to maintain the goal and performance because the benefits are high. On the contrary, imposed tasks or activities (*have to*) are generally low valued and, if costs increase, the individual may not deploy further effort to maintain performance and seek for an alternative preferred goal. Fatigue is thus considered as an adaptive function that allows the individual redirecting its actions towards higher valued ones according to one's motivational priorities.

According to Hockey, cognitive demands or workload are not basically responsible for fatigue. Instead, it is the deployed mental effort – seen as a controlled response to the perception and appraisal of demands – that triggers fatigue. Also, it is assumed that the possibility to exert control over work moderates the importance of fatigue effects, even under high workload (Hockey & Earle, 2006; Karasek, 1979; Karasek & Theorell, 1990). Hockey has proposed a Compensatory Control Model (CCM) in order to conceptualize his ideas of control management and conflicts between goals. I will only briefly describe the first version of the model and enter into more details for the second and the third versions, which are more elaborated.

The Compensatory Control Model: 1st version

The Compensatory Control Model (CCM) was initially built up in the context of performance under stressors and high workload (Hockey, 1993, 1997, 2005) and integrates the idea of a central executive or supervisory system (Norman & Shallice, 1986) to control effort. This model was thus more specifically dedicated to the understanding of task performance and effort. Fatigue was not directly part of the model and was considered as the result of increasing effort. This first conceptualizing represented control as two levels: a lower level (*Loop A*, in blue in **Figure 4**) dedicated to routine performance and an upper level (*Loop B*, in red in **Figure 4**) that regulates both task goals and effort via the supervisory controller. In this model, *overt performance* is driven by internal states, which in turns, determine output criteria for behavior (i.e., how fast, how much, or how long to work, the order of actions, etc.). The *action monitor* serves to compare and adapt the current activity with the target/desired output. The lower-level Loop A represents automatic control routines for well-learned skills and does not require effort regulation to maintain performance. By contrast, the higher-level Loop B is needed as soon as discrepancy between performance and desired output is too large to be resolved by routine corrections. In this case, the *effort monitor* is sensitive to increasing control demands in the lower loop and accounts for subjective effort in the face of increased task demands. This perception of change in *external load* (or strain) makes control to shift towards a higher-level: the *supervisory controller*. However, the model does not predict that effort will automatically be increased to meet task demands. Rather, the prediction of this model when the individual has to manage increased strain is twofold: the individual can increase his effort to maintain performance or he can maintain or reduce his effort, which leads to performance decrements.

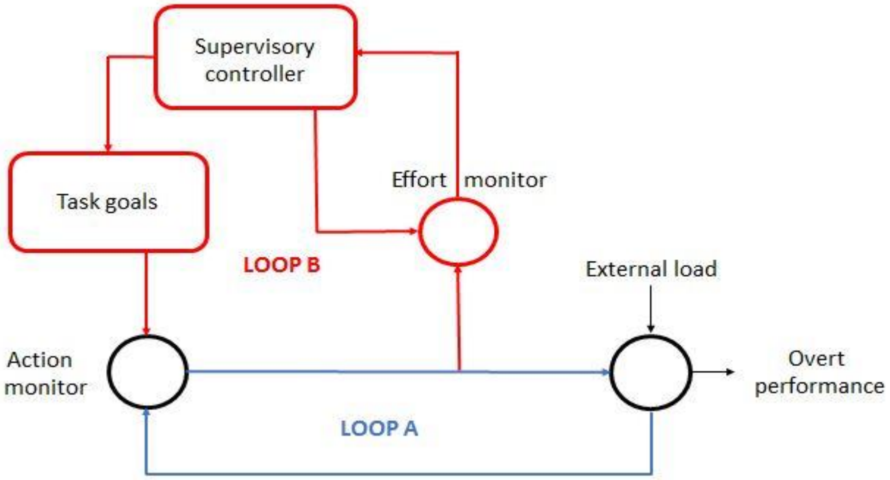

Figure 4. First Version of the Compensatory Control Model (CCM) of Performance Regulation. Loop A represents routine regulatory activity and Loop B represents effort-based control relying on the supervisory controller. Adapted from Hockey (1997).

This first model of Compensatory Control considered executive functions (i.e., the supervisory controller) as a single and undifferentiated entity responsible for both goal and effort management. Hockey extended this first model to propose a more elaborated representation of the links between the executive functions as well as the localization of fatigue.

The Compensatory Control Model: 2nd version

This model (**Figure 5**) posits that a *reference goal* (G) is maintained via direct *feedbacks* from *overt performance*. Similarly to the first version of the CCM, small deviations between the goal and the outcome can be adjusted by the implementation of automatic routine procedures while higher deviations require the central executive (*executive functions*) to exert controlled effort. When executive functions are activated due to the maintenance of performance being threatened, the *effort monitor* can require the *effort control* to implement one of these two solutions: (1) *increase the effort budget* and stabilize performance, which increases costs; (2) *maintain the effort budget* and impair performance, which minimizes costs. The second solution is submitted to the *goal selection* component which (3) *maintains the goal* at lower performance or (4) *changes the goal* according to one’s current motivational needs (g1, g2…). According to this model, the feeling of fatigue would be relieved when the discomfort or conflict triggered by the imbalance between the current goal and the outcome (overt performance) is resolved. Therefore, the model also predicts that changing one’s goal could be as efficient as taking a rest since goal activation will return to its maximum.

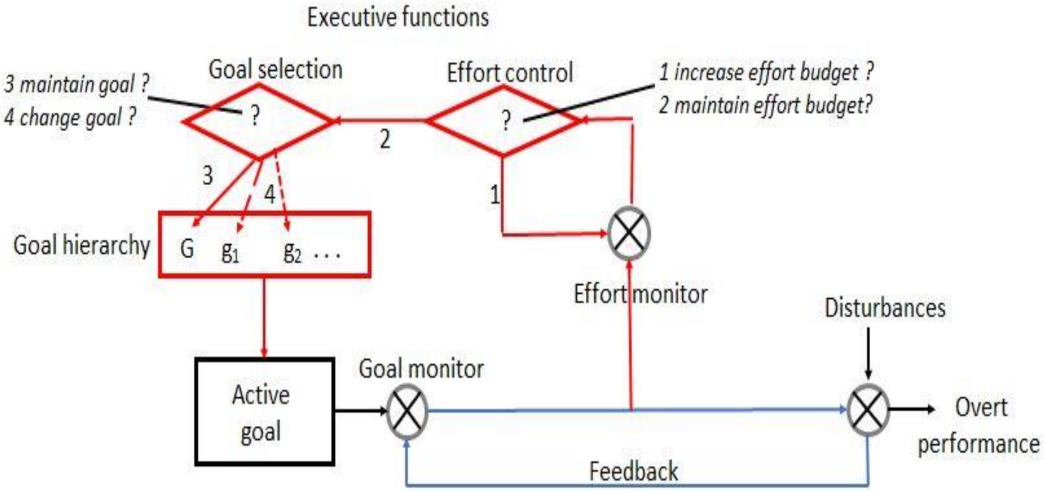

Figure 5. Second Version of the Compensatory Control Model. This model shows expanded executive functions and goal management options. Adapted from Hockey (2011). See text for explanation.

As compared to the first version, this second version of the motivational control theory of fatigue modelled two distinct functions for goal management and effort control, where effort was only considered as an optional mechanism. Indeed, increased effort is only required when goal maintenance is compromised and feelings of fatigue were considered as the result of this optional increased effort. However, Hokey later argued that fatigue is likely to start at the very beginning of the task, in the form of a feeling of cognitive discomfort triggered by alternatives that compete against the current task goal (Hockey, 2013). Since such effect occur before the need to deploy effort, the previous consideration of fatigue as being only the result of increased effort appeared to be insufficient.

Moreover, Hockey (2013) also newly claimed that there exist two types of task interruptions. On the one hand, fatigue may be considered as an emotion and adaptive function that allows the individual to leave the current activity and reconsider alternative goals according to its motivational priorities. When the current task goal is no longer valued, the costs associated with increased effort become greater than the benefits and executive control will allow a switch in attention from the current task goal to other competitor goals that are preferred and more meaningful for the individual. Hockey referred to this first type of interruption as the *top-down motivational regulation*. On the other hand, Hockey also proposed that lower level events such as bodily needs or external events may also lead to an automatic interruption, which Hockey referred to as *bottom-up distraction*.

Also, based on neuroimaging evidence that the PFC was more dedicated to goal maintenance while the anterior cingulate cortex (ACC) was more linked to conflict detection and outcome evaluation (e.g., Botvinick et al., 2001; Miller & Cohen, 2001; Sarter et al., 2006), Hockey's newest model distinguishes not between two but three executive processes: goal regulation, effort management, and performance evaluation (i.e., conflict detection), which was not represented as a separate function in previous versions of the model.

The Compensatory Control Model: 3rd version

In his third version of the model (**Figure 6**), the current task goal (G) is maintained by a first executive process: the *goal regulation*. Minor deviations between the goal and the outcome are detected by the *action monitor* that receives negative feedback, and can be automatically managed in the lower control loop by routine procedures. According to Hockey, these subtle disturbances might be responsible for the early-onset of fatigue that takes the form of feeling of cognitive discomfort.

However, major deviations may also occur. They could be due to two different sources: 1) top-down source such as competitor goals (g1, g2,…) that are more valued by the individual; 2) bottom-up distraction such as *cognitive events*, *somatic events* and *environmental events*. These more important conflicts are detected in a higher control loop by the second executive process: the *performance evaluation*. This function assesses threats to the current goal and sends signal to the goal regulator to reinstate the goal.

The model also assumes that the individual defines an initial effort budget (reference level) to the task. If the deployed effort remains in the limits of the allocated budget, no supplementary executive action is needed. However, if the quantity of effort exceeds the budget, performance evaluation has to recruit an increase in budget from the third executive function: the *effort regulation* system. As already mentioned, it is the deployed effort to meet task demands that would be responsible for the strain-induced fatigue in the higher control loop, which is more important than the early-onset of fatigue that take place in the lower loop. If the costs are evaluated to be too high relative to the expected benefits, the increased effort budget will not be granted and there will be two possible endings:1) to maintain or reduce effort at the expense of performance; 2) to abandon the current goal to favor a competitor.

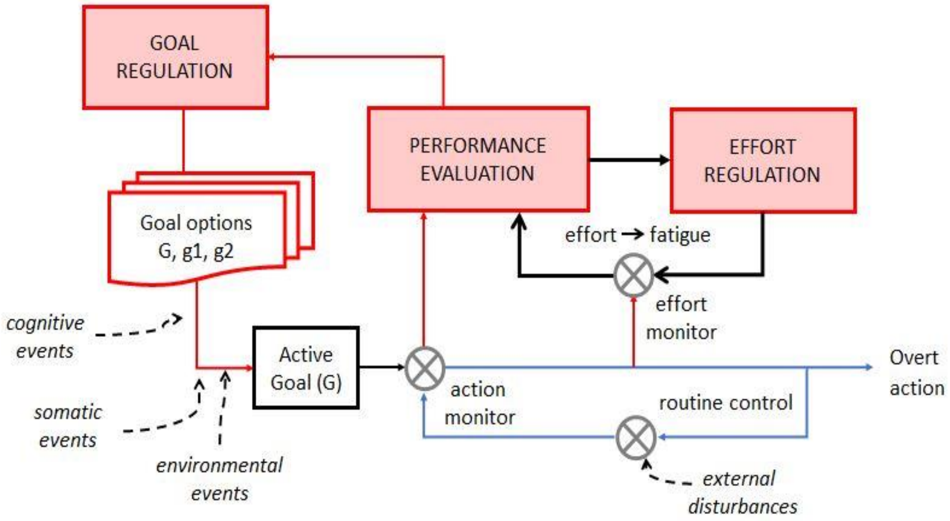

Figure 6. Third Version of the Compensatory Control Model. Compared to the previous version, this model assumes three distinct executive processes – goal regulation, performance evaluation, and effort regulation – in the upper loop. In addition to top-down interruptions (competitor goals), this new model also takes bottom-up distractions (cognitive, somatic, and environmental events) into account as potential sources of interruption. Adapted from Hockey (2013). See text for explanations.

After this detailed presentation of Hockey’s contribution, I will turn to models integrating new proposals about mental effort. The first two models also comprise the idea of costs/benefits computation towards a particular activity or behavior but with different conceptions of effort. The first one proposes that putting increased effort into an activity will eventually *discount the rewarding value* of that activity. The second one proposes that performing a cognitive activity is likely to increase the so-called *opportunity costs* (i.e., the fact of not being able to perform alternative activities). The third one is a little bit an “outsider” in the sense that effort is considered as *adding value* to the activity instead of reducing its rewarding worth. Afterwards, I will move towards models integrating the *dopaminergic system* and related cerebral areas to the costs/benefits (or effort/reward) evaluation and towards models predicting *pathological fatigue*. I will then close this chapter by presenting some *confounding variables* that are relevant to take into account when planning to study cognitive fatigue.

Cognitive Fatigue as Effort Discounting

Müller and Apps (2018) proposed a neurocognitive account of the multidimensional nature of fatigue and how it impacts motivation. According to these authors, fatigue increases with sustained effort and partially decreases with rest. The rate of fatigue also depends on the intensity of the effort. Furthermore, the authors claimed that motivation is a domain-general process characterized by costs/benefits assessment, and modulated by fatigue. This framework is mostly based on the well-recognized concept of *discounting effort* according to which effort cost assessment will diminish the value of the reward (see **Box 3**; Apps et al., 2015; Bonnelle et al., 2015; Chong et al., 2017; Hartmann et al., 2013; Kool et al., 2010; Le Heron et al., 2017; Shenhav et al., 2013; see also Westbrook et al., 2013 and Westbrook & Braver, 2015 for the cognitive effort discounting (COGED) paradigm). Therefore, as fatigue rises, people's evaluation of effort costs increases, which consequently decreases the subjective value of the reward: it is said that the reward value is discounted by effort. When the reward is devalued, motivation declines in parallel with performance impairments. The fact that exerting effort renders subsequent actions more effortful can be understood thanks to cognitive control theories (see **Box 4**).

Box 4. Cognitive Control Account

According to the cognitive control framework, attaining the optimal signal-to-noise ratio for a particular cognitive operation in a population of neurons is effortful. Moreover, repeatedly performing a cognitive operation (as it is the case in fatigue paradigms) may lead to neuronal adaptation (Grill-Spector et al., 2006). Therefore, increasing fatigue would lead to a decrease in the signal-to-noise ratio of a population of neurons, which is referred as neuronal fatigue. This cost (i.e., reduction in signal-to-noise ratio) can be overcome by the execution of a greater intensity control until information is appropriately processed (Kurzban et al., 2013; Manohar et al., 2015; Shenhav et al., 2017) at the expense of greater mental effort. Consequently, if exerting effort for a particular cognitive operation (or behavior) subsequently leads to a greater cost for performing the same operation (or behavior), its rewarding value will decrease. This theory may explain why fatigued people are less prone to engage in effortful behavior which was previously highly valued.

Based on the cognitive control account, Müller and Apps (2018) proposed that as fatigue increases, overcoming the increased costs requires a greater intensity control signal to reach optimal signal-to-noise ratio in the neuronal population dedicated to the behavior. Since providing a greater intensity control signal is effortful, it devalues the rewards associated with action. The authors also proposed a model in which they integrated the abovementioned notions by representing connections between cerebral areas coding for neuronal fatigue with those assessing the costs/benefits ratio of a particular behavior **(Figure 7**).

According to this model, fatigue arises with sustained effort within circuits that are recruited during a cognitive or physical task. These circuits comprise interoceptive (posterior insula (PI)), sensorimotor (premotor cortex (PM), supplementary motor area (SMA), and somatosensory cortex (Somat)), as well as widespread cognitive areas (**Figure 7**). The authors also proposed that these “fatigued “systems – or systems susceptible to neuronal fatigue – have connections with areas dedicated to goal-directed behavior such as dorsal ACC, DLPFC, and anterior insula (AI). These higher-level areas underpin the costs/benefits evaluation of a particular behavior to determine if it is worth exerting or not. In this view, fatigue serves to decrease the value attributed to exerting subsequent efforts (i.e., discounting effort) as compared to exerting alternative actions.

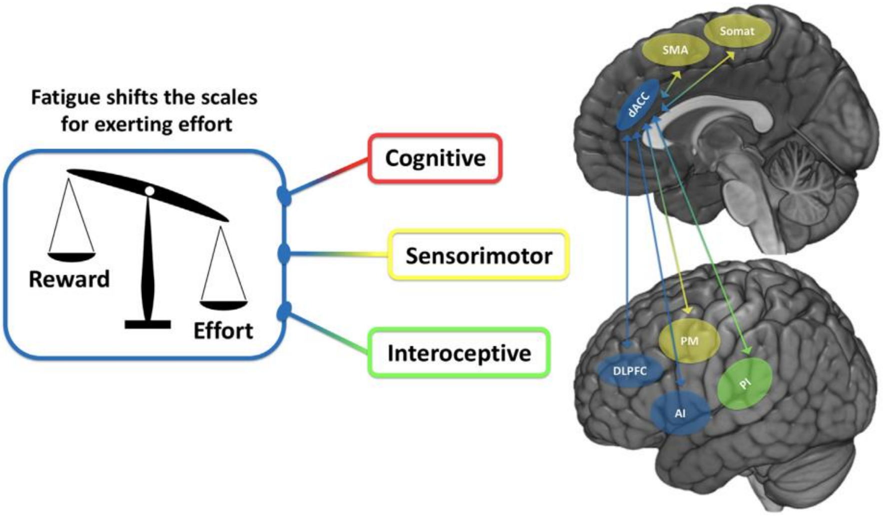

Figure 7. Proposed Systems in the Brain Underlying Motivational Fatigue. Fatigue can arise in interoceptive and sensorimotor systems (including but not limited to green and yellow areas) as well as in cognitive areas widespread across the brain. These three categories of areas are the "fatigued circuits" with extended effort during a cognitive or physical task. The DLPFC, the AI, and the dorsal ACC form a core "goal-directed" circuit evaluating the costs and benefits of exerting effort into behaviors. Connections between interoceptive, sensorimotor and cognitive systems to the goal-directed costs/benefits circuit allows fatigue to increase the weighting of effort costs in subsequent costs-benefits evaluations. Consequently, people are less motivated to exert effort, leading to performance decrements and in the degree to which actions are valued. Premotor cortex (PM), dorsolateral prefrontal cortex (DLPFC), anterior insula (AI), posterior insula (PI), dorsal anterior cingulate cortex (dACC), supplementary motor area (SMA), somatosensory cortex (Somat). Reprinted with permission from Müller and Apps (2018).

With reference to cognitive control theories, this model can be summed-up as follows: as fatigue increases in regions involved in task performance, greater input into those regions is required to obtain the same output. This change in how much effort will be required to perform a task is monitored within other regions – insula, DLPFC, and dACC. This network is also involved in the costs/benefits evaluation of effort. Thus, the monitoring of task executing regions by this network will serve to increase the costs associated with exerting subsequent effort. Therefore, neuronal fatigue within regions involved in task performance will impact subsequent motivation through the insula, the dACC, and DLPFC network. In agreement with this model, Chong et al. (2017) carried out a study in which people had to choose to exert effort for a reward while varying the intensity of the effort. Their results showed that the insula, the dACC, and the DLPFC were involved in the effort-discounted value of rewards.

Mental Effort as Opportunity Cost

According to Kurzban et al. (2013), certain mental processes cannot be allocated to multiple purposes at the same time. This is what the authors defined as the adaptive problem of *simultaneity*. The solution to simultaneity resides in *prioritizing among possible computations* – that is, identifying which of the various actions or computations is worth performing. The authors illustrated this problem in foraging organisms, which can feed in only one patch at a time and must decide when to stay in their current patch and when to search for a new one (Charnov, 1976). Solving the problem of prioritization requires the assignment of *costs and benefits* to the different options. Feeding at the current patch carries *opportunity costs:* the value of the next-best alternative (i.e., searching a new location).

The allocation of mental processes to a task (X) carries opportunity costs equal to the value of the next-best use of those mental processes (doing other tasks A, B, C,…) because the systems required for the task (X) cannot be simultaneously used for alternatives (A, B, C,…). Based on previous work (Boksem et al., 2005; Boksem & Tops, 2008; Botvinick, 2007; Hockey, 2011; Kool et al., 2010; Lorist et al., 2005), Kurzban et al. (2013) proposed that the conscious experience of mental effort results from mechanisms measuring the opportunity costs of the current task, motivating the reallocation of computational processes away from the present task and toward the next best alternative (Kurzban, 2010).

Organisms solve the prioritization problem by estimating the *utilities* of different possible actions, and then selecting the action that has the maximal expected utility. As an example, consider a research participant asked to perform math calculations with the possibility of having his or her smartphone nearby. The model predicts that doing math in the presence of the smartphone will be *perceived as more effortful* than in the case of the smartphone was absent, because the opportunity cost of performing math is higher in presence of the smartphone. If the experimenter leaves the room, the participant will reassess the utility of doing the math problems, probably cease this activity and shift to his smartphone.

In the same vein of ideas, there also exist cases in which a person will finally decide to divide her processing capacity between two actions – the current action and the next-best action – rather than restraining to only one. This is exactly what the model of Kurzban et al. (2013) is trying to predict.

The following equation represents how the utility – or marginal value gained – of performing two tasks at once (e.g., math and smartphone) varies as a function of the utility of performing only one task (math) and the utility of performing only the other (smartphone), when doing two tasks at once achieves a fixed fraction (β) of the utility of doing each task separately:

$$U(a_1, a_2) = \beta \ \times \big(U(a_1, a_1) + U(a_2, a_2)\big)$$

where a_1 and a_2 represent two tasks; $U(a_1,a_1)$ is the utility of doing only task a_1; $U(a_2,a_2)$ is the utility of doing only task a_2; and $U(a_1,a_2)$ is the utility of doing tasks a_1 and a_2 simultaneously; β is an index of diminishing marginal utility.

The *relative utility* (*RU*) of the next-best action (a_2) is defined as the fraction of its utility by the utility of the first best action a_1,

$$RU(a_2) = \frac{U(a_2, a_2)}{U(a_1, a_1)}$$

The conditions under which a person should allocate their processing capacity simultaneously to both tasks is expressed as follows:

$$U(a_1, a_2) > U(a_1, a_1) \ when \ \beta + \beta \times RU(a_2) > 1$$

Figure 8 also illustrates when a person should divide their processing capacity between two actions rather than restraining to only one. This is the case when the relative utility of the next-best action ($RU(a_2)$) is high, and when there is diminishing marginal utility to devoting processing capacity entirely to one task (i.e., β is high). When the marginal value gained from dedicating capacity to the best task – the utility of doing only the first task – is *less than* the marginal value gained from dividing processing capacity – the utility of performing both tasks simultaneously –, then processing capacity should be divided between the two tasks.

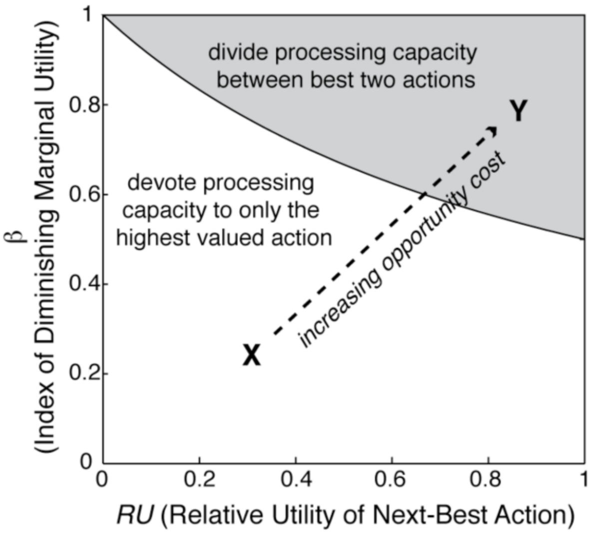

Figure 8. Mental Effort as Opportunity Cost. This model tries to predict when people should focus attention on only the first best action or to divide attention between two actions. This choice is determined by the relative utility (*RU*) of the next-best action but also by the fractional value (β) one gains when dividing processing capacity. Under low opportunity costs, people will devote processing capacity to only the first best action. However, with increasing opportunity costs, people will feel an increased sense of effort and be motivated to divide their mental processes between the two best actions in a way that reduces performance, moving from position *x* to position *y*. Reprinted with permission from Kurzban et al. (2013).

Similar to this model, some other interpretations of human choice come from optimization theories implemented in the artificial intelligence field. For example, it has been proposed that the best algorithm determining choice is the one that maximizes the *value of computation* (VOC), which is the difference between the expected utility gained from its computation minus the expected cost of its required resources (e.g., time of computation). Lieder et al. (2014) have applied this optimality principle to human cognition, proposing that individuals select cognitive strategies based on their relative VOC (Griffiths et al., 2015; Lieder & Griffiths, 2015; Lieder et al., 2012, 2014). In other words, people should rationally perform a costs/benefits analysis comparing the advantages of a selected cognitive strategy and the cost its computations entails (Lieder et al. 2014). Following this principle, mental effort should be deployed to achieve an optimal balance between the expected utility of its outcome (e.g., performance accuracy) and the opportunity cost of its required time (Shenhav et al., 2017).

In the same vein, Shenhav et al. (2013) have also proposed the *expected value of control* (EVC) theory in which control signals are specified along two dimensions: an identity dimension (e.g., what to attend) and an intensity dimension (e.g., how strongly to attend) that influence the likelihood of obtaining reward, or avoiding punishment. These factors define an overall reward rate at the expense of a certain cost with increasing control intensity. Therefore, the EVC is defined as the difference between the expected reward rate and the expected cost associated with a given configuration of control signals. Similar to the VOC model, the optimal control allocation is the one that maximizes the EVC.

An Alternative Framework: Effort Adds Value

The concept of effort has been somewhat renewed by Inzlicht et al. (2018) in their paradox of effort theory. As the authors explain, effort has long been considered costly, felt difficult or aversive, and linked to feelings of anxiety, stress, fatigue, and frustration. Effort is often avoided and the volition to exert effort is known to decrease after having already exerted a certain amount of effort (Inzlicht et al., 2014). However, Inzlicht et al. (2018) newly proposed that effort can also *add value* and be experienced as rewarding *per se*. The authors took the example of crafted objects that we effortfully assemble (e.g., IKEA furniture) and that are more valued than preassembled ready-to-use ones (Norton et al., 2012). It is also the case for people appreciating effortful challenges such as climbing huge mountains: these challengers would value their activity for the required effort. This view is a little bit different from that according to which people will deploy effort in order to get high reward and minimize costs. Instead, this model predicts that people will value rewards to a greater extent if these rewards have required a certain effort.

In the same vein, the *martyrdom effect* also suggests that value of an action can increase from its anticipated effort (Olivola & Shafir, 2013). For example, the willingness to contribute to a charitable cause increases when the fundraising process is expected to be painful and effortful: people often prefer taking part into challenges such as running 5-miles rather than easier activities such as attending a picnic or simply give money from home. Another pattern that would explain the volition of people to exert effort is the *learned industriousness*. According to this latter one, if effort is constantly paired with reward, a conditioned association will be created, and people become more willing to deploy that effort (Eisenberger, 1992). Finally, the authors also evoke the *need for cognition*, which describes people's intrinsic tendencies to engage in cognitive activities (Cacioppo et al., 1996).

Most of the time, effort is sought because it increases the value of its product (Kruger et al., 2004) rather than the value of the effort itself. However, the authors proposed an alternative view according to which people can also seek effort because the effort itself possess a rewarding value (Cacioppo et al., 1996; Kaufman, 1999; Loewenstein, 1999). Accordingly, Inzlicht et al. (2018) have represented a function according to which increasing effort intensity will depend on the increase of the product of effort (**Figure 9 A**) or on the increase of the value of effort itself (**Figure 9 B**).

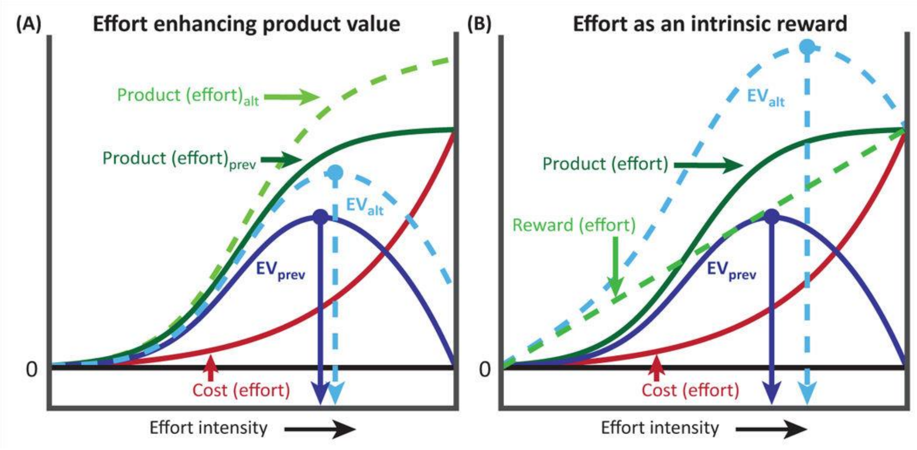

Figure 9. Two Alternative Formulations for the Positive Valuation of Effort. This figure represents what has been suggested by previous work (represented by prev) as well as by this alternative framework (represented by alt) for the case in which the product of effort is rewarding (A) and for the case in which the effort itself is valued as an intrinsic reward (B).

According to previous work, the expected value (EV) of effort (EV_{prev}; dark blue lines) is the difference between the expected product of the effort ($Product(effort)_{prev}$; dark green lines) and the cost of exerting effort (Cost(effort); red lines). The individual can select their optimal effort investment by setting the effort intensity that maximizes its EV (unbroken vertical arrow). According to the alternative framework, there are two ways of valuing effort: (A) as an amplification in the value of the effort's product with increasing effort intensity (from dark green to light green values), and/or (B) as an amplification of the value of the effort intensity itself. Each of these alterations (A and B) results in an alternate set of expected value of effort (EV_{alt}; broken blue lines) and corresponding changes in the optimal level of effort (broken vertical arrow). Reprinted with permission from Inzlicht et al. (2018).

Fatigue, Dopamine, and the Reward System

The neurotransmitter dopamine (DA) plays an important role in high level cognitive functions such as working memory and cognitive control. Several neuropsychological studies have suggested a direct association between altered dopamine transmission in the prefrontal cortex and cognitive deficits (Brozoski et al., 1979; Müller et al., 1998). Some authors have also postulated a non-linear relationship – an inverted U-shaped relation – between cerebral dopamine and cognitive performance in working memory tasks (**Figure 10**; Cools & D'Esposito, 2011; Cools & Robbins, 2004; Goldman-Rakic et al., 2000). In other words, an intermediate – optimum – level of dopamine is needed for an efficient cognitive functioning, while too much but also too little dopamine would be deleterious (see Tunbridge et al., 2006 for a review).

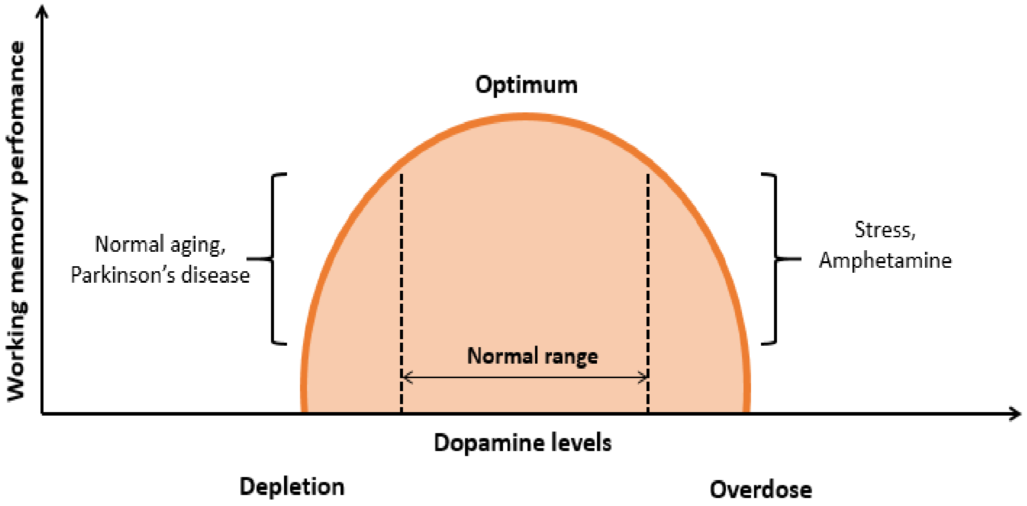

Figure 10. Inverted U-Shaped Relationship between Working Memory Performance and Cerebral Dopamine Levels. This function shows that an optimal DA level is required for high working memory functioning, while too much or too little DA is deleterious. Adapted and simplified from Goldman-Rakic et al. (2000) as well as Cools and D'Esposito (2011).

Dopamine is a neurotransmitter belonging to the catecholamine family and is the precursor of adrenalin, and noradrenalin. From a functional point of view, dopamine plays a role in goal-directed behavior. Dopaminergic neurons origin from the midbrain to project towards different cortical and subcortical regions (Li et al., 2009). In the human brain, the dopaminergic system is divided into three main routes (**Figure 11**). The nigrostriatal pathway connects the substantia nigra pars compacta (SNc), located in the ventral midbrain to the dorsal striatum in the forebrain, more precisely the caudate nucleus and putamen. The mesolimbic pathway – also called the reward pathway – takes its roots in the ventral tegmental area (VTA) in the midbrain and extends to cerebral limbic regions: accumbens nucleus, amygdala, hippocampus, and ACC. Finally, the mesocortical pathway also starts in the VTA to project towards the neocortex: orbitofrontal prefrontal cortex (OFC), the mid DLPFC, and the cingulate cortex (Li et al., 2009; Manard & Collette, 2014).

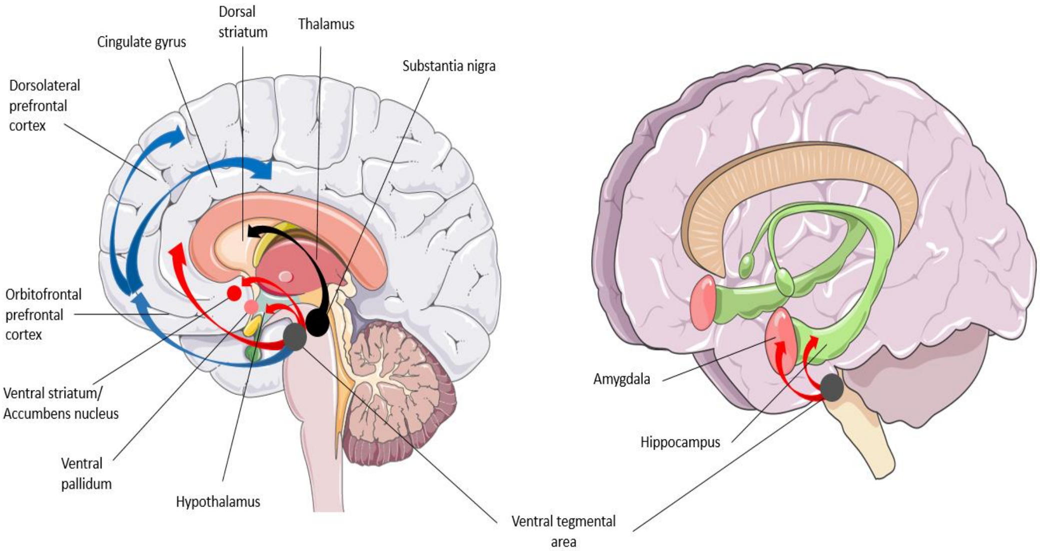

Figure 11. The Three Main Dopaminergic Pathways. The nigrostriatal pathway (in black) starts from the substantia nigra to reach the striatum; the mesolimbic and mesocortical pathways, often called the meso-cortico-limbic pathway, both start in the ventral tegmental area (VTA). The mesolimbic pathways (in red) then projects towards limbic regions (accumbens nucleus (NAc), amygdala, hippocampus, anterior cingulate cortex (ACC)) while the mesocortical pathway (in blue) projects towards the neocortex (orbitofrontal prefrontal cortex (OFC), mid dorsolateral prefrontal cortex (DLPFC), and cingulate cortex).

Given the implication of dopamine in the reward system as well as in prefrontal areas, this neurotransmitter has revealed to be very relevant in explaining cognitive fatigue, so much that several authors have built their theoretical model based on a dopaminergic hypothesis. For example, cognitive fatigue has been associated with a down-regulation of the dopaminergic system in striato-thalamo-cortical fibers (Chaudhuri & Behan, 2000, 2004; Lorist et al., 2009). Likewise, fMRI studies on patients with MS – the most frequently used model of cognitive fatigue – have consistently shown abnormal activation or connectivity strength in BG and PFC (DeLuca et al., 2008; Finke et al., 2015; Tartaglia et al., 2008). Dopamine in midbrain areas has also been suggested to preserve motivation during fatigue onset (Moeller et al., 2012). Lorist et al. (2005) also suggested that the consequences of fatigue, such as failures in monitoring, can be explained by inadequate levels of DA transmission in the striatum and ACC. Chaudhuri and Behan (2000) also proposed that inadequate DA level in BG, which disrupts the integration of perceived reward, is linked to fatigue in several diseases. Similarly, Dobryakova et al. (2013) assumed that fatigue might occur as a result of reduced DA availability in the BG, leading to reduced firing of striatal DA neurons in response to a rewarding outcome.

Costs/Benefits Calculation

In agreement with most of the previous presented models, Tops et al. (2004) proposed that mental fatigue can be viewed as an effort/reward imbalance: if the task effort is believed to result in sufficient reward, people will continue the task. By contrast, when the task effort is higher than the reward, the motivation starts to disappear and people show task-disengagement as well as feelings of fatigue. Similarly, Boksem and Tops (2008) claimed that people are basically motivated by obtaining rewards but also by avoiding punishment. In this view, people will expend energy if costs are low and rewards are high. In the case of long-lasting cognitive tasks, the expended energy will progressively become greater than the reward, and motivation will eventually drop. From an evolutionary point of view, the feeling of fatigue can be considered as “a drive to abandon behavior” (Boksem & Tops, 2008, p.126) which is useful for the individual because it will make them disengage from the task as soon as the energetic costs are excessive as compared to the provided benefits. Interestingly, Boksem and Tops built their framework of cognitive fatigue strongly based on the neural "reward system" driven by dopamine. Their model can be summed-up as follows (see also **Figure 12**):

The OFC is known to integrate information from different sensory inputs but also to estimate the reward value of stimuli (Kringelbach, 2005; Walter et al., 2005). Similarly, the basolateral amygdala (BLA) is known to process the appetitive values of stimuli such as positive reinforcement (Cardinal et al., 2002) but also aversive values of stimuli such as negative reinforcement and punishment (LeDoux, 1996; Seymour et al., 2007). The insula is known to encode the aversive value of events such as the consequences (i.e., costs and punishments) of our decisions (Small et al., 2001; Nitschke et al., 2006). These three structures thus assess the appetitive/rewarding and aversive/punishing value of stimuli or events.

This reward-related information is conveyed from these three structures to the ACC, which will goal-direct behavior in a way that is expected to lead to the highest reward and the lowest aversive outcomes. The implementation of this calculated strategy into the appropriate behavior is underpinned by projections from ACC to the NAc. When the outcome of a behavior is better or worse than expected, dopaminergic projections from the VTA increase the appropriate neuronal pattern in the PFC and the ACC by strengthening connections that lead to this rewarding behavior, or reduce the neuronal activation in the case of unsuccessful behavior. In addition to the appetitive/aversive evaluation of outcome to bias behavior, decision-making also takes the energetic costs triggered by the behavior into account. In this view, the insula would code the current physiological state and energetic resources while the ACC would code the estimated effort to reach the expected reward. Afterwards, ACC projections towards the BLA and the NAc modulate the energy dedicated to the behavior.

In conclusion, a particular behavior will be implemented if the change from the current state to the future state is highly valued, both in terms of appetitive/aversive consequences but also in terms of energetic costs for the body. An increase in perceived effort as compared to the expected rewards will result in a down regulation of DA activity in NAc and midbrain DA, creating the feeling of fatigue that drives the organism to abandon behavior that is valued too costly as compared to its benefits.

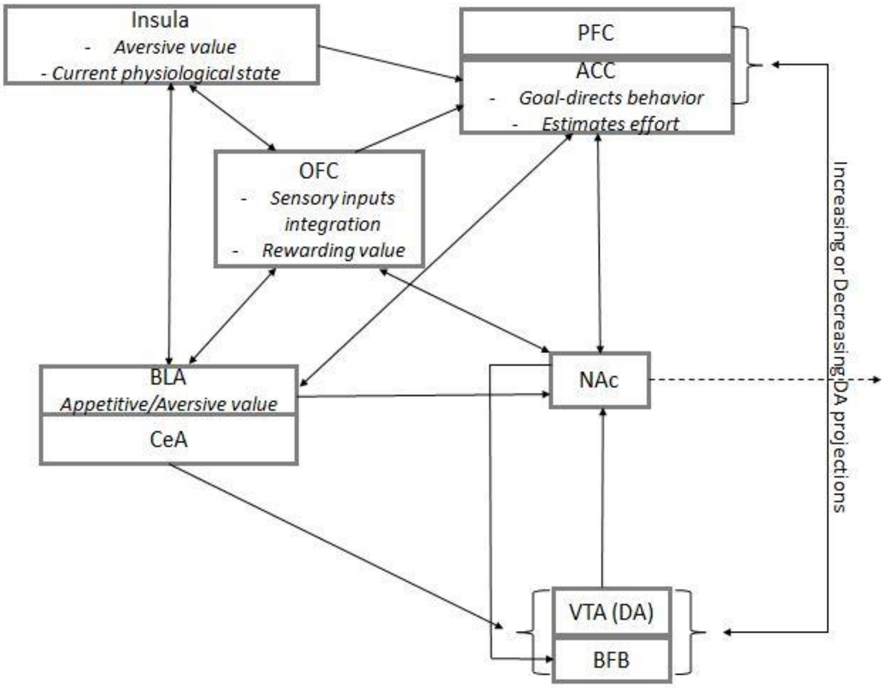

Figure 12. Cognitive Fatigue as Costs and Benefits Calculation. The OFC, BLA, and insula code the appetitive and aversive value of stimuli or actions. This information is transmitted to the ACC, which goal-directs behavior in the most rewarding and least punishing direction. The implementation of this strategy into behavior is underpinned by ACC projections towards the NAc. When outcomes are better or worse than expected, the VTA relays this information to the PFC and the ACC, strengthening connections to promote the rewarding behavior or inducing extinction in case of unrewarding behavior. In addition to the reward/punishment evaluation, decision-making also assesses the energetic cost linked to the execution of the behavior. The current physiological state and energetic resources are coded by the insula while the estimated effort to reach the expected reward is coded by the ACC. Afterwards, ACC projections towards the BLA and the NAc modulate the energy dedicated to the behavior. Therefore, a particular behavior will be implemented if it is highly valued, both in terms of rewarding/punishing consequences but also of bodily energetic costs. ACC = Anterior Cingulate Cortex; BLA = Basolateral Amygdala; CeA=Central Nucleus of the Amygdala; OFC = Orbitofrontal Cortex; PFC = Prefrontal Cortex; NAc = Nucleus Accumbens; VTA = Ventral Tegmental Area; BFB = Basal Forebrain; DA = Dopamine. Adapted from Boksem and Tops (2008).

Box 5. Limbic System and Limbic Loop

Limbic System: set of regions involved in emotional processing from sensory inputs. They comprise the thalamus, the anterior hypothalamus, the hippocampus, the amygdala, and the cingulate gyrus. This system also has strong interconnections with VTA, BG, PFC, and ventral striatum (VS; including the nucleus accumbens).

Limbic Loop: originates in ACC and projects towards the VS (particularly the nucleus accumbens), the ventral pallidum (VP), and the thalamus, which in turn projects to ACC, closing the loop. The mesolimbic pathway – or the reward pathway – also projects into the limbic loop, in particular from the brainstem (VTA) towards ACC and VS (Pierce & Kumaresan, 2006). Therefore, it has been proposed that the limbic loop processes reward (Croxson et al., 2009; Kable & Glimcher, 2007; Matsumoto et al., 2007; Pessiglione et al., 2007). Interestingly, Verguts et al. (2015) also proposed the limbic loop as the neural substrate of effort.

A Neurocomputational Model of Effort

In their neurocomputational model of effort, Verguts et al. (2015) tried to model how effort, underpinned by the limbic loop (see **Box 5**), can be optimally allocated as a function of reward, cost, and task difficulty.

The authors started by defining a first utility function as:

$$U(effort) = E(reward) \; - effort\ cost$$

where *E(reward)* stands for the expected reward.

Given that *E(reward)* can be expressed as a function of *effort* and task *difficulty* and that the *effort cost* can be expressed as a function of *effort* level, this first equation was rewritten as:

$$U(effort) = r\frac{effort}{difficulty \; + effort} - c \cdot effort$$

where *r* and *c* represent expected reward and cost, respectively.

Since the effort that maximizes the previous equation is the *optimal effort*, it and can be expressed as a function of reward (*r*), cost (*c*), and task difficulty:

$$optimal\ effort = \sqrt{\frac{difficulty\ \cdot r}{c}} - difficulty$$

In this model, the authors proposed that reward and cost feedback (detected by the VTA in **Figure 13**) is used for learning a stimulus-action association in the motor loop, but also for choosing when and whether to invest effort in the limbic loop (ACC, VS, VP, and thalamus in **Figure 13**).

Learning to exert effort is thus supported by dopaminergic projections from the VTA towards the ACC and the value (Reward/Cost) is represented by the dotted line in **Figure 13**. The ACC codes the stimulus value [$V(s)$] and values of actions (a) for a given stimulus [$Q(s, a)$]. In this model, effort consists in increasing signal-to-noise ratio (SNR) in cortical areas (Cohen et al., 2007; McClure et al., 2005), which the authors called *boosting*, taking two possible values: Boost or No Boost (a or a').

One of these options is chosen in ACC according to this rule:

$$\Pr(\mathrm{a}) = \frac{\exp\left(\gamma\ Q_n^{\pi}(s, a)\right)}{\sum_{a'} \exp\left(\gamma\ Q_n^{\pi}\ (s, a')\right)}$$

In other words, the probability of choosing an option (a) will be determined as a function of the value of this option relative to the value of an alternative option (a'). When the Boost option is chosen, the Boost value [$Q(s, B)$ in **Figure 13**] in ACC is activated. Otherwise, the No-Boost value [$Q(s,$ no $B]$ in **Figure 13**) in ACC is activated. This information is transmitted from the ACC to the VS (nucleus accumbens) (Basar et al., 2010; Heimer et al., 1997), from the VS to the VP and to the thalamus, and back to the ACC to activate the boosting unit in the ACC (B in **Figure 13**) with value ACC_{Boost}. Finally, this activation of the boosting unit (B) modulates the choice for an appropriate action ("Actions" box in **Figure 13**).

An action k is chosen according to this rule:

$$\Pr(k) = \frac{\exp(ACC_{Boost}\ \sum_i w_{ik}^{SR}\ x_i)}{\sum_{k'} exp(ACC_{Boost} \sum_i w_{ik'}^{SR}\ x_i)}$$

where $x_i = 1$ if stimulus i is presented and $x_i = 0$ if stimulus i is not presented; and where w^{SR} represents neural network weights between a stimulus and action representation. This stimulus-representation association is assumed to be already acquired by previous learning.

In other words, the probability of choosing an action (*k*) depends on the neural network weight between the stimulus *i* and the representation of action *k* relative to the neural network weight between the stimulus *i* and the representation of an alternative action *k*'.

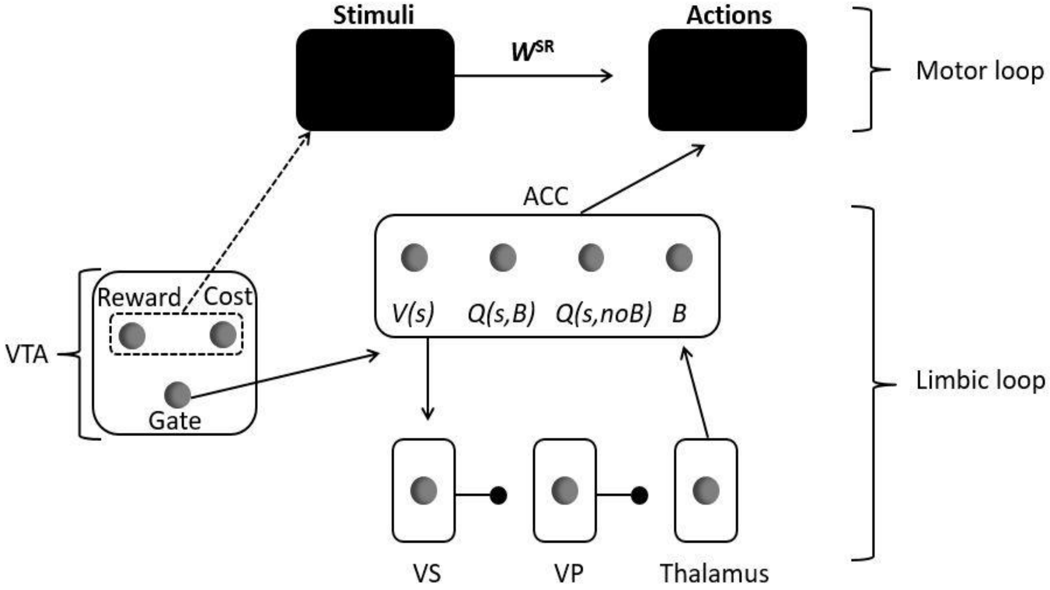

Figure 13. A Neurocomputational Model of Effort. The dashed line represents reward and cost feedback that influences both the motor loop and the limbic loop. In the limbic loop, the ACC codes the stimulus value [*V*(*s*)] and values of options for a given stimulus: *Q(s, B)* or *Q(s, noB)*. When the Boost option is chosen, the unit *Q*(*s*, *B*) is activated in the ACC. This information is transmitted from ACC to the VS, VP and thalamus, and back to the ACC to activate the boosting unit (*B*). This activation modulates the choice for an appropriate action in the Actions box. The activation of a particular action also depends on the neural network weight (w^{SR}) characterizing the association between the stimulus and that action. This weighed association is assumed to have been previously learned through reward and cost feedback on the motor loop. Adapted from Verguts et al. (2015).

Models of Pathological Fatigue

To close this first chapter, I will present three influential models that have been built in the first place in order to understand pathological fatigue such as that experienced by people with CFS. However, these models are also used in some paper discussions to explain underlying mechanisms that would take place in normal conditions of cognitive fatigue.

Co-Conditioning Theory

According to the co-conditioning theory (Tanaka & Watanabe, 2010), fatigue can be defined as a homeostatic and functional impairment caused by overwork and/or stress. When an organism becomes fatigued, an alarm signal (i.e., inhibitory system) may occur to prompt the individual to take a rest and to avoid further overwork. After repetitive experiences of overwork/stress, the organism may express the alarm signal as well as the fatigue sensation in response to an unconditioned stimulus (impaired homeostasis) that has been paired with the conditioned stimulus (overwork/stress or the expectation of overwork/stress). For example, if hormonal reactions (e.g., cortisol release) have been linked several times to overwork/stress, then the next manifestation of these hormonal actions will push the organism to experience fatigue even in the absence of overwork/stress. Therefore, the individual will be tempted to rest or diminish his activity before he really stands in situation of overwork/stress. The threshold that triggers the alarm signal and the fatigue sensation is also lowered, what is called central sensitization. In patients with CFS, this conditioning is preserved even after the homeostatic and functional disturbances have gone and may explain the persisting alarm signal to take a rest and the severe fatigue sensation experienced.

Dual Regulation System of Fatigue

A little bit after the proposition of the co-conditioning theory, Ishii et al. (2014a) went a step further and proposed a dual regulation model of fatigue. In this model, mental workload activates the *mental facilitation system* (see **Figure 14**), which the authors defined as a neural circuit interconnecting the limbic system, the BG, thalamus, and frontal cortex. An increase in motivational input (i.e., increased dopaminergic drive) to this facilitation system serves as a compensatory mechanism to maintain task performance in the presence of mental fatigue. However, prolonged or excessive activation of this facilitation system may cause impaired energy metabolism and oxidative damage, leading to a disruption and difficulties in driving this system adequately.

In parallel with the facilitation system, mental workload also activates the *mental inhibition system* (presented in the previous model), which has been postulated to play the role of a biological alarm signal under conditions of fatigue and requires us to take a rest to avoid disrupting homeostasis (Boksem & Tops, 2008; Tanaka & Watanabe, 2010). This inhibition system comprises the insular cortex (IC) and the posterior cingulate cortex (PCC) and activation of this system impairs cognitive task performance. However, similarly to the facilitation system, overactivation of the inhibition system is dysfunctional. Indeed, according to the Co-Conditioning Theory (Tanaka & Watanabe, 2010), repeated and prolonged mental workload causes activation of the mental inhibition system through central sensitization and/or classical conditioning (Tanaka & Watanabe, 2010). Consequently, the organism may express the alarm signal even in the absence of mental workload. In other words, there is an overactivation or an abnormal use of the inhibitory system, which has been found in CFS patients (Tanaka et al., 2006).

The balance between the activation of the two – facilitation and inhibition – systems determines whether performance of the cognitive task is impaired, maintained, or improved. This model also assumes that there exists three causes of acute mental fatigue: 1) insufficient activation of the mental facilitation system; 2) enhancement of the mental inhibition system; and 3) a combination of the two first causes. Similarly, there are three causes of chronic mental fatigue: 1) disruption of the mental facilitation system; 2) central sensitization/classical conditioning of the mental inhibition system; 3) a combination of the two. These alterations result in severely reduced cognitive task performance that are present in CFS.

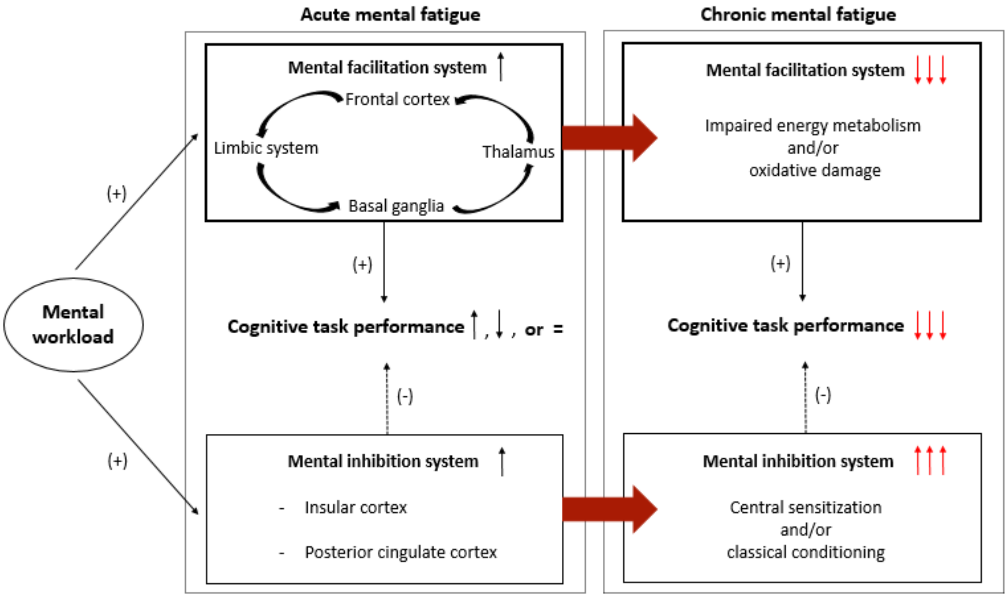

Figure 14. Dual Regulation System of Fatigue. Acute mental workload activates the mental facilitation system underpinned by a thalamic-frontal loop that maintains or improves cognitive task performance. In parallel with this, mental workload also activates the inhibition system underpinned by the IC and the PCC that impairs task performance. Repeated and prolonged mental workload triggers dysfunction of the facilitation system due to impaired energy metabolism or oxidative damage but also overactivation of the inhibition system through central sensitization or classic conditioning. These alterations in the dual regulation system result in severely reduced cognitive task performance that are common in chronic mental fatigue. Adapted from Ishii et al. (2014a).

Perceived Effort as a Lack of Sensory Attenuation

Finally, Kuppuswamy (2017) built her model based on the hypothesis that fatigue (both physical and cognitive) should be considered as a single construct and is an inference in the first place. In order to illustrate the basic idea of how human beings perceive effort, she decided to base her model on the active inference framework of sensorimotor control in order to explain perceived motor effort (i.e., physical fatigue). However, the author assumed that similar principles are also at play in the experience of cognitive fatigue and further proposed that this framework may also explain pathological fatigue.

According to the active inference framework (Brown et al., 2013), outputs from the cortico-motor system are in the form of descending predictions (*efferents*) while inputs from the somatosensory systems are ascending sensory inputs (*afferents*) (**Figure 15**). The comparison between descending proprioceptive predictions and ascending sensory inputs lead to sensory *prediction errors*.

To perceive the consequences of our movements, we have to be aware of sensory errors. By contrast, to be able to engage in movement (e.g., muscle contraction), there is a necessary transient attenuation in the precision of prediction errors (i.e., attenuation in ascending prediction errors) reporting the information that no movement has been produced. In other words, we have to transiently keep our attention away from sensory errors signaling that we are not moving. This function of decreasing the precision of sensory prediction errors is commonly referred to as *sensory attenuation*. Sensory attenuation has been demonstrated in the force matching task. When one is required to match an externally applied force, one typically underestimates the force we produce and classically produces a higher force (Shergill et al., 2003). This overshooting results from the attenuation of the intensity of the sensory consequences of a self-generated motor act, which results in a given force being perceived as less forceful. Under circumstances of normal sensory attenuation, proprioceptive prediction errors from muscle contraction are suppressed, which our brain interprets as “less or no effort”. By contrast, in the absence of sensory attenuation, the same muscle contraction will be accompanied by higher prediction errors (i.e., the fact that no movement or weak movement has been elicited), which the brain interprets as “the movement requires more effort than expected.”

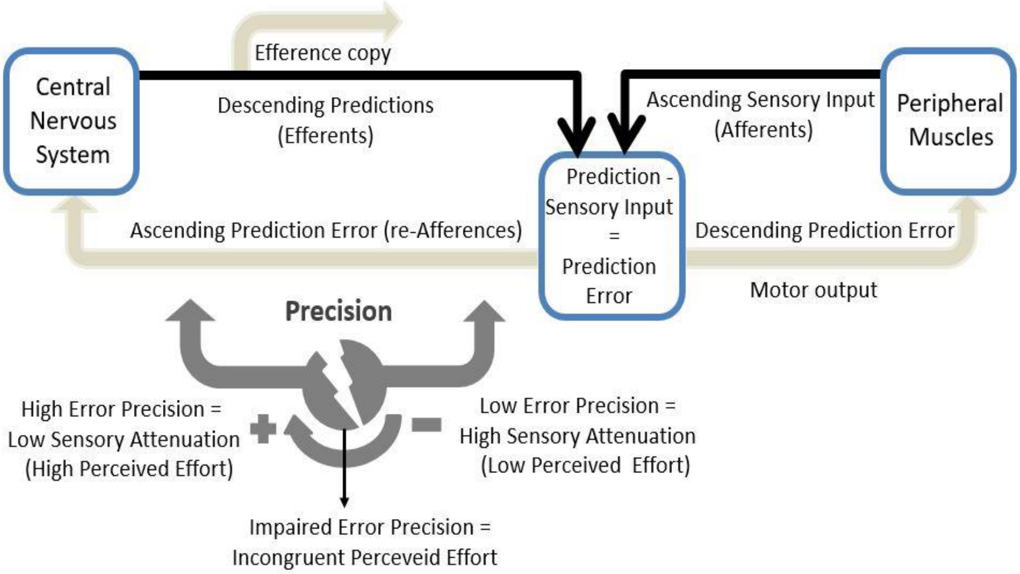

Figure 15. Perceived Effort as a Lack of Sensory Attenuation. The descending commands from the brain specify sensory predictions (efferents) that are compared with the incoming sensory signals (afferents). The comparison between these two pieces of information gives rise to sensory prediction errors. To attend or not to attend to the sensory prediction errors, which drive motor output, depends on the precision the brain affords them. When precision is high, the sensory attenuation is low, which leads to high perceived effort. On the contrary, when precision is decreased, the sensory attenuation is high, which results in perceived effortlessness. In conditions of impaired sensory attenuation, incongruent perceived effort may arise, leading to feeling of fatigue. Adapted from Kuppuswamy (2017).

This model may also explain pathological fatigue which is characterized by a report of high effort in performing simple activities of daily living that normally require low levels of effort. Indeed, under dysfunctional sensory attenuation, the brain is unable to ignore the afferent somatosensory consequences of movement, and everyday motor actions are experienced as effortful. Prolonged experience of high perceived effort could therefore eventually lead to the report (or symptom) of chronic pathological fatigue.

Confounding Variables of Cognitive Fatigue

Before entering into **Chapter 2**, which will be dedicated to the presentation of empirical studies of cognitive fatigue in young people, I will identify a set of variables that are likely to interfere with the results that can be drawn from experimental studies and should thus be taken into account by researchers in the field.

Firstly, as mentioned by Hockey (2013), one of the major variable that we should be aware of in cognitive fatigue studies is *practice effect* or learning. That is, in absence of extended practice before the real recording of performance, the evolution of performance will typically show improvement in the first time blocks of tasks before impairment later in the session.

Secondly, Hockey (2013) also mentioned that some studies have already shown a so-called "end-spurt" in which better performance is observed in the very last time period of a task as compared to previous periods of reduced effectiveness. This phenomenon appears *when the end of the task is in sight.* Therefore, studies nowadays do not inform research participants of the duration of the protocol and take care of the environment (e.g., no clock or watch, or smartphone allowed in the testing room).

Thirdly, it is also worth mentioning here that *sleep disturbances* are potential confounding factors of cognitive fatigue (Akerstedt et al., 2004). For example, some studies using a sleep deprivation protocol to induce fatigue have found evidence of cognitive impairments (Asplund & Chee, 2013; Duffy et al., 2009; Lim & Dinges, 2008; Martella et al., 2011; see also McCoy & Strecker, 2011 for a review on effects of different types of sleep disturbances on cognition). Therefore, sleep quality must be taken into account in cognitive fatigue studies.

Fourth, some cognitive functions as well as cognitive fatigue have been found to vary as a function of the *time of day* (Blain et al., 2016; Esposito et al., 2014). Therefore, well-informed studies impose a fixed moment during the day to carry out experimental studies (e.g., all sessions start at 9 a.m.) or pay attention to balance morning and afternoon sessions between the different conditions of their experiment. Related to this issue, it has also been shown that performing a task at ones optimal time of day depending on *chronotype* prevents performance decrement to a certain extent (Lara et al., 2014). Importantly, chronotypes tend to shift to an "earlier" pattern with advancing age (Roenneberg et al., 2004). Therefore, it seems important to take both the distribution of chronotype and the time of day into account, most importantly when age groups are compared.

Fifth, several studies have also shown that the *effect of caffeine* improves cognitive functions and modulates fatigue (Azevedo et al., 2016; Klaassen et al., 2013; Lorist & Tops, 2003; van den Berg et al., 2019). Therefore, most experimental studies require their participants to refrain from caffeine consumption at least during the day of the experiment.

Finally, the *effect of lighting* is also likely to interfere with the global ergonomics (Hu et al., 2018), which renders this factor important for long-lasting tasks.

Intermediate Summary

To sum-up, cognitive fatigue has first been associated with the energy depletion hypothesis according to which people progressively become exhausted because their limited energy supply vanish after having performed a long-lasting work. This idea has been somewhat questioned but still remains up to date and is demonstrated in studies showing that rest breaks relieve cognitive fatigue. Afterwards, models have explained cognitive fatigue by integrating the notion of voluntarily controlled effort invested in the task. It is the case when people compute the costs/benefits or effort/reward balance to decide whether or not to deploy effort in a particular behavior or task. Using a somewhat different view of the costs/benefits hypothesis, Müller and Apps (2018) proposed that the deployed effort may discount the value of rewards. According to the opportunity cost model (Kurzban et al., 2013), effort arises from the existence of many other options that the individual is not allowed to perform, sometimes pushing the individual to share its mental capacity between two activities depending on their relative utility. Finally, dopaminergic inputs from the VTA as well as some other cerebral areas (e.g., BG, ACC, OFC) have been postulated to underpin cognitive fatigue (Boksem & Tops, 2008) and effort (Verguts et al., 2015).

This Thesis work is aimed at investigating cognitive fatigue in young, middle-aged, and older people. To this end, three studies using either the Time-on-Task approach (**Study 1** and **Study 2**) or the Probe approach (**Study 3**) were implemented. Therefore, the next chapter will be dedicated to the presentation of studies having investigated cognitive fatigue in the young population. The two following chapters will be dedicated to the presentation of models of cognitive and cerebral aging (**Chapter 3**) and to studies having investigated cognitive fatigue in middle-aged and older people (**Chapter 4**).

Chapter 2: Empirical Studies in Young People

This chapter will begin with the presentation of the Time-on-Task and the Probe approaches, followed by the presentation of empirical studies having used one or the other approach. Studies using the Time-on-Task approach are divided into behavioral, electroencephalographic (EEG) and magnetoencephalographic (MEG), neuroimaging, brain connectivity, and motivation-related studies. Experiments using the Probe approach are less numerous than Time-on-Task studies. The corresponding section is divided into behavioral and neuroimaging probe studies. The Probe approach part also comprises a section about workload, which has been essentially investigated using this approach. Finally, we present a section devoted to studies interested in the subjective feelings of fatigue. As previously mentioned, the two first studies (behavioral data) of this Thesis work were based on the Time-on-Task approach while the third study (fMRI data) was based on the Probe approach.

Time-on-Task and Probe Approaches

As well explained by Hockey (2013), researchers belonging to the fatigue field, already in the nineteenth century, have been interested in two main questions about the effects that work triggers on fatigue. The first one is related to the time course of fatigue: how does performance vary – or to what extent is performance impaired – as a function of the continuous time spent on the task? Secondly, researchers have also been interested in the specificity of the fatigue state. In other words, are fatigue effects specific to the task that induced them or are they transferable to any other cognitive activities? These two types of questions have led to two experimental approaches in the cognitive fatigue literature: the *continuous work method* – or *Time-on-Task paradigm* – and the *probe method* (Hockey, 2013). In the first approach, a cognitive task is generally administered to the participants for a relatively long-lasting period of time that can range between a few minutes to several hours. The second approach implied to start the experiment by administering a first so-called *loading task* followed by a *probe task* in order to test whether induced fatigue by the first task is transferable to the second task. The probe task can also be administered before (as a baseline measure) and after the loading task (experimental condition) as well as before and after a control task (control condition).

Obviously, one or the other approach will be favored as a function of the question of interest. The first one serves to answer questions about how long is it necessary to perform the same task to undergo its fatiguing effect. Or, as it is the case in my first experimental study, to answer questions such as “Will a long-lasting task trigger differential fatigue effects as a function of the different age groups being studied?” The second approach is aimed at determining whether performance on the probe task is weakened by the previous performance of the loading task. Regarding the energy depletion hypothesis previously presented in **Chapter 1**, it was believed that work had a general effect on the body’s limited energy supply, leading to the assumption that fatigue triggers general effects and impairs all subsequent mental activities (Kraepelin, 1902). However, there was also an alternative prediction of the energy depletion hypothesis according to which fatigue effects were transferable only to functions that were depleted by the loading task. In this sense, Robinson (1923) proposed that impairments are observable only for probed mental operations sharing the same task requirements as the loading task. This probe approach was originally appraised in the context of ego-depletion, according to which a limited inner resource is depleted by exerting self-control overtime. This framework also proposed that exerting self-control on a primary task will impair the capacity of exerting self-control on a subsequent task (Inzlicht & Schmeichel, 2012). Similarly, it has been proposed that transfer effects are possible when the two tasks are underpinned by similar neural substrates (van der Linden & Eling, 2006; van der Linden et al., 2003). Evidence for the specific effect of fatigue would be in agreement with the motivational hypothesis according to which performance impairment are primarily due to a loss of interest and a motivation drop. Indeed, if a general fatigue effect would not allow any recovery from a change between the loading and the probe task, a specific fatigue effect will result in a certain degree of recovery because motivation is reset.

In the following lines, readers will be presented with different experimental (e.g., behavioral, neuroimaging, electrophysiological) studies that based their protocol on one of these two – continuous *versus* probe – approach. However, for the sake of clarity, it is important to mention at this stage that the two approaches are sometimes used in combination in the same study. Therefore, it is likely that one study that I will present under the subheading “Time-on-Task” would have correctly been presented under the subheading “Probe approach”. For example, the continuous approach can be used as the primary task for the probe approach to induce fatigue in participants before administering them with the probe task. In this case, it is possible to assess both Time-on-Task effects on the long-lasting task as well as transfer effects on the probe task. The continuous approach is also used between two sessions of resting-state fMRI to investigate the cerebral changes induced by performing a long-lasting task. Likewise, the continuous approach can be used between two assessments of subjective feelings. In those cases, the authors are not interested in transfer effects as such but rather in how much cerebral activity (or subjective feelings) have been altered (or modified) by the long-lasting task.

Above and beyond these two main approaches, we can also differentiate between different subtypes of studies. Noteworthy, there are studies trying to target the motivation during the task to be performed by proposing incentives to the participants. These types of studies are often used in the context of the continuous approach to test whether, after a certain amount of time, performance decrements can be relieved by some rewarding financial incentives (Boksem & Tops, 2008). Therefore, some of these studies will be presented in the "Time-on-Task approach" section.

Beyond the time spent on the task – or *temporal fatigue hypothesis* -, certain authors also assume that task difficulty or workload demands – referred as the *cognitive load hypothesis* – are also likely to trigger cognitive fatigue. These studies manipulate task demands and assume that "higher the cognitive load, higher the cognitive fatigue" (Borragán et al., 2017).

However, there exists an alternative view that distinguishes between different types of cognitive fatigues (Hancock & Desmond, 2000; May & Baldwin, 2009). According to these authors, cognitive overload (or active task-related fatigue) but also cognitive underload (or passive task-related fatigue) are likely to trigger cognitive fatigue. Generally, researchers resorting to this type of studies assess cognitive fatigue by administering two task conditions to their participants: a high load *versus* a low load. These high and low conditions can also be used in the context of the probe approach to test whether there is a differential transfer effect as a function of the loading (high *versus* low) task. In this manuscript, I will present studies that investigated the cognitive load hypothesis in the "Probe approach" section.

Finally, I will close **Chapter 2** by presenting results focusing on subjective fatigue.

Time-on-Task Approach

In these last few years, the concept of cognitive fatigue has particularly emerged in the literature bearing on the young population. From a behavioral point of view, many studies using a Time-on-Task paradigm to induce cognitive fatigue have shown that fatigued people are characterized by increases in reaction times and/or reduced accuracy (Boksem et al., 2005, 2006; Fan et al., 2019; Faber et al., 2012; Guo et al., 2016; Guo et al., 2018; Hopstaken et al., 2015a ; Hopstaken et al., 2015b; Hopstaken et al., 2016; Kato et al., 2009; Lorist, 2008; Lorist et al., 2009; Lorist et al., 2005; Lorist et al., 2000; Möckel et al., 2015; Petruo et al., 2018; Shigihara et al., 2013; Wang et al., 2014; Wang et al., 2016).

For example, Trejo et al. (2005) required their participants to perform mental arithmetic problems continuously during 3 hours until they felt exhausted and found increased RT with Time-on-Task. Cognitive fatigue induced by a 3 hour visual attention task has also been shown to alter the ability to focus one's attention on the task at hand and to enhance distractibility and difficulties ignoring irrelevant information (Boksem et al., 2005). Using a Flanker task during 2 hours, Faber et al. (2012) also showed that cognitive fatigue disrupted selective attention and was associated with difficulties suppressing irrelevant information. Other studies have shown that cognitive fatigue induced by a 2 hour continuous task is associated with a reduced action monitoring as well as a decrease in response preparation as indexed by inadequate adjustments of behavior after errors (i.e., the inability to use previous information to reconfigure task set) (Boksem et al., 2006; Lorist, 2008; Lorist et al., 2005; Lorist et al., 2000).

In addition to these very long-lasting paradigms, it is also worth mentioning that tasks of shorter durations can also trigger performance decrements (Mizuno et al., 2014; Smolders & de Kort, 2014). It is for example the case for the Psychomotor Vigilance Task (PVT) that has been shown to trigger increased RTs as well as subjective feelings of fatigue in participants performing it during *only* 20 minutes (Gui et al., 2015; Lim et al., 2010).

Electroencephalographic and Magnetoencephalographic Studies

Historically, cognitive fatigue has mostly been investigated using electroencephalographic (EEG) and Event-Related Potential (ERP) measures, because of the feasibility of these methods for long-lasting recording. Since EEG has a high temporal resolution, these studies have particularly used the Time-on-Task paradigm – as compared to the probe method – to assess task-related changes (Arnau et al., 2017; Boksem et al., 2005, 2006; Fan et al., 2019; Guo et al., 2016; Guo et al., 2018; Hopstaken et al., 2015a; Hopstaken et al., 2016; Käthner et al., 2014; Kato et al., 2009; Lorist, 2008; Lorist et al., 2009; ; Lorist et al., 2005; Lorist et al., 2000; Liu et al., 2016; Möckel et al., 2015; Papadelis et al., 2007; Petruo et al., 2018; Tanaka et al., 2012; Wang et al., 2016; Wascher et al., 2014).

For example, the increase in theta (i.e., 4-7 Hz) and lower-alpha (i.e., 8-10 Hz) band power has been classically linked to cognitive fatigue installation (Arnau et al., 2017; Boksem et al., 2005; Borghini et al., 2014; Craig et al., 2012; Papadelis et al., 2007; Wascher et al., 2016). In the same vein, decreased arousal and alertness during high demanding attentional activities have been associated with increase in the 6-10 Hz band (Klimesch, 1999; Oken & Salinsky, 1992).

Regarding changes in ERPs under cognitive fatigue, Boksem et al. (2005) showed an association between the automatic reorientation of attention to irrelevant stimuli with a larger negativity in the N1 latency range. As this N1 reorienting effect did not change with Time-on-Task, the authors suggested that goal-directed attention (top-down) is negatively affected by mental fatigue, while stimulus-driven attention (bottom-up) remains unaffected. However, certain studies did not show any differential impact of mental fatigue between controlled *versus* automatic processes (Lorist, 2008). Otherwise, a reduction in the error-related negativity (Ne/ERN) amplitude has been considered a marker of impaired action monitoring underlaid by the ACC (Boksem et al., 2006; Fan et al., 2019; Lorist et al., 2005) while the decrease in contingent negative variation (CNV) would be the sign of the inability to slow down after committing an error (Boksem et al., 2006). In 2015, Hopstaken et al. (2015a) required their participants to perform a 2-hour N-Back task and showed a significant decrease in P3 amplitude with Time-on-Task. Wascher et al. (2014) used a spatial stimulus-response-compatibility task for 4 hours. The results showed that occipital alpha power increased rapidly and reached its maximal amplitude after 1 hour already, whereas frontal theta continuously increased with Time-on-Task. Therefore, occipital alpha was related to task disengagement while frontal theta was suggested to represent increased effort to maintain performance and the resort the executive control capacities.

Very interestingly, the ERP methodology has also been able to show the temporality of compensatory mechanisms under cognitive fatigue. Wang et al. (2016) administered a modified cued version of the Stroop task (Cohen et al., 1999) during 160 minutes to young participants and showed that a late ERP component from an anterior frontal region followed an inverted U-shaped curve as a function of the time spent on the task (**Figure 16**). In other words, the amplitude of that late component progressively increased during the first 80 minutes of task (compensation phase) to maintain performance and then progressively decreased during the last 80 minutes (decompensation phase). Moreover, the error rate as well as long RT trials (RT longer than 2s.) were similar to the beginning time block during the compensation phase but significantly increased during the decompensation phase.

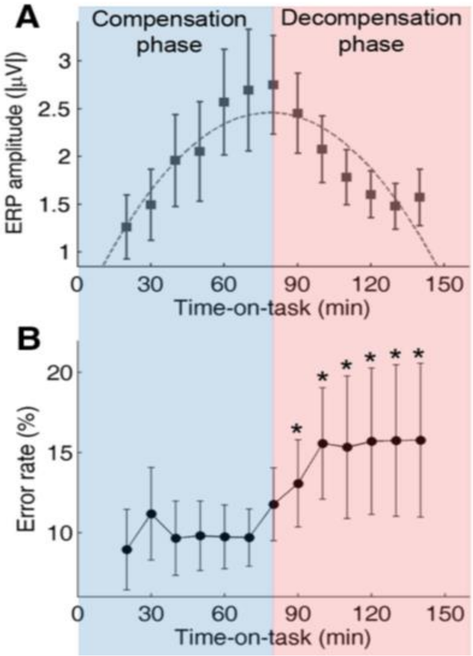

Figure 16: Wang et al. (2016)'s Data. A. ERP amplitude of a late ERP component (640–1272 ms) in the anterior frontal region following an inverted U-shaped curve with Time-on-Task. The compensation phase (blue shaded) took place between 0-80 min and the decompensation phase (pink shaded) during the subsequent 80-160 min. **B.** Percentage of error rate during compensation and decompensation phase. Adapted from Wang et al. (2016).

Some studies using magnetoencephalography (MEG) have also shown changes in neural activities that are caused by performing cognitive fatigue-inducing tasks (Ishii et al., 2013, 2014b, 2014c, Ishii et al., 2015; Tanaka et al., 2014a, 2014b). For example, Ishii et al. (2013) administered three 25-minute sessions of 0-Back and 2-Back tasks and showed reduced alpha band power in the occipital region with Time-on-Task. This reduction was significantly greater in the 2-Back as compared to the 0-Back task. Also using an N-back task, Tanaka et al. (2014a) showed that cognitive fatigue induced by a 10-minute 2-Back task resulted in a post-task increase in beta band power in the prefrontal brain area, which had previously been associated with diminished alertness and arousal (Okogbaa et al., 1994). Ishii et al. (2014b) administered their participants with a decision experiment in which they performed reverse Stroop test trials[3] and were intermittently asked to decide whether they wanted to take a rest or continue. In the control condition, participants also performed Stroop trials but were instructed to press a key intermittently without making any decision. The results showed that levels of decrease in theta, alpha, and beta band power were greater in experimental trials – when the participant opted to rest – than those in control trials and that the DLPFC and the PCC were implied in the decision to rest in the presence of fatigue.

Other Physiological Markers Used in these Studies

Besides electrophysiological measures such as EEG, other physiological markers have been linked to cognitive fatigue. Several studies have shown association between eye-related measures (e.g., blink duration, proportion of long blinks, blink frequency, or pupil size) with drowsiness (Caffier et al., 2003), vigilance drops (McIntire et al., 2014), load and effort (Beatty, 1982; Kahneman, 1973; Kahneman & Beatty, 1966), as well as cognitive fatigue (Gergelify et al., 2015; Guo et al., 2018; Herlambang et al., 2019; Martins & Carvalho, 2015; Tian et al., 2019). For example, baseline pupil diameter (Hopstaken et al., 2015a; Hopstaken et al., 2016) as well as stimulus-evoked pupil dilation (Hopstaken et al., 2015b) have been found to decrease with Time-on-Task. Some studies (e.g., Gilzenrat et al., 2010; Murphy et al., 2014) have provided evidence that the LC–NE[4] system regulates task engagement and is correlated to changes in pupil dynamics. Two modes of the LC–NE system have been proposed (Aston-Jones & Cohen, 2005): the phasic mode is characterized by intermediate baseline levels of NE and strong stimulus-evoked bursts of NE release. This mode supports high task engagement and has been associated with an intermediate pupil diameter and large stimulus-evoked dilations (Gilzenrat et al., 2010; Jepma & Nieuwenhuis, 2011). In the tonic mode, both

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[3] Participants had to indicate the meaning of the presented word (“red”, “blue”, or “yellow”) regardless of the ink color.

[4] LC-NE is the abbreviation for locus coeruleus-central norepinephrine.

baseline and stimulus-evoked levels of NE are high. Therefore, this mode is associated with reduced task engagement, increased pupil diameter, and lowered relative stimulus-evoked dilations. Interestingly, Cazzoli et al. (2014) showed that oculomotor markers can be used to distinguish between different sources of fatigue (chronotypical factors *versus* Time-on-Task induced fatigue). These authors showed that performing a free-visual exploration task for about 25 minutes at non-optimal time of the day triggered a significant increase in the mean visual fixation duration during the task. By contrast, the mean saccadic speed progressively decreased throughout the duration of the task, but was not influenced by the lack of synchronicity between chronotype and time of the day. Finally, some studies have focused on aircraft pilots or car drivers, showing, for example, that the percentage of time the eyes closed during a specific period as well as blinking frequency amplitude increased monotonically with increasing fatigue or sleepiness (Bergasa et al., 2006; Galley et al., 2003; Zhang et al 2019).

Autonomic nervous system (ANS)[5] variables have also been linked to cognitive fatigue (Mizuno et al., 2011; Pattyn et al., 2008; Smith et al., 2019; Zhang & Yu 2010). Drowsiness has been linked to decreased heart rate (HR) values during driving tasks (for a review, see Borghini et al., 2014). Likewise, it has been shown that HR decreases while heart rate variability (HRV) increases with cognitive fatigue (Egelund, 1982; Mascord & Heath, 1992). In 2015, Gergelyfi et al. administered their participants with a 120-minute Sudoku task and found that subjective feeling of fatigue increased and performance worsened in parallel with increased blink rate and HRV. Melo et al. (2017) required their participants to perform a Go/NoGo task for 50 minutes and found a decrease in parasympathetic activity (rMSSD and pNN50) with Time-on-Task. Moreover, frequency-related measures of HRV (LF/HF) were linked to self-reported scales of attention and drowsiness. As mentioned earlier, several studies have constantly shown that EEG is a reliable physiological indicator of cognitive fatigue (Jagannath & Balasubramanian, 2014; Lal & Craig, 2001, 2002). Likewise, electrocardiography (ECG) has been used as a measure of ANS to detect driver fatigue (Jiao et al., 2004; Lal & Craig, 2001; Li et al., 2003). However, these techniques have some practical

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[5] ANS controls involuntary functions and is divided into sympathetic and parasympathetic nervous system. Heart rate variability (HRV) may be described as the time difference between two successive heartbeats. Recognized HRV indicators are the following: time domain indicators comprise NN.mean (mean of normal to normal interval), rMSSD (root mean square of successive differences), PNN50 (the proportion of NN50 divided by total number of NNs), and frequency-domain indicators comprise TP (total spectral power), HF (high frequency from 0.15 Hz to 0.4 Hz), LF (low frequency from 0.04 Hz to 0.15 Hz), VLF (very low frequency from 0.0033 Hz to 0.04 Hz) and the LF/HF ratio (Huang et al., 2018).

limitations (electrode to fix on the scalp or on the subject's body, skin preparation, etc.). Consequently, researchers have progressively sought for material fitting real-life situations. In this regard, capacitive ECG (cECG) is a non-contact method[6] to record the cardiac activity. Using this technique during a 120-minute simulated driving task, Balasubramanian and Bhardwaj (2018) have shown that both LF (an index of sympathetic modulation) and HF (index of parasympathetic modulation) increased while the LF/HF ratio decreased with Time-on-Task. This finding is similar to results from other studies in which LF/HF decreased in drowsy state (Byeon et al., 2006; Sun & Yu, 2014), while it increased in greater mental workload or alertness (Sato et al., 1998). Also in a wish to develop smarter device, Huang et al. (2018) equipped their participants with a wearable ECG during an 80-minute quiz comprising logical problems and memory tests and found that TP and LF were the most important indicators of cognitive fatigue.

Finally, not directly linked to cognitive fatigue (because no fatiguing task was used) but still relevant to this work, Spangler et al. (2018) were able to show that rMSSD measured during 5 minute during rest (participants watched a grey screen while remaining still and relaxed) was inversely related to the ex-Gaussian parameter τ (tau)[7] extracted from the RT distribution of a short Stroop task. The authors interpreted this result as people with high baseline HRV can better prevent attentional lapses.

Neuroimaging Studies

From a cerebral functional point of view, some neuroimaging experiments have also investigated brain activities during a long-lasting cognitive task (Asplund & Chee, 2013; Coull et al., 1996; De Joux et al., 2013; Derosière et al., 2015; Gui et al., 2015; Lim et al., 2016; Lim et al., 2010; Paus et al., 1997; Sturm et al., 1999; Tajima et al., 2010). Globally, these studies show that decreased activation of fronto-parietal areas is associated with cognitive fatigue. For example, Lim et al. (2010) required their participants to perform the PVT continuously for 20

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[6] While estimating driver fatigue, cECG electrodes are fixed on the surface of the seat upholstery and not required to be fixed on the subject's body.

[7] The ex-Gaussian distribution will be entered into details just before the Experimental part of this work because it is the basis of the first research article presented. In short, the ex-Gaussian function is characterized by three parameters (μ (mu) and σ (sigma) represent the Gaussian component while τ (tau) represent the exponential component). τ is an index of the density of extreme RTs made by the participant.

minutes in combination with arterial spin labeling (ASL) perfusion fMRI. Their results showed that decreased cerebral blood flow (CBF) in a right-lateralized fronto-parietal network between pre-task and post-task rest was correlated with performance decline. The authors claimed that fatigue has a persistent effect on the fronto-parietal network classically associated with attentional functioning and assumed this network would mediate Time-on-Task effects. Likewise, Gui et al. (2015) also adopted the PVT during 20 minutes to investigate changes in the amplitude of low-frequency fluctuation (ALFF) of the resting-state blood oxygen level-dependent (BOLD) time courses[8]. The results showed decreased ALFF in DMN regions after as compared to before the task but also that pre-test resting ALFF in the DMN (PCC and medial prefrontal cortex) predicted subjects' subsequent performance decline. In other words, the higher the initial ALFF in DMN regions – representing more flexibility in reallocating brain resources from task-negative to task-positive network –, the more stable the behavioral performance during the 20-min PVT. This hypothesis was also supported by a trend for a negative correlation between activation increase in a region belonging to the fronto-parietal network (middle frontal gyrus) and reaction time increase during the task.

Using positron emission tomography (PET), Paus et al. (1997) found that performing a continuous 60-minute auditory vigilance task was associated with decreased activity in the thalamus, frontal, parietal, and temporal areas in the right hemisphere. Coull et al. (1996) investigated selective *versus* non-selective attention tasks using PET and found performance decline parallel with decreased activity in the right fronto-parietal network with Time-on-Task during the non-selective task. In their review of PET studies, Sturm et al. (1999) identified a network comprising right frontal, parietal, thalamic, and brainstem areas to be co-activated with alerting and orienting attention. It was thus suggested that the classical decreased CBF in those regions may be explained by reduced alertness with Time-on-Task. Tajima et al. (2010) required their participants to perform a 35-minute fatigue-inducing task twice and identified the medial orbitofrontal cortex to be positively correlated with subjective sensation of fatigue measured directly after the PET session.

Contrary to studies showing fatigue-related decreases in the fronto-parietal network, Lim et al. (2016) administered the Blocked Symbol Decoding Task (BSDT) during about 14

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[8] ALFF is defined as the total power within the frequency range between 0.01 and 0.1 Hz, and thus measures the strength or intensity of low frequency oscillations of resting-state BOLD time courses. It is a marker of regional spontaneous neural activity changes.

minutes in-scanner and showed increased activity in fronto-parietal areas as well as decreased deactivation in the DMN with Time-on-Task. The authors suggested that Time-on-Task would only trigger decreased fronto-parietal activity in simple tasks as it is the case for binary decision paradigms (target *versus* non-target). By contrast, they claimed that more complex tasks – like theirs – would rather trigger increased activity of the fronto-parietal network, allowing sustaining controlled attention during a long-lasting period. Regarding the decreased deactivation in the DMN, it has been suggested that the failure to suppress activity in this network while performing a cognitive task would reflect disengagement from the task at hand (Weissman et al., 2006). Given DMN activity is linked to mind-wandering (Christoff et al., 2009), this result was also in agreement with studies showing that mind-wandering parallels Time-on-Task (Smallwood & Schooler, 2006).

Connectivity Studies

As Qi et al. (2019) mentioned in their paper reporting the last new insights from the Brain Connectome project, the univariate analysis approach was generally employed in the studies summarized above while the interconnectivity between brain regions and the integrity of the cortical network under cognitive fatigue was not investigated at this point. As previously presented in **Chapter 1**, Ishii et al. (2014a) showed that mental fatigue is not only caused by impaired activity in task-related brain regions, but also modulated by mental facilitation and inhibition systems that regulate the activity of task-related brain regions. Therefore, network analysis seems also very relevant for studying the neural mechanisms of mental fatigue (Qi et al., 2019).

Some connectivity studies have tried to identify how brain networks were modulated by Time-on-Task effect (Giessing et al., 2013; Gui et al., 2015; Lorist et al., 2009; Sun et al., 2014a; Sun et al., 2014b; Taya et al., 2018; ten Caat et al., 2008). Using a Go/No-Go task, Giessing et al. (2013) aimed at investigating brain functional reorganization associated with attentional task performance. The results showed that Time-on-Task impaired behavioral performance and led to less efficient network topology (i.e., increasing clustering and shorter connection distance). As previously mentioned, Gui et al. (2015) used a PVT continuously for 20 minutes with ALFF to identify brain regions that were vulnerable to cognitive fatigue. Their connectivity analyses showed reduced anti-correlation between the PCC and the right middle PFC after the task, suggesting that task-positive and task-negative networks mediate

Time-on-Task effects. Taya et al. (2018) investigated the changes in topology of subnetworks of resting-state fMRI after cognitive fatigue induction by a visual oddball task taxing selective attention. Their results suggested that fronto-parietal subnetworks have a flexible topological architecture allowing compensation for impaired performance triggered by cognitive fatigue.

In 2009, Lorist et al. used EEG coherence as a measure of synchronization between neural networks in a paradigm in which participants performed a continuous 2-hour task switching. The results showed higher coherence value in the fronto-parietal network for switch trials, as compared to repetition trials. However, the results also showed a widespread and non-specific effect of mental fatigue on EEG power and coherence across multiple frequency bands. This increase in neuronal activity and stronger synchronization did not favor efficient behavioral performance. According to the authors, this non-specific and widespread effect on power and coherence measures of Time-on-Task can be explained by the action of the dopaminergic system. Accordingly, decreased dopamine levels in mentally fatigued participants would be responsible for increased noise levels, which in turn, increase power and coherence. These increased parameters further negatively affect the quality of information processing. Sun et al. (2014a) used a 5-minute PVT to assess changes in functional connectivity in the lower alpha EEG band power. The results showed a global reshape of the topology in cortical connectivity networks under fatigue state. Furthermore, there was an asymmetrical pattern of connectivity in fronto-parietal regions with higher connectivity on the right hemisphere associated with sustained attention. Interestingly, significant decrease with cognitive fatigue were observed in left, but not right, fronto-parietal connectivity. This study showed that changes in functional network connectivity due to cognitive fatigue are already observable with a relatively short time scale.

Similar disintegrated network topology have been reported in fatigue studies that used simulated driving paradigms (Kong et al., 2015; Zhao et al., 2017). However, in comparison with cognitive task paradigms in which subjects were typically required to perform the prolonged execution of various cognitive tasks, prolonged driving mostly reduced alertness ability. In order to investigate fatigue-related mechanisms between these two types of cognitive activities, Dimitrakopoulos et al. (2018) compared the topological alterations of functional brain networks in the theta EEG band between two fatigue-inducing tasks: a 1-hour low-intensity simulated driving *versus* a high-demanding half-hour PVT. If both paradigms impaired behavioral performances, PVT and simulated driving were related to different network reorganizations. While a common disrupted global integration was revealed in both fatigue tasks (i.e., increased path length, a measure of parallel information efficiency), simulated driving was also associated with increased local segregation (i.e., increased clustering). This result supports the fact that connectivity analyses may help identify different network topologies between different types of fatigue such as active (i.e., the PVT task) *versus* passive (i.e., simulated driving) task related fatigue (May & Baldwin, 2009).

Motivation by Rewarding Incentives

Rewarding incentives have been associated with better performances in tasks requiring executive functions. For example, Krebs et al. (2010) showed in a Stroop task that stimuli linked to the delivery of monetary reward were answered faster than non-rewarding stimuli. This phenomenon also seems to play a role in situations of prolonged demands, suggesting that motivation is one of the key mechanisms to maintain performance in a long time course (Sarter et al., 2006). Lorist et al. (2009) used a 2-hour switching task to induce cognitive fatigue followed by a motivational manipulation which consisted in social comparison and monetary incentives to perform well for 20 additional minutes. This resulted in a slight nonsignificant decrease in EEG coherence but more efficient behavior. Interestingly, Boksem et al. (2006) investigated whether increasing motivation could allow recovering performance on a 2-hour monitoring task (a modified version of the Simon task). In order to modify motivation, the authors told the participants that they would receive financial reward if they belonged to the best performers. The results showed that this monetary incentive improved their performance. Thus, this experiment shows that motivation can modulate performance under fatigue. However, it also appeared that participants did not react in the same way to motivation. Indeed, participants chose a strategy focusing on speed or accuracy but did not improve both speed and accuracy. It was thus suggested that fatigue is probably more than an effort/reward imbalance and involves adaptive strategies that are under the voluntary control of the individual to keep performance at an acceptable level under adverse internal circumstances. This assumption was further supported by a study of the same group (data not published) in which participants were told that accuracy was more rewarding than speed. Indeed, participant increased their accuracy but not speed after the motivation phase.

Similarly, Hopstaken et al. (2015a, 2015b) administered their participants a 2 hour N-Back task and showed decreased performance, decreased pupil diameter – index of psychophysiological arousal – as well as increased subjective fatigue with the time spent on the task. However, all measures improved after participants were informed that the remaining duration of the experiment will depend on their performance. In 2016, Hopstaken et al. changed their paradigm a little bit to investigate mental fatigue as induced by a long-lasting cognitive task (N-Back) containing task-unrelated distractor stimuli (human faces). The results showed that task engagement and performance decreased with Time-on-Task. Like in their previous studies, they increased motivation by the same "remaining-time" incentive. Afterwards, task engagement and performance were restored and irrelevant stimuli were ignored. In the same vein, Herlambang et al. (2019) administered their participants with a 2.5 hour working memory task containing 14 blocks that alternated between monetary reward and non-reward. The results showed that accuracy in the rewarding blocks remained constant while it declined in the non-rewarding blocks. Furthermore, the non-rewarding blocks were also associated with more distraction, less cognitive effort, more eye blinks, and fewer saccades.

The global pattern of above results strongly suggests that, even after a long-lasting continuous performance, resources may not be completely depleted as it was proposed by the energy depletion hypothesis. Instead, these results are rather in agreement with the costs/rewards imbalance (Boksem & Tops, 2008; Tops et al., 2004) and opportunity cost theories (Kurzban, 2010; Kurzban et al., 2013). With increasing Time-on-Task, the rewards of the experimental task stay the same while the opportunity cost of not engaging in other possible activities increases (Kurzban et al., 2013). This results in an imbalance between the costs and rewards of the task and eventually leads to disengagement. However, certain types of incentives may reset motivation and restore performance to a certain extent.

Probe Approach

As previously mentioned, the probe approach has been originally used in the context of ego-depletion and then progressively extended to the cognitive fatigue domain. Studies resorting to this approach are interested in the question of "are fatigue effects specific and transferable only to the *fatigued* process or are they general and transferable to *any* cognitive function?"

In this regard, van der Linden et al. (2003) found that, after having performed a 2-hour cognitively demanding task (a scheduling task), participants displayed more preservation on the Wisconsin Card Sorting Test (WCST) as well as prolonged planning time on the Tower of London (TOL), suggesting impaired executive functioning under cognitive fatigue.

Another well-recognized and cited study in the field is that of Persson et al. (2007) who required their participants to perform a probe task (verb generation) with high (MANY) or low (FEW) interference[9] before and after a working memory task (Sternberg task) with high (HIGH) and low (LOW) interference conditions. Regarding transfer effect, the process-specific hypothesis assumes that performance changes between pre- and post-task will depend on the specific cognitive processes (i.e., a high level of interference) required by the loading and the probe tasks. For the probe task, interference resolution index (IR-scores) were computed in pre- and post-task by subtracting the RTs of FEW interference trials from that of the MANY interference trials. Afterwards, transfer effects were assessed by a 2 (HIGH, LOW) x 2 (Pre, Post) ANOVA on the IR-scores. The results showed that IR-scores increased after the loading task (Sternberg) in the HIGH interference group but not the LOW interference one (**Figure 17 A**). The authors concluded that high interference conditions of the working memory (Sternberg) and verb generation tasks were mediated by a common resource-limited cognitive mechanism. To ascertain the specificity of this transfer effect between the working memory task and the probe task, the same authors conducted a second experiment in which the probe task was identical (verb generation) but the loading task was replaced by the stop-signal task which also comprised HIGH (i.e., high proportion of stop trials) and LOW (i.e., low proportion of stop trials) conditions. However, this task does not tax exactly the same cognitive process than the verb generation task. Indeed, the stop-signal is more related to response inhibition and has been associated with right, rather than left, inferior prefrontal function (Aron et al., 2003) while the verb generation task is more related to interference resolution *per se*. According to their hypothesis, the authors did not find evidence of transfer effect between these two tasks that tax different functional mechanisms and rely on different neuronal substrates (**Figure 17 B**).

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[9] For the verb generation task, participants had to generate silently a verb in response to a visually presented noun (see Persson et al., 2004). In the MANY condition, participants were presented with nouns having several appropriate associated responses (e.g., BALL—THROW, KICK, BOUNCE) while in the FEW condition, participants were presented with nouns having one dominant response, or only a few associated responses (e.g., SCISSORS—CUT).

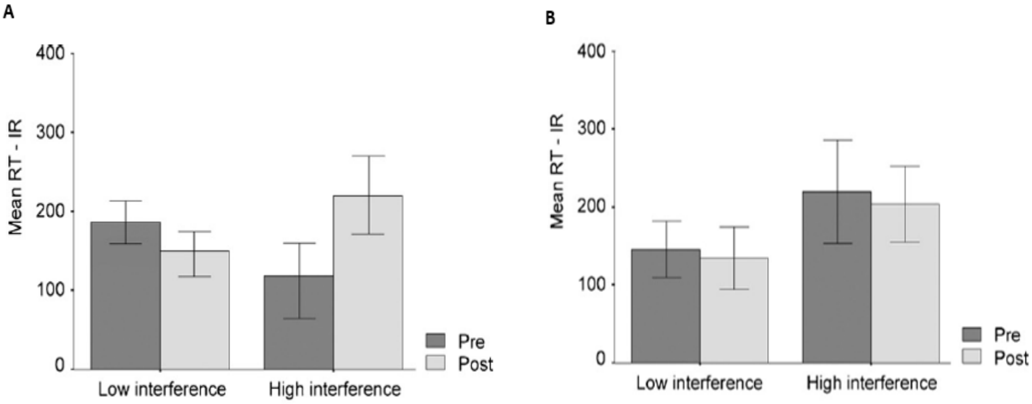

Figure 17. Persson et al. (2007)'s Data. Mean interference resolution scores as a function of group (High/Low interference), and time (Pre/Post loading task). **A.** Sternberg as loading task and verb generate as probe-transfer task; **B.** Experiment 2—Stop-signal as loading task and verb generate as probe-transfer task. Reprinted with permission from Persson et al. (2007).

Besides Time-on-Task paradigms, some studies investigating brain activity have also used the probe method (Esposito et al., 2014; Lim et al., 2010; Nakagawa et al., 2013; Persson et al., 2013; Tanaka et al., 2014b). As previously mentioned, an ASL perfusion fMRI study showed that a prolonged PVT task was associated with a decrease in the right fronto-parietal attentional network during post-task rest and correlated with performance decline (Lim et al., 2010). Otherwise, Persson et al. (2013) administered their participants with the same protocol as Persson et al. (2007) in order to investigate transfer effects between a loading task (Sternberg) with high and low interference condition and a probe task (verb generation) during fMRI acquisition. The results of this study showed that the high level interfering condition – as compared to the low interfering condition – triggered impaired performances but also a left-to-right shift in activated cerebral regions. This pattern of activation resembles that of older people in situation of cerebral compensation: a reduction in regions normally recruited for the task in parallel with an increased activation in normally non-recruited regions for that task (Persson et al., 2004; Reuter-Lorenz, 2002). Therefore, the authors proposed the possibility that a classically observed pattern of activation in older people is also present in cognitively fatigued young people. In 2014, Esposito et al. required their participants to perform an intensive training of 4 hours (theoretical training and sustained practice with a flight simulator) followed and preceded by an N-Back task as well as resting-state fMRI. As compared to the control condition in which participants were free to choose their activities, the intensive training increased resting-state activity in the early visual processing and to a lesser extent in the DMN networks while it decreased activity in the front-parietal executive network. The early visual network has been previously associated with EEG alpha rhythm (Mantini et al., 2007), particularly in exhausted states (Boksem et al., 2006; Kamei et al., 1998; Schrauf et al., 2011). Considering that alpha oscillations represent inhibition of cortical processing (Pfurtscheller et al., 1996; Worden et al., 2000), the increased resting-state activity in this network after a period of induced fatigue pointed towards increased inhibition of the neural activity in the early visual system implied by exhaustion. The authors proposed that cognitive fatigue does not necessarily alter resting-state activity in task-positive or task-negative networks because it would have implied an opposite pattern between early visual and DMN networks. Rather, they claimed that cognitive fatigue is more likely to affect resting-state activity of networks that are associated with sensory inhibition or excitation (as is the case for the visual network) as well as networks associated with intrinsic or extrinsic neural processes (as is the case for the DMN and the fronto-parietal networks). Nakagawa et al. (2013) used visual and auditory divided attention tasks with low and high attentional loads in fMRI. They found fatigue-induced deactivation from pre to post-session on task-related activity in the frontal, temporal, occipital, and parietal cortices, in the cerebellum and in the midbrain for both the low and the high conditions of their attentional task. Moreover, a significant interaction effect was found in the midbrain (i.e., more deactivation in the high-load condition). According to the authors, this larger deactivation in the midbrain may reflect the suppression of the negative feedback system that normally triggers recuperative rest in the face of overload to maintain homeostasis. The authors assume that suppressing this system can be seen as a compensatory effort against fatigue-induced performance deteriorations in many situations at the expense of comfort. Otherwise, this system has been postulated to be underlined by the striato-thalamo-cortical loop connecting the neostriatum with the prefrontal cortex (Boksem & Tops, 2008; Chaudhuri & Behan, 2000) and interacts with midbrain dopaminergic neurons to flexibly modulate resource allocation (Krebs et al., 2012). Failures in dopaminergic input to the striato-thalamo-cortical loop have been linked to failures to integrate motivational input and in turns, to cognitive fatigue (Chaudhuri & Behan, 2000; Dobryakova et al., 2013; Lorist et al., 2009).

Workload

Somehow related to the probe approach are studies investigating the influence of the workload level on cognitive fatigue (Borragán et al., 2017; Käthner et al., 2014; Nakagawa et al., 2013; Shigihara et al., 2013). In a very interesting study, Borragán et al. (2017) based their design on the Time-based Resource-sharing model (TBRS; Barrouillet et al., 2004) which proposes that the available time to process cognitive demands is responsible for inducing cognitive load. Therefore, they assumed that limiting the time available to process cognitive demands should increase cognitive load, eventually increasing cognitive fatigue. In this experiment, the authors administered their participants with the Time Load Dual Back (TLDB) which is a dual task combining the classic N-Back working memory updating task (Kirchner, 1958) with an interfering task (odd/even decision task). In the TLDB, digits and letters are alternatively displayed and participants are instructed to either (a) indicate if the letter is the same as the previous letter (1-Back task), or (b) indicate whether the digit is odd or even. To manipulate the limited time to process information, the stimulus time duration (STD) can be adjusted to be long *versus* short, leading to the low *versus* high cognitive load conditions[10]. The results were in agreement with the hypothesis and showed that task performance was globally higher in the low load condition, as compared to the high load one. Moreover, there was also an interaction between Time-on-Task and cognitive load showing that performance decreased faster with Time-on-Task in the high load condition as compared to the low one. Therefore, shortening the available time to process information – i.e., increasing time pressure – increased cognitive load, which in turn triggered higher levels of cognitive fatigue. However, there was a dissociated effect of the cognitive load on subjective fatigue and sleepiness as assessed by VAS. While subjective fatigue increased more in the high load condition than in the low condition, the subjective sleepiness increased more in the low condition than in the high one. The authors proposed that the low condition was too easy to process, leading participants into a cognitive underload state and to a feeling of boredom accompanied by higher subjective sleepiness. This explanation supports the existence of different types of fatigue that is further assumed in the following experiment.

In **Chapter 1** I presented the overload *versus* underload theory (Hancock & Desmond, 2000; May & Baldwin, 2009). Accordingly, very high demanding but also very low

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[10] This STD is calculated on an individual basis in a pre-test session in order to create low and high condition that are adjusted to each participant.

demanding tasks are likely to trigger cognitive fatigue. A very well speaking study is the one of Shigihara et al. (2013) who aimed at investigating two types of cognitive fatigue by administering their participants with 0-Back and 2-Back tasks continuously for 30 minutes. Moreover, participants were also required to perform the Advanced Trail Making Test (ATMT; Kajimoto et al., 2007)[11] during 30 minutes as well as to fill-in subjective scales just before and just after the N-Back session. Performance decrements on the ATMT, as indexed by increased error count after as compared to before the N-Back session, were found after both the 0-Back and the 2-Back. However, decreased performances (i.e., increase in mean RT) during the N-Back session were found in the 0-Back but not in the 2-Back condition. Moreover, the level of sleepiness was greater after having performed the 0-Back but not after the 2-Back. The authors explained this surprising result by the fact that there exist two types of cognitive fatigue respectively triggered by cognitive overload or cognitive underload. In this case, a possible explanation is that boredom triggered by the easiness of the low-demanding 0-Back did not elicit enough interest and deployed effort, leading to task disengagement. As an alternative explanation, the authors also proposed that the cognitive underload triggered by the 0-Back activated the inhibition system, which in turn, altered task performance and enhanced subjective feeling of sleepiness.

Contrary to the above mentioned studies, Borragán et al. (2016) used a probe approach in order to test positive rather than negative transfer effects. Indeed, their hypothesis was that diminished cognitive control, triggered by cognitive fatigue, will eventually facilitate procedural sequence learning. The authors administered their participants with high and low cognitive load conditions of the TLDB as the fatiguing loading task, followed by a visuo-motor procedural learning task: the Serial Reaction Time Task (SRTT). In agreement with their hypothesis, RTs in the SRTT were faster following the high load condition of the TLDB as compared to the low load condition. The authors proposed that the high load condition has triggered diminished cognitive control resources that normally oppose automatic procedural learning.

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[11] Contrary to the classical TMT, the ATMT is presented on a laptop display and participants use touch sensor screen instead of paper-pencil.

Subjective Cognitive Fatigue

As mentioned earlier, it is informative to distinguish between objective cognitive fatigue (i.e., performance decrements) and subjective sensation of fatigue (Kluger et al., 2013). According to Hockey (2013), the subjective sensation of fatigue should even be considered the first marker of cognitive fatigue. Most of the above-mentioned studies have used subjective fatigue scales in their protocol and I will describe some of these results in the following lines.

By performing a visual attention task for 3 hours, participants in Boksem et al.'s (2005) study reported evidence of increased aversion to continue task performance with the time spent on the task using VAS. Interestingly, this aversion to continue a task has been previously thought to be a very reliable marker of mental fatigue installation (Hockey, 1997; Holding, 1983; Meijman, 2000). Moreover, increase in alpha power in this study correlated with the increase in subjective fatigue. By contrast, Ishii et al. (2013) found that decreased in alpha power due to a long-lasting N-Back task was related to subjective fatigue level as assesses by VAS. Hopstaken et al. (2015a) found that after 2 hours performing an N-Back task, participants reported higher level of subjective fatigue: task engagement decreased with Time-on-Task, as assessed by the RSME (Zijlstra, 1993). Kato et al. (2009) found an increase of subjective fatigue on the mental symptoms subscale of the Fatigue Scale (Chalder et al., 1993) after a 60-min performance on a Go/NoGo task. Likewise, Guo et al. (2016) found that after performing a 63-minute dual visual task, the mean in KSS (Akerstedt & Gillberg, 1990) increased from the first time interval (0-35min.) of task to the second interval (36-60min.). As previously presented, Borragán et al. (2016) administered their participants with the TLDB comprising a high and a low load conditions followed by the SRTT as the probe task. Interestingly, RTs in the SRTT were less impacted after the high load condition as compared to the low load condition, which the authors explained by a facilitation of sequential procedural learning under decreased cognitive control. However, scores on VAS for fatigue were found to be higher after the high load condition as compared to the low load condition, suggesting that performing the TLDB under high cognitive control triggered more cognitive fatigue than under lower cognitive control. Tanaka et al. (2014a) used MEG to investigate the neural activity associated with cognitive fatigue induced by a continuous attentional task during 10 minutes. Their results showed that increased beta-frequency band power in the right middle frontal gyrus was negatively associated with subjective mental stress but positively associated with boredom and sleepiness, as assesses by VAS. In 2018, Guo et al. required their participants to perform a simulated driving task (driving group) during 90 minutes or to watch videos (control group) and showed that only the driving group reported higher level of subjective fatigue after the experiment as assessed by the Profile of Mood States Short Form (POMS-SF; Chen et al., 2002).

However, it is important to note that increases in subjective fatigue level are not always associated with declines in objective performance. As already presented, Tajima et al. (2010) found a positive association between activity in medial orbitofrontal cortex during a 35-minute ATMT and subjective sensation of fatigue using VAS. However, while subjective level of fatigue increased during the time course of the fatiguing task, performance was not altered. In the same vein, Gergelyfi et al. (2015) found that after performing 120 minutes of Sudoku, people reported higher subjective fatigue on a modified version of the Multidimensional Fatigue Inventory (MFI; Gentile et al., 2003) and Intrinsic Motivation Inventory (IMI) but that people with large increases in subjective fatigue also tended to show better performance on a working memory task that followed each Sudoku block. Likewise, Esposito et al. (2014) investigated scores on the RSME (Zijlstra, 1993) and on an N-Back task after participants had performed an intensive training condition *versus* a leisure control condition. The results showed that the sustained performance in the training condition induced an increased self-reported level of exhaustion compared to the control condition. Moreover, they also found a significant increase of mental effort expenditure to maintain the same performances (i.e. same error rates) in the N-Back task after the training condition than after the control condition. This pattern of result – performance maintenance parallel with increased mental effort – is in agreement with Hockey’s framework. Finally, Herlambang et al. (2019) used an original paradigm in which they alternated between rewarding and non-rewarding blocks during a 2.5 hour working memory task. While subjective feeling of fatigue, as assessed by VAS continuously increased with Time-on-Task, the level of mental effort alternated between higher and lower deployed effort as a function of the reward and non-reward blocks. Moreover, even if participants experienced subjective fatigue, accuracy remained stable in the rewarding blocks and declined in the non-rewarding blocks.

Chapter 3: Models of Cognitive and Cerebral Aging

Cognitive Modifications in Normal Aging

It is now well-established that normal (or healthy) aging is associated with cognitive decline (Craik & Salthouse, 2000), particularly in tasks involving “fluid” mental operations such as executive functions (EFs) (De Beni & Borella, 2015; Podell et al., 2012; Salthouse et al., 2003; West, 2000). For example, aged people have been shown to experience difficulties in inhibition, shifting, problem resolution, as well as strategic planning (Crawford et al., 2000). Related to the EFs, working memory has also been related to fluid operations, suggesting its weakening with advancing age (Kirova et al., 2015; Solesio-Jofre et al., 2017; Van der Linden et al., 1994). By contrast, “crystallized” mental operations such as vocabulary or general knowledge decline in the very last stage of life or remain preserved forever (Jones & Conrad, 1933; Kaufman et al., 1989).

Moreover, although high level cognitive functioning globally decreases in efficiency with age, all functions are not impaired to the same extent, with some remaining well preserved (Borella et al., 2009; Collette & Salmon, 2014; Cona et al., 2013; Ludwig et al., 2011; Salthouse et al., 2003; Taconnat & Lemaire, 2014; Vallesi et al., 2010). For example, it has been showed that older people have difficulties maintaining and manipulating two mental plans in working memory but not alternating between these plans (Kray et al., 2004; Verhaeghen & Cerella, 2002). Regarding the function of updating in working memory, aged people would encounter difficulties specifically suppressing irrelevant (i.e., not relevant anymore) information from working memory while their storage abilities are maintained (De Beni & Palladino, 2004). Likewise, in the inhibitory domain, voluntary/intentional abilities are known to show an age-related decrease while automatic inhibition remains efficient (Collette et al., 2009; Hogge et al., 2008). Besides the EFs, age-related cognitive modifications are observable in other domains: processing speed, mathematical reasoning, memory, language, visuo-spatial abilities (Harada et al., 2013; Park & Reuter-Lorenz, 2009; Salthouse, 2009).

Analytic versus General Approach of Decline

All these abovementioned cognitive impairments can be seen according to two different theoretical approaches. The analytical approach claims that cognitive aging directly impairs the cognitive components for which decreased performances are observed. For example, a more important interference effect in a Stroop task will be interpreted as a deficit in conflict monitoring or interference resolution in older people. By contrast, the global approach suggests that age-related cognitive differences are explained by general factors ranging from diminished working memory resources (Craik et al., 1990) to sensorial function integrity (Li & Lindenberger, 2002). Somewhat related to this global approach, some influential frameworks have also suggested that the age-related decline in most cognitive functions can be primarily explained by a limited number of "proxy" cognitive functions such as processing speed – the processing speed hypothesis (Salthouse, 1996) – or inhibitory impairment – the inhibitory hypothesis (Hasher & Zacks, 1988).

Processing Speed and Inhibition Hypotheses

Today, processing speed is well-recognized to decrease with age (Albinet et al., 2012; Cona et al., 2013; Manard et al., 2014; Salthouse, 1992, 1993, 1994a, 1994b, 1996, 2000; Salthouse & Babcock, 1991; Salthouse & Meinz, 1995; Salthouse et al., 2000). Slowdown in processing speed has been shown to explain age-related performances decreases in other functions such as inhibition (Verhaeghen & De Meersamn, 1998), episodic memory (Fastenau et al., 1996), or language (Waters & Caplan, 2001). Therefore, processing speed seems to be the most influent mediator between age and fluid cognition (De Ribaupierre & Lecerf, 2006; Salthouse & Meinz, 1995).

Against the processing speed hypothesis, inhibitory abilities have also been suggested to explain some age-related effects in various cognitive tasks (e.g., Borella et al., 2007; Borella et al., 2006; Persad et al., 2002). According to Hasher and Zacks (1988), inhibition is one of the first cognitive processes to decline with age (see also Persad et al., 2002; Radvansky et al., 2005) and would be a major source of working memory impairment in aging people. Inhibition would be useful, on the one hand, to filter information that can potentially reach working memory and, on the other hand, to limit competition between several responses during the process of the output. In agreement with this view, Miyake et al. (2000; see also Friedman et al., 2011; Friedman et al., 2008) proposed that all EFs involve an inhibitory capacity to suppress task-irrelevant distractors, which is considered to be a basic unit of working memory or executive functioning by certain authors (e.g., Dempster & Corkill, 1999; Zacks et al., 1996) but also as a "fundamental regulatory mechanisms" (Hasher et al., 2007) of cognition.

In agreement with these two hypotheses, my first study (**Gilsoul et al., 2019**; see **Appendix 1)** aimed at investigating to what extent decreased executive performance associated with normal aging could be influenced by a lower efficiency of some *non-executive* processes also prone to decline in normal aging. The two principal mediators we investigated were processing speed and attention (based on the model of van Zomeren & Brouwer, 1994) with the hypothesis that a slowdown in processing speed and/or weaker attentional functions may – at least partially – explain executive difficulties associated with normal aging. To this end, we administered 104 young and 71 older participants with a large battery of executive, attentional and processing speed tasks. Mediation analyses were performed to test whether processing speed and attention would mediate the effect of age on inhibition, shifting, updating, and dual-task coordination. Our results showed that attention variables had only slight age effects and almost no mediating effect. By contrast, processing speed was found to be an important mediator of age with significant partial mediation found for shifting, updating, and dual-task coordination. In a more exploratory way, based on Hasher and Zacks (1988)'s hypothesis, we also investigated if inhibition could be a potential mediator and found it to partially mediate the age effect on the other three executive functions.

Frontal-Executive Aging Hypothesis

According to the executive-frontal aging hypothesis, the aging process triggers cerebral neuroanatomical changes that are particularly marked in the frontal lobes, in parallel with PFC functioning decline (West, 2000). It is thus assumed that cognitive functions that are underpinned by the PFC would be the first to decline with age, as compared to cognitive functions relying on other cerebral regions (West, 1996). Following this view, the executive control would be one the first functions to be altered in normal aging (West, 1996, 2000). In agreement with this hypothesis, some studies have shown that aging is associated with frontal neuroanatomical modifications. For example, Lindberg (2012) found a reduction in volume of brain areas that are situated in the frontal lobes, this reduction being more important in prefrontal regions, such as the OFC, than in limbic regions such as the ACC or the hippocampus (Isingrini, 2004). Likewise, performance decreases in working memory have already been associated with reduction in right-lateralized cortical regions including medial orbitofrontal gyrus as well as inferior and superior frontal gyri (Nissim et al., 2017). Age-related declines in EFs have also been shown to correlate with white matter reduction in certain cerebral regions (O'Sullivan et al., 2001). While decreases in processing speed and working memory seem related to white matter reduction in anterior regions, decreases in inhibition and flexibility have been linked to reduction in posterior regions (Kennedy & Raz, 2009).

However, if the executive-frontal aging hypothesis may explain some evidence found in studies (De Beni & Borella, 2015; Podell et al., 2012; Salthouse et al., 2003; West, 2000), it is not sufficient to support the whole set of cognitive deficits that are commonly attributed to the aging process. Indeed, some cognitive functions that are underpinned by other cerebral regions also decrease in efficiency with aging. For example, it has been shown that visuo-spatial attention, principally relying on parietal cortex, undergoes efficacy decline with age (see Greenwood, 2000 for a review). Furthermore, it has progressively become apparent that the executive functioning could not be only attributed the frontal lobe. Cerebral imaging studies converge to the conclusion that the EFs imply frontal as well as parietal regions (see Collette & Van der Linden, 2002 for a review). For example, Manard et al. (2016) have shown that age-related executive performances were associated with grey matter volume decrease in anterior, posterior as well as subcortical regions. Therefore, it has become clear that other theoretical frameworks were necessary to take all age-related cerebral and cognitive modifications into account.

Beyond the "local-regional" approach that focused on the frontal lobe, other authors have attempted to explain age-related cognitive functioning – decreases as well as maintenance – in terms of cerebral networks that expand beyond the frontal lobe. In this sense, the concept of reserve has become very interesting to account for age-related compensatory mechanisms.

Cerebral Reserve, Cognitive Reserve, and Compensation Hypotheses

According to Stern (2002), the concept of reserve is twofold, comprising passive models – brain reserve and threshold – as well as active models – cognitive reserve. Many authors have proposed passive models such as the brain reserve (Katzman, 1993), the neuronal reserve (Mortimer et al., 1981), or the threshold model (Satz, 1993). The latter one is well established and proposes that there exist individual differences in brain reserve capacity (BRC), namely brain size and synapse quantity. According to this model, there is a critical threshold of BRC below which clinical or functional manifestations emerge. Therefore, a particular brain lesion will not lead to the same clinical deficit in patients, depending on their respective BRC. In brief, passive models are essentially quantitative and assume fixed cut-off of brain matter below which functional impairment will occur (Stern, 2002). However, these models are not able to explain individual differences in how the brain processes cognitive or functional tasks following brain damage.

Besides passive models, Stern (2002) developed the concept of active models of reserve – cognitive reserve hypothesis – in which the brain is considered to actively attempt to compensate for brain damage or increasing cognitive demands. In that context, Stern (2002, 2009) proposed that cognitive reserve can be divided into two components: the *neural reserve* and the *neural compensation*.

First, the *neural reserve* refers to a more flexible and efficient utilization of brain networks or cognitive strategies that are less prone to disruption. The neural reserve component encompasses two possibilities: differences in recruitment of the same network and differences in the ability to recruit alternate networks. Regarding differences in recruitment of the *same network*, a well-recognized response to increasing task difficulty is increased activation of areas involved in an easier version of the task and/or the recruitment of additional brain areas or networks (Grady et al., 1996; Grasby et al., 1994; Gur et al., 1988; Rypma et al., 1999). For a given difficulty, more skilled individuals typically show less task-related recruitment than less skilled individuals. It is also proposed that a person with more neural reserve will show increased and/or additional recruitment of brain areas and networks at a higher difficulty level of the task. Regarding differences in the ability to recruit *alternate networks*, Stern (2002) suggested that a person with more neural reserve may rely on a large array of networks to solve a problem. As an analogy, a mathematician might be able to solve a math problem in many different ways, while a less skilled individual might have only one possible solution.

Second, the *neural compensation* refers to the utilization of alternative cerebral networks and strategies that are not normally used by healthy brains (or young brains), to compensate for brain damage (or normal aging) when habitually implicated cerebral areas are altered. What really distinguishes between neural reserve and neural compensation is the fact that a different network, not normally used for the task at hand, will be recruited by the more impaired group as compared to the unimpaired group in case of neural compensation.

According to the cognitive reserve hypothesis, two patients having the *same* amount of BRC but different levels of cognitive reserve will not show the same functional impairment after a brain lesion. The patient with more cognitive reserve can tolerate a larger lesion before undergoing some clinical deficits. In that context, the critical threshold at which functional manifestations arise varies from one individual to another, depending on their flexibility or efficiency in recruiting cerebral networks. The concept of cognitive reserve thus helps explain the finding of many studies that higher levels of intelligence, education, and occupational attainment are good predictors of better resistance to brain damage before experiencing clinical and functional deficits: these people process tasks in a more efficient manner. Regarding Alzheimer's disease (AD), Stern (2009) also proposed that people with high cognitive reserve can wait until a more advanced level of cerebral AD pathology before experimenting clinical deficits, as compared to people with lower cognitive reserve. However, once a certain threshold of cerebral lesions is reached, people with high cognitive reserve will experiment more abrupt clinical declines given the pathology will have spread to a larger extent.

Besides patients with brain damage, cognitive reserve is also present in healthy people and underpins a more flexible and efficient utilization of brain networks or cognitive strategies in response to increased cognitive demands (neural reserve) or the recruitment of alternative networks to compensate for healthy age-related difficulties (neural compensation). The cognitive reserve hypothesis may thus help explain the intra and inter-individual heterogeneity that is commonly found in neuropsychological evaluation in older people (Calso, 2017). A classical hypothesis is that people with a higher level of cognitive reserve would better resist to age-related effects and would have better cognitive performances as compared to aged people with a lower level of cognitive reserve. For example, Roldán-Tapia et al. (2012) showed better performances on executive and intelligence subtests in aged people with a high cognitive reserve, as indexed by the educational level, the occupational attainment, and the vocabulary level. A main factor of cognitive reserve in older people is the educational level (see Bennett et al., 2003; Meguro et al., 2001; Springer et al., 2005) but it has also been suggested that different factors of cognitive reserve would differentially impact executive processes (Hultsch et al., 1999; James et al., 2011; Le Carret et al., 2003; Shimamura et al., 1995).

Cerebral Compensation versus Dedifferentiation Hypotheses

The idea of cognitive reserve (Stern, 2002, 2009) have echoed in other theoretical framework aimed at explaining age-related cognitive performance and activity. In this regard, three main ideas have motivated the neurocognitive aging research.

Firstly, age-related decreases in cerebral activation – as compared to that of younger people – accompanied by poor performances have classically been attributed to *under-utilization* of cognitive strategies but also, from a structural point a view, to cerebral atrophy (Reuter-Lorenz & Cappell, 2008). If those underactivations associated with poor performances seemed relatively trivial to interpret, determining whether age-related cerebral overactivations are beneficial, detrimental, or useless was much less straightforward and has been the focus of many research (Reuter-Lorenz & Lustig, 2005). Therefore, as a second idea, increases in cerebral activity in older people associated with weaker performances than that of young people have been interpreted as the result of *inefficient utilization* of cognitive strategies as well as resulting from a *dedifferentiation* process due to impaired specificity and selectivity of neuronal systems (Reuter-Lorenz & Cappell, 2008). Thirdly, age-related increases in brain activation parallel to equivalent performance to that of young people have been considered as *compensatory processes* (Cabeza, 2002; Cabeza et al., 2002; Cabeza et al., 2004; Reuter-Lorenz & Lustig, 2005). This compensation hypothesis of age-specific overactivations further predicts that, even if performance is similar between young and older groups, overactivation across individuals in the older group should be correlated with higher performance (Reuter-Lorenz & Lustig, 2005).

The idea of neural reserve (Stern, 2002, 2009) has been applied in the CRUNCH hypothesis (*compensation-related utilization of neural circuits hypothesis;* Reuter-Lorenz & Cappell, 2008). This model assumes that, in general, older people show a higher recruitment of neural resources at a lower level of task demand as compared to young people, which allows them to achieve a similar performance level to that of young people. These age-related overactivations are interpreted as a sign of compensation only if older people reach the same level of performance as young people but also if the activation pattern in the older group is positively correlated with cognitive performance. However, the model also assumes that, as demands increase, a resource ceiling is reached. Once this threshold is passed, the older brain is not able to compensate anymore and performance as well as cerebral activation become weaker than that of young people (**Figure 18**).

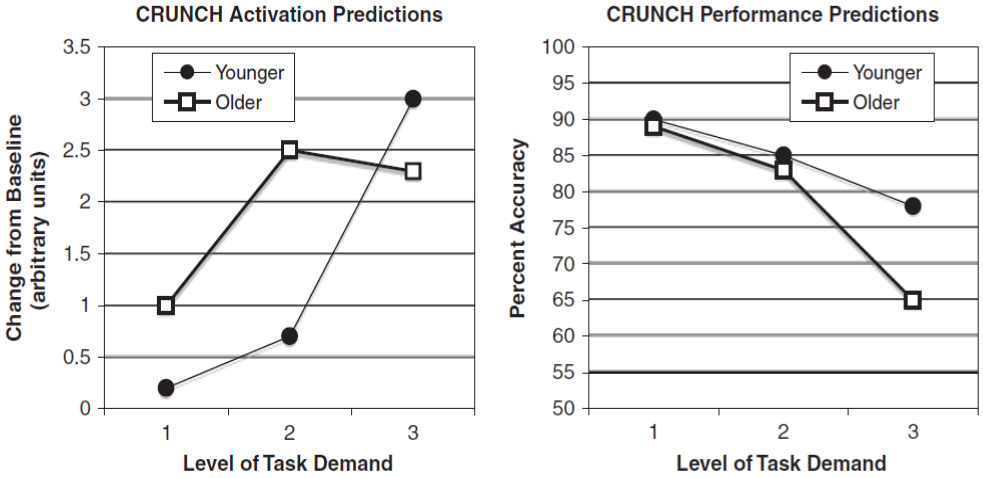

Figure 18. Patterns of Activation and Performance Levels Predicted by the CRUNCH. The left graph shows increased recruitment of neural resources in response to increasing task demand, which is a ‘‘normal’’ neural response that is also evident in younger individuals. Moreover, the left graph also shows how, relative to young people, older adults show overactivation at lower task demands while they show underactivation at higher level of task demand within the same region of interest. According to the CRUNCH, compensatory recruitment at low demand enables older people to maintain an equivalent performance level to that of young people. The right graph shows how, as task demands increase, older adults reach a resource ceiling, and performance level becomes weaker than that of young people. Adapted from Reuter-Lorenz and Cappell (2008).

More closely related to the neural compensation of Stern (2002, 2009), the PASA pattern (*Posterior-Anterior Shift in Aging*) has consistently been reported in the literature bearing on visual stimuli in normal aging (Davis et al., 2008; Dennis & Cabeza, 2008; Grady et al., 1994). This pattern suggests that older individuals would compensate sensory deficits – that are underpinned by posterior areas – by recruiting areas such as PFC normally dedicated to higher level cognitive processes. Therefore, healthy aging brain would be characterized by a decrease in occipito-temporal activation in parallel with increased activity in anterior regions. From a more temporal point of view, another well-recognized pattern is the ELSA (*Early to Late Shift in Aging*) which is characterized by an early reduction in brain activity followed by a later increase in brain activity (Dew et al., 2012).

According to the HAROLD model (*Hemispheric Asymmetry Reduction in Older Adults;* Cabeza, 2002), cerebral activity of older people tends to be less lateralized than that of young people during cognitive tasks. For example, during working memory tasks, PFC activity is normally left-lateralized for verbal stimuli and right-lateralized for spatial stimuli (Smith & Jonides, 1997). In elderly people, however, the PFC appears to be bilaterally activated for these two types of tasks (Reuter-Lorenz et al., 2000; see **Figure 19 left side**). The same pattern of focal, left PFC activity in young adults and bilateral PFC activation in older adults were also shown in verbal long-term memory (Cabeza et al. 1997, Grady et al. 1999; see **Figure 19 right side**). Similarly, cerebral activity underpinning inhibition is rather lateralized in the right hemisphere, including a network of prefrontal and parietal areas, in the young population (Garavan et al., 1999). By contrast, older people show a bilateral activation of this fronto-parietal network (Nielson et al., 2002). Briefly, it seems that the engagement in cognitive tasks lead older people to recruit a similar network to young people as well as supplementary contralateral areas.

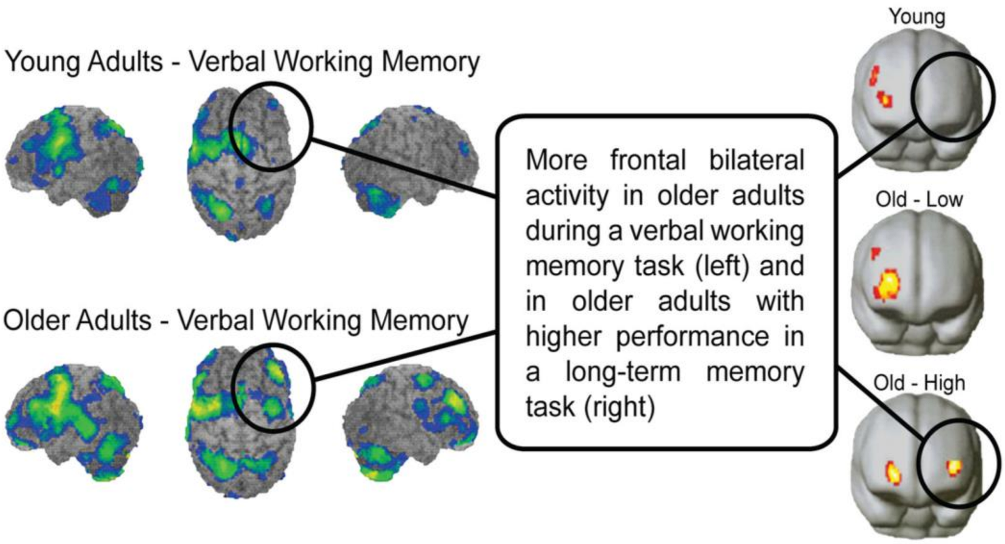

Figure 19. Hemispheric Asymmetry Reduction in Older Adults. (Left side) Left lateralized frontal engagement in young adults during a verbal working memory task; in older adults, an additional right frontal engagement is observed (Reuter-Lorenz et al., 2000). (Right side) Right lateralized engagement in young adults and low-performing older adults during a long-term memory task, and bilateral frontal engagement in high-performing older adults (Cabeza et al. 2002). Reprinted from Park and Reuter-Lorenz (2009)

The question raised by this model is when can hemispheric asymmetry reduction be interpreted as a compensatory mechanisms *versus* as dedifferentiation? The compensatory view has been supported by studies showing that bilateral activity in older people helped counteract age-related cognitive deficits (Cabeza et al., 1997) or was associated with enhanced cognitive performance (Reuter-Lorenz et al., 2000). The dedifferentiation hypothesis has been supported by increases in correlations among different cognitive measures but also between cognitive and sensory measures with advancing age (Baltes & Lindenberger, 1997). However, the compensation and dedifferentiation views are not necessarily exclusive. For example, Cabeza (2002) proposed that dedifferentiation can play a compensatory role in the aging brain in the sense that older people's cognitive performance seems to benefit from a decrease in differentiation.

Cabeza (2002) further proposes two possible origins for these hemispheric asymmetry reductions: the psychogenic origin and the neurogenic origin. The first one assumes that cerebral activity changes – namely, a more bilateral activity – in older people, as compared to young people –, would be due to modifications inside the cognitive architecture. In other words, cerebral activity changes because older people resort to different cognitive strategies to perform a task. The second one assumes that cerebral activity changes are due to modifications inside the neuronal architecture: there are that functional modifications in cerebral regions as well as in their connections.

Some other theoretical frameworks have also postulated compensatory mechanisms in normal aging but went a step forward by proposing more complex models that integrated several ideas from PASA pattern, CRUNCH, and HAROLD hypotheses.

A First Model of Age-Related Compensation

Cabeza and Dennis (2013; see **Figure 20**) proposed a model of age-related compensation according to which older people would attempt to compensate for their cognitive deficits by recruiting reserve neuronal resources, which will eventually lead to successful compensation or unsuccessful compensation. More precisely, this model consists of three hypothetical constructs (represented by rectangles) and four measurable variables (represented by ovals). The *neural resources* component refers to the total capacity of the brain for cognitive processing and can be assessed using neuroimaging measures (e.g., MRI, DTI, PET). The *neural supply* component refers to the amount of neural resources being deployed for cognitive processing and can be assessed using functional measures such as fMRI, ERPs, and MEG. The construct *cognitive processing* refers to the cognitive operations and strategies being performed (attention, memory, etc.) and is represented by behavioral performance (accuracy, response times). Finally, the construct *task demands* refers to the quantity and quality of required cognitive processing. This model proposes that resource reduction, classically observed in normal aging, leads to a decrease in neural supply, which in turn leads to a decline in cognitive processing. Consequently, older adults have difficulties coping with task demands. When cognitive processing implemented by the individual does not meet task demands, there is a mismatch. To meet task demands, older adults attempt to compensate (which is referred as "*attempted compensation*") by recruiting reserve neural resources, which increases the neural supply component. This increase in neural supply may take the form of increased activity in the same brain regions or in alternative brain regions and/or as increased connectivity. To echo the CRUNCH model, the authors also proposed that "*attempted compensation*" is a natural response of the brain that can be encountered in young people to increase their neural supply in response to enhanced task demands (Reuter-Lorenz & Cappell, 2008). This attempted compensation to solve the mismatch between cognitive processing and task demands may lead to enhanced cognitive processing ("*successful compensation"*) *versus* no change or even worse performance ("*unsuccessful compensation "*). According to Cabeza and Dennis (2013), it is important to distinguish between attempted compensation and successful compensation because different predictions in functional activity can be stated.

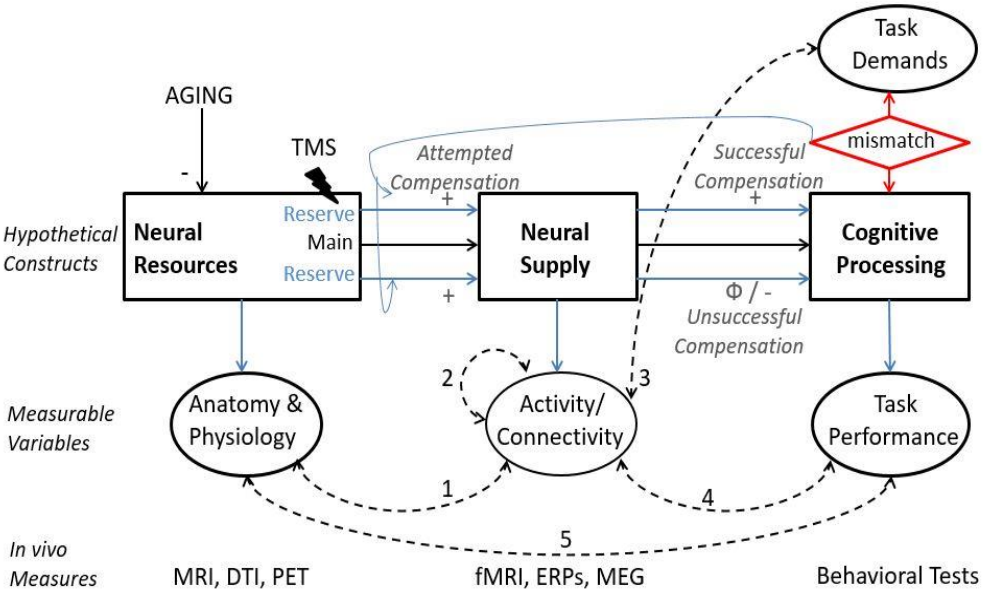

Figure 20. A Model of Age-Related Compensation. The model consists in three hypothetical constructs (rectangles) and four measurable variables (ovals). A mismatch between available cognitive processing resources and task demands leads to the recruitment of reserve neural resources, which increases the neural supply. It is referred as "attempted compensation". The increase in neural supply may enhance cognitive processing and performance ("successful compensation") or not ("unsuccessful compensation"). Regarding the relationships between measurable variables, dashed arrows 1 and 3 are inverted-U functions (as neural resources or task demands increase, activity/connectivity first increases but eventually declines). Dashed arrow 2 refers to relationships between activities in different brain regions. Dashed arrow 4 is critical for distinguishing between successful compensation and unsuccessful compensation. Finally, dashed arrow 5 refers to the link between brain resources (e.g., PFC volume) and task performance (e.g., executive control). Adapted from Cabeza and Dennis (2013).

The Scaffolding Theory of Aging and Cognition

Park and Reuter-Lorenz (2009) proposed the Scaffolding Theory of Aging and Cognition (STAC, **Figure 21**) as a neurofunctional account detailing the effects of age on cognition. According to this model, older people are affected by varying degrees of *neural challenges* and *functional deterioration*. Neural challenges are age-related structural changes in the brain including cortical thinning and regional atrophy, loss of white matter integrity, and dopamine depletion. Functional deterioration refers to age-related brain activity such as dedifferentiation of ventral-visual and motor areas (Bernard & Seidler 2012; Park et al. 2004; Voss et al. 2008), decreased memory-related recruitment of medial temporal lobe regions (Cabeza et al. 2004; Gutchess et al. 2005) and increased activation of the default mode network (Park & Reuter-Lorenz 2009; Reuter-Lorenz & Park, 2010).The *level of cognitive function* of an individual depends on both the consequences of these above-mentioned negative features but also on a beneficial process, which is referred in the model as *compensatory scaffolding*. Compensatory scaffolding can be considered a form of “positive” plasticity that accompanies aging since it counteracts the adverse effects of neural and functional declines. Examples of compensatory scaffolding include greater activation or additional recruitment of prefrontal brain regions (Davis et al., 2008; Gutchess et al., 2005), as well as bilateral recruitment for tasks normally requiring left or right lateralized activations (Cabeza, 2002; Cappell et al., 2010; Reuter-Lorenz et al., 2000; for a review, see Cabeza & Dennis, 2013). The neurogenesis is also considered in the model as a potential source of positive plasticity that may contribute to compensatory scaffolding (Fuchs & Flügge, 2014; Lövdén et al., 2013). According to this model, scaffolding is seen as a mediator between neural challenge/functional deterioration and the level of cognitive performance. Finally, it is also possible to enhance neural scaffolding activity by some explicit interventions that include various lifestyle activities such as exercise, intellectual engagement, new learning, and cognitive training.

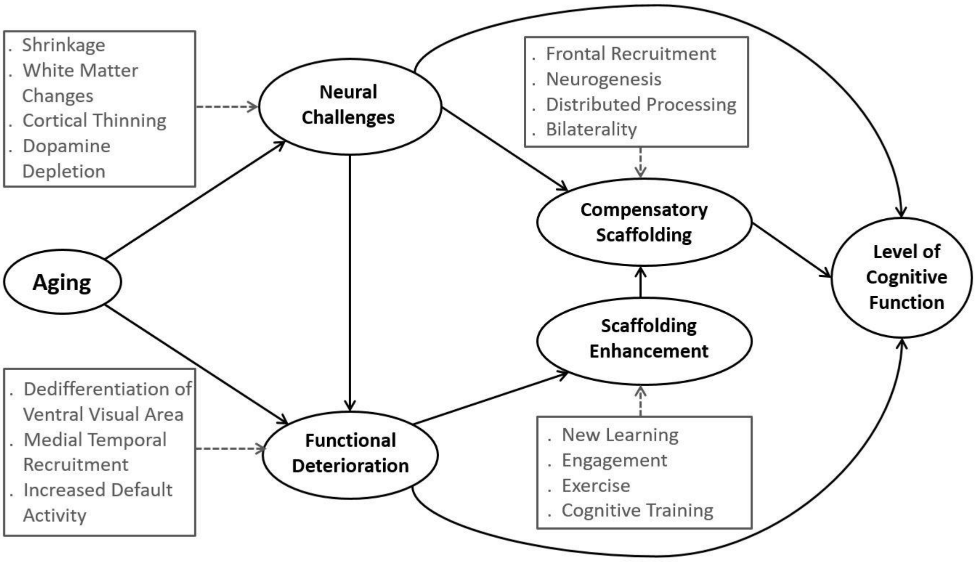

Figure 21. The Scaffolding Theory of Aging and Cognition (STAC). According to this model, older people are affected by varying degrees of neural challenges and functional deterioration. Neural challenges are age-related structural changes while functional deterioration refers to age-related brain activity such as dedifferentiation of ventral-visual and motor areas, decreased recruitment of medial temporal lobe regions, and increased activation of the default mode network. The level of cognitive function of an individual depends on both the consequence of these above-mentioned negative features but also on a beneficial compensatory scaffolding. This latter concept is a form of positive plasticity that counteracts the adverse effects of neural and functional decline. Examples of compensatory scaffolding include greater activation or additional recruitment of prefrontal brain regions as bilateral recruitment for tasks that are normally left or right lateralized. Finally, scaffolding activity can also be enhanced by activities including exercise, intellectual engagement, new learning, as well as cognitive training interventions. Adapted from Park and Reuter-Lorenz (2009).

A feature of this first version of the STAC model (Park & Reuter-Lorenz, 2009) is that it accounted for individual differences in cognitive functioning at one specific time point: the late adulthood. Interestingly, the same authors proposed a new version of the STAC (STAC-r; Reuter-Lorenz & Park, 2014) that integrates new developments in the field such as longitudinal influences on neural structure and function, genetic, health, as well as life-style variables that potentially influence cognition. Thus, the main feature of the revised model is the assumption that not only aging but also life-course experience variables impact the structure and function of the brain, which affect the development of compensatory scaffolding.

As compared to the first version, the STAC-r (**Figure 22**) incorporates two outcome variables: *Rate of Cognitive Change* and *Level of Cognitive Function*. The rate of cognitive change represents the importance of cognitive decline over time, which in turn influences the level of cognitive function. STAC-r also includes two new constructs that represent the combined contributions of life experiences, genetics, and environmental influences, operating to either enhance or deplete brain resources.

The first construct – called *Neural Resource Enrichment* – includes variables that enhance brain structure or function such as intellectual and social activities, the educational level (Amieva et al., 2014), physical fitness (Head et al., 2012), multilinguism (Alladi et al., 2013), or enriched leisure activities (Landau et al., 2012). Neural enrichment could directly enhance or preserve brain structure and function by promoting efficient connectivity, increasing cortical thickness, or increasing synaptic density. Moreover, neural enrichment has also another pathway allowing increasing the capacity for compensatory scaffolding, providing additional protection against age-related neural deficits. Therefore, highly educated older adults with normal cognitive function are expected to support greater neural degradation than less educated older people (Stern, 2002, 2012).

The second construct – *Neural Resource Depletion* – represents negative influences on brain structure, neural function and ultimately cognition. These factors comprise variables such as the APOE-4 gene (Slooter et al., 1998), amyloid and tau deposits (Mielke et al., 2014), vascular risk factors (de Frias et al., 2014), or stress (McEwen, 2007).

In sum, the authors assume there are many beneficial and detrimental factors influencing the brain, some of them are predetermined by genetics whereas others are acquired (exercise, nutrition, intellectual engagement, etc.).

In the original STAC model, brain structure and function were represented by *neural challenge* and *functional deterioration*, both of which were affected only by age-related detrimental influences. By contrast, STAC-r assumes a life-course perspective and proposes the possibility that brain structure and function change bi-directionally, reflecting both positive and negative effects of life-course experiences.

The component called "*Scaffolding Enhancement*" of the first version is referred as "*Intervention*" in the STAC-r. This component represents the incorporation of the potential benefits of formal interventions, enhancing compensatory scaffolding and, in turn, cognitive function. STAC-r also incorporates the possibility that these interventions have a direct influence on brain structure and function. Training could cause changes in neural structure through volumetric increases and network connectivity, or by affecting compensatory mechanisms. For example, some studies have found that post-training improvements in older adults are associated with reduced activity in regions that were overactive in pre-training, suggesting that training can also improve the efficiency of neural function (Heinzel et al., 2014; Meinzer et al., 2013).To engage in complex learning tasks or in enriched activities favors self-initiated processing, which can stimulate plasticity and create neural scaffolds (Lövdén et al., 2010).

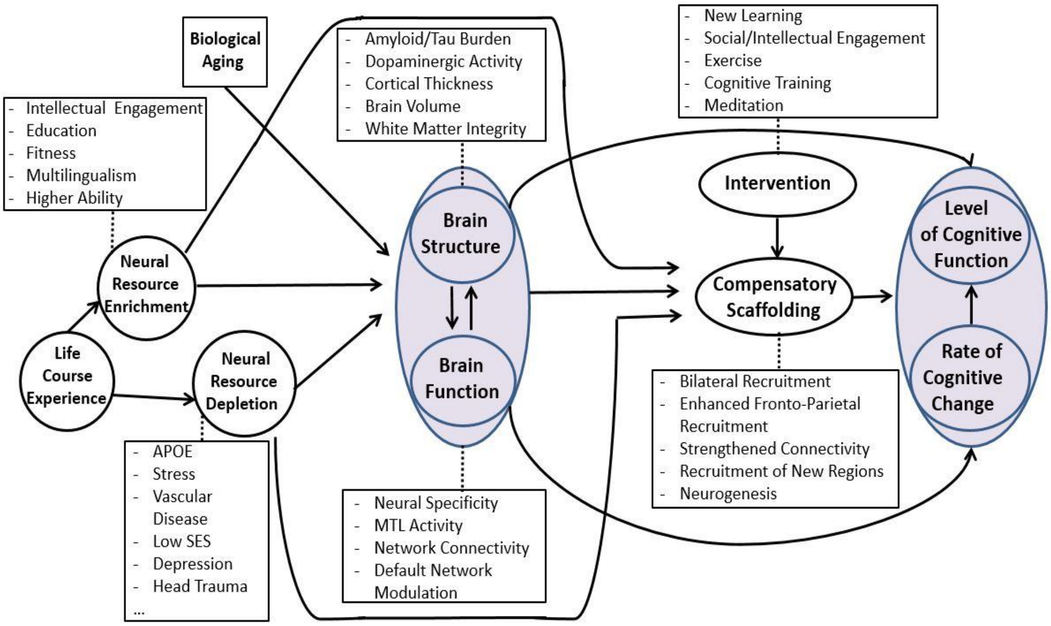

Figure 22. A Conceptual Model of the Scaffolding Theory of Aging and Cognition-revised (STAC-r). Adapted from Reuter-Lorenz and Park (2014). Details are in the text.

Brain Resources, Genetics, and Dopamine

Other interesting theories about cognitive aging emphasize brain resource depletion that can manifest by neuronal death, synaptic loss, but also degradation of the dopaminergic system. These neuronal declines inherent to the process of aging have also been postulated to differ as a function of the genetic background of the individual. I will start by presenting a model focusing on age-related magnification of genetic effects on cognitive performance. Thereafter, I will come back on the inverted U-shaped curve linking DA levels to cognitive performance that was presented in the first part of the introduction (**Chapter 1**) but, in this case, the authors propose to add a genetic influence on the link between DA signaling and performance in normal aging.

The Resource Modulation Hypothesis

Several authors (for example, Lindenberger et al., 2008; Nagel et al., 2008) have postulated that genetic background effects on cognition should be magnified as soon as individuals undergo decreases in their brain resources. These latter comprise neurochemical (e.g., dopaminergic decline), structural (e.g., neuronal loss), as well as functional (e.g., inefficient use of cerebral network) resources. The resource modulation hypothesis claims that decreases in brain resources triggered by normal aging increases the effect of common genetic variations on cognitive performance (Lindenberger et al., 2008). Consequently, genetic polymorphisms should exert more important effects on cognitive functions in aging, as compared to young adulthood. In **Figure 23**, there is a nonlinear relationship linking brain resources and cognitive performances. This means that people possessing optimal brain resources will be characterized by high level performances and that inter-individual differences relying on genetic background will be weak. By contrast, genetic effects are more prone to trigger marked performance difference between individuals when brain resources move away from the optimal level, as it is the case in normal aging.

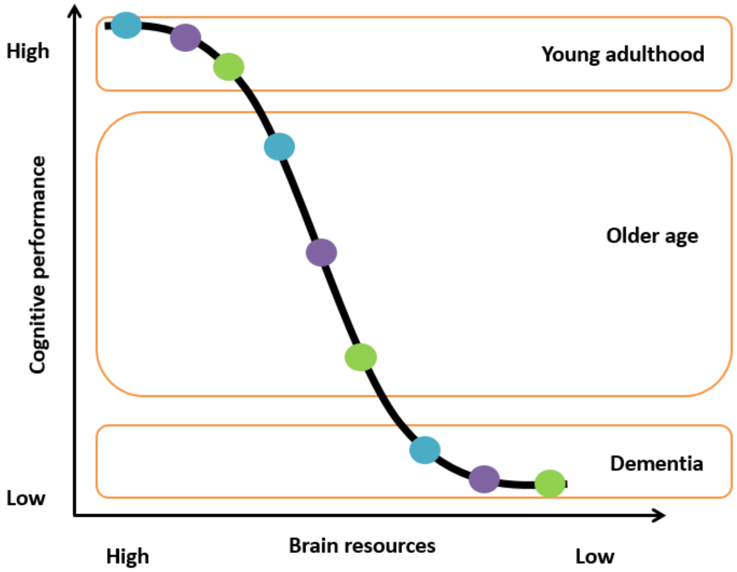

Figure 23. The Resource Modulation Hypothesis. This model posits that losses in chemical and structural brain resources associated with normal aging modulate the effects of common genetic variation on cognitive performance. The colored circles represent three different individuals possessing different genetic backgrounds (different combinations of genetic polymorphisms), from very beneficial background (blue individual) to less beneficial background (green individual) for cognitive task performance. For individuals with optimal brain resources – young people –, cognitive performances are high and relatively homogenous between the different individuals. By contrast, individuals moving from the top of the curve – older people –, are characterized by more varying cognitive performance between individuals as a function of their respective genetic background. Finally, individuals with important depletions in brain resources – such as in dementia – are all very low performing and homogenous. Adapted from Lindenberger et al. (2008).

In addition to brain atrophy, neuronal death, or white matter deficits, the aged brain is also characterized by deficits in dopaminergic transmission in the PFC (Li, 2012, 2013; Li et al., 2001). These deficits include reductions in DA concentration, D1 and D2 receptor density, as well as DA transporter availability (Bäckman et al., 2006; Li et al., 2009) which mediate age-related cognitive deficits such as difficulties in working memory tasks (Braver & Barch, 2002). In agreement with this view, correlations between the DA system and cognitive performance have been shown for a variety of tasks in healthy aging (Bäckman et al., 2000;

Erixon-Lindroth et al., 2005; Volkow et al., 1998). In addition to DA disruption in the PFC, declines in striatal DA availability and transmission may also have an impact on *frontal* processes, given striatal projections towards PFC (Cummings, 1993; Eslinger & Grattan, 1993).

Similarly, Li (2012) suggested that different life stages are associated with different DA levels and thus, with different performance levels during cognitive tasks. While the most favorable period would range between 18 and 30 years, childhood and normal aging are characterized by lower DA levels. This author also proposed that life span affects neuromodulation, such a DA transmission, which may in turn influence genotype effects on cognition. As previously mentioned in the introduction, the relation between DA levels and cognitive performance has been suggested to follow an inverted U-shaped curve (Cools & D'Esposito, 2011). Interestingly, Li (2012) further proposes that this nonlinear function also predicts that genetic effects on cognitive performance would be more important when DA signaling moves away from the optimal level. Non optimal levels are found in childhood, normal aging, following DA antagonist intake, but also in conditions of stress and stimulant consumption (see **Figure 24**; Li et al., 2010; Lindenberger et al., 2008).

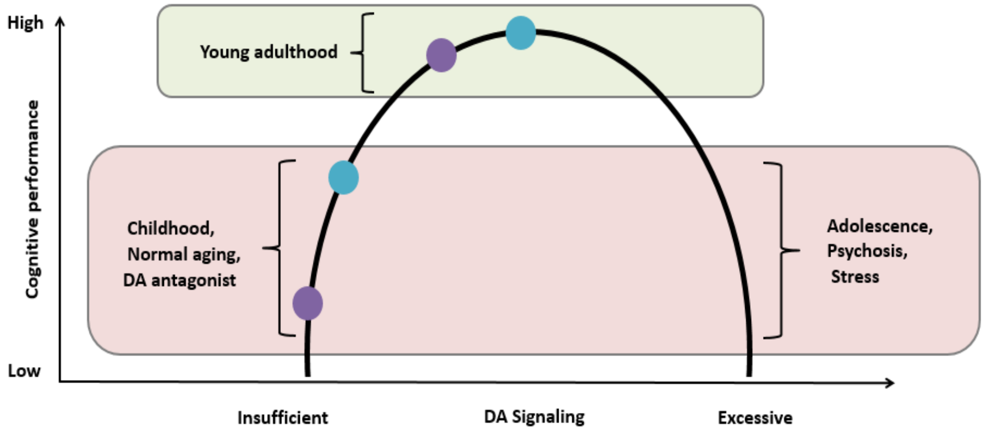

Figure 24. Age and Genetic Effects on the Inverted U-Shaped Curve Linking Dopamine and Performance. This relationship between DA signaling and performance implies that the effects of dopamine-relevant genes may be more evident in life periods or conditions in which DA signaling is insufficient or excessive. Colored circles represent two different individuals possessing different genetic background, from very beneficial allelic variants (blue individual) to non-beneficial variants (purple

individual) for DA signaling. Genetic-related effects on cognitive performance are amplified when individuals move away from the optimal DA signaling level. Adapted from Li (2012).

This model was supported by a study in which the authors administered young and older people with a spatial working memory task (Nagel et al., 2008). The results showed that older individuals with DA-beneficial gene alleles were more efficient in accuracy and response times than older participants with less DA-beneficial allelic variant. It was concluded that genetic effects on cognition were amplified in aging because allele-related differences were only observable in the older group but not in the young one. According to Nagel et al. (2008), normal aging that is associated with DA decline would trigger a shift towards the left side of the inverted U-shaped curve linking DA signaling and cognitive performance. Moreover, individual with less favorable allelic variants for DA system would be characterized by a more important left-sided slide.

These evidence of DA disruption in normal aging is really relevant for this work given the well-recognized implication of the DA system in cognitive fatigue.

Selective Engagement of Cognitive Resources

Hess (2014) proposed a theoretical account characterizing the relationship among aging-related variations in cognitive resources, motivation, and engagement in cognitively demanding activities. According to his framework, normal aging is associated with an *increase in the costs* of cognitive activity (Hess & Ennis, 2012). These costs, in turn, are assumed to influence the motivation to engage in cognitively demanding activities. As a consequence, age-related decreases in cognitive resources will influence the *selection of processes* in which older people will engage. Hess proposed that this motivated selection process is an adaptive function linked to changes in developmental goals associated with specific periods of life. In agreement with this view, the socioemotional selectivity theory (Carstensen et al., 1999) suggests that an increased perception of limited future time in older age results in a focus on emotional wellbeing, meaning that older people are more prone to choose stimuli promoting positive affect (e.g., social partners or activities). Older people seem thus to adjust goal priorities with changing life circumstances, selectively engaging in activities promoting resource conservation and maximizing performance in valued activities.

Therefore, according to this framework, the concept of *self-relevance* (e.g., perceived benefits, concerns, and meaningfulness) has an important influence on cognitive engagement in later life. The author hypothesized that self-related interest of a given task will play a role in determining engagement, and this to a larger extent in older adults than in young or middle-age people. A very nice example comes from an experiment in which older people classically show impairment in reading speed in the presence of distracting text due to a decline in inhibitory function (e.g., Carlson et al., 1995). However, when the passage to be read is rendered relevant to the age group, older adults' reading speed and memory improve (Germain & Hess, 2007). In other words, the inhibitory function of older people is more efficient when personal relevance of the task is increased, this effect being weaker in the young group.

According to Hess (2014), the motivation to engage in activities is determined, in part, by perceptions of the benefits of engagement relative to the costs, referred as *benefit–cost ratios* (BCRs). In this framework, costs represent effort expenditure or investment of mental energy. The individual will not engage in an activity if BCRs fall below his threshold of engagement or if the costs no longer justify expenditure of resources. At any given level of perceived benefit, greater costs will result in lower BCRs. Hence, tasks with low-to-medium perceived benefits have little chance to exceed the threshold of engagement for older adults (**Figure 25**). In other words, for reaching a given threshold of engagement (or level of BCR), older people need much more perceived task benefits than young people. Moreover, adjustments in the threshold of engagement may also occur, with older people exhibiting increases in the criterion (i.e., minimum BCR) as compared to young people. This threshold adjustment would be modulated by intrinsic motivation to engage in cognitively demanding activities as a function of its self-relevance for the individual.

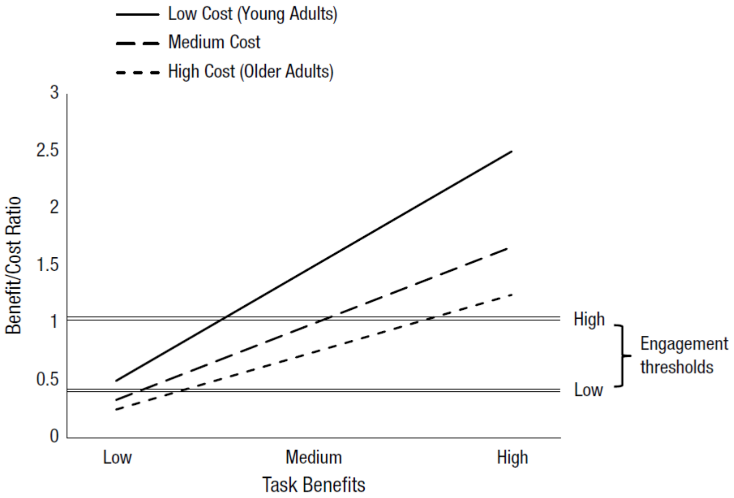

Figure 25. Selective Engagement of Cognitive Resources. This graph represents benefit–cost ratios (BCRs) associated with a task that varies in level of costs (Low, Medium, High) and as a function of the age group. Costs for a same task are assumed to be lower for young than for older people. Resource engagement is more likely for tasks associated with BCRs above the engagement threshold. Two hypothetical engagement thresholds are also represented (High, Low), the High threshold being associated with aging. Increased costs and engagement thresholds (or BCR) in later life result in a reduction of tasks falling above the threshold for engagement as well as increasing levels of discrimination between tasks with high versus low-to-medium benefits. Reprinted with permission from Hess (2014).

Chapter 4: Empirical Studies in Older and Middle-aged People

Empirical Studies in Older People

As mentioned in the previous chapter, it is now well established that normal aging triggers diminished cognitive functioning efficiency (Collette & Salmon, 2014; Crawford et al., 2000; Salthouse et al., 2003; West, 1996; West, 2000). Fatigability in older people has been shown to disrupt the regulation of the inflammatory response following an acute cognitive stress (Lin et al., 2014) and has been linked to conditions like depression (Hayslip et al., 1990) but also to negative health consequences as the individual ages (Avlund et al., 2007). However, very few studies have investigated the process of cognitive fatigue in older ages.

Precursor studies of cognitive fatigue having explored age-related differences are probably those investigating continuous vigilance tasks, such as the well-recognized Mackworth Clock-Test (Mackworth, 1948). As described in **Chapter 1**, this test consists very simply in a pointer traveling the face of a clock at regular steps and including infrequent double steps. The task of the participant is to press a key as accurately and quickly as possible when he detects these unexpected double steps. As a measure of the time spent on the task, attention is expected to decrease. Using this task in a longitudinal and multicohort study, Giambra and Quilter (1998) found that age did not affect the number of hits but that mean RTs increased from middle age (40-49 years) to older age (60-74 years). In a substudy from the previous one, the same team (Giambra et al., 1988) also assessed the strategy used during the task (ranging from “active/conscious involvement in the task” to “passive involvement in the task”) but did not find any difference in strategy between age groups.

The following lines describe the most influential studies in the field which are “truly assessing” cognitive fatigue in older ages. Similar to the young population, studies presented here also rely on either the continuous approach or the probe approach. Sometimes, authors also resort to a combination of these two paradigms, allowing to test both Time-on-Task effects on the loading task as well as the impact of this long-lasting test on probed measurements.

Among the existing studies in older people, Holtzer et al. (2011) administered a variant version of the Attention Networks Test (ANT) to older adults during about 35 minutes and showed that cognitive fatigue impacted the executive attention component while the alerting and the orienting attentional processes were not impaired at all. According to the authors, this finding provides support to theoretical models that consider the frontal basal ganglia pathway as a core substrate of cognitive fatigue (Chaudhuri & Behan, 2000, 2004). This finding in older people is also in agreement with findings in young people according to which top-down control is more likely to be affected by cognitive fatigue while stimulus-driven bottom-up attention would remain unaltered (Boksem et al., 2005).

In 2002, Falkenstein et al. administered young and older people with a 4-hour battery comprising the Go/NoGo paradigm that was presented in the first and in the last time block. The results did not show any Time-on-Task effect on task performance, neither in the young nor in the older group. However, the older group showed a reduced latency of the P3 component linked to the Go trials, which was assumed to represent compensatory processes. By contrast, Wascher and Getzmann (2014) required their participant to perform an inhibition of return task and found higher Time-on-Task effect in the older as compared to the young group. This effect was attested by an increase in time needed to inhibit irrelevant information with time on task, specifically in older people.

According to Wascher et al. (2016), it is worth mentioning that most working activities that require physical and cognitive effort also contain periods in which monotonous cognitive tasks have to be performed. Such periods can be related to the passive task-related fatigue previously presented (May & Baldwin, 2009). Therefore, the authors claimed that age-related effects on passive fatigue should be of central interest because age affects frontal structures that are implicated in motivation to sustain performance in non-demanding situations (Berridge & Robinson, 1998). Wascher et al. (2016) thus created tasks reflecting real workflow while remaining experimentally controlled. Participants had to perform three tasks: a monotonous stimulus-response task (the Simon task), a self-paced cognitive task (the d2-task), and a physical task (moving and sorting boxes of different weights and sizes) in a repetitive sequence for about 4–5 hours. This paradigm was coupled with a mobile EEG continuously recording while participants were freely moving and dealing with the tasks. The results showed that subjective fatigue remained rather stable in younger adults during the entire shift but increased for older adults. However, this subjective fatigue was highly related to the task performed. After the monotonous task, fatigue ratings were substantially increased compared to the physical task and this pattern of results was more pronounced in the young group. Moreover, subjective feelings of demotivation by the monotonous task were observed in the young but not in the older group. This enhanced impact of monotony in young people was also mirrored in behavioral and neurophysiological data. At the end of the shift, accuracy on the monotonous task was lower in young than in older participants. Regarding the EEG recording, young people showed increased alpha activity in this monotonous task, suggesting that younger adults might have switched to a state of attentional withdrawal. By contrast, older people seemed to deal better with monotony and cognitive fatigue markers in this group were more widespread across tasks. In particular, early synchronizations in the EEG might indicate that older adults were far more driven by external signals. Globally, while young people seemed more affected by monotony or passive task-related fatigue with Time-on-Task, older people rather showed decline executive control and processed information in a stimulus-driven manner.

Similarly, Arnau et al. (2017) administered young and older people a cognitive task (Simon task) during 3 hours including breaks of various durations. Performance declined and spectral power in the theta, alpha, and beta range increased as a function of the time spent on the task but there was no significant difference between the two groups. However, EEG recording showed that frontal theta power became larger with Time-on-Task for older compared to young people, which was interpreted as compensatory processes. In young people, there was a saturation in occipital alpha suggesting impaired performance due to the monotony of the task. According to the authors, the absence of behavioral difference between young and older people could be explained by the triggering of two different types of cognitive fatigue in the two groups (May & Baldwin, 2009). Indeed, older participants might suffer more severely from a depletion of cognitive resources due to task demands with increasing Time-on-Task compared to younger participants, which led them to resort to compensatory mechanisms to maintain performance. By contrast, young people experienced cognitive underload due to the monotony of the task. Therefore, compensation and higher motivation in older people *versus* lower motivation in young people may explain the lack of behavioral differences between the two groups.

Very interestingly, Terentjeviene et al. (2018) made young and older men perform a 2-hour Go/NoGo task that was preceded and followed by a large set of measures: anthropometric measurement, cortex excitability (TMS), hand-grip strength, prefrontal cortex activity (fNIRS during 5-minute rest and a switching task), cognitive functions, and self-assessment questionnaires (comprising emotion, mood, and perceived workload). The results evidenced more signs of cognitive fatigue in young as compared to older men. For example, RT length but also intraindividual variability (as measured by the CVRT) of the "Incorrect NoGo" increased with the time spent of the task only in the young group. Also, handgrip strength decreased more in young than in older men after the 2-hour Go/NoGo task. Moreover, even if both groups felt increased subjective fatigue after this long-lasting task, young people experienced more fatigue and effort but also drops of energy and intrinsic motivation as compared to older people. The authors thus concluded that psychological strain during the 2-hour Go/No task was higher for young people than for the elderly, which is consistent with the results of Wascher et al. (2016) as well as Arnau et al. (2017) showing that young people experienced more fatigue from a monotonous cognitive task than older people.

Using a 160-minute cued Stroop task in a sample of older people, Burke et al. (2018) showed preserved accuracy but increased RTs, subjective fatigue, as well as pupil diameter with Time-on-Task. The maintenance of accuracy throughout the task was explained by a speed-accuracy tradeoff since older people are known to favor accuracy at the expense of speed (Salthouse, 1979).

In 2019, Samuel et al. decided to extend to an older population their Stroop-EEG protocol of 2016 that focused only on young people (see Wang et al., 2016 in **Chapter 2**). Thus, they administered a group of 14 young people and a group of 16 older people the same cued Stroop task continuously for about 2 hours[12] in parallel with high-density EEG. Regarding the young group, the authors were particularly interested in determining to what extent neural compensatory mechanisms classically found in older people can be generalized to neural responses of cognitively fatigued young people. Regarding older adults, compensatory mechanisms are engaged at baseline to counteract the deleterious effects of cognitive decline (Davis et al., 2008; Dew et al., 2012). However, if baseline performance is globally lower in older compared to young people, behavioral decreases with long-lasting tasks are not always observable in older people as compared to young people (Arnau et al., 2017; Falkenstein et al., 2002; Philip et al., 1999; Terentjeviene et al., 2018; Wascher et al., 2016). Therefore, the question was: how does the brain respond to cognitive fatigue in older people and is neural

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[12] As the authors themselves recognized, there was a noticeable limitation in their study. Indeed, the cued Stroop task was initially designed to be administered during 3 hours. However, due to technical issues or abandons, they finally administered the task during 160 minutes in the young group but only during 100 minutes in the older group. Therefore, Time-on-Task effects in the two age groups are not really comparable.

compensation the key to explaining the absence of performance deterioration in this group?" As in Wang et al. (2016), two times of interest (TOI) were analyzed: 1) an *early* period (150–300 ms), in which sensory and early attentional processes are active (Atkinson et al., 2003; Weinstein, 1995); and 2) a *late* period (300–1000 ms) in which higher-order attention and conflict-related processing are active (Perlstein et al., 2006; West, 2003). The results in the young group showed that behavioral performance declined with Time-on-Task. Regarding the early component, ERP amplitude decreased in both occipital-temporal and central-frontal regions as a function of the time spent on the task, suggesting progressive impairments of early sensory and attentional discrimination processes. Similarly, ERP in occipital-temporal region during the late period decreased with Time-on-Task. By contrast, ERP in central-frontal regions during the late period increased with time-on-task. Interestingly, the rate of the early ERP amplitude decrease in occipital-temporal region (i.e. posterior decrease) and the rate of the late ERP amplitude increase in central-frontal regions (i.e. anterior increase) were correlated. This posterior decline followed by anterior increase is similar to the PASA compensation pattern observed in prior cognitive aging research (Davis et al., 2008), suggesting that sensory decline can be triggered by cognitive fatigue, and that the frontal compensatory activity can be recruited. Moreover, these rates of ERP changes predicted the rate of change in behavioral performance (CVRT): declining ERPs (impairment) were associated with impaired performances while increasing ERPs (compensation) were associated with the maintenance of task performance. In addition to the PASA pattern, the authors also concluded that young people exhibited the early to late shift activation (ELSA) pattern within the central-frontal region: decline in early neural processing was compensated by increase in late neural processing. Regarding the older group, however, there was no evidence of behavioral impairment (change in RT, error rate, or CVRT increase) with Time-on-Task. This result is in agreement with prior studies showing that older adults are able to maintain performance under cognitive fatigue (Arnau et al., 2017; Falkenstein et al., 2002; Terentjeviene et al., 2018; Wascher et al., 2016). Neurophysiologically, early ERP amplitudes decreased with Time-on-Task, suggesting progressively impaired sensory and early attention-related processing. However, late ERP amplitudes did not change with Time-on-Task, suggesting the absence of compensatory neural activity in the older cohort. Whether this absence of compensatory activity is due to capacity limitations or the lack of necessity to compensate is difficult to ascertain in the current paradigm. Globally, these results suggest that young and older adults coped with cognitive fatigue differently by exhibiting differential responses as a function of Time-on-Task at both the behavioral level and the neural level.

In 2019, Ren et al. moderated the conclusions about the absence of compensatory mechanisms in older people under cognitive fatigue found by the previous study (Samuel et al., 2019). The authors conducted an experiment in which they administered 46 older adults with a letter-location task (dual 1-Back) and the Color-word of the Stroop task during fMRI scanning. An 18-item VAS with items related to mood and energy (e.g. tired, keeping your eyes open is difficult, lively, efficient) was used to assess subjective fatigue before and after MRI acquisitions. The authors decided to divide the total sample into two groups – a low-CF *versus* a high-CF – based on participants' score changes in perceived cognitive fatigue (CF) before and after the MRI scan. The total duration of the fatiguing tasks (30 minutes) were divided into six time blocks of 5 minutes and CVRT was calculated within each time block. Performance changes with Time-on-Task were calculated as the difference between Block 6 and Block 1 with lower scores indicating better cognitive performance. Regarding fMRI connectivity measures, the Posterior-Anterior Shift (PAS) score was calculated as Block 6 (Anterior – Posterior) – Block 1 (Anterior – Posterior), allowing to estimate the amount of shift from posterior to anterior regions with Time-on-Task. The results showed that task performance (CVRT) became impaired with Time-on-Task (Block 6 *versus* Block 1) in the high-CF group as compared to the low-CF group. The interaction between time blocks and groups revealed that decreased connectivity of the cortical-striatal network with Time-on-Task was related to higher perceived cognitive fatigue. Moreover, increased posterior-anterior shift (or increased reliance on the anterior part of the cortico-striatal network) was related to better cognitive performance in older people belonging to the low-CF group, while it was related to worse cognitive performance in the high-CF group. These results thus suggest that the compensatory PASA pattern in older people performing a long-lasting task may only be applicable to older adults without vulnerability to CF.

Empirical Studies in Middle-aged People

Mild cognitive changes can also be observed in middle-aged people (Bielak et al., 2013; Cansino et al., 2015; He et al., 2013; Park et al., 2013; Strozyk & Jentzsch, 2012; Wolkorte et al., 2014) but to a much lesser extent than in older people. Moreover, this 40- to 60-year-old population is fully immersed in active life and has to deal with cognitive challenges every day. Consequently, given their relatively well preserved cognitive resources and their engagement in social and professional life, this population could be expected to resist cognitive fatigue better than older people and in a way similar to young people. However, it would also make sense to predict the opposite. That is, because middle-aged have to deal with many responsibilities and numerous stressors (child caring, job, etc.) every day, they would be potentially at risk to undergo deleterious cognitive fatigue effects. However, up to now, very few studies investigating cognitive fatigue in middle-aged are available in the literature.

Among the few existing studies, de Jong et al. (2018) required young and middle-aged participants to perform a typewriting task and a mouse targeting task during 120 minutes, in combination with EEG recording. The results showed that the average typing speed was lower in middle-aged people than young people but decreased with Time-on-Task in both groups. Moreover, typing speed of the last word of the sentence to be typed did not change with Time-on-Task in young people while it decreased in middle-aged people. Otherwise, young people had diminished typing accuracy (i.e., increase in typing errors) and used the backspace key more often with Time-on-Task as compared to middle-aged people. In this latter group, the percentage of error-corrections was positively associated with the time to complete a sentence, indicating that correcting errors takes time in middle-aged people, while this relation was absent in the young group. Also, error-corrections speed was slower than correct typewriting speed in the young group while it was the opposite in the middle-aged group. Moreover, the P3 amplitude decreased with Time-on-Task, parallel with the increased typing time and errors in the young group, suggesting that task disengagement in this group was linked to diminished typewriting efficiency. In the middle-aged group, there was an opposite trend: an increase in the amplitude of the P3 was associated with an increase in general inter-key interval. From these findings, the authors concluded that cognitive fatigue was more likely to impair the quality of processing in young people while it was more likely to impair processing speed in middle-aged people, suggesting that young people rather favored speed performance while middle-aged people rather acted in an error-aversive manner.

In 2014, Klaassen et al. had a group of 13 young and a group of 16 middle-aged male schoolteachers perform two sessions of a parametric version of the working memory Sternberg task using fMRI: one directly after a control condition (i.e., watching documentary videos or reading magazines) and one directly after a fatiguing condition (i.e., a battery of executive tasks) during 1.5 hour each. Brain activity associated with the Sternberg task was grouped into low load (3 + 4 letter string) and high load (5 + 6 letter string). Subjective rating scales – the short version of the Profile of Mood States (Wald & Mellenbergh, 1990) as well as the NASA Task Load Index (Hart & Staveland, 1988) targeting fatigue and effort – were completed upon arrival (time 0), between the control or fatigue condition and the fMRI session (time 1), and after the scanning session (time 2). The results showed that there were more errors during six letter trials than during five letter trials and RT increased significantly between four and five letter trials. Regarding age group effects, there was no group differences on the number of errors, but RT were globally slower in middle-aged than in young participants. Regarding the condition effect, the fatiguing condition triggered more errors than the control condition but there was no difference between the two conditions on RT. Also, perceived fatigue and effort ratings were higher in the fatigue than the control condition at time 1 and time 2. Regarding brain activation, there were two main findings. Firstly, middle-aged people showed greater activation during the Sternberg encoding phase in the fronto-parietal network – the left DLPFC and left superior parietal cortex – than young people, this result being independent from the cognitive load (low *versus* high) or the condition (control *versus* fatiguing). According to the CRUNCH model (Reuter-Lorenz & Cappell, 2008), age-related over-activations, particularly in PFC regions, have typically been interpreted as functional compensation in response to cognitive decline, when it allows equivalent performance between age groups. As it was the case in this study, the authors tentatively suggested that this global fronto-parietal overactivation in middle-aged as compared to young may have fulfilled a compensatory role. It could be surprising that this overactivation was not modulated by the cognitive load or the condition. However, the authors interpreted this as a plateauing of load-dependent activation after about 4 or 5 items (Cappell et al., 2010; Nagel et al., 2009; Schneider-Garces et al., 2010), which would indicate compensatory activation was reached in these brain areas.

Secondly, the results also showed that load-dependent activation in dorsomedial prefrontal cortex (DMPFC) during the encoding phase was more elevated in middle-aged people as compared to young people in the control condition. By contrast, this load-dependent DMPFC activation did not differ between the groups in the fatigue condition. These results can be explained by the fact that middle-aged people reduced their load-dependent DMPFC activity in the fatigue condition as compared to the control condition while young people showed an increase in this load-dependent DMPFC activity from the control to the fatigue condition. According to the CRUNCH model (Reuter-Lorenz & Cappell, 2008), aging people show a higher recruitment of certain cerebral regions at a lower level of the task as compared to young people, which would allow them to achieve a similar performance level to that of young people. However, once a certain degree in cognitive demands of the task is exceeded, the aged brain is not able to compensate anymore – the CRUNCH threshold is reached – and performances of aged people become weaker than that of young people. Therefore, Klaassen et al. (2014) proposed that middle-aged people resort to compensatory mechanisms more quickly than young people but also that they reach their CRUNCH point – reflecting the exhaustion in neuronal resources – much more rapidly.

In 2016, Klaassen et al. carried out a relatively similar study to that of 2014. They required a group of 14 young and a group of 15 middle-aged male schoolteachers to perform a memory encoding-recognition task using fMRI after a control and a fatiguing task on two separate weekends. In this *subsequent memory paradigm* (Paller & Wagner, 2002), items presented during the encoding phase are classified according to performance on a subsequent recognition task. Cerebral activation to items that were successfully remembered was subtracted from activation to items that were forgotten in each participant as first-level contrasts and entered into second-level analyses consisting in a two (control *versus* fatigue) by two (young *versus* middle-aged) full factorial model. The results showed that perceived fatigue ratings were higher following the fatigue than the control condition at time 1 and at time 2 but did not differ between young and middle-aged people. Regarding RTs, responses to subsequently recognized words were slower than responses to subsequently forgotten words, suggesting that the encoding processes benefitted from more prolonged study of word stimuli. There was no effect of age group or condition on recognition performance nor on confidence levels attributed to the recognition. Activation related to successful encoding was found in the ACC in both young and middle-aged adults. However, middle-aged males showed greater successful encoding activation than young males in the left DMPFC, DLPFC and OFC. Also, there was a greater activation in the right ACC in the control than in the fatigue condition independently of age groups, suggesting this area plays a role in the experience of cognitive fatigue that is not restricted to the aging brain.

Moreover, there was a trend for an interaction between age group and fatigue condition in the left ACC: activation in this area was greater in middle-aged than young adults in the control condition. In light of the CRUNCH hypothesis (Reuter-Lorenz & Cappell, 2008), this may indicate neural compensation to maintain performance at an equivalent level. Indeed, it can be hypothesized that middle-aged teachers recruited more neural resources than younger teachers in relation to similar levels of cognitive performance. Furthermore, middle-aged adults showed significantly reduced activation in the fatigue compared to the control condition, whereas no significant activation change was evident in young adults. According to Klaassen et al. (2016), this reduction in response to the fatigue induction may indicate that, due to increased compensation, a so-called resource ceiling is reached earlier in the middle-aged teachers compared to the young. However, according to the CRUNCH model, decrease in brain activation due to the reach of the compensatory limit should be accompanied by a decline in performance, which was not observed. These findings should thus be interpreted with caution. Finally, the authors proposed that changes in ACC activity from the control to the fatigue condition could also correspond to a difference in effort.

Intermediate Summary

From this presentation of studies, it appears that older people resist relatively well to cognitive fatigue (no important decrease in performance) as compared to young people. It has been proposed that they are more motivated and less prone to boredom triggered by the long-lasting and repetitive nature of most cognitive fatigue paradigms. At the cerebral level, some studies have shown compensatory mechanisms in older people (Arnau et al., 2017; Wascher et al., 2016) but not all (Samuel et al., 2019). Regarding middle-aged, very few studies exist and they seem to show a faster resort to compensatory resources than young people (Klaassen et al., 2014; Klaassen et al., 2016). However, while studies focusing on older people used a Time-on-Task approach, those focusing on middle-aged people mostly used a Probe approach. More crucially, no study has ever assessed cognitive fatigue effects in middle-aged and older people in a same protocol. Therefore, it seemed crucial to carry out studies investigating young, middle-aged, and older people inside a same framework.

In this sense, the present Thesis work assessed these three age groups through three studies using the Time-on-Task approach (**Study 1** and **Study 2**) as well as the Probe approach (**Study 3**). The two first studies will allow to determine whether Time-on-Task differentially affect behavioral performance as a function of age (**Study 1**) but also whether allowing people to take breaks during the task relieves performance in the same way for the three age groups (**Study 2**). The third study (**Study 3**) will enable to investigate whether cerebral activity after having performed a fatiguing task, relatively to a control one, vary as a function of age and working memory load.

Experimental Part

Objectives and Hypotheses

Nowadays, human beings are increasingly cognitively solicited until a relatively advanced age. Several studies conclude to an important impact of cognitive fatigue on behavioral performances (e.g., slowdown in RT, increased errors) but also on task-related cerebral networks. However, based on the set of models and studies presented in the Theoretical Introduction, it is obvious that middle-aged as well as older populations have scarcely been the focus of thorough studies bearing on cognitive fatigue. Investigating cognitive fatigue as a function of age is crucial given the increasing retirement age and that aging people are also characterized by diminished cognitive functioning efficiency (Collette & Salmon, 2014; Crawford et al., 2000; Salthouse et al., 2003; West, 1996, 2000). Indeed, cognitive fatigue is a prevalent cause of accidents in everyday life (Dinges, 1995; Shen et al., 2008) but also in the workplace (McCormick et al., 2012) and can lead to tragic consequences in certain professions such as airplane pilots (Bartlett, 1943), car-train drivers (Brown, 1994; Campagne et al., 2004; Kecklund & Akerstedt, 1993; Torsvall & Akerstedt, 1987), firefighters (Aisbett & Nichols, 2007; Aisbett et al., 2012; Ferguson et al., 2016), as well as intensive care unit physicians (Maltese et al., 2016). From a medical point of view, repetitive cognitive fatigue can sometimes turn into burnout (Maslach et al., 2001), triggering costs for the public health care system but also for the employers (Ricci et al., 2007). Understanding how cognitive fatigue affects aging people may help prevent its negative consequences. From a theoretical point of view, investigating cognitive fatigue with advancing age will help understand whether compensatory mechanisms are implemented to counteract fatigue effects or whether some age groups reach their limit of cerebral compensation.

Consequently, the main objective of this Thesis work was to investigate the impact of cognitive fatigue on behavioral tasks as well as on cerebral activity, systematically in young, middle-aged, and older samples.

Briefly, **Study 1** aimed at assessing the changes in RTs (more precisely, the ex-Gaussian parameters; see below) during an uninterrupted long-lasting Stroop task as a function of the time spent on the task and the three age groups. **Study 2** was globally based on the same design as **Study 1** but with the new objective of investigating the hypothesized beneficial influence of short breaks on performance. Therefore, participants had also to perform a long-lasting Stroop task but were allocated either to a “No Break” condition in which they had to perform the Stroop task in an uninterrupted way (as in **Study 1**) or to a “Break” condition in which they were able to take 5-minute breaks during the task. Finally, **Study 3** assessed the impact of a cognitively fatiguing condition *versus* a control condition on cerebral activity during an N-Back task (Kirchner, 1958) performed in an fMRI scanner, again in young, middle-aged, and older participants. To make a link between theory and practice, **Study 1** and **Study 2** belong to the *Time-on-Task approach* since RT data were analyzed as a function of the time blocks of the task itself (i.e., the Stroop task) while **Study 3** belongs to the *Probe approach* given it assessed the impact of an initial task (fatiguing or control) on a subsequent task (i.e., the N-Bask task).

In the following lines, the experimental approach of **Study 1** will be fully developed in order to help the reader grasp the rationale behind the ex-Gaussian approach and the reasons why this approach is more appropriate to investigate RT data as compared to mean and median of RT. **Study 2** will be presented to a lesser extent because it is based on the same design as **Study 1** except for the addition of a new condition (Break; No Break). Afterwards, **Study 3** and its hypotheses will be developed.

In **Study 1**, a long-lasting 160-minute Stroop task comprising three items types (Congruent, Incongruent, and Neutral) was administrated without interruption to young, middle-aged, and older participants. In the literature, cognitive fatigue has been associated with decreased behavioral performance with Time-on-Task. However, if young people have been found to show reduced accuracy as well as increased RTs, performance patterns seem different in middle-aged and older people. From a behavioral point of view, middle-aged people are more consistently found to preserve accuracy at the expense of speed (de Jong et al., 2018; Wolkorte et al., 2014). Similarly, older people performing a 160-minute Stroop task have already been found to have preserved accuracy but slowed speed (Burke et al., 2018), what the authors explained by a speed-accuracy tradeoff in the favor of accuracy in older people (Salthouse, 1979). Therefore, we decided to capitalize on RT data in order to compare our groups on a measure that is sensitive to the three age populations. However, the question we were asking at the beginning of this Thesis work was the following: *What best represents RT data?*

As Wang et al. (2014) mentioned, studies investigating cognitive fatigue often use a well-established procedure consisting in comparing the mean RT between the different time blocks of a long-lasting fatiguing task (such as a 160-minute Stroop). However, reaction time data are rarely normally distributed but instead tend to be positively skewed, meaning that they show a right-tailed asymmetry representing extreme RTs made by the participant (Heathcote et al., 1991).Therefore, the classical use of the mean (or median) of RT would lead to erroneous conclusions because central tendency measures are only useful for symmetrical distributions. Likewise, in some studies, individuals' RTs are ranked from the fastest to the slowest and then grouped into separate RT bins (e.g., 10 bins containing each 10% of RTs) in which mean or median RTs are calculated. This type of procedure is methodologically limited for several reasons. The first issue is that several means or medians are extracted from only one distribution. Secondly, there is a higher risk to get biased estimates since each mean or median is calculated from only 10% of the distribution. A third issue related to this bin approach in the context of cognitive fatigue is to consider only the slowest 10% of RTs (the tenth bin) as the outcome of interest. This procedure would be meaningful if we were able to ensure that cognitive fatigue is a discreet process that is not present on 90% of RTs but is restricted to RTs belonging to the last bin. By contrast, if we consider cognitive fatigue as a continuous phenomenon, it is likely that some previous bins (e.g., bins 7 to 9) already contain slowed RTs (Schmiedek et al., 2007).

Given all these reasons, it has been proposed that a distributional analysis is the most appropriate way to describe RT data because it allows to extract parameters from the entire distribution (Heathcote et al., 1991). Among the various theoretical mathematical models that can be used to describe RT distributions, the ex-Gaussian distribution has proven to fit RT data very well (Dawson, 1988; Heathcote et al., 1991; Hohle, 1965, Lacouture & Cousineau, 2008; Luce, 1986; Ratcliff & Murdock, 1976; Schmiedek et al., 2007). The ex-Gaussian distribution is the convolution of the Gaussian and exponential distributions (Burbeck & Luce, 1982; Luce, 1986) and is characterized by three parameters: μ and σ are respectively the mean and the standard deviation of the Gaussian component and τ is the mean of the exponential component. More concretely, a change in μ reflects a shift in the RT distribution while a change in τ represents a change in the thickness of the tail of the distribution – the density of extreme RTs made by the participant (Schmiedek et al., 2007; see red-colored area under the curve in **Figure 27**). The sum of μ and τ is equal to the mean RT. In other words, μ represents the mean of the distribution that has been cleaned from its extreme values. Therefore, considering the classic mean RT as the main outcome can be misleading because an increase in τ may be counteracted by a decrease in μ, triggering a null effect on the resulting mean RT. Likewise, it is possible that two different conditions lead to the same value of mean RT even if they have two different distributional shapes (Balota et al., 2008; Spieler et al., 1996; Tse et al., 2010). These properties further support the resort to distributional analyses, particularly in the context of cognitive fatigue in which extreme reaction times are interesting to catch, rather than means and medians. **Figure 27** represents an example of probability density function (PDF) of the ex-Gaussian distribution that was fitted to an individual RT distribution in a single participant.

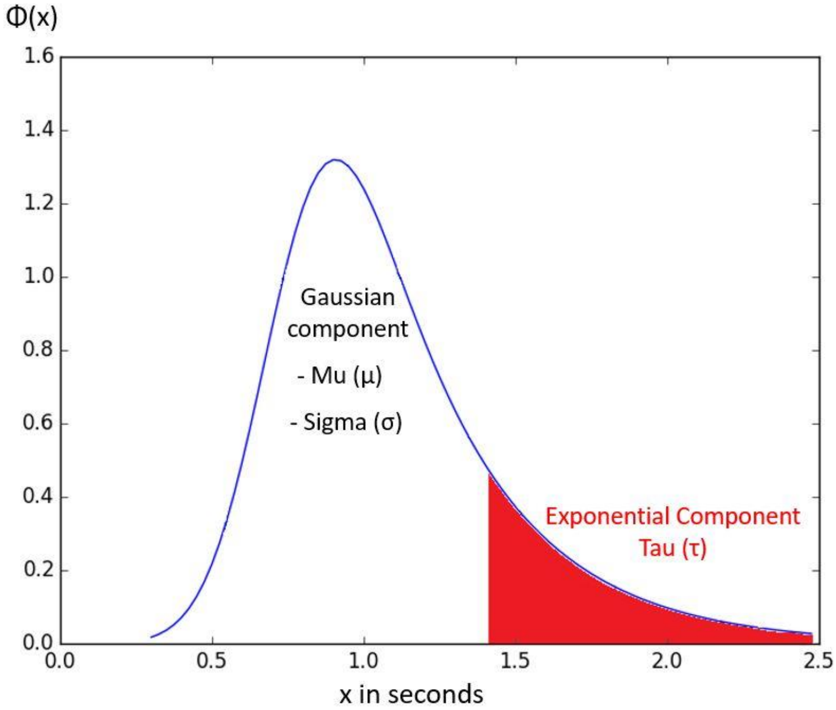

Figure 27. Probability Density Function (Φ(x)) of the Ex-Gaussian Function. X represents RT data limited to 2.5 seconds by trial in our Stroop task. The Gaussian component is characterized by μ and σ while the exponential component is represented by τ.

The area under the curve of a PDF defines the density of the function in a specific range. Finding the parameter values of a probability function that best represents the distribution of empirical data is sometimes trivial. For example, regarding the Gaussian function, the algebraic mean and standard deviation of the empirical data are the most accurate estimates of the mean and standard deviation of the best-fitting Gaussian function. However, the task of getting the best estimations of the parameter values can be more complex (Lacouture & Cousineau, 2008).

To paraphrase Lacouture and Cousineau (2008), to find the values of a probability function that best represent the ex-Gaussian function, an iterative approach known as *maximum likelihood estimation* allows the best-fitting parameters to be estimated. Given a data set and a probability density function with specific parameter values, the likelihood value (LogL criterion) provides an indication of the goodness of fit between the data and the function. To find the parameter values that correspond to a minimum of the *minus LogL criterion*, a search of the parameter space is required. Systematically trying all possible values would be time consuming. This is particularly the case for functions comprising several parameters defining a multi-dimensional space (Lacouture & Cousineau, 2008). To solve this problem, algorithms such as the *Simplex* method that allow to find a minimum of a multi-parameter function have been implemented (Cousineau et al., 2004; Lacouture & Cousineau, 2008). Regarding our **Study 1**, we decided to use an algorithm based on the simplex method described by Nelder and Mead (1965) coupled with a greedy approach. Our algorithm is available on osf.io/8d7hb (see **Supplementary Materials** of **Study 1** for further details).

A direct relation between the ex-Gaussian parameters and functional cognitive processes is not easy to establish. However, RTs are classically thought to result from two different components (Hohle, 1965; Luce, 1986): the time to make a decision about the response – the *decision component* – and the time to physically make the response – the *transduction component*. As mentioned in Dawson (1988), reaction times allocated to the transduction component are believed to be normally distributed (with a mean of μ and a standard deviation of σ), while reaction times allocated to the decision component are assumed to be exponentially distributed (with a mean of τ). As a consequence, a distribution of reaction times following the ex-Gaussian function would be able to capture both transduction and control-decision processes (Lacouture & Cousineau, 2008).

Beyond this *transdution versus decision* distinction, Inzlicht and Schmeichel (2012) have proposed that mean RTs can be divided into motivational and executive control processes when the individual is ego-depleted (Muraven & Baumeister, 2000). In that context, τ parameter has been linked to higher level executive control processes (Brewer, 2011; Schmiedek et al., 2007; Unsworth et al., 2010) while μ has been associated with motivational processes (Bresin et al., 2011).

Therefore, the resort to the ex-Gaussian approach is a promising method to more precisely catch which component of the RT distribution is affected by cognitive fatigue as induced by our Time-on-Task paradigm. Will cognitive fatigue trigger a right-sided move of the entire curve or, rather, will it increase the number of extreme RTs made by the participant? The ex-Gaussian approach may also help disentangle which cognitive processes are more likely to be affected by Time-on-Task. Indeed, it is possible to distinguish between changes in the transduction component and motivational aspects of the RTs *versus* changes in the decision component and executive control processes, which is not possible when using the simple mean and median of RT.

Relevant to our study, Wang et al. (2014) assessed the changes in the ex-Gaussian parameters in young people using a modified version of a computerized Stroop task (Cohen et al., 1999) during 3 hours and found a significant increase in τ, while μ and σ were not found to change with Time-on-Task. However, up to now, no study has ever applied the ex-Gaussian approach to discriminate between age groups in the context of cognitive fatigue.

In **Study 1**, we thus aimed at investigating the effect of cognitive fatigue as induced by Time-on-Task on the ex-Gaussian parameters in three age groups (young, middle-aged, and older). The 160-minute Stroop duration was artificially divided into four successive time blocks of forty minutes in which the ex-Gaussian parameters were extracted for each individual RT distribution and for each item types (Congruent, Incongruent, Neutral).

Since older people basically experience cognitive decline compared to young people, we assumed that a greater fatigue effect induced by our long-lasting task would be observed in this population. However, as the older age group seems to resist cognitive fatigue relatively well as compared to young people (Arnau et al., 2017; Falkenstein et al., 2002; Philip et al., 1999; Samuel et al., 2019; Terentjeviene et al., 2018; Wascher et al., 2016), difficulties could be observed only on the most resource-demanding Incongruent items in both young and older people. These difficulties should be observed to a larger extent in older than young people due to baseline cognitive decline in older people.

Regarding middle-aged people, a hypothesis was more difficult to establish given the very few existing studies. However, as this population shows relatively well preserved cognitive resources and is able to deal with cognitive challenges every day, we hypothesized middle-aged to be able to resist cognitive fatigue in a similar way to young people, namely they would show increase in τ with Time-on-Task only on Incongruent items, but the installment of cognitive fatigue could occur earlier than in young people.

From the past to now, fatigue induced by Time-on-Task has been associated with the energy *depletion hypothesis* according to which people become fatigued because they possess a limited energy-resource supply that is depleted after a period of work (Hockey, 2013). Interestingly, rest breaks have been proposed to decrease fatigue by enabling the organism to restore its exhausted energy levels by temporarily disengaging from work or task demands (Meijman & Mulder, 1998). Therefore, **Study 2** aimed at investigating the influence of breaks on task-performance and subjective feelings during a long-lasting task. The same 160-minute Stroop task was administered to young, middle-aged, and older people. However, participants were allocated either to a Breaks condition or a NoBreak condition. This latter one was exactly the same as in **Study 1**. In the Breaks condition, participants were allowed to take a 5-minute break every forty minutes. As in **Study 1**, the ex-Gaussian function was fitted to each individual's RT distribution in each block for each item type. Anticipating on the results, **Study 1** only shows a significant Time-on-Task effect (i.e., block effect) on τ but not μ and σ. Therefore, analyzes for **Study 2** were restricted to τ.

As for **Study 1**, we predict that τ should significantly increase with Time-on-Task (Wang et al., 2014). Also as in **Study 1**, we expected a Group by Time-on-Task by Item interaction on τ, with τ increasing particularly on Incongruent items (i.e., the most demanding items) in all age groups but quicker in middle-aged than young and to a larger extent in older than in young people.

More relevant to this study, we predict that the Breaks condition would be associated with smaller τ values than the NoBreak condition. More crucially, if rest breaks are beneficial for cognitive performance and relieve fatigue (Finkbeiner et al., 2016; Meijman & Mulder, 1998), we should observe a Condition by Time-on-Task interaction showing τ increase with time in the NoBreak condition but not in the Breaks condition. Given age has rarely been a variable of interest in break studies, we tentatively propose that the three age groups should benefice from breaks and show τ invariance with Time-on-Task in the Breaks condition.

In **Study 3**, young, middle-aged, and older participants were allocated either to a control condition in which they were watching non-demanding videos, or to a fatigue condition in which they performed a long-lasting Stroop task (during 100 minutes for young and 80 minutes for middle-aged and older). Afterwards, all participants were required to perform an N-Back task with three working memory loads (1-Back, 2-Back, 3-Back) during fMRI acquisition. In this study, the 1-Back load serves as a baseline allowing to assess brain activity related to the 2-Back (2-Back > 1-Back) and to the 3-Back (3-Back > 1-Back) loads.

Young people classically recruit fronto-parietal areas during working memory tasks (Collette & Van der Linden, 2002; D'Esposito, 2007; Jonides et al., 1997; Jonides et al., 1993; Miller & Cohen, 2001; Owen et al., 2005), increase cerebral activity as a function of the working memory load (Braver et al., 1997; Jonides et al., 1997; Nyberg et al., 2009; Rypma et al., 1999) and modulate fronto-parietal activity in situations of cognitive fatigue (Coull et al., 1996; Lim et al., 2016; Lim et al., 2010; Nakagawa et al., 2013; Paus et al., 1997). Therefore we suggest fronto-parietal activity will be higher in young people in the fatigue condition as compared to young people in the control condition for the 2-Back as well as for the 3-Back loads.

Hypotheses regarding middle-aged and older groups will be stated based on the CRUNCH hypothesis (Reuter-Lorenz & Cappell, 2008) presented in **Chapter 3**. As a reminder, the CRUNCH hypothesis posits that aging people show a higher recruitment of neural resources at a lower level of task demands as compared to young people, which allows them to achieve a similar performance level to that of young people. However, as task demands increase, the resource ceiling is more likely to be reached because the aging brain is not able to compensate anymore. In this case, cerebral activity becomes weaker than that of young people and performance starts to decrease. Given middle-age people could be considered an intermediate age with more preserved cerebral resources, we expect middle-aged people to show higher fronto-parietal activity in the fatigue as compared to control condition for the 2-Back load relatively to the same contrast in young people and this should be accompanied by similar performance in the fatigue and the control condition (compensatory response). However, we predict a reduced activity in the fatiguing condition as compared to the control condition for the more resource-demanding 3-Back load relatively to the same contrast in young people, with reduced performance in the fatigue compared to the control condition (no compensation).

Regarding older people, predictions are less straightforward as this age group has been shown to resist cognitive fatigue relatively well as compared to young people (Arnau et al., 2017; Falkenstein et al., 2002; Philip et al., 1999; Samuel et al., 2019; Terentjeviene et al., 2018; Wascher et al., 2016). We predict they should show a less marked difference in cerebral activity between control and fatigue condition for the 2-Back load relative to the same contrast in young people, and this should be accompanied by similar performance in fatigue and control conditions (no need to compensate). However, given their more impaired cerebral resources and vulnerability to higher cognitive load (CRUNCH hypothesis; Reuter-Lorenz & Cappell, 2008), we expect a reduced difference in activity between the fatiguing condition and the control condition for the 3-Back load relatively to the same contrast in young people but at the expense of performance in both fatigue and control conditions.

General Discussion

Nowadays lifestyles, constantly soliciting human cognitive functions, have progressively turned cognitive fatigue into a pervasive symptom, even in the healthy population. Unfortunately, in certain cases, cognitive fatigue has revealed to be the cause of accidents in everyday life (Dinges, 1995; Shen et al., 2008) but also in the workplace (McCormick et al., 2012). It seemed therefore crucial to study cognitive fatigue, both at the behavioral as well as at the cerebral level. Cognitive fatigue can arise from performing an uninterrupted long-lasting task but can also have after-effects on a subsequent task. It is why we decided to investigate this topic thanks to both the Time-on-Task (behavioral studies) and the Probe approaches (fMRI study).

In addition, today's societies are characterized by increased life expectancy, resulting in people staying at work until a relatively advanced age. Studying how cognitive fatigue influences behavioral efficiency as well as cerebral activity with advanced age seemed therefore of great relevance and was the main objective of the Thesis work. Given the elderly are recognized to show baseline cognitive declines (Collette & Salmon, 2014; Crawford et al., 2000; Salthouse et al., 2003; West, 1996, 2000), there were reasons to believe that cognitive fatigue may also impact this population.

To paraphrase Lachman (2004), situated *somewhere in between younger and older people*, middle-aged individuals have poorly been the focus of research studies, probably because of the difficulty acceding to this population. Otherwise, midlife has been postulated as the most challenging life period (Lachman, 2004). Indeed, it is the time when people have to deal and arrange at best many spheres of their lives: from caring for children and sometimes for parents, being efficient at work, keeping a social life, to everyday house duties.

This general discussion will recall the main results of the three studies, confront our findings with the main models of cognitive fatigue, and propose future perspectives. Given **Study 1** and **Study 2** were behavioral studies based on the Time-on-Task approach and shared the same experimental protocol except for the new condition in **Study 2**, they will be discussed together. **Study 3** was an fMRI study based on the Probe approach and will be discussed separately afterwards.

Principle Results from Study 1 and Study 2

In **Study 1,** we found a dissociated pattern of age effect and Time-on-Task effect on the ex-Gaussian parameters. While age had a significant effect on μ, Time-on-Task significantly led to increase in τ, representing an increase in extreme RTs made by the participants. Reaction times have been proposed to result from two successive components: the time to make a decision about the response and the time to implement the motor-transduction components of the response (Hohle, 1965; Luce, 1986). Interestingly, the ex-Gaussian parameters have also been linked to different functional cognitive processes (Dawson, 1968; Lacouture & Cousineau, 2008): μ would represent the time to perform the motor component of the response (in short, the motor speed) while τ would represent the time dedicated to the decision process (in short, the decision speed). Our first results thus suggested that age is more likely to negatively influence motor speed but not decision speed, which is in agreement with previous studies (Eckert et al., 2010; Falkenstein et al., 2006; Roggeveen et al., 2007; Yordanova et al., 2004). By contrast, Time-on-Task is more prone to alter decision speed but not motor speed. This result was in line with Wang et al. (2014) who also found Time-on-Task influence on τ but not μ in a sample of young people. This result is also in agreement with studies linking τ to executive control processes (Brewer, 2011; Unsworth et al., 2010). This pattern of results seems also logical regarding cognitive fatigue studies in general. Indeed, most studies have linked cognitive fatigue to decreased accuracy and/or increased RTs particularly in task requiring executive functions like inhibition (Kato et al., 2009), task switching (Lorist et al., 2009), working memory updating (Hopstaken et al., 2015a, 2015b; Hopstaken et al., 2016), planning and preparation (Lorist, 2008; Lorist et al., 2000; van der Linden et al., 2003), or action monitoring (Boksem et al., 2006; Lorist et al., 2005).

Based on results from **Study 1**, statistical analyses of **Study 2** – which were dedicated to the investigation of breaks as candidates to relieve cognitive fatigue – only focused on the τ parameter. As a reminder, **Study 2** comprised participants from **Study 1** to form the NoBreak condition and we recruited new participants to compose the Breaks condition, which were matched as much as possible to participants of the first study on demographic data.

Study 2 revealed that both young and middle-aged people showed Time-on-Task effect on τ, while it was not the case for the older group (similar results in middle-aged and older but not in young participants were found in **Study 1**). Performance declines or RTs increases during a long-lasting cognitive task have been consistently shown in young people (Boksem et al., 2005, 2006; Hopstaken et al., 2015a, 2015b; Hopstaken, 2016; Kato et al., 2009; Lorist, 2008; Lorist et al., 2009; Lorist et al., 2005; Lorist et al., 2000; van der Linden et al., 2003). Regarding the middle-aged population, studies directly targeting cognitive fatigue are scarce, making it more difficult to discuss our data. In 2018, de Jong et al. found decreased speed with Time-on-Task in middle-aged people performing a 120-minute typewriting task. From a cerebral point of view, Klaassen et al. (2014; Klaassen et al., 2016) found evidence of a faster reach of cerebral compensatory threshold (CRUNCH hypothesis; Reuter-Lorenz & Cappell, 2008) in their middle-aged group relatively to their young group. Our findings thus seem in agreement with the existing literature. Older people have not systematically been reported to suffer from cognitive fatigue protocols more than young people, which has been attributed to a better resistance to task monotony than young people (Arnau et al. 2017; Falkenstein et al., 2002; Philip et al., 1999; Terentjeviene et al., 2018; Wascher et al., 2016). Accordingly, our results showed τ invariance with Time-on-Task in the older group (as in **Study 1**).

How to Explain our Results with Cognitive Fatigue Models

Cognitive Fatigue as a Combination of Overload and Underload?

Somewhat influenced by the nineteenth century industrialization context, cognitive fatigue has long been postulated as the result of energy depletion, giving rise to widespread expressions like “I’m depleted” or “I run out of energy”. According to this view, people become fatigued after a long-lasting time performing a work because their limited energy diminishes along the task, until a state of depletion. In agreement with the energy depletion hypothesis, the “overload theory” (Grier et al., 2003; Helton & Russell, 2011; Helton & Warm, 2008) attributes Time-on-Task declines to a depletion of resources due to high task demands or high workload. By contrast, the “underload theory” (Pattyn et al., 2008; Smallwood & Schooler, 2006) posits that fatigue-related decreases in performance are due to task disengagement or attentional withdrawal because of the monotonous or boring nature of the task. As presented in **Chapter 1**, more recent studies suggest that either cognitive overload or cognitive underload are likely to trigger Time-on-Task cognitive fatigue (Boksem et al., 2006; Boksem & Tops, 2008; May & Baldwin, 2009; Saxby et al., 2008).

Study 2 showed that breaks seemed beneficial for maintaining performance and stabilizing feelings of sleepiness, motivation and fatigue during a long-lasting period (160 minutes). This result partially supports the energy depletion hypothesis since rest breaks are classically thought to restore energy levels that have progressively vanished during task by temporarily interrupting task engagement (Meijman & Mulder, 1998). However, if the energy depletion was supported to some extent, it appeared not to be the only explanation of fatigue development. Indeed, the VAS for effort was still rated higher *After* as compared to *Before* the task in the Breaks condition. As it is well-exposed in Hockey's work, cognitive fatigue literature has progressively integrated other factors – such as motivation, the meaning of the goal, the cost/benefits calculation, etc. – likely to explain cognitive fatigue, below and beyond the energy depletion hypothesis. In addition to our findings on effort assessment, the fact that our task did not solely trigger depletion or an overloaded state was also suggested with the Item by Block interaction showing that τ increased only on Neutral items with Time-on-Task. We related this result to the underload hypothesis, given the higher predictability and monotony of these items as compared to the others. Therefore, we propose our global Time-on-Task effect may have resulted from some energy depletion due to the long-lasting and exhausting duration of our task, which was relieved by breaks. Moreover, we propose that our Time-on-Task effect also resulted from underload/boredom because of the meaningless goal of the task as attested by effort deployment to maintain performance even in the presence of breaks.

Interestingly, Arnau et al. (2017) proposed that a same task may be differentially experienced – triggering an overload or an underload state – as a function of age. More precisely, young people are assumed to suffer from task monotony (underload) while older people would suffer from resource depletion (overload). In their results, Arnau et al. did not find age-related differences in performance with Time-on-Task. They attributed it to the fact that young people decreased their motivation as well as performance because they undergone task monotony while older adults demonstrated higher motivation and resorted to compensatory mechanisms (i.e., larger EEG frontal theta power) allowing to maintain performance against energy depletion. This result is also in agreement with other studies showing a better resistance to task monotony in older as compared to young people (Terentjeviene et al., 2018; Wascher et al., 2016).

Since our results suggest both the energy depletion/overload (i.e., performances were maintained thanks to breaks) but also the underload (i.e., effort was still rated higher in the presence of breaks) acted in combination in Time-on-Task effect, we propose young and middle-aged people probably showed performance decrements as a result of a combined effect of depletion and monotony. By contrast, older people probably mostly faced the depletion effect but not the monotony effect. However, future investigations, such as using a continuous EEG recording during the 160-minute Stroop task, are needed to establish that cognitive fatigue is differentially experienced (monotony *versus* depletion) as a function of age. In Future Perspectives, we also proposed that administering participants with a motivational paradigm, in which rewarding incentives will only relieve cognitive fatigue in the case of motivation drop or boredom but not in the case of energy depletion, would help clarify whether cognitive fatigue is differentially experienced as a function of age.

Cognitive Fatigue as Opportunity Cost?

As an alternative view, we propose that performing such a long-lasting Stroop task has probably triggered opportunity costs in our participants. According to Kurzban et al (2013), all mental activities cannot be performed at the same time, resulting in individuals prioritizing their activities. However, prioritization carries opportunity cost that is simply the value of the next-best alternative. Kurzban et al. proposed that the conscious experience of mental effort results from mechanisms measuring the opportunity costs on the current task, sometimes leading to the reallocation of processes away from the present task and towards the next best alternative (Kurzban, 2010). Generally, humans solve the prioritization problem by estimating the *utilities* of different possible actions, and then selecting the action that has the maximal expected utility. In **Chapter 1**, I used the example given by Kurzban et al. of a research participant asked to perform math calculations having his or her smartphone nearby. The model predicts that doing math in the presence of the smartphone will be perceived as more effortful than in the absence of the smartphone, because the opportunity cost of performing math is higher in the presence of the smartphone. Similarly, a research participant may be performing our meaningless task while thinking about many other more interesting activities that he or she was not performing during that time. If it was probably the case for young people, we think it may have been even more the case for middle-aged people who had many everyday responsibilities. Regarding older people, we do not intend to say that they have nothing else more interesting to do but it is possible they had less urgent activities or demands to meet at the time they performed our task. To test this hypothesis, we should have administered our participants with additional questionnaires asking whether they were fully focused on the task or were thinking about something else (e.g., what they have to do after the experiment, exams that are coming, not to forget a medical appointment, etc.) during task performance. Likewise, questionnaires administered at some time points during the Stroop task would have helped reveal what participants were actually thinking about when performing the task. However, this method would create undesired interruptions that can be assimilated to breaks. Such types of investigations have been implemented to assess mind-wandering episodes during task performance (Stawarczyk & D'Argembeau, 2016). Interestingly, Stawarczyk et al. (2011) developed an experience sampling method allowing isolating stimulus-independent and task-unrelated thoughts (SITUTs) from other kinds of distractions (i.e., irrelevant sensory perceptions and interfering thoughts related to the appraisal of the current task). They found that those SITUTs impaired performance at the Sustained Attention to Response Task (SART; a Go/No-Go task). Moreover, the content of SITUTs were often linked to the anticipation and planning of future events, supporting the opportunity cost hypothesis.

Cognitive Fatigue as Costs/Benefits Ratio?

Tops et al. (2004) proposed that cognitive fatigue results from an effort/reward imbalance. People will keep on the task if rewards are worth enough compared to the deployed effort. In the case of insufficient rewards, motivation decreases, people become fatigued, and finally disengage. In the same vein, Boksem and Tops (2008) assumed that people are going to expend more energy if costs are low and rewards are high. In the case of long-lasting cognitive tasks, the expended energy will progressively become greater than the reward, and motivation will eventually drop. Therefore, it is possible that the Time-on-Task effect in our studies was due to rewards being too low as compared to the deployed effort. Participants in **Study 1** and **Study 2** were compensated 5 euros for their participation, which is probably a weak reward relative to the devoted time. Besides the money-like reward, the nature of the task itself (monotonous, meaningless) may also be considered low-rewarding in the present work.

It is worth mentioning that we intentionally low remunerated participants in order to not trigger an artifacted motivation effect. Indeed, several studies have shown that presenting people with rewarding incentives (such as money) help restore performance to its initial levels

(Boksem et al., 2006; Herlambang et al., 2019; Hopstaken et al., 2015a, 2015b ; Hopstaken et al, 2016; . Krebs et al., 2010; Lorist et al., 2009).

Cognitive Fatigue and the Selective Engagement of Cognitive Resource in Older

If the low rewarding feature of our protocol may explain cognitive fatigue effect in young and middle-aged, why did older people not suffer from Time-on-Task? We propose that cost/benefit balance may not be the same as a function of age. According to the selective engagement of cognitive resources model (Hess, 2014), older people are more likely to engage in processes that promote positive affect and are beneficial for self-esteem. We thus propose that performing our Stroop task, which was boring but not so difficult, may have induced a positive affect in older people who felt they managed the task well. Accordingly, Freund (2006) observed that older adults exhibited higher levels of persistence on a simple sensorimotor task when the focus was on maintenance (i.e., instructions to match an already achieved level of performance) as opposed to improvement in functioning (i.e., instructions to do as well as possible). The opposite was true for younger adults. This study suggests that the rewarding nature of a task will not be attributed to the same characteristics as a function of age. While young people will favor novelty and more challenging tasks at the expense of punctual failures, older people may rather favor the feeling of mastering a task and maintaining performance along the task. This proposal may also explain why our sample of older participants did not seem to suffer from Time-on-Task on the Stroop task despite its lengthy and low-interesting nature.

Future Perspectives for Study 1 and Study 2

In this section, we propose future perspectives allowing either to test new hypotheses, or testing some theoretical models. For example, **Study 1** and **Study 2** showed Time-on-Task effects in middle-aged but not older people, suggesting it is not the age *per se* that influences cognitive fatigue during a long-lasting task but rather the life stage. Therefore, assessing several life characteristics in middle-aged seems interesting in order to help explain why this group underwent Time-on-Task effect while older people did not. As previously mentioned, **Study 2** seemed to show that both depletion and boredom were at play to trigger cognitive fatigue. However, it was not possible to disentangle whether one or the other age group was more prone to depletion *versus* boredom. Therefore, we propose that administering a motivational paradigm, which implies that rewarding incentives will relieve cognitive fatigue only if it is due to a lack of motivation or boredom but not if it is due to depletion, would allow to better determine how cognitive fatigue is experienced as a function of age. Finally, given nowadays obligations of working until an advanced age, we dedicate a longer section of future perspective to breaks. If **Study 2** allowed to show that the different age groups benefited from breaks to the same extent, it only tested one type of breaks. It is possible that different types of breaks (e.g., different length, different nature, or given at different intervals) are differentially beneficial to people as a function of age.

As a first perspective, we propose that investigating Time-on-Task effects using shorter blocks than ours (i.e., 40 minutes) would help reveal finest temporal fatigue-related effect. In our studies, we decided to use relatively long blocks in order to have enough RT data to properly fit the ex-Gaussian function to RT distributions. Regarding the main effect of Block, this procedure allowed us to show increased τ in Block 4 (i.e., after 120 minutes of task) relatively to the beginning blocks. However, it is possible that the Time-on-Task effect was present sooner. Likewise, analyzing RT distributions with a sliding window (e.g., assessing RTs in 8 overlapping time blocks of 20 minutes instead of 4 non-overlapping blocks of 40 minutes) would allow an even better characterization of temporal effects of cognitive fatigue.

As a second perspective, we propose that measuring life characteristics of participants would help explain individual differences in the sensitivity to cognitive fatigue, and more particularly for middle-aged people. Midlife has already been postulated to be the most challenging life period (see **Box 6**) due to the many responsibilities and facets of life they have to deal with. Accordingly, we also carried out a supplementary study (data not presented in this Thesis work[13]) in which we recruited a sample of 78 middle-aged participants (40 to 65 years; $N_{Males} = 30$; mean age males = 52.13 ± 6.55; $N_{Females} = 41$; mean age females = 50.73 ± 5.23 for women; 7 participants excluded) that were administered with a 100-minute Stroop task but were also screened on a large battery of self-reported questionnaires comprising, among others, socio-demographic, health, depression, quality of life and subjective fatigue state ratings, as well some objective ratings such as BMI, pupillometry during a 5-minute PVT, handgrip strength, and blood pressure. Future analyses will thus be dedicated to the

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[13] Because of technical issues due to Covid-19, the sample needed for planned statistical analyses could not be completed but data acquisition is still ongoing.

investigation of the links between self-reported questionnaires and objective health-related measures on fatigue-related performance.

As a third perspective, we propose to investigate the effect of manipulating motivation by rewarding incentives on our long-lasting Stroop task. To this end, participants will be asked to perform the task during 120 minutes and, at this time, a screen will appear signaling that they would receive a certain amount of money if they perform well for the remaining time. This procedure would allow to further test to what extent the energy depletion hypothesis may explain results from the two first studies. Indeed, if cognitive fatigue is triggered by depleted resources, therefore proposing money to keep on performing should normally not restore performance. By contrast, if cognitive fatigue is caused by a lack of interest performing the task, then rewarding incentives may help restore performance by enhancing motivation. As proposed earlier, it is also possible that cognitive fatigue is differentially experienced as a function of age. Therefore, we propose that young people (and probably middle-aged people), that were assumed to mostly suffer from task length and monotony, should benefit from monetary incentives while older people, who were assumed to compensate for resource depletion, should not be largely influenced by a motivational manipulation.

As a fourth perspective, more specifically related to **Study 2**, we propose it should be interesting to test the effect of varying breaks. Basically, we decided to administer short breaks (5 minutes) because long breaks were found to be associated with an immediate performance rebound followed by later decrements (Lim & Kwok, 2016; Lim et al., 2016). However, studies remain scarce and it remains a possibility that the length of breaks has not the same effect on performance as a function of age. Arnau et al. (2017) proposed short and long breaks to young and older participants during a 3-hour Simon task. They found that frontal theta power decreased over breaks only in older people, which was interpreted as compensatory processes counteracting resource depletion with Time-on-Task. However, the authors did not discuss the difference between short and longer breaks.

Also related to **Study 2**, we propose it would be interesting to test the effects of breaks of different nature than "rest breaks". As cited in Mathiassen et al. (2014), dating back more than 100 years, Sechenov proposed that any type of ‘‘diverting’’ activity – physical or mental – would positively influence recovery from fatigue. Accordingly, Mathiassen et al. proposed that "cognitive breaks" would help recover from fatigue during repetitive manual work. Closer to the cognitive fatigue domain, Blasche et al. (2018) compared the effects of four conditions (no break, unstructured break, physical break, relaxing break) on fatigue and vigor scales during classes of 4-hour. They found that if rest breaks were beneficial when performing mental tasks, their effect can be further improved by engaging in physical or relaxing activities. Beyond cognitive fatigue triggered by the task itself, we should also mention that sitting during many hours (i.e., having a sedentary behavior) is detrimental for cognition (Baker et al., 2018; Voss et al., 2014; see Flack et al., 2017 for a systematic review). Studies comparing sitting with a sit-stand work position found that the sitting position resulted in more fatigue and lower energy (Dutta et al., 2014) as well as reduced focus and productivity (Pronk et al., 2012) than the sit-stand position. Therefore, future studies should be dedicated to the comparison of a long-lasting task performed in a sitting *versus* a standing position and/or sitting breaks versus standing-physical breaks.

The Attention Restoration Theory (ART; Kaplan, 1995; Kaplan & Kaplan, 1989) posits that looking at natural scenes or biological movement may help restore attention (Herzog et al., 1997; Kaplan, 1995). According to this model, direct (actively controlled) attention and effortless (passively controlled) attention are considered distinct systems, with the active one being prone to fatigue and depletion (Kaplan, 1995). One way to facilitate the recovery of actively controlled attention resources is to engage the effortless (passively controlled) attention system. This can be easily achieved by presenting people with natural scenes or natural movement (Berto, 2005; Herzog et al., 1997). People are thought to typically perceive these scenes as effortlessly fascinating and as promoting a sense of being away from everyday concerns, and as being compatible with their needs (Kaplan & Kaplan, 1989). Based on this theory, studies have included different types of breaks in their protocols, such as looking at a green (natural) *versus* concrete rooftop (Lee et al., 2015) or looking at dog (natural) *versus* robots videos (Finkbeiner et al., 2016). Globally, results showed higher benefits from breaks including natural stimuli at both the performance (Lee et al., 2015) and the well-being level (Finkbeiner et al., 2016).

Finally, **Study 2** assessed break effects on a laboratory-like protocol: a 160-minute task with short breaks that were imposed every 40 minutes. This study does not directly reflect real work conditions where breaks are sometimes of varying length and are taken at more irregular intervals. We propose future studies should vary all the above-mentioned parameters (i.e., the types of breaks, the length of breaks, the imposed *versus* deliberated nature of the breaks) in different age groups in order to find what is the most beneficial to maintain performance at different ages.

Principle Results from Study 3

Study 3 showed the expected effects of age (young > middle-aged > older) and working memory load (1-Back > 2-Back > 3-Back).This study also revealed lower accuracy (d') in the N-Back task following the fatigue compared to the control condition while cerebral activity did not largely differ between these two conditions. Subjective feelings of sleepiness and demotivation were globally higher after the manipulation session independently of the condition but subjective feelings of effort were higher after the fatigue but not after the control condition, suggesting that the fatigue condition led to a higher deployment of cognitive resources. A Group by Condition interaction was observed for the criterion index (C), showing that middle-age participants adopted a more liberal decision criterion in the fatigue condition than in the control condition. We tentatively attributed this finding to a decrease of controlled processes following cognitive fatigue induction. At the brain level, no large age-related effects were found for middle-aged people. However, a group effect was observed for older participants, mainly characterized by decreases of activity in bilateral fronto-parietal areas and increased activity in left anterior brain areas. We did not show large changes in brain activity between the fatigue and the control conditions. However, age-related fatigue effects were observed in the older (but not the middle-aged) group. Masking the fatigue by the control condition revealed small foci of increased activity in frontal areas (cingulate and OFC) as well as decreased activity (anterior and posterior regions) in older as compared to young people, particularly for the 2-Back load.

How to Explain our Results with Cognitive Fatigue Models

The Specificity of Transfer Effect?

Study 3 did not show large differences in cerebral activity between the control and the fatigue condition. As proposed in the discussion of that study, it is possible that our loading task (i.e., the Stroop task) did not fully transfer fatigue effects to the probe task (i.e., the N-Back task) because these two tasks did not exactly tax on the same cognitive resources and cerebral substrates. The N-Back task requires WM updating and mainly involves prefrontal and fronto-parietal areas (Owen et al., 2005). Tasks such as the Stroop task mainly involve inhibition and rely on fronto-parietal areas but also on some additional specific areas: inferior and middle frontal gyri, occipital, and temporal regions, as well as some subcortical regions including the caudate nucleus, the thalamus, the putamen, and the cerebellum (Niendam et al., 2012). According to the process-specific hypothesis, transfer effects are only possible when the two successive tasks rely on the same specific process as well as on overlapping neural representations. This proposal has been supported by studies showing transfer effects between two tasks sharing the same cognitive requirements (Persson et al., 2013; Persson et al., 2007).

An alternative explanation to this absence of marked difference between the control and the fatigue conditions is that the control condition also induced a certain state of sleepiness and demotivation due to the long-lasting duration of watching videos. Indeed, subjective sleepiness and demotivation were higher at T2 as compared to T1, independently of the condition. However, the effort scale was rated higher after the fatigue but not after the control condition, suggesting higher deployment of cognitive resources and effort to perform the fatiguing condition. We also found that accuracy (d') was smaller in the fatigue than in the control condition but also that middle-aged were more liberal (i.e., adopted a more risky strategy) following the fatigue than the control condition. Therefore, our results suggest small but significant behavioral effects of the fatiguing condition but not of the control condition. We thus propose that our fatigue condition was well more fatiguing and effortful than the control condition but that cerebral effects were weak because of the divergence in cerebral networks required by the two tasks.

If the latter proposal is true, why did older people seem to show more fatigue-related effects as compared to young people? Masking the fatigue by the control condition revealed increases and decreases in activity in older as compared to young people, suggesting fatigue effects specifically in the older sample. We propose it can be explained by the fact that older people basically show cerebral dedifferentiation while performing a task, contrary to young people. This has been proposed by several hypotheses (HAROLD, PASA, ELSA) assuming that older participants recruit the same cerebral network than young people to perform a task, but also additional areas that are not normally required by the task. Therefore, if older people show a lack of specificity in the cerebral network they used to perform a task, there is chance that they used common networks between the two tasks and underwent fatigue effects. In brief, transfer effect may be less process-specific in older brains because cognitive processes also rely on less specific networks.

In **Chapter 1**, I presented the energy depletion hypothesis according to which people become cognitively fatigued because of the depletion of a limited cognitive resource. I also made the distinction between general and specific transfer effects. If the transfer of fatigue effects appears to be process-specific, this would mean that depleted resources are limited to the specific process that was required by the task. This result would have some implications in the workplace, because cognitive fatigue triggered by a long workday may be relieved to some extent by varying the tasks.

However, as already discussed for **Study 2**, it remains difficult to distinguish between energy depletion and motivation-like hypotheses to explain cognitive fatigue. On the one hand, the specificity of transfer effects would signify that the depleted limited resources are restricted to the cognitive processes required by the task and that other cognitive processes remain unaffected. On the other hand, evidence for the specific effect of fatigue could also be partially in agreement with the motivational hypothesis according to which fatigue effects (e.g., performance impairments) are primarily due to a loss of interest in the current goal and to a motivation drop (Hockey, 2013). Accordingly, changing the task goal may result in a certain degree of recovery because motivation that progressively vanished on the previous task is now reset thanks to the new task goal. In this case, cognitive fatigue is not discussed in terms of depleted energy but rather in terms of motivation loss or goal extinction, that are renewed when the individual changes activity (Hockey, 2013).

If the lack of marked difference between the control and the fatigue condition has been discussed as a lack of process-specific requirement between the two successive tasks, this study alone cannot attest it. In order to do that, future studies proposing an inhibition task during fMRI (or a WM updating task during the fatigue condition) should help answer this question.

Cognitive Fatigue as Costs/Benefits Ratio?

Older people in the fatigue condition showed less deactivation in cingulate areas in 2- and 3-Back load as well as in orbitofrontal area in 3-Back load relatively to fatigued young people. These two cerebral areas belong to the limbic loop and are core structures of some fatigue and effort-related models. According to Boksem and Tops (2008)'s model, a particular behavior will be implemented if it is highly valued, both in terms of appetitive/aversive consequences and in terms of energetic costs for the body. To this end, the OFC integrates sensory information and estimates the reward value of stimuli (Kringelbach, 2005; Walter et al., 2005) while the insula gauges the aversive value (costs and punishments) of our decisions (Small et al., 2001; Nitschke et al., 2006). This reward/aversive-related information is conveyed to the ACC, which also receives dopaminergic inputs from VTA to goal-direct behavior and estimate effort. Likewise, the model proposed by Verguts et al. (2015) proposes that ACC codes stimulus value as well as values of different options for a given stimulus and that learning to exert effort is supported by dopaminergic projections from the VTA towards the ACC. Therefore, the lower deactivation in the ACC and in the OFC found in older people relative to young people in the fatigue condition may be explained by a higher estimation of the deployed effort to perform the most challenging 3-Back WM load.

Cognitive Fatigue and the Selective Engagement of Cognitive Resource in Older

According to Boksem and Tops (2008), VTA projections towards the ACC normally strengthen connections in the case of rewarding behavior while induce extinction in the case of unrewarding behavior. As previously mentioned, older people will decide to engage in activities that promote self-esteem and are positively valued (Hess, 2014). Accordingly, older people will often favor activities in which they are high-performing instead of activities more prone to failures. Since the N-Back task is relatively difficult, it is also possible that more fatigue effects were observable in older people because the task was globally perceived as low-rewarding. Indeed, ACC activation is also linked to error detections (Botvinick et al., 2001; Cohen et al., 2000; Kerns et al., 2004), which may have triggered a negative affect and a poor feeling of self-efficacy in older people. By contrast, the N-Back task might have been perceived as challenging and stimulating, and to some extent rewarding, in young and middle-aged people.

Cognitive Fatigue in Time-on-Task versus Probe approach

Interestingly, our two first studies rather showed an absence of Time-on-Task on behavioral performance in older people. This finding was attributed to a better resistance to task monotony from older people and was in agreement with previous studies which used a Time-on-Task approach (Arnau et al., 2017; Terentjeviene et al., 2018; Wascher et al., 2016). By contrast, our Probe approach fMRI study rather showed an absence of transfer effects in young and middle-aged while there were some fatigue effects in older, relatively to young people. We propose that the process-specific hypothesis of transfer effect may be true in young and middle-aged people while it could be less important in older people that are less specific in the cerebral network they recruit to perform a task (i.e., dedifferentiation). Whether this proposal is true or not, it seems that older individuals may be able to resist long-lasting paradigms but show post-task fatigue effects at the cerebral level.

By contrast, middle-aged people had a profile that resembles more that of young people. Middle-aged people showed Time-on-Task effects in **Study 1** and **Study 2**, possibly due to task monotony. Contrary to older people, there was an absence of fatigue-related cerebral effects in middle-aged in **Study 3**, probably because their cerebral networks are efficient and are differentially recruited by the different cognitive processes required by the tasks.

However, very few studies have investigated cognitive fatigue in middle-aged and older people using a Probe approach. Future studies are thus needed to better understand whether cognitive fatigue effects are more or less at play in middle-aged and aging people as a function of the methodology (Time-on-Task or Probe approach) that is used.

Future Perspectives for Study 3

Study 3 did not show large differences between the control and the fatigue condition on N-Back performance or on cerebral activity. We proposed it is possibly due to the lack of commonalities between the loading and the probe task while transfer effects of fatigue might be process-specific. As previously mentioned, it should be interesting to administer an inhibition task during fMRI or a WM updating task during the fatigue condition in order to test the hypothesis of process-specific transfer effects of cognitive fatigue.

However, if global performance on the N-Back did not seem impaired by the preceding fatigue condition, we did not test whether correct and incorrect answers (or rapid and slower RTs) were differentially distributed along the task. It is possible that performance following the fatigue and the control condition were similar on average but that performance diminished (or RTs increased) from the beginning to the end of the N-Back task following the fatigue condition, while staying relatively stable following the control condition. Likewise, fMRI data were analyzed using a block design. It is possible that using event-related analyses would help reveal a profile of brain responses varying from the beginning to the end of the task. Consequently, further analyses will be dedicated to testing whether Time-on-Task effects directly measured on the N-Back task following the fatiguing and the control conditions show age-related differences in fatigue effects on cerebral activity and behavioral performance.

Cognitive fatigue is associated with the DA system (Boksem & Tops, 2008; Chaudhuri & Behan, 2000, 2004; Dobryakova et al., 2013). Otherwise, it has been proposed that genetic effects are more important when brain resources (e.g., the DA system) diminish such as when the individual ages (Lindenberger et al., 2008; Nagel et al., 2008). It has been proposed that genotype effects on cognition may be modulated by age-related changes in neuromodulation such as in DA transmission (Li, 2012). In other words, genetic effects on cognition are more likely to reveal inter-individual difference in populations with diminished resources than in young people. Therefore, futures analyses should be dedicated to the investigation of relevant variants of genes such as the *COMT* val158met SNP which is particularly involved in DA regulation. Regarding the *COMT*, Val/Val homozygotes are characterized by lower baseline levels of DA as compared to Met/Met homozygotes. These different genotypes may trigger individual differences on cognition that would be even more important as the individual ages. Such analyses would allow to determine whether some DA-related SNPs would allow a better resistance to cognitive fatigue in individuals possessing the most beneficial allelic variants, more particularly in older populations.

As dopamine seems to play an important role in cognitive fatigue, we propose it can also explain cognitive fatigue in pathological populations. Accordingly, cognitive fatigue has been frequently reported in psychological conditions such as depression (Demyttenaere et al., 2005; Lavidor et al., 2002) and neurological illnesses such as PD or MS (Chaudhuri & Behan, 2000; Kluger et al., 2013), which have been explained by a down-regulation of the dopaminergic system in striato-thalamo-cortical fibers (Chaudhuri & Behan, 2000, 2004; Lorist et al., 2009). Likewise, MS patients have been characterized by abnormal activation or connectivity strength in the BG and in the PFC (DeLuca et al., 2008; Finke et al., 2015; Tartaglia et al., 2008). Chaudhuri and Behan (2000) also proposed that inadequate dopamine levels in the BG are linked to fatigue in several diseases. Abovementioned models could partially explain cognitive fatigue in these pathologies. Dopaminergic projections from the VTA towards the ACC normally strengthen in the case of rewarding behavior and normally decrease in the case of unsuccessful behavior (Boksem & Tops, 2008). It is possible that pathologies such as PD or MS are characterized by inefficient dopaminergic projections between the VTA and the ACC, leading to the inability to distinguish between rewarding and non-rewarding behaviors and to an undifferentiated implementation of everyday behaviors. Accordingly, Dobryakova et al. (2013) assumed that fatigue might occur as a result of reduced DA availability in the BG, leading to reduced firing of striatal DA neurons in response to a rewarding outcome. Future studies are needed to test which mechanisms are at play to trigger cognitive fatigue in healthy young, healthy aging, as well as in pathological populations. We propose our protocols could be used in pathological populations and then be confronted to our results. It would allow to test whether a young MS patient (or an older PD patient) experiences cognitive fatigue more like young, middle-aged, or older people. Likewise, it could allow to test whether cerebral areas influenced by DA projections (e.g., the ACC and the OFC) are activated to the same extent as in older people in pathology characterized by dopamine dysregulation.

Conclusions

This Thesis work adds some new findings to the existing literature. First of all, we showed that cognitive fatigue as measured by a Time-on-Task paradigm seems to increase the density of extreme RTs made by the participants (represented by τ parameter). This means that when people become fatigued, they do not progressively become slower but rather start to display a larger number of longer RTs, which can be assimilated to periodic attention drops. This result also suggests that cognitive fatigue more particularly affects the decision component of response while the motor-transduction component remains unaffected (Hohle, 1965; Luce, 1986). This result can thus explain everyday accidents as well as attention drops in airplane pilots (Bartlett, 1943) or large speed variations already found in car or train drivers under cognitive fatigue (Brown, 1994; Campagne et al., 2004; Kecklund & Akerstedt, 1993; Torsvall & Akerstedt, 1987).

Secondly, we assumed it was particularly important to investigate age-related effects on cognitive fatigue because life expectancy has progressively increased these last decades and because people are often required to work until an advanced age. Moreover, older people are characterized by baseline cognitive changes as compared to younger people, rendering this population at risk to suffer more from fatigue effects. Middle-aged people are less studied in the literature. However, we assumed they also could be the target of cognitive fatigue given their challenging everyday lives as compared to the other age groups. Our data showed that middle-aged but not older people underwent Time-on-Task effects while we found the reverse age effect when using the Probe approach. We propose middle-aged may resemble young people in the way they experience cognitive fatigue and are more sensitive to task monotony and boredom while older people may be more resisting to long-lasting and relatively easy tasks but more sensitive to challenging tasks following fatigue induction. However, it is possible that we did not show large transfer effects of fatigue in young and middle-aged people with our Probe approach because the two successive tasks did not exactly rely on the same processes and networks. Therefore, future studies are needed to test the process-specific hypothesis and whether the Probe approach still differentially impacts people as a function of age when the two successive tasks rely on the same cognitive process.

Thirdly, we were interested in the effects of breaks and how they are beneficial in the different age groups. We showed that the Time-on-Task effect was relieved by the presence of breaks (i.e., performance was maintained) but that the rating of effort still remained higher after as compared to before the task, even in the presence of breaks. Therefore, we propose that cognitive fatigue may not be due to only one process in particular but that it can be induced by a combination of both energy depletion and boredom. More crucially, it is also possible that a same task is experienced as more or less depleting or boring as a function of age (Arnau et al., 2017). Future studies, manipulating for example a motivational variable, are needed to test whether cognitive fatigue is differentially experienced as a function of age. More importantly, we found that our short punctual rest breaks that were given at regular intervals seemed beneficial to the same extent for the three age groups. This result suggests that adaptations in daily life, and more particularly in the workplace, should not be difficult to implement in order to guarantee a better maintenance of cognitive efficiency. However, future studies should be dedicated to determining whether different types of breaks are differentially beneficial as a function of age.

Regarding the confrontation of our results with the existing literature, we tried to discuss our findings on the Time-on-Task studies with some cognitive fatigue models. However, it is not easy to determine which model best fits our data. For example, it is not possible to distinguish whether cognitive fatigue triggered by the long-lasting Stroop task was due to a costs/benefits imbalance or whether it was due to opportunity costs triggered by the task. We propose that administering participants with additional questionnaires (i.e. how did participants perceive the task?; what were they thinking about during the task? etc.) or with the experience sampling method of mind-wandering episodes (Stawarczyk et al., 2011) during task may help distinguish between different interpretations. Regarding **Study 3**, we found fatigue-related increases in cerebral activity in older relative to young participants in the ACC and in the OFC. This finding was discussed thanks to the model of Boksem and Tops (2008) as well as the model of Verguts et al. (2015) linking dopaminergic inputs from the VTA towards the ACC in order to goal-direct behavior and estimate effort. Accordingly, we propose that considering some dopamine-relevant genes, such as the *COMT*, would allow to characterize individual differences in cognitive fatigue, particularly in older populations in which genetic effects on cognition are amplified (Lindenberger et al., 2008; Nagel et al., 2008).

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List of Publications

Articles

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Gilsoul, J., Libertiaux, V., & Collette, F. (under review). Cognitive fatigue in young, middle-aged, and older: A response time distribution approach.

Gilsoul, J., Libertiaux, V., & Collette, F. (in preparation). Cognitive fatigue in young, middle-aged, and older: Do breaks matter?

Gilsoul, J., Bahri, M. A., Phillips, C., Depierreux, F., Salmon, E., Maquet, P., & Collette, F. (in preparation). Age-related changes in cerebral activity during a working memory task following cognitive fatigue: An fMRI investigation

Posters and Oral Communications as First Author

Gilsoul, J., Libertiaux, V., & Collette, F. (2019, May 14). How does cognitive fatigue affect Young, Middle-aged, and Older people? A distribution analysis of Time-on-Task effect by fitting the ex-Gaussian parameters to the response time distributions. Paper presented at Annual Meeting of the BAPS 2019, Liège, Belgique. http://hdl.handle.net/2268/238941

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Marcotte, C., Simon, J., **Gilsoul**, J., & Bastin, C. (2018, May 18). Impact of the number of alternatives in a forced choice recognition memory task on performance in normal aging. Poster session presented at Annual Meeting of the Belgian Association for Psychological Sciences, Gent, Belgium. http://hdl.handle.net/2268/223617

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Appendix

Appendix 1

Do Attentional Capacities and Processing Speed Mediate the Effect of Age on Executive Functioning?

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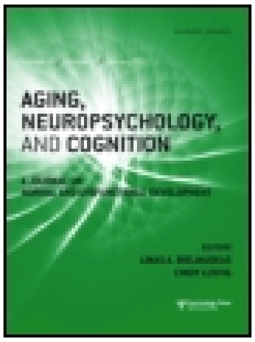

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Do attentional capacities and processing speed mediate the effect of age on executive functioning?

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ABSTRACT

The executive processes are well known to decline with age, and similar data also exists for attentional capacities and processing speed. Therefore, we investigated whether these two last *nonexecutive* variables would mediate the effect of age on executive functions (inhibition, shifting, updating, and dual-task coordination). We administered a large battery of executive, attentional and processing speed tasks to 104 young and 71 older people, and we performed mediation analyses with variables showing a significant age effect. All executive and processing speed measures showed age-related effects while only the visual scanning task performance (selective attention) was explained by age when controlled for gender and educational level. Regarding mediation analyses, visual scanning partially mediated the age effect on updating while processing speed partially mediated the age effect on shifting, updating and dual-task coordination. In a more exploratory way, inhibition was also found to partially mediate the effect of age on the three other executive functions. Attention did not greatly influence executive functioning in aging while, in agreement with the literature, processing speed seems to be a major mediator of the age effect on these processes. Interestingly, the global pattern of results seems also to indicate an influence of inhibition but further studies are needed to confirm the role of that variable as a mediator and its relative importance by comparison with processing speed.

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Executive functions; attention; speed of processing; mediation analyses

Introduction

Executive processes were first described in the context of the central executive system of working memory (Baddeley, 1986) and the Supervisory Attentional System (Norman & Shallice, 1986) and were related to the integrity of frontal lobes. Thereafter, several authors (Damásio, 1995; Miyake et al., 2000; Stuss & Benson, 1986) have contributed to the fractioning of these processes. In their neuroanatomical model based on frontal lesion studies, Stuss and Levine (2002) describe four types of frontal abilities that are specific and interconnected: (a) the executive functions (EFs) comprise processes such as inhibition, planning, mental shifting, decision taking, etc.; (b) auto-regulation and decision taking capacities (for the influence of emotion on these processes, see Damásio, 1995, 2010); (c) energization is dedicated to energy

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Supplemental data for this article can be accessed here.

mobilization and allocation in order to quickly initiate goal-directed responses (Stuss, 2006); and (d) metacognitive functions allow the representation of one's own mental states (autonoetic consciousness) or that of other people (Theory of Mind) (Stuss, 2008, 2011; Stuss & Levine, 2002). Finally, in their hierarchical model of consciousness levels, Stuss and Anderson (2004) propose that EFs process information coming from sensorial systems and monitor goal-directed responses as a function of the stimulus.

Of particular relevance for our present study, the EFs can be defined as a set of high-level abilities required to deal with new, dangerous or complex situations. These functions are well needed to the production of behaviors that are goal-directed. The existence of the four distinct EFs of inhibition, shifting, updating, and dual-task coordination is now well acknowledged, based on single-case analyses of brain-damaged patients and individual difference studies in various target populations (e.g., Burgess & Shallice, 1996a, 1996b; Duncan, Johnson, Swales, & Freer, 1997; Lehto, 1996; Robbins et al., 1998). However, a commonality of processes in executive functioning was also evidenced by Miyake et al. (2000). Using confirmatory factor analyses, these authors have demonstrated that, although dissociable, inhibition, shifting, and updating functions remain intercorrelated. Miyake and colleagues proposed these intercorrelations could correspond to processes related to the maintenance of task goals and contextual information in working memory and/or some "basic" inhibitory processes necessary for EFs to operate properly.

However, this commonality of processes could also be related to the intervention of attentional functioning and processing speed. As these mechanisms are constantly solicited, whatever cognitive activity we are engaged in (for a review, see Rabinovich, Tristan, & Varona, 2015), it could be expected that these variables play a certain role on executive functioning. In agreement with that proposal, Collette et al. (2005) showed that the functions of shifting, updating, and inhibition recruited common parietal areas previously associated with attentional processes, more particularly attentional reorienting (Corbetta & Shulman, 2002; Dove, Pollmann, Schubert, Wiggins, & Yves von Cramon, 2000; Gurd et al., 2002) and selective attention (Behrmann, Geng, & Shomstein, 2004; Coull & Frith, 1998; Wojciulik & Kanwisher, 1999. Moreover, a recent confirmatory factor analysis in young participants showed that these three EFs, and also dual-task coordination, are directly influenced by processing speed and sustained attention, these two processes being underlay by alertness capacity (Hogge, 2008).

Like executive functioning, attention is far from a unitary cognitive function (Posner & Boies, 1971). However, the actual characterization of its different components as well as their interrelations has not yet been well established. Corbetta and Shulman (2002) postulated the existence of two cerebral networks responsible for different attentional functions. The first one is known as the dorsal attention network (DAN) (comprising the dorsal parietal and frontal cortices) and is involved in the cognitive goal-directed selection of sensory information and responses (top-down attention). The second one is known as the ventral attention network, is centered on the right temporoparietal junction, and is dedicated to the detection of behaviorally relevant stimuli (stimulus-driven attention). Corbetta, Patel, and Shulman (2008) further postulated that both dorsal and ventral attention networks are also activated during reorienting processes. Based on the definitions of Posner and Petersen (1990), attentional functioning is currently frequently investigated by the Attentional Network Test (ANT; Fan, McCandliss, Sommer, Raz, & Posner, 2002) that simultaneously assesses the efficiency of the alerting, orienting, and executive attention brain networks[1] (Lu, Fung, Chan, & Lam, 2016; Mahoney, Verghese, Goldin, Lipton, & Holtzer, 2010; Zhou, Fan, Lee, Wang, & Wang, 2011).

One of the most influential attentional models in clinical practice was proposed by van Zomeren and Brouwer (1994), which distinguishes between "intensity" and "selectivity" of attentional processes. The *intensity* axe opposes alertness and sustained attention. Alertness refers to the ability to quickly react to a recurrent stimulus that is presented at irregular intervals, the stimulus being or not preceded by an alerting cue (tonic vs. phasic alertness). Sustained attention characterizes one's abilities to maintain an attentional investment during relatively long periods in order to react to frequent stimulations. The *selectivity* axe opposes selective attention and divided attention. The former function refers to a set of mechanisms allowing the focalization of attentional resources on a specific and limited part of information in order to maximize processing efficiency. By contrast, the latter one is relatively similar to the concept of dual-task coordination and refers to the simultaneous processing of many sources of information but also to the conjoint realization of many tasks. The van Zomeren and Brouwer's model was selected to assess attentional functioning in the present study. As we conceptually distinguish between attention and executive concepts and as we were intended to fully assess the different components of attention, we preferred to use an attentional model that did not emphasize executive aspects of attentional functioning.

Finally, processing speed refers to the way people can implement fast response times (or reaction times) because of time-pressure or to avoid a decrease of performance (as in working memory tasks). While the simple time reaction tasks measure alertness, choice reaction time tasks are often used to assess the rapidity with which an individual carries out an elementary cognitive operation on the proposed stimuli. Consequently, choice reaction time tasks are classically used to measure processing speed (Chiaravalloti, Christodoulou, Demaree, & DeLuca, 2003).

It is now well-established that normal aging is associated with cognitive decline (Craik & Salthouse, 2000), particularly in tasks involving EFs (De Beni & Borella, 2015; Podell et al., 2012; Salthouse, Atkinson, & Berish, 2003; West, 2000). In a cerebral point of view, prefrontal activity during cognitive tasks tend to be less lateralized in aged people in comparison to young people. This reduction in hemispheric asymmetry could be attributed to two different processes: while some authors tend to assume a compensatory function (Cabeza, 2002), others claim the existence of a dedifferentiation process (Li & Lindenberger, 1999). The hypothesis of dedifferentiation raises the question of the separability of executive processes in aging. Some studies tend to show a dedifferentiation process in EFs (De Frias, Dixon, & Strauss, 2006; Delaloye et al., 2009; Hedden & Yoon, 2006). For example, De Frias, Dixon, and Strauss (2006) were intended to test the factorial structure of four executive functioning indices (Hayling, Stroop, Brixton, and Color Trails). Their confirmatory factor analyses evidenced that a single-factor model gave the best fit to the data. However, individual differences among the four tasks were not fully attributed to the EF factor. Therefore, the authors suggested that independent features may further explain the commonality between the executive tasks. In 2009, Delaloye et al. also failed to replicate the three-factor model of Miyake et al. (2000) in older people. In a very interesting study, De Frias, Dixon, and Strauss (2009) examined the structure of the EFs (inhibition, shifting, and updating) between three groups of older individuals characterized by different cognitive status: cognitively elite (CE), cognitively normal (CN), and cognitively impaired (CI). Their analyses confirmed a three-factor model for the CE group and a one-factor fit for the two other groups. The authors concluded that CE older adults are maybe aging in a more successful manner, leading them to exhibit an executive functioning structure resembling that of young people. By contrast to these studies, Vaughan and Giovanello (2010) demonstrated, thanks to structural equation modeling, that the three main EFs postulated in Miyake et al. (2000) are also better represented by a three-factor model in older people.

Moreover, although the executive functioning decreases in efficiency with age, the different functions do not undergo a general decline. Rather, many studies evidence that if some aspects become impaired with aging others remain well preserved (Borella, Delaloye, Lecerf, Renaud, & De Ribaupierre, 2009; Collette & Salmon, 2014; Cona, Arcara, Amodio, Schiff, & Bisiacchi, 2013; Ludwig, Fagot, & de Ribaupierre, 2011; Salthouse, Atkinson, & Berish, 2003; Taconnat & Lemaire, 2014; Vallesi, Hasher,& Stuss, 2010). For example, with regard to shifting abilities, older people would meet difficulties to maintain and to manipulate two mental plans in working memory but not to alternate between these plans (Kray, Eber, & Lindenberger, 2004; Verhaeghen & Cerella, 2002). Regarding updating, aged people would meet difficulties in the process that consist in suppressing irrelevant (i.e., no more relevant) information in working memory but have preserved storage abilities (De Beni & Palladino, 2004). In the inhibitory domain, voluntary/intentional abilities seem well to decrease with age while automatic inhibition would be preserved (Collette, Germain, Hogge, & Van der Linden, 2009; Hogge, Salmon, & Collette, 2008). In this sense, Borella, Ludwig, Dirk, and De Ribaupierre (2011) showed a lack of correlation between their two inhibition measures (interference index and negative priming index), leading them to the assumption that inhibition is a multidimensional construct (Borella, Carretti, & De Beni, 2008; Borella, Delaloye, Lecerf, Renaud, & De Ribaupierre, 2009; De Ribaupierre, 2001; De Ribaupierre, Borella, & Delaloye, 2003; Ludwig, Borella, Tettamanti, & De Ribaupierre, 2010). Another example comes from Shilling, Chetwynd, and Rabbitt (2002), who administered aged people with four inhibitory tasks considered as being variants of the Stroop task and found low correlations between these different measures. This finding suggests, on the one hand, that inhibition is not a unitary process and, on the other hand, that aging does not impair inhibition in all of its different aspects.

All these cognitive impairments are usually seen according two different theoretical approaches. The *analytical approach* claims that cognitive aging would directly impair the cognitive components for which decreased performances are observed. For example, a greater interference effect in a Stroop task will be interpreted as a deficit in the inhibitory function in older people. By contrast, the *global approach* suggests that the cognitive differences linked to age might be explained by a number of general cognitive factors ranging from diminished working memory resources (Craik, Morris, & Gick, 1990) and decreased processing speed (Salthouse, 2000) to sensorial function integrity (Li & Lindenberger, 2002). Today, cognitive decline seems to be viewed as being explained by some general factors as well as impairment in some specific cognitive components. Therefore, it would be very interesting to test whether certain nonexecutive factor such as processing or attention would explain some decrements in EFs in normal aging.

Indeed, with advancing age, some changes are also reported in nonexecutive processes that could influence executive functioning efficiency. Furthermore, there is a general agreement that processing speed decreases with age (Albinet, Boucart, Bouquet, & Auddifren, 2012; Cona, Arcara, Amodio, Schiff, & Bisiacchi, 2013; Manard, Carabin, Jaspar, & Collette, 2014; Salthouse, 1992, 1993, 1994a, 1994b, 1996, 2000; Salthouse & Babcock, 1991; Salthouse & Meinz, 1995; Salthouse et al., 2000).

As very well summed up in Lecerf, De Ribaupierre, Fagot, and Dirk (2007), cognitive performances in older people are mediated by processing speed (De Ribaupierre, 1995; Salthouse, 1992), working memory (Baddeley, 1986; Baddeley & Hitch, 1974), and inhibition (Hasher & Zacks, 1988). Some authors further assume that these three mechanisms are simultaneously playing a role (De Ribaupierre, 2000). It seems that processing speed is the most influent mediator between age and fluid cognition (De Ribaupierre & Lecerf, 2006; Salthouse & Meinz, 1995). In that context, processing speed seems to be particularly relevant to explain the age-related inhibitory decline (De Ribaupierre, 1995; Hogge, Salmon, & Collette, 2008; Salthouse, 1992; Salthouse & Meinz, 1995; Verhaeghen & Cerella, 2002; Verhaeghen & De Meersman, 1998). Likewise, Fisk and Sharp (2004) found an age effect on shifting but neither on inhibition nor updating when processing speed is controlled. By contrast, other authors did find this influence of processing speed for the function of shifting (Kray & Lindenberger, 2000; Salthouse et al., 2000) as well as updating (Sylvain-Roy, Lungu, & Belleville, 2015). Finally, some studies have shown that difficulties in dual-task coordination are not necessarily met when processing speed is controlled (Baddeley, 2001).

If the influence of processing speed on cognition seems well established, no study has ever tried to assess the effect of attentional variables on executive efficiency in normal aging although some studies have shown performance decrements in some attentional measurements. When related to the model proposed by van Zomeren and Brouwer (1994), these studies tend to suggest the presence of an age effect more often on the *selectivity* axe of attentional functions, namely selective and divided attention (Haring et al., 2013; Jefferies et al., 2015; Maylor & Lavie, 1998; Passow et al., 2014; Störmer, Li, Heekeren, & Lindenberger, 2013) as compared to the *intensity* one (Mani, Bedwell, & Miller, 2005).

In that context, the objective of the present study was to determine to what extent decreased executive performance associated with normal aging could be influenced by a lower efficiency of some nonexecutive processes also prone to decline in normal aging. Here we propose that a slowdown of processing speed and weaker attentional functions may—at least partially—explain executive difficulties associated with normal aging. To comprehensively capture the relationships between these variables, we administered a large battery of executive, attentional, and processing speed tasks and carried out mediation analyses (Baron & Kenny, 1986) in a large sample of young and older participants to determine the respective contribution of the attentional system, the processing speed, but also their interaction to the executive abilities in normal aging.

Method

Our study comprised an initial sample of 104 young participants aged from 18 to 42 years and an initial sample of 71 older participants aged from 57 to 81 years. Participants were part of the Caucasian ethnicity and were all French speakers. Young people were recruited from areas inside the Province of Liège (Wallonia part of Belgium) mostly thanks to advertising in MyULiège website and thanks to word of mouth. Young participants were mostly students as well as members of the scientific community of the University of Liège (mostly outside of the Faculty of Psychology and Educational Sciences). Older people were recruited thanks to advertising in University for third age standing at Liège and thanks to word of mouth. Obviously, participants were not included in the study if they were part of home retirement because of the lack of autonomy in everyday life situations that would further impact the executive functioning efficiency of older people. They all have a normal or properly corrected vision and a normal or properly corrected audition. The repartition of the highest degree level achieved by our participants according to the Belgian educative system is also shown (online supplementary Table 14). All participants gave their informed consent to participate, and the study was approved by the Ethics Committee of the Faculty of Psychology and Educational Sciences of the University of Liège and was in accordance with the Declaration of Helsinki (1964). Participants had no neurological or psychiatric problem, were free of medication that could affect cognitive functioning, and reported being in good health.

Four aged people were excluded from analyses because their scores on the Mattis Dementia Rating Scale (Mattis, 1976) were equal to or under 129 on 144 (Monsch et al., 1995).[2] Our final samples comprised 104 young participants and 63 older participants. Demographic data are given in Table 1. In order to be sure that our young and older groups did not greatly differ from each other in terms of intellectual capabilities, we decided to take the educational level as well as the Mill Hill score into account. The education variable was measured by adding the number of successful educational years since the primary school of the Belgian educative system. The Mill Hill scale (Deltour, 1993) is a verbal task assessing crystallized intelligence linked to lexical knowledge (i.e., vocabulary). This task is made of 33 items. For each item, participants had to determine, among six possibilities, the semantically nearest word of a given target word. The dependent variable is the total number of correct answers. We observe that the young group has a higher level of education than the older group [$t(165) = -5.71$, $p < .001$]. However, the groups also differ on the Mill Hill scale (Deltour, 1993), with an advantage for the aged participants [$t(165) = 2.21$, $p = .03$]. Taken together, these results suggest that our two groups are similar in terms of cultural background.

The whole administration of tasks was divided into two sessions of approximately 1 hr 45 min each, which were separated by a few days (from 1 to 15 days as a function of participants' availabilities). Participants were tested individually in a testing room free of visual or auditory disturbance.

Table 1. Demographic data contrasting the young group and the older group.

	Young		Older	
	Raw scores	*Z*-scores	Raw scores	*Z*-scores
Gender (male/female)	44/60	–	38/25	–
Age (years)***	24.68 (5.18)	−.75 (.25)	66.38 (5.83)	1.24 (.28)
Education (years)***	14.81 (2.23)	.32 (.88)	12.68 (2.49)	−.52 (.98)
Mill Hill*	24.94 (3.83)	−.13 (.94)	26.37 (4.35)	.22 (1.06)
Mattis DRS score	–	–	138.87 (4.15)	

For the raw scores, values are means and (*SD*) except for the distribution of gender. *Z*-scores were also performed through each group and means and (*SD*) of these *Z*-scores inside each group are presented.
*$p < .05$; **$p < .01$; ***$p < .001$.

Cognitive battery

A battery of 21 tasks was administered to assess executive, attentional, and processing speed performances of our two samples of participants. The executive processes of inhibition, shifting, updating, and dual-task coordination were assessed by three tasks each. With regard to attentional functioning, the processes of selective and sustained attention were assessed by two tasks each while only one task of phasic alertness was administered. Finally, four tasks were used to determine processing speed. Table 2 presents the considered outcomes for all tasks[3] and Table 3 the raw mean performances in each group. We also present reliability of the executive and processing speed tasks used in online supplementary Table 15. These reliability estimates have been extracted from large sample studies. As the attentional tests were taken from the well-recognized and validated battery of Zimmermann and Fimm (1994), we do not present their reliability estimates. Correlation matrices between the EFs and processing speed measures are presented respectively in Tables 4 and 5.

Executive tests

Inhibition (Stroop, anti-saccade, and stop-signal tasks). Our computerized version of the Stroop test (Stroop, 1935) consists of naming the ink color (blue, red, yellow, or green) of 144 words written in blue, red, yellow, or green. Participants had to give their answers verbally as quickly and accurately as possible; the anti-saccade test (adapted from Roberts, Hager, & Heron, 1994) consists of 108 arrows appearing in the left or in the right of the computer screen and oriented to the left, to the right, or to the top. Before the apparition of each arrow, a blank square always appears in the opposite side of the

Table 2. Outcomes of the executive, attentional, and processing speed tasks.

Tasks	Outcomes
Stroop	Difference of the median RT between interfering (e.g., the word blue written in red) and neutral items (e.g., %%% symbols written in red)
Anti-saccade	Proportion of correctly detected arrows from the whole set of presented arrows
Stop-signal	A diminution index was computed by subtracting the median RT of the trials of the control part from the median RT of the trials that required a response through the entire task
Plus-minus	Difference in median RT between trials with and without shifting
Number-letter	Difference in median RT between trials with and without shifting
Local-global	Difference in median RT between trials with and without alternation
Tone monitoring	Percentage of correct detections of the fourth presentation of each kind of sound
Semantic keep track	Mean percentage of correct responses
Letter memory	Percentage of consonants correctly ordered for the series comprising 5–10 consonants
PASAT	Percentage of correct responses
Brown–Peterson	Percentage of correctly ordered responses for the intervals of 5, 10, and 20 s
Divided attention	Mean RT for the visual and auditory items
Phasic alertness	Difference in median RT between trials with and without warning signal, divided by the median RT of trials for all items
Visual scanning	Median RT for the condition without target detection
Ocular motility	Difference in median RT for central and peripheral targets
Visual irregularity	Number of nondetected irregularities (omissions)
Target detection	Difference in median RT between the second and the first part of the task
Letter comparison	Median RT for similar items
Tonic alertness	Median RT for items without warning signal
Articulatory speed	Mean RT for the repetition of the three pairs of words
Grapho-motor addition	Number of correct additions

RT = reaction time.

Table 3. Raw mean scores (*SDs*) for each executive, attentional, and processing speed measure in the two groups.

	Young	Older
Stroop	143.65 (70.76)	247.49 (128.4)
Anti-saccade	89.95 (9.79)	62.14 (17.18)
Stop-signal	113.12 (152.17)	214.52 (218.36)
Plus-minus	184.33 (161.08)	375.13 (264.71)
Number-letter	624.99 (249.48)	1045 (443.44)
Local-global	186.26 (138.65)	378.92 (292.53)
Tone monitoring	55.03 (22.13)	35.14 (15.36)
Semantic keep track	84.06 (6.98)	72.77 (10.57)
Letter memory	73.29 (16.47)	58.73 (14.85)
PASAT	81.92 (10.02)	61.95 (14.99)
Brown–Peterson	90.51 (8.53)	76.25 (16.6)
Divided attention	640.35 (67.36)	701.98 (90.43)
Phasic alertness (index)	0.04 (0.08)	0.04 (0.13)
Visual scanning	3552.45 (1076.29)	5244.63 (1788.91)
Ocular motility	43.3 (67)	69.24 (160.66)
Visual irregularity detections	4.15 (5.39)	7.03 (9.65)
Target detection	95.53 (39.19)	98.96 (59.74)
Letter comparison	578.97 (90.57)	771.11 (121.76)
Tonic alertness	229.56 (29.86)	289.27 (55.6)
Articulatory speed	4423.43 (811.33)	5582.76 (1177.29)
Grapho-motor addition	51.51 (11.32)	42.56 (9.63)

Table 4. Correlation matrices between the executive measures across the two groups.

Inhibition		Stroop	Stop-signal	Anti-saccade
Stroop	Pearson's correlation	1	.011	.301***
	p-value		.897	.000
Stop-Signal	Pearson's correlation		1	.289***
	p-value			.000
Anti-saccade	Pearson's correlation			1
	p-value			
Shifting		Plus-minus	Number-letter	Global-local
Plus-minus	Pearson's correlation	1	.248**	.149
	p-value		.002	.068
Number-letter	Pearson's correlation		1	.175*
	p-value			.030
Global-local	Pearson's correlation			1
	p-value			
Updating		Tone monitoring	Semantic keep track	Letter memory
Tone monitoring	Pearson's correlation	1	.351***	.412***
	p-value		.000	.000
Semantic keep track	Pearson's correlation		1	.579***
	p-value			.000
Letter memory	Pearson's correlation			1
	p-value			
Dual-task		PASAT	Brown–Peterson	Divided attention
PASAT	Pearson's correlation	1	.612***	.346***
	p-value		.000	.000
Brown–Peterson	Pearson's correlation		1	.148
	p-value			.058
Divided attention	Pearson's correlation			1
	p-value			

*p < .05; **p < .01; ***p < .001.

presentation of the arrow. Participants had to give the direction of the appearing arrow thanks to the keyboard. Therefore, they had to inhibit their reflex gaze orientation to the blank square in order to detect the orientation of the arrow; the stop-signal task (Logan & Cowan, 1984) is divided into two parts. The control part is composed of 24 words

Table 5. Correlation matrix between the four processing speed measures across the two groups.

		Letter comparison	Tonic alertness	Articulatory speed	Grapho-motor addition
Letter comparison	Pearson's correlation	1	.625***	.437***	.434***
	p-value		.000	.000	.000
Tonic alertness	Pearson's correlation		1	.417***	.399***
	p-value			.000	.000
Articulatory speed	Pearson's correlation			1	.311***
	p-value				.000
Grapho-motor addition	Pearson's correlation				1
	p-value				

* $p < .05$; ** $p < .01$; *** $p < .001$.

belonging to living or no-living categories. For each trial, participants had to decide as quickly and accurately as possible if the word belongs to the living or no-living entities thanks to the keyboard. The test part is based on the same principle as the control part but is composed of 192 items with 25% being presented with a sound signal occurring after the presentation of the item. For these items, participants had to keep themselves from answering.

Shifting (plus-minus, number-letter, and local-global tasks). The plus-minus task (Jersild, 1927; Spector & Biederman, 1976) is divided into three parts in which participants had to react orally as quickly and accurately as possible to numbers that are verbally presented. In the first part, they had to add 3 to each number (30 in total). In the second part, they had to subtract 3 from each number (30 in total). In the third part, they had to alternate between adding and subtracting 3 from each number (31 in total); The Number–Letter task (Rogers & Monsell, 1995) is divided into three parts in which a digit-letter pair (e.g., 7G) appears on the screen at each trial. In the first part, pairs (32 in total) appear only in the two bottom quadrants and participants had to make an even/odd judgment about the digit thanks to the keyboard. In the second part, pairs (32 in total) appear only in the two upper quadrants and participants had to make a vowel/consonant judgment about the letter. In the third part, pairs (128 in total) appear in pseudorandom clockwise order in the four quadrants and participants had to make an even/odd judgment when the pair was presented in the bottom quadrants and a vowel/consonant judgment when the pair was presented in the upper quadrants; the Local-Global task (Navon, 1977) is composed of 96 geometrical shapes (square, circle, triangle, cross) that are shaped by smaller squares, circles, triangles, or crosses. Participants had to orally determine the number of sides (1, 2, 3, or 4) of the global level of the geometrical shapes when they appeared in blue on the screen versus of the local level of the shapes when they appeared in red.

Updating (tone monitoring, letter memory, and semantic keep track tasks). The tone monitoring task (adapted from the Mental Counters task developed by Larson, Merritt, & Williams, 1988) is composed of high, medium, and low-pitched sounds presented in a pseudo-random order. Participants had to press the keyboard when each of these sounds was presented for the fourth time; the letter memory task (adapted from Morris & Jones, 1990) is composed of 42 series of consonants (4, 5, 6, 7, 8, 9, or 10) visually presented in a pseudo-random order. For each trial, participants had to orally give the four latter presented consonants; the semantic keep track task (adapted from Yntema, 1963) was composed of 27 series of words belonging to different semantic categories and presented in a pseudo-random order. For each series, participants had to orally give the last word belonging to each category (three or four categories for each series).

Dual-task coordination (PASAT, Brown–Peterson, and divided attention tasks). The Paced Auditory Serial Addition Test (PASAT; Gronwall, 1977; Gronwall & Sampson, 1974) is composed of five series of 21 digits randomly presented on the screen. Participants had to add each digit with the following one and to give the result orally. The time interval between each digit decreases from the first to the last series; in the Brown–Peterson task (Brown, 1958; Peterson & Peterson, 1959), participants had to memorize three consonants successively appearing on the screen. After a certain time delay (0, 5, 10, or 20 s), they had to recall the three letters in the correct order. During the time interval, participants had to repeat, in the backward order, some digit pairs that are given by the experimenter; the divided attention task from TEA battery (Zimmermann & Fimm, 1994) was also administered and consists of the simultaneous presentation of visual and auditory information among which specific items have to be detected.

Attentional tests

Alertness. In the phasic alertness task from the TEA battery (Zimmermann & Fimm, 1994), participants have to react to visual stimuli preceded or not by an auditory warning signal.

Selective attention (ocular motility and visual scanning tasks). In the ocular motility task from the TEA battery (Zimmermann & Fimm, 1994), a target or a neutral stimulus appears to the left or to the right of a fixation point. A target stimulus also appears in the center of the screen at irregular intervals. Participants had to react to the target stimuli; in the visual scanning task from the TEA battery (Zimmermann & Fimm, 1994), participants had to determine whether or not a target stimulus was present in a 5 × 5 matrix.

Sustained attention (visual irregularity detection and target detection tasks). In the visual irregularity detection task (Zimmermann & Fimm, 1994), a texture moves from a rectangle to another during 15 min. Participants had to detect irregularities in this alternation; in the target detection task (Zimmermann & Fimm, 1994), participants had to press the keyboard each time they saw a black circle, which could appear on the screen with or without blank circles. The task was divided into two parts of 5 min.

Processing speed tests

Processing speed (letter comparison, tonic alertness, articulatory speed, and grapho-motor speed tasks). In an adapted version of the letter comparison task (Salthouse, 1991, 1993; Salthouse & Babcock, 1991), participants had to decide as quickly and accurately as possible whether the two consonants of each consonant pair appearing on the screen were identical or different thanks to the keyboard; the tonic alertness task from the TEA battery (Zimmermann & Fimm, 1994) required to respond as fast as possible to the presentation of a visual stimulus; in the articulatory speed task, participants had to repeat a pair of words five times as quickly as possible; in the grapho-motor task (adapted from Salthouse & Coon, 1994), participants had to execute as many additions as possible during 1 min on digits from 1 to 9 (e.g., 4 + 3).

Composite score computation and statistical analyses

All analyses were carried out thanks to SPSS18 (SPSS Inc. Released 2009. PASW Statistics for Windows, Version 18.0. Chicago: SPSS Inc). Since we were interested in the effect of age on executive functioning that is modulated by attentional and processing speed measures, we decided to include in mediation analyses only measures for which we observed an age effect. Therefore, in order to determine which variables were predicted by age, we carried out hierarchical multiple regression analyses by systematically controlling for the influence of gender and educational level in the first step of the model (see Table 6).

Since we had many measures for each assessed component (21 tasks in total), we decided to compute composite scores through both groups. Anticipating the results (Table 6), since all the executive measures showed an age effect, all of these variables were used for the computation of the composite scores. Theoretically based on the definitions of Baddeley (1986) and Miyake et al. (2000), we therefore created four

Table 6. Hierarchical multiple regression analyses for the prediction of each function by age controlled for gender and educational level.

Dependent variables	ΔR^2	ΔF	*df*	*b*	β	*t*	*p*
Executive variables							
Stroop ***	.106	22.29	1, 154	−.016	−.344	−4.72	<.001
Anti-saccade***	.408	163.83	1, 162	−.032	−.676	−12.8	<.001
Stop-Signal***	.158	29.4	1, 155	−.02	−.423	−5.42	<.001
Plus-minus***	.069	14.07	1, 156	−.013	−.278	−3.75	<.001
Number-letter***	.261	59.69	1, 159	−.026	−.54	−7.73	<.001
Local-global***	.145	27.78	1, 151	−.019	−.395	−5.27	<.001
Tone monitoring***	.116	23.98	1, 161	−.017	−.361	−4.9	<.001
Semantic keep track***	.179	44.35	1, 163	−.021	−.448	−6.66	<.001
Letter memory***	.092	18.76	1, 159	−.015	−.319	−4.33	<.001
PASAT***	.278	79.32	1, 163	−.027	−.559	−8.91	<.001
Brown–Peterson***	.116	29.56	1, 162	−.017	−.362	−5.44	<.001
Divided attention***	.098	19.26	1, 162	−.016	−.333	−4.39	<.001
Attentional variables							
Phasic alertness	.000	.048	1, 162	−.001	−.018	−.22	.827
Visual scanning***	.171	39.57	1, 163	−.021	−.439	−6.29	<.001
Ocular motility	.005	.77	1, 163	−.003	−.072	−.88	.382
Visual irreg. detections	.021	3.7	1, 162	−.007	−.155	−1.92	.056
Target detection	.008	1.33	1, 162	−.005	−.095	−1.15	.251
Processing speed variables							
Letter comparison***	.322	95.97	1, 163	−.029	−.602	−9.8	<.001
Tonic alertness***	.222	55.7	1 162	−.024	−.499	−7.46	<.001
Articulatory speed***	.196	42.61	1, 155	−.022	−.472	−6.53	<.001
Grapho-motor addition**	.05	10.29	1, 162	−.011	−.236	−3.21	.002

Analyses were performed on *Z*-scores.

b = unstandardized coefficient of the last entered variable, namely age; β = standardized coefficient of the last entered variable, namely age; *t* = *t*-test value on the last coefficient, namely age; ΔR^2 = variation in R^2 from the step without age to the step including age as predictor; ΔF = variation in *F* from the step without age to the step including age as predictor; *df* = degrees of freedom.

*$p < .05$; **$p < .01$; ***$p < .001$.

executive composite variables with the three tasks associated with each of the following components: inhibition, shifting, updating, and dual-task coordination. The executive composite scores were created according to the method proposed by Keefe et al. (2004). We first standardized the raw scores ($\frac{x-\bar{x}}{\sigma}$) by using the mean and the standard deviation of the whole sample. We also applied a "zero minus *Z*-scores" correction on certain variables in order to get all of our measures in the same direction. Then, we averaged together the *Z*-scores representing the same function (e.g., *Z*-scores on Stroop, anti-saccade, and stop-signal tasks were averaged together to form the composite score of inhibition). Finally, these four newly created composite scores were further transformed into *Z*-scores in order to keep each measure in a same scale.

Regarding the attentional variables, we were also initially interested in creating composite scores for the different aspects of the attentional system, theoretically based on van Zomeren and Brouwer's model (1994). Since only the visual scanning measure was significantly impacted by age after the control of the gender and the educational level ($p < .001$, Table 8), we did not need to compute any composite score for the attentional variables. Rather, the visual scanning variable constituted the only attentional mediator in our analyses.

As no theoretical model allowed us to group together the various measures of processing speed, we decided to compute a composite score by including the measures that showed an age-related effect and significantly correlated to each other across our two groups. Since all the measures of processing speed were predicted by age (Table 6) but also correlated with each other (all $r > .30$ and all $p < .001$; see Table 5), we computed a single composite score with our four speed variables.

Finally, we also created an interaction variable between processing speed and attentional functioning mediators to test the hypothesis that the relationship between executive functioning and processing speed was differently impacted by the attentional function. This crossed variable was obtained by multiplying the processing speed composite score and the visual scanning score.

We carried out mediation models, based on Baron and Kenny's recommendations (1986), with attentional functioning, processing speed, and the interaction between attentional functioning and processing speed as mediators (Figure 1). For example, in order to test the mediating effect of processing speed on the relation between age and inhibition, the following criteria should be met: (a) age has a significant effect on inhibition (path c); (b) age has a significant effect on processing speed (path a); (3) processing speed has a significant effect on inhibition after having controlled for age (path b); and (d) in order to get a total mediation, the effect of age on inhibition has to become nonsignificant after having controlled for processing speed (path c′). Otherwise, we will be in the presence of partial mediation. To ensure the significance of the mediation effect, we did use the Sobel test (Sobel, 1982) whose significance threshold was corrected using the Bonferroni correction to control for the overall error rate (α/12 tests = .004). Finally, to further reinforce our results, we conducted step-by-step stepwise regressions each time we got corrected and noncorrected significant mediation effects. We used this strategy to confirm the results obtained in our mediation models. Once again, we controlled for gender and education level in a forced first bloc. Given the large number of statistical analyses, we adjusted the

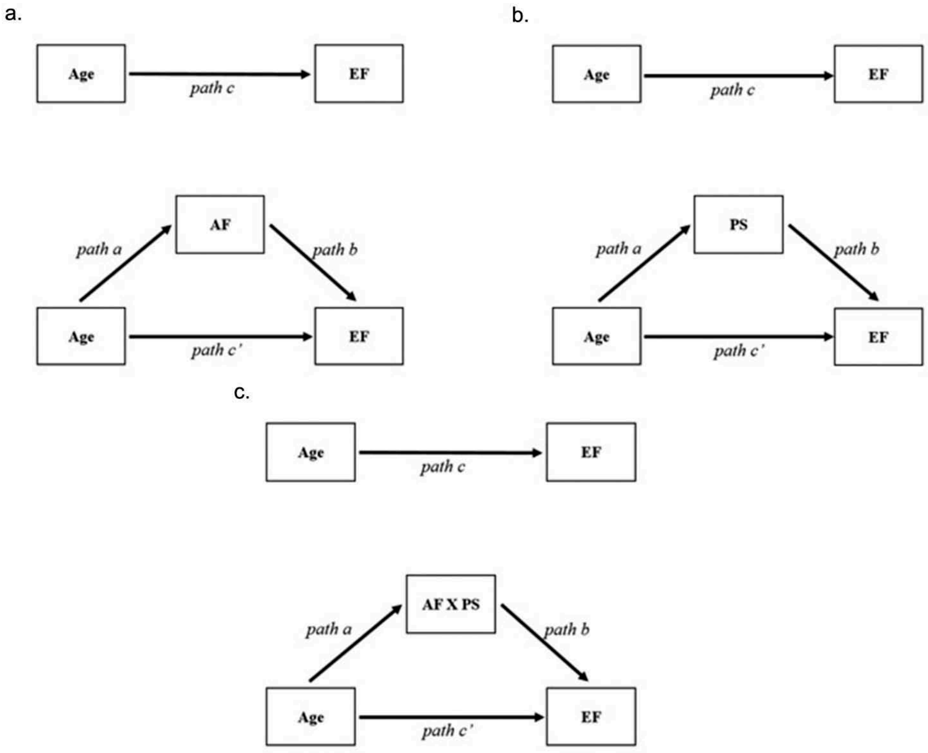

Figure 1. Illustrations of the mediation models with attentional functioning (AF, model A), processing speed (PS, model B), and the interaction between AF and PS (model C) as mediators. For each illustration, the two upper boxes with path c represent the simple model, namely the effect of age on the executive functioning. By contrast, the three-box models represent the mediation models where AF (A), PS (B), and AF × PS (C), respectively, mediate the effect of age on the executive functioning.

EF = executive functions, namely, inhibition, shifting, updating, and dual-task coordination standardized composite scores; AF = attentional functioning (namely, *Z*-score of the visual scanning measure); PS = processing speed standardized composite score.

alpha threshold of the stepwise regressions to control for the overall error rate by setting *F* probability at .005 to enter a variable and at .01 to remove a variable.

Results

Effect of aging

Hierarchical multiple regression analyses revealed that all executive (all $p < .001$) and processing speed (all $p < .01$) variables were predicted by age after controlling for gender and educational level. However, regarding attentional variables, only the visual scanning task ($p < .001$) was predicted by age (Table 6). Therefore and as indicated in the "Method" section, we created four composite scores representing inhibition, shifting, updating, and dual-task coordination to represent our four EFs whereas the visual scanning task was the only variable representing the attentional functioning.

Table 7. Standardized composite scores (and *SD*) in each group.

	Young	Older
Inhibition***	.54 (.56)	−.91 (.91)
Shifting***	.49 (.57)	−.84 (1.03)
Updating***	.46 (.78)	−.75 (.87)
Dual-task coordination***	.5 (.65)	−.83 (.92)
Processing speed***	.54 (.64)	−.89 (.84)
Visual scanning [a]***	.4 (.67)	−.65 (1.11)

These composite scores were created by performing the mean of the *Z*-scores of tasks representing the same construct. Then, the five composite scores obtained were further standardized (transformed into *Z*-scores).

[a] Visual scanning is not part of a composite score. Given that this variable was the only attentional variable predicted by age, we only took the *Z*-score of visual scanning as representative of the attentional system.

Comparison of young and older participants on composite scores:

*$p < .05$; **$p < .01$; ***$p < .001$.

Moreover, given that all processing speed measures were significantly correlated with each other [all $r > .30$ and all $p < .001$], we also computed a composite score representing processing speed (Table 7).

Mediation effects

The following tables present the meditation models with visual scanning (Table 8), processing speed (Table 9), and the interaction between visual scanning and processing speed (Table 10) separately considered as mediators. Gender and educational level were always entered as the first step in all of the regression models.

Results of the first mediation model (Figure 1(A)) show that, after the control of age, visual scanning performance increases the percentage of explained variance of updating [ΔR^2 = 7%, $t(162) = 4.844$, $b = .324$, $p < .001$], which is also confirmed by a significant Sobel test [$Z = -3.95$, $p < .001$]. A mediation effect of visual scanning performance for the effect of age on shifting [ΔR^2 = 2%, $t(159) = 2.53$, $b = .173$, $p = .012$] as well as on dual-task coordination [ΔR^2 = 1%, $t(162) = 2.226$, $b = .142$, $p = .027$] was also observed. However, Sobel tests on these functions do not survive the Bonferroni correction ($\alpha < .004$): for shifting [$Z = -2.37$, $p = .018$] and for dual-task coordination [$Z = -2.1$, $p = .036$]. Importantly, all these mediation effects remain partial given that the fourth step of analysis shows that age always remains significant after the control of visual scanning (all $p < .001$). By contrast, even if visual scanning increases the percentage of explained variance of inhibition [ΔR^2 = 1%, $t(161) = 2.047$, $b = .127$, $p = .042$], a Sobel test on this mediation model is not significant even when the uncorrected p threshold is taken into account [$Z = -1.95$, $p = .051$].

With regard to the second mediation model (Figure 1(B)), results show that, after the control of age, processing speed increases the percentage of explained variance for shifting [ΔR^2 = 7%, $t(159) = 4.734$, $b = .368$, $p < .001$], for updating [ΔR^2 = 5%, $t(162) = 3.836$, $b = .319$, $p < .001$], and for dual-task coordination [ΔR^2 = 14%, $t(162) = 3.326$, $b = .545$, $p < .001$]. These mediating effects are further confirmed by Sobel tests for shifting [$Z = -4.19$, $p < .001$], for updating [$Z = -3.54$, $p < .001$], and for dual-task coordination [$Z = -6.22$, $p < .001$]. Once again, these results suggest that processing speed is only a partial mediator since the fourth step of analysis shows, for these three EFs, that age remains significant after the control of processing speed (all

Table 8. Mediation models of the age effect on each executive function with visual scanning as mediator.

		Inhibition				Shifting				Updating				Dual-task coordination			
		B	*SE*	Beta	*t*	*B*	*SE*	Beta	*t*	*B*	*SE*	Beta	*t*	*B*	*SE*	Beta	*t*
Path b	R^2 adjusted; R^2; ΔR^2	.101; .112; .112***				.161; .171; .171***				.195; .205; .205***				.244; .253; .253***			
	1. Gender	.137	.152	.068	.904	−.012	.147	−.006	−.082	−.048	.143	−.024	−.336	−.053	.139	−.026	−.383
	Education	.134	.030	.341	4.531***	.162	.029	.413	5.649***	.176	.028	.448	6.309***	.195	.027	.497	7.222***
	R^2 adjusted; R^2; ΔR^2	.541; .549; .437***				.464; .474; .303***				.396; .407; .202***				.509; .518; .266***			
	2. Gender	−.021	.109	−.010	−.190	−.139	.119	−.069	−1.175	−.160	.125	−.079	−1.281	−.181	.112	−.090	−1.613
	Education	.043	.022	.110	1.939	.086	.024	.220	3.563***	.114	.026	.289	4.442***	.124	.023	.315	5.367***
	Age	−.033	.003	−.700	−12.535***	−.028	.003	−.583	−9.593***	−.023	.003	−.476	−7.441***	−.026	.003	−.546	−9.482***
	R^2 adjusted; R^2; ΔR^2	.550; .561; .011*				.482; .494; .020*				.468; .481; .074***				.521. .533; .014*			
	3. Gender	−.017	.108	−.008	−.156	−.134	.117	−.066	−1.147	−.149	.117	−.074	−1.269	−.176	.111	−.088	−1.588
	Education	.033	.023	.084	1.446	.073	.024	.187	2.999**	.087	.025	.221	3.534**	.112	.023	.285	4.794***
	Age	−.031	.003	−.644	−10.444***	−.024	.003	−.509	−7.657***	−.016	.003	−.334	−4.988***	−.023	.003	−.484	−7.625***
	Vis. scan.	.127	.062	.127	2.047*	.173	.068	.169	2.528*	.324	.067	.324	4.811***	.142	.064	.142	2.226*
Path c′	R^2 adjusted; R^2; ΔR^2	.101; .112; .112***				.161; .171; .171***				.195; .205; .205***				.244; .253; .253***			
	1. Gender	.137	.152	.068	.904	−.012	.147	−.006	−.082	−.048	.143	−.024	−.336	−.053	.139	−.026	−.383
	Education	.134	.030	.341	4.531***	.162	.029	.413	5.649***	.176	.028	.448	6.309***	.195	.027	.497	7.222***
	R^2 adjusted; R^2; ΔR^2	.249; .263; .151***				.295; .308; .136***				.390; .401; .196***				.353; .365; .112***			
	2. Gender	.109	.139	.054	.782	−.037	.135	−.018	−.270	−.080	.124	−.040	−.646	−.078	.128	−.039	−.605
	Education	.076	.029	.194	2.646**	.109	.028	.278	3.903***	.110	.026	.280	4.247***	.145	.027	.370	5.450***
	Vis. scan.	.414	.072	.415	5.760***	.402	.072	.393	5.615***	.473	.065	.473	7.304***	.358	.067	.358	5.368***
	R^2 adjusted; R^2; ΔR^2	.550; .561; .298***				.482; .494; .186***				.468; .481; .080***				.521; .533; .168***			
	3. Gender	−.017	.108	−.008	−.156	−.134	.117	−.066	−1.147	−.149	.117	−.074	−1.269	−.176	.111	−.088	−1.588
	Education	.033	.023	.084	1.446	.073	.024	.187	2.999**	.087	.025	.221	3.534**	.112	.023	.285	4.794***
	Vis. scan.	.127	.062	.127	2.047*	.173	.068	.169	2.528*	.324	.067	.324	4.811***	.142	.064	.142	2.226*
	Age	−.031	.003	−.644	−10.444***	−.024	.003	−.509	−7.657***	−.016	.003	−.334	−4.988***	−.023	.003	−.484	−7.625***

Steps 3 (path b) and 4 (path c′) required by Baron and Kenny (1986) for mediation models. ΔR^2 = variation in R^2 from the previous to the present step; *B* = unstandardized coefficient; *SE* = standard error; Beta = standardized coefficient; *t* = *t*-test value on the last coefficient; Vis. scan. = visual scanning.

*$p < .05$; **$p < .01$; ***$p < .001$.

Table 9. Mediation models of the age effect on each executive function with processing speed as mediator.

		Inhibition				Shifting				Updating				Dual-task coordination			
		B	*SE*	Beta	*t*	*B*	*SE*	Beta	*t*	*B*	*SE*	Beta	*t*	*B*	*SE*	Beta	*t*
Path b	R^2 adjusted; R^2; ΔR^2	.101; .112; .112***				.161; .171; .171***				.195; .205; .205***				.244; .253; .253***			
	1. Gender	.137	.152	.068	.904	–.012	.147	–.006	–.082	–.048	.143	–.024	–.336	–.053	.139	–.026	–.383
	Education	.134	.030	.341	4.531***	.162	.029	.413	5.649***	.176	.028	.448	6.309***	.195	.027	.497	7.222***
	R^2 adjusted; R^2; ΔR^2	.541; .549; .437***				.464; .474; .303***				.396; .407; .202***				.509; .518; .266***			
	2. Gender	–.021	.109	–.010	–.190	–.139	.119	–.069	–1.175	–.160	.125	–.079	–1.281	–.181	.112	–.090	–1.613
	Education	.043	.022	.110	1.939	.086	.024	.220	3.563***	.114	.026	.289	4.442***	.124	.023	.315	5.367***
	Age	–.033	.003	–.700	–12.535***	–.028	.003	–.583	–9.593***	–.023	.003	–.476	–7.441***	–.026	.003	–.546	–9.482***
	R^2 adjusted; R^2; ΔR^2	.549; .560; .011*				.527; .539; .065***				.443; .456; .049***				.654; .663; .144***			
	3. Gender	.006	.109	.003	.054	–.084	.112	–.042	–.751	–.111	.120	–.055	–.926	–.099	.095	–.049	–1.042
	Education	.028	.023	.072	1.218	.050	.024	.127	2.081*	.081	.026	.207	3.133**	.069	.020	.174	3.352**
	Age	–.029	.003	–.611	–8.64***	–.018	.003	–.370	–5.107***	–.014	.004	–.289	–3.679***	–.011	.003	–.226	–3.662***
	Speed	.152	.076	.150	2.001*	.368	.078	.363	4.734***	.319	.083	.319	3.836***	.545	.065	.545	8.326***
Path c′	R^2 adjusted; R^2; ΔR^2	.101; .112; .112***				.161; .171; .171***				.195; .205; .205***				.244; .253; .253***			
	1. Gender	.137	.152	.068	.904	–.012	.147	–.006	–.082	–.048	.143	–.024	–.336	–.053	.139	–.026	–.383
	Education	.134	.030	.341	4.531***	.162	.029	.413	5.649***	.176	.028	.448	6.309***	.195	.027	.497	7.222***
	R^2 adjusted; R^2; ΔR^2	.344; .356; .244***				.453; .463; .292***				.400; .411; .206***				.628; .635; .382***			
	2. Gender	.162	.130	.080	1.247	.003	.119	.001	.023	–.041	.123	–.020	–.334	–.044	.097	–.022	–.450
	Education	.037	.028	.094	1.305	.055	.026	.141	2.150*	.085	.027	.217	3.167**	.072	.021	.182	3.379**
	Speed	.561	.072	.554	7.839***	.613	.066	.605	9.329***	.509	.068	.509	7.539***	.694	.053	.694	13.058***
	R^2 adjusted; R^2; ΔR^2	.549; .560; .204***				.527; .539; .076***				.443; .456; .045***				.654; .663; .028***			
	3. Gender	.006	.109	.003	.054	–.084	.112	–.042	–.751	–.111	.120	–.055	–.926	–.099	.095	–.049	–1.042
	Education	.028	.023	.072	1.218	.050	.024	.127	2.081*	.081	.026	.207	3.133**	.069	.020	.174	3.352**
	Speed	.152	.076	.150	2.001*	.368	.078	.363	4.734***	.319	.083	.319	3.836***	.545	.065	.545	8.326***
	Age	–.029	.003	–.611	–8.64***	–.018	.003	–.370	–5.107***	–.014	.004	–.289	–3.679***	–.011	.003	–.226	–3.662***

Steps 3 (path b) and 4 (path c′) required by Baron and Kenny (1986) for mediation models. ΔR^2 = variation in R^2 from the previous to the present step; *B* = unstandardized coefficient; *SE* = standard error; Beta = standardized coefficient; *t* = *t*-test value on the last coefficient; Speed = processing speed.

*$p < .05$; **$p < .01$; ***$p < .001$.

Table 10. Mediation models of age effect on each executive function with the interaction between visual scanning and processing speed as mediator.

		Inhibition				Shifting				Updating				Dual-task coordination			
		B	*SE*	Beta	*t*	*B*	*SE*	Beta	*t*	*B*	*SE*	Beta	*t*	*B*	*SE*	Beta	*t*
Path b	R^2 adjusted; R^2; ΔR^2	.101; .112; .112***				.161; .171; .171***				.195; .205; .205***				.244; .253; .253***			
	1. Gender	.137	.152	.068	.904	−.012	.147	−.006	−.082	−.048	.143	−.024	−.336	−.053	.139	−.026	−.383
	Education	.134	.030	.341	4.531***	.162	.029	.413	5.649***	.176	.028	.448	6.309***	.195	.027	.497	7.222***
	R^2 adjusted; R^2; ΔR^2	.541; .549; .437***				.464; .474; .303***				.396; .407; .202***				.509; .518; .266***			
	2. Gender	−.021	.109	−.010	−.190	−.139	.119	−.069	−1.175	−.160	.125	−.079	−1.281	−.181	.112	−.090	−1.613
	Education	.043	.022	.110	1.939	.086	.024	.220	3.563***	.114	.026	.289	4.442***	.124	.023	.315	5.367***
	Age	−.033	.003	−.700	−12.535***	−.028	.003	−.582	−9.593***	−.023	.003	−.476	−7.441***	−.026	.003	−.546	−9.482***
	R^2 adjusted; R^2; ΔR^2	.556; .567; .018*				.501; .513; .039***				.421; .435; .029**				.514; .525; .007			
	3. Gender	−.03	.107	−.015	−.275	−.156	.114	−.078	−1.365	−.17	.122	−.084	−1.393	−.186	.112	−.093	−1.666
	Education	.036	.022	.092	1.628	.077	.024	.196	3.262**	.104	.025	.266	4.139***	.119	.023	.303	5.149***
	Age	−.032	.003	−.677	−12.181***	−.026	.003	−.552	−9.326***	−.021	.003	−.447	−7.058***	−.025	.003	−.532	−9.159***
	Vis. scan. × speed P.	−.115	.045	−.136	−2.551*	−.181	.051	−.202	−3.565***	−.147	.052	−.174	−2.861**	−.074	.047	−.087	−1.562
Path c′	R^2 adjusted; R^2; ΔR^2	.101; .112; .112***				.161; .171; .171***				.195; .205; .205***				.244; .253; .253***			
	1. Gender	.137	.152	.068	.904	−.012	.147	−.006	−.082	−.048	.143	−.024	−.336	−.053	.139	−.026	−.383
	Education	.134	.030	.341	4.531***	.162	.029	.413	5.649***	.176	.028	.448	6.309***	.195	.027	.497	7.222***
	R^2 adjusted; R^2; ΔR^2	.152; .167; .055**				.232; .247; .075***				.248; .262; .056**				.266; .28; .027*			
	2. Gender	.113	.148	.056	.764	−.044	.141	−.022	−.314	−.072	.138	−.036	−.518	−.069	.137	−.034	−.508
	Education	.116	.029	.296	3.973***	.143	.028	.366	5.157***	.158	.027	.402	5.76***	.183	.027	.465	6.749***
	Vis. scan. × speed	−.202	.062	−.24	−3.285**	−.249	.062	−.278	−3.992***	−.205	.058	−.242	−3.528**	−.142	.057	−.168	−2.477*
	R^2 adjusted; R^2; ΔR^2	.556; .567; .399***				.501; .513; .266***				.421; .435; .174***				.514; .525; .246***			
	3. Gender	−.03	.107	−.015	−.275	−.156	.114	−.078	−1.365	−.17	.122	−.084	−1.393	−.186	.112	−.093	−1.666
	Education	.036	.022	.092	1.628	.077	.024	.196	3.262**	.104	.025	.266	4.139***	.119	.023	.303	5.149***
	Vis. scan. × speed	−.115	−.045	−.136	−2.551*	−.181	.051	−.202	−3.565***	−.147	.052	−.174	−2.861**	−.074	.047	−.087	−1.562
	Age	−.032	.003	−.677	−12.181***	−.026	.003	−.552	−9.326***	−.021	.003	−.447	−7.058***	−.025	.003	−.532	−9.159***

Steps 3 (path b) and 4 (path c′) required by Baron and Kenny (1986) for mediation models. ΔR^2 = variation in R^2 from the previous to the present step; *B* = unstandardized coefficient; *SE* = standard error; Beta = standardized coefficient; *t* = *t*-test value on the last coefficient; Vis. scan. = visual scanning; Speed = processing speed.

**p* < .05; ***p* < .01; ****p* < .001.

$p < .001$). By contrast, processing speed increases the percentage of explained variance of inhibition [$\Delta R^2 = 1\%$, $t(161) = 2.00$, $b = .152$, $p = .047$] but Sobel test is not significant even when the uncorrected p threshold is taken into account [$Z = -1.94$, $p = .052$].

Finally, after the control of age, the mediator representing the interaction effect between visual scanning and processing speed variables (Figure 1(C)) increases the percentage of explained variance of inhibition [$\Delta R^2 = 1.8\%$, $t(161) = -2.55$, $b = -.115$, $p = .012$], shifting [$\Delta R^2 = 3.9\%$, $t(159) = -3.57$, $b = -.181$, $p < .001$], updating [$\Delta R^2 = 2.9\%$, $t(162) = -2.86$, $b = -.147$, $p = .005$] but Sobel tests are not significant even when the uncorrected p threshold is taken into account [$Z = -1.4$, $p = .16$ for inhibition; $Z = -1.56$, $p = .12$ for shifting; $Z = -1.45$, $p = .15$ for updating]. Furthermore, the interaction between visual scanning and processing speed did not increase the percentage of explained variance of dual-task coordination [$\Delta R^2 = 0.7\%$, $t(162) = -1.56$, $b = -.074$, $p = .12$]. Globally, there was no significant mediation effect between age and executive functioning by the interaction between visual scanning and processing speed.

Confirmatory stepwise analyses

In order to fully support these results, we carried out confirmatory stepwise regression analyses (Table 11) for the corrected and noncorrected significant mediation effects. The results show that visual scanning increases the explained variance of updating beyond the effect of age [$\Delta R^2 = .074$, $\beta = .324$. $p < .001$] but not for the other EFs. Regarding processing speed, this variable adds supplementary explained variance to shifting once age is taken into account [$\Delta R^2 = .065$, $\beta = .363$. $p < .001$]. Interestingly, processing speed is chosen as the first explicative variable for updating [$\Delta R^2 = .206$, $\beta = .319$. $p < .001$] and dual-task coordination [$\Delta R^2 = .382$, $\beta = .545$. $p < .001$] before age, showing again the contribution of this variable to explained variance.

Exploratory analyses: inhibition as a mediator?

We finally tentatively explored a *mediation by inhibition hypothesis* by carrying out *a posteriori* mediation analyses (see Table 12) of age by the function of inhibition on the three other EFs: shifting, updating, and dual-task coordination. We found that, after the control of age, inhibition increases the percentage of explained variance of shifting [$\Delta R^2 = 1.8\%$, $t(158) = 2.362$, $b = .206$, $p = .019$], updating [$\Delta R^2 = 2\%$, $t(161) = 2.478$, $b = .218$, $p = .014$], and dual-task coordination [$\Delta R^2 = 2\%$, $t(161) = 2.811$, $b = .224$, $p = .006$]. These results are further supported by significant Sobel tests [$Z = -2.31$, $p = .02$ for shifting; $Z = -2.41$, $p = .016$ for updating; $Z = -2.7$, $p = .007$ for dual-task coordination] but only for uncorrected p values. As for the other mediators, these exploratory results suggest that inhibition would be only a partial mediator since the fourth step of analysis shows that age remains significant after the control of inhibition (all $p < .001$). However, confirmatory step-by-step stepwise analyses performed for these mediation effects did not retain inhibition as a predictor of the other EFs once gender, educational level, and age were taken into account (see Table 13).

Table 11. Confirmatory stepwise analyses relative to the visual scanning and processing speed.

		Shifting					Updating					Dual-task coordination			
		B	*SE*	Beta	*t*		*B*	*SE*	Beta	*t*		*B*	*SE*	Beta	*t*
Visual scanning	R^2 adjusted; R^2; ΔR^2	.161; .171; .171***				R^2 adjusted; R^2; ΔR^2	.195; .205; .205***				R^2 adjusted; R^2; ΔR^2	.244; .253; .253***			
	1. Gender	−.012	.147	−.006	−.082	1. Gender	−.048	.143	−.024	−.336	1. Gender	−.053	.139	−.026	−.383
	Education	.162	.029	.413	5.649***	Education	.176	.028	.448	6.309***	Education	.195	.027	.497	7.222***
	R^2 adjusted; R^2; ΔR^2	.464; .474; .303***				R^2 adjusted; R^2; ΔR^2	.396; .407; .202***				R^2 adjusted; R^2; ΔR^2	.509; .518; .266***			
	2. Gender	−.139	.119	−.069	−1.175	2. Gender	−.160	.125	−.079	−1.281	2. Gender	−.181	.112	−.090	−1.613
	Education	.086	.024	.220	3.563***	Education	.114	.026	.289	4.442***	Education	.124	.023	.315	5.367***
	Age	−.028	.003	−.583	−9.593***	Age	−.023	.003	−.476	−7.441***	Age	−.026	.003	−.546	−9.482***
						R^2 adjusted; R^2; ΔR^2	.468; .481; .074***								
						3. Gender	−.149	.117	−.074	−1.269					
						Education	.087	.025	.221	3.534**					
						Age	−.016	.003	−.334	−4.988***					
						Vis. scan.	.324	.067	.324	4.811***					
Processing speed	R^2 adjusted; R^2; ΔR^2	.161; .171; .171***				R^2 adjusted; R^2; ΔR^2	.195; .205; .205***				R^2 adjusted; R^2; ΔR^2	.244; .253; .253***			
	1. Gender	−.012	.147	−.006	−.082	1. Gender	−.048	.143	−.024	−.336	1. Gender	−.053	.139	−.026	−.383
	Education	.162	.029	.413	5.649***	Education	.176	.028	.448	6.309***	Education	.195	.027	.497	7.222***
	R^2 adjusted; R^2; ΔR^2	.464; .474; .303***				R^2 adjusted; R^2; ΔR^2	.400; .411; .206***				R^2 adjusted; R^2; ΔR^2	.628; .635; .382***			
	2. Gender	−.139	.119	−.069	−1.175	2. Gender	−.041	.123	−.020	−.334	2. Gender	−.044	.097	−.022	−.450
	Education	.086	.024	.220	3.563***	Education	.085	.027	.217	3.167**	Education	.072	.021	.182	3.379**
	Age	−.028	.003	−.582	−9.593***	Speed	.509	.068	.509	7.539***	Speed	.694	.053	.694	13.058***
	R^2 adjusted; R^2; ΔR^2	.527; .539; .065***				R^2 adjusted; R^2; ΔR^2	.443; .456; .045***				R^2 adjusted; R^2; ΔR^2	.654; .663; .028***			
	3. Gender	−.084	.112	−.042	−.751	3. Gender	−.111	.120	−.055	−.926	3. Gender	−.099	.095	−.049	−1.042
	Education	.050	.024	.127	2.081*	Education	.081	.026	.207	3.133**	Education	.069	.020	.174	3.352**
	Age	−.018	.003	−.370	−5.107***	Speed	.319	.083	.319	3.836***	Speed	.545	.065	.545	8.326***
	Speed	.368	.078	.363	4.734***	Age	−.014	.004	−.289	−3.679***	Age	−.011	.003	−.226	−3.662***

ΔR^2 = variation in R^2 from the previous to the present step; *B* = unstandardized coefficient; *SE* = standard error; Beta = standardized coefficient; *t* = *t*-test value on the last coefficient; Vis. scan. = visual scanning; Speed = processing speed.

**p* < .05; ***p* < .01; ****p* < .001.

Table 12. Mediation models of the age effect on shifting, updating, and dual-task coordination with inhibition as mediator.

		Shifting				Updating				Dual-task coordination			
		B	*SE*	Beta	*t*	*B*	*SE*	Beta	*t*	*B*	*SE*	Beta	*t*
Path b	R^2 adjusted; R^2; ΔR^2	.160; .170; .170***				.200; .210; .210***				.244; .253; .253***			
	1. Gender	−.018	.149	−.009	−.123	−.030	.143	−.015	−.208	−.048	.140	−.024	−.344
	Education	.161	.029	.410	5.583***	.179	.028	.455	6.398***	.196	.027	.498	7.207***
	R^2 adjusted; R^2; ΔR^2	.463; .472; .303***				.405; .416; .206***				.512; .520; .267***			
	2. Gender	−.140	.119	−.069	−1.171	−.138	.124	−.069	−1.112	−.172	.113	−.085	−1.521
	Education	.086	.024	.220	3.542**	.116	.025	.296	4.570***	.125	.023	.317	5.405***
	Age	−.028	.003	−.581	−9.550***	−.023	.003	−.480	−7.560***	−.026	.003	−.547	−9.503***
	R^2 adjusted; R^2; ΔR^2	.478; .490; .018*				.423; .437; .021*				.532; .543; .022**			
	3. Gender	−.146	.118	−.072	−1.238	−.134	.123	−.066	−1.092	−.167	.111	−.083	−1.511
	Education	.077	.024	.198	3.193**	.107	.025	.272	4.216***	.115	.023	.293	5.033***
	Age	−.021	.004	−.435	−5.051***	−.016	.004	−.328	−3.733***	−.019	.004	−.391	−4.941***
	Inhibition	.206	.087	.205	2.362*	.218	.088	.218	2.478*	.224	.080	.223	2.811**
Path c′	R^2 adjusted; R^2; ΔR^2	.160; .170; .170***				.200; .210; .210***				.244; .253; .253***			
	1. Gender	−.018	.149	−.009	−.123	−.030	.143	−.015	−.208	−.048	.140	−.024	−.344
	Education	.161	.029	.410	5.583***	.179	.028	.455	6.398***	.196	.027	.498	7.207***
	R^2 adjusted; R^2; ΔR^2	.397; .408; .238***				.377; .389; .179***				.464; .474; .220***			
	2. Gender	−.111	.126	−.055	−.878	−.091	.127	−.045	−.721	−.117	.118	−.058	−.989
	Education	.091	.026	.233	3.524**	.118	.026	.301	4.531***	.129	.024	.328	5.310***
	Inhibition	.521	.065	.518	8.002***	.449	.065	.449	6.884***	.500	.061	.498	8.237***
	R^2 adjusted; R^2; ΔR^2	.478; .490; .082***				.423; .437; .049***				.532; .543; .069***			
	3. Gender	−.146	.118	−.072	−1.238	−.134	.123	−.066	−1.092	−.167	.111	−.083	−1.511
	Education	.077	.024	.198	3.193**	.107	.025	.272	4.216***	.115	.023	.293	5.033***
	Inhibition	.206	.087	.205	2.362*	.218	.088	.218	2.478*	.224	.080	.223	2.811**
	Age	−.021	.004	−.435	−5.051***	−.016	.004	−.328	−3.733***	−.019	.004	−.391	−4.941***

Steps 3 (path b) and 4 (path c′) required by Baron and Kenny (1986) for mediation models. ΔR^2 = variation in R^2 from the previous to the present step; *B* = unstandardized coefficient; *SE* = standard error; Beta = standardized coefficient; *t* = *t*-test value on the last coefficient.

*$p < .05$; **$p < .01$; ***$p < .001$.

Table 13. Confirmatory stepwise analyses relative to the mediation by inhibition hypothesis.

		Shifting					Updating					Dual-task coordination			
		B	*SE*	Beta	*t*		*B*	*SE*	Beta	*t*		*B*	*SE*	Beta	*t*
Inhibition	R^2 adjusted; R^2; ΔR^2	.160; .170; .170***				R^2 adjusted; R^2; ΔR^2	.200; .210; .210***				R^2 adjusted; R^2; ΔR^2	.244; .253; .253***			
	1. Gender	−.018	.149	−.009	−.123	1. Gender	−.030	.143	−.015	−.208	1. Gender	−.048	.140	−.024	−.344
	Education	.161	.029	.410	5.583***	Education	.179	.028	.455	6.398***	Education	.195	.027	.498	7.207***
	R^2 adjusted; R^2; ΔR^2	.463; .472; .303***				R^2 adjusted; R^2; ΔR^2	.405; .416; .206***				R^2 adjusted; R^2; ΔR^2	.512; .520; .267***			
	2. Gender	−.140	.119	−.069	−1.171	2. Gender	−.138	.124	−.069	−1.112	2. Gender	−.172	.113	−.085	−1.521
	Education	.086	.024	.220	3.542**	Education	.116	.025	.296	4.570***	Education	.124	.023	.317	5.405***
	Age	−.028	.003	−.581	−9.550***	Age	−.023	.003	−.480	−7.560***	Age	−.026	.003	−.547	−9.503***

ΔR^2 = variation in R^2 from the previous to the present step; *B* = unstandardized coefficient; *SE* = standard error; Beta = standardized coefficient; *t* = *t*-test value on the last coefficient.
$^*p < .05$; $^{**}p < .01$; $^{***}p < .001$.

Discussion

The aim of this study was to determine the potential mediating effect of processing speed and attentional processes on age-related effects in executive functioning. Accordingly, we administered a large battery of executive, attentional and processing speed tasks. We observed age effects on the visual scanning attentional task, and on all executive and processing speed measures. We also evidenced a partial mediation effect of visual scanning abilities on updating performance as well as a partial effect of processing speed on shifting, updating, and dual-task performance. These results were also supported by confirmatory stepwise analyses. However, processing speed and attentional factors were not mediators of the age effect on inhibitory abilities, and an exploratory analysis seems to indicate that inhibition could also be a mediator for the three remaining executive variables. Nevertheless, these *mediation by inhibition* effects were not further supported by confirmatory stepwise analyses.

Age effects on executive, processing speed, and attentional tasks

Our results are in agreement with previous data by showing that all executive variables were predicted by age (Collette & Salmon, 2014; Crawford, Bryan, Luszcz, Obonsawin, & Stewart, 2000; Salthouse, Atkinson, & Berish, 2003; West, 1996, 2000). Nevertheless, some studies indicated that not all aspects of executive functioning decrease with advancing age, with a preservation of automatic inhibitory processes and specific alternation processes in shifting task (e.g., Hogge, Salmon, & Collette, 2008; Kray, Eber, & Lindenberger, 2004). The generalized age-related effect across tasks observed here can be explained by the use of only controlled inhibitory tasks and shifting tasks that were not designed to disentangle local and global alternation processes.

Likewise, and as it could have been expected from several previous studies (Albinet et al., 2012; Cona, Arcara, Amodio, Schiff, & Bisiacchi, 2013; Manard, Carabin, Jaspar, & Collette, 2014; Salthouse, 1992, 1993, 1994a, 1994b, 1996, 2000; Salthouse & Babcock, 1991; Salthouse & Meinz, 1995; Salthouse et al., 2000), all processing speed variables were predicted by age. Salthouse proposed that perceptual speed is more involved in the relationship between age and cognition than motor speed (Salthouse, 1993, 1994b). We consider tasks administrated here as involving perceptual speed as they all require processing auditory or visual information before producing the response.

With regard to attentional functions, we found that only performance on the visual scanning task, requiring selective attention abilities, was significantly predicted by age. It is somewhat consistent with studies having shown an age effect on selective attention (Haring et al., 2013; Jefferies et al., 2015; Maylor & Lavie, 1998; Passow et al., 2014; Störmer et al.,2013) and no effect on sustained attention (Quigley, Andersen, & Müller, 2012). Nevertheless, it is not in agreement with studies demonstrating an age effect on alertness (Festa-Martino, Ott, & Heindel, 2004; Pate, Margolin, Friedrich, & Bentley, 1994) and sustained attention (Mani, Bedwell, & Miller, 2005). However, attentional abilities remain rarely explored with a large range of tasks in older people.

Here, we decided to use van Zomeren and Brouwer's model (1994) in order to fully assess attention in its different components. This model is still greatly used in the clinical practice, allowing to apply a well-recognized and validated battery of attention tasks (Zimmermann

& Fimm, 1994). Nonetheless, we cannot exclude the possibility that the use of other attention models, such as the one of Corbetta and Shulman (2002) but also the one of the three attention networks based on Posner and Petersen (1990), could have led to slightly different results. For example, administering tasks assessing the dorsal attention network (DAN) and the ventral attention networks (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002) would have maybe allowed evidencing some age effect on goal-directed attention vs. stimulus-driven attention. Indeed, as aging is well recognized to primarily impact EFs (De Beni & Borella, 2015; Podell et al., 2012; Salthouse, Atkinson, & Berish, 2003; West, 2000), it would be interesting to test whether the more controlled top-down attention (DAN) is more diminished than the bottom-up attention (ventral attention network) during normal aging. Likewise, we cannot exclude that different results could have emerged if we were using the ANT (Fan, McCandliss, Sommer, Raz, & Posner, 2002). However, the few studies having used the so-called[4] Attentional Network Test (Fan, McCandliss, Sommer, Raz, & Posner, 2002) to simultaneously assess the processes of alerting, orienting, and executive attention have shown a larger negative age effect on the executive network than on the two other networks (Mahoney et al., 2010; Lu, Fung, Chan, & Lam, 2016; Zhou, Fan, Lee, Wang, & Wang, 2011). These results can be considered as relatively similar to those obtained here with separate attentional and executive tasks. Similarly, the investigation of canonical resting-states brain networks in young and older people showed that the executive control network (ECN) was the most affected by age, followed by the DAN (Zhang et al., 2014). Therefore, it seems that attentional functions decrease to a lesser extent with age as compared to EFs.

The absence of age-related effect on our attentional tasks could also be related to the control of educational level. Indeed, previous studies that showed an attentional decrease in older people did not systematically take the educational level into account (Festa-Martino, Ott, & Heindel, 2004; Haring et al., 2013; Jefferies et al., 2015; Mani, Bedwell, & Miller, 2005; Maylor & Lavie, 1998; Passow et al., 2014; Pate, Margolin, Friedrich, & Bentley, 1994) while educational level has been related to various measures assessing cognition in aging (Meguro et al., 2001; Springer, McIntosh, Winocur, & Grady, 2005). Therefore, it is possible that the level at which people are educated is correlated with attentional functions that are particularly needed in school learning (Posner & Rothbart, 2014). Consequently, our control for the educational level may challenge the previously found age effect on attentional variables.

Correlations between the executive tasks

Globally, we have some evidence of convergent validity. For each EF, there are maximum two tasks that do not significantly correlate with each other while the others are well correlated. However, our methodology was more theorically driven than data-driven. Indeed, we decided to perform these grouping of tasks theoretically based on Miyake's model (2000). Nonetheless, there are very obvious reasons to explain the lack of correlations between certain tasks supposed to tap the same EF.

In a theoretical point of view, Harnishfeger (1995) distinguished between intentional vs. nonintentional inhibition but also between cognitive vs. behavioral inhibition. In agreement with this conception, many studies suggest the existence of different inhibitory mechanisms (e.g., Borella, Delaloye, Lecerf, Renaud, & De Ribaupierre, 2009; Hamilton & Martin, 2005; Nassauer & Halperin, 2003; Rush, Barch, & Braver, 2006). For example, Borella, Delaloye, Lecerf, Renaud, and De Ribaupierre (2009) evidence weak correlation between inhibition indices of two version of a same inhibition task as well as between different inhibition tasks. Nassauer and Halperin (2003) evidenced some difference in performances between perceptive vs. motor inhibition in young people. Likewise, Rush, Barch, and Braver (2006) evidenced weak correlation in young and older people between different inhibitory tasks comprising a Stroop task and a stop-signal task. Given the cognitive nature of the Stroop task and the motor nature of the stop-signal task, our lack of correlation may suggest these tasks would assess different aspects of the inhibition function (Rush, Barch, & Braver, 2006). As mentioned in the introduction, Borella, Ludwig, Dirk, and De Ribaupierre (2011) failed to find correlation between their two inhibition measures (interference index and negative priming index). This finding pleads in favor of the assumption of multidimensional inhibition (Borella, Carretti, & De Beni, 2008; Borella, Delaloye, Lecerf, Renaud, & De Ribaupierre, 2009; De Ribaupierre, 2001; De Ribaupierre, Borella, & Delaloye, 2003).

In a same vein, the lack of correlation between two shifting tasks could be due to the fact that they bear on different mechanisms. Indeed, the required alternation inside the plus-minus task is fully predictable and therefore is initiated in an endogenous way while the required alternation inside the global-local task is not predictable at all and is therefore initiated in an exogenous way (Salmon et al., 2010).

Likewise, Fournier, Larigauderie, and Ganoac'h (2004) evidenced different processes of dual-task coordination: (a) the ability to simultaneously maintain and manipulate visuospatial information; (b) the ability to simultaneously maintain and manipulate verbal information; and (c) the ability to coordinate different types of processing that do not need any storage. Given that the Brown–Peterson is a very good example of task requiring to simultaneously maintain and manipulate verbal information while the divided attention task requires coordination without any storage, the lack of significant correlation between these two tasks is understandable.

Attention and processing speed as mediators of the age-related decline on executive functioning

The attentional variable "visual scanning" significantly mediated the effect of age on the updating function. However, this mediation effect was a partial one, meaning that age remains a significant predictor of updating despite the presence of that mediator. Therefore, we can assume that the decrease in updating efficiency in older people is primarily explained by age but also by selective attention. In the updating tasks, participants have to continuously switch their attentional focus to the most recently presented information, a process requiring selective attention abilities very close to the ones necessary to sequentially inspect the matrix of stimuli in the visual scanning task. However, no mediator effect of that attentional variable was observed for the EFs of shifting, inhibition, and dual-task coordination. As a whole, these results do not agree with our initial hypothesis that attentional efficiency would influence executive performance in normal aging. This hypothesis was based on a neuroimaging study claiming the existence of common neural substrates between executive and attentional processes (Collette et al., 2005) and a recent confirmatory factor analysis indicating that attentional processes could in part drive the commonality of EFs (Hogge, 2008). Actually, the absence of mediation effect by visual scanning seems logical for dual-task coordination that requires to separate one's attentional resources between different cognitive activities. This notion is just opposed to the function of selective attention in van Zomeren and Brouwer's model (1994). Likewise, shifting has already been considered as a complementary component of divided attention (van Zomeren & Brouwer, 1994). Indeed, shifting can intervene as soon as people have to switch their attention between several activities they are engaged in and they are not actually able to simultaneously manage. By contrast, the absence of mediation effect of age by visual scanning on inhibition is more difficult to explain as selective attention and inhibition are often considered to act conjointly to select target information and suppress irrelevant one (Neill, Valdes, & Terry, 1995). As the visual scanning task mainly assesses the external orientation of attention and does not require any need of inhibition, we therefore suggest that the task could not be the most adequate to explore a mediation effect of age by selective attention on inhibition.

However, two alternative hypotheses have to be considered to explain the lack of mediation effect by attention: the *mediation by inhibition hypothesis* and the *dedifferentiation hypothesis*. Regarding the *mediation by inhibition hypothesis*, Miyake et al. (2000; see also Friedman et al., 2008; Friedman, Miyake, Robinson, & Hewitt, 2011) proposed that all EFs involve an inhibitory capacity to suppress task-irrelevant distractors, which is considered to be a basic unit of working memory or executive functioning by certain authors (e.g., Dempster & Corkill, 1999; Zacks, Hasher, & Radvansky, 1996) but also as a "'fundamental regulatory mechanisms'" (Hasher, Lustig, & Zacks, 2007) of cognition. Otherwise, inhibition is considered as one of the first cognitive processes to decline with age (Hasher & Zacks, 1988; Persad, Abeles, Zacks, & Denburg, 2002; Radvansky, Zacks, & Hasher, 2005). Hasher and Zacks (1988) proposed that a reduction in inhibition would be a major source of decrement in working memory of aging people. It is the reason why some authors assumed that it could explain some deficits in other cognitive tasks (e.g., Borella, Carretti, Cornoldi, & De Beni, 2007; Borella, Carretti, & Mammarella, 2006; Persad, Abeles, Zacks, & Denburg, 2002). Consequently, inhibition could be a mediator variable between age and executive abilities. We assessed that hypothesis in exploratory *post-hoc* analyses and evidenced a partial mediation of the age effect by inhibition on the three other EFs. These results are in agreement with studies explaining the common activation of EFs by a certain implication of inhibition mechanisms that allow people suppressing irrelevant distracting stimuli and keeping focused on the current task goals (Miyake et al., 2000; Wojciulik & Kanwisher, 1999). However, as these exploratory results were not confirmed by stepwise analyses, further studies are necessary to confirm the potential role of inhibition as a mediator for executive efficiency in aging.

Otherwise, only young participants were included in studies having shown the influence of attentional processes on the EFs (Collette et al., 2005; Hogge, 2008) while the organization of executive functioning seems to be modified in aging. Indeed, some data indicates that aging is associated with a *dedifferentiation* of the executive processes (De Frias, Dixon, & Strauss, 2006; Delaloye et al., 2009; Hedden & Yoon, 2006), leading to a grouping of factors (e.g., flexibility and inhibition, De Frias, Dixon, & Strauss, 2006; flexibility and updating, Adrover-Roig, Sesé, Barceló, & Palmer, 2012). Moreover, there would also exist a reduction in the distinctiveness of neural representations, as well as changes in the ability of different neural regions to communicate with each other (Goh, 2011). On this basis, we can tentatively propose that the more diffuse cognitive and brain representations in aging lead to changes in the relationships between attentional and executive variables by comparison with young participants. This interpretation obviously needs to be specifically explored in future studies.

According to our initial hypothesis, the processing speed variable significantly partially mediated the effect of age on shifting, updating, and dual-task coordination. These results are in great agreement with the literature showing a large influence of the slowdown of processing speed on different aspects of cognition in aging (Albinet et al., 2012; Cona, Arcara, Amodio, Schiff, & Bisiacchi, 2013; Manard, Carabin, Jaspar, & Collette, 2014; Salthouse, 1992, 1993, 1994a, 1994b, 1996, 2000; Salthouse & Babcock, 1991; Salthouse & Meinz, 1995; Salthouse et al., 2000). Moreover, processing speed was chosen as the first explicative variable for updating and dual-task coordination in stepwise analyses. These results are particularly interesting given that outcome measures for updating and dual-task coordination were all except one expressed in other measures than reaction time. This suggests that processing speed is at least as useful in predicting performance in terms of level of accuracy as in terms of reaction time. However, our procedure does not allow us to disentangle on which mechanisms processing speed acts to mediate the effect of age. For example, it is possible that older participants meet certain difficulties to perform adequately all required cognitive operations due to the paced nature of the tasks (*a limited time mechanism*) or that the processed information decreases in availability over time (due to longer response times, *a simultaneity mechanism*) (see Salthouse, 1996).

Finally, if the mediating effect of processing speed on shifting (Kray & Lindenberger, 2000; Salthouse et al., 2000), updating (Fisk & Sharp, 2004), and dual-task coordination (Baddeley, 2001) is consistent with the literature, our results are far from the common findings according to which the control of processing speed dramatically decreases the effect of age on inhibition (De Ribaupierre, 1995; Hogge, Salmon, & Collette, 2008; Salthouse, 1992; Salthouse & Meinz, 1995; Verhaeghen & Cerella, 2002; Verhaeghen & De Meersman, 1998). As mentioned in the “Method” section, it is also the reason why many authors (De Frias, Dixon, & Strauss, 2006; Delaloye et al., 2009; Ludwig, Borella, Tettamanti, & De Ribaupierre, 2010) rightly prefer to adopt relative scores that control for individual differences—namely, baseline *processing speed* individual difference—in their analyses instead of simple difference score. However, since we were interested in the mediation effect of processing speed between age and inhibition, we used simple difference score (MacLeod, 1991). Therefore, we would say that even without computing interfering score controlled for baseline processing speed we did not find any mediation effect of processing speed between age and inhibition. If we had controlled for baseline processing speed in our interference scores, our absence of result could have been attributed to this choice of score computation. As it was not the case, our data greatly evidence that inhibition with advancing age is not mainly explained by a slowdown in processing speed.

Moreover, many of these studies systematically used the Stroop task to assess inhibition. A recent study by Wolf et al. (2014) investigating the effect of age on inhibition and processing speed found that inhibition, as measured by the Stroop task, would decrease with age by itself and that this decrement cannot be explained by a general slowing. Furthermore, as previously discussed, inhibition seems itself to be a mediator variable and is postulated to play a very central role in cognition (e.g., Hasher & Zacks, 1988). So, we could postulate that inhibition plays a role as important as processing speed to explain changes in complex cognition including executive functioning associated with normal aging. For example, Van der Linden et al. (1999) using latent-construct structural equation modeling showed that significant relationships between age and language performance are mediated by reductions in speed, resistance to inference and working memory. Further studies will be obviously necessary to test these hypotheses.

Future perspective

In future investigation, it would be interesting to analyze the relation between age, processing speed, attention, EFs, and the cognitive reserve built by older people throughout the life span. According to Stern (2002), the concept of cognitive reserve relates to brain network utilization efficiency in the sense of a more efficient synaptic processing or the use of alternative brain networks when required. In the aging context, the classical hypothesis is that people with a higher level of cognitive reserve would better resist to deleterious age effects and would have better cognitive performances as compared to aged people with a lower level of cognitive reserve. With regard to this latter point, Roldán-Tapia, García, Cánovas, and León (2012) evidenced better performances on a Stroop task, the Trail Making Test, and different WAIS subtests in aged people with a high cognitive reserve, as indexed by the educational level, the occupational attainment, and the vocabulary level. A main factor of cognitive reserve in older people is the educational level (see Bennett et al., 2003; Meguro et al., 2001; Springer, McIntosh, Winocur, & Grady, 2005). Consequently, we consider that variability in cognitive reserve did not impact our results as we controlled for the educational level in the first step of all analyses. Interestingly, different factors of cognitive reserve would have an impact on specific executive processes (Hultsch, Hertzog, Small, & Dixon, 1999; James, Wilson, Barnes, & Bennett, 2011; Le Carret, Lafont, Mayo, & Fabrigoule, 2003; Shimamura, Berry, Mangels, Rusting, & Jurica, 1995). Therefore, future investigation should take those different cognitive reserve factors into account and to test the possible influence of each factor on our mediation analyses.

Conclusion

Results obtained here emphasize that processing speed is the most prominent mediator explaining age-related effects on executive functioning, even if this effect is partial and does not totally suppress the effect of age. It is in great agreement with Salthouse's work assuming a large influence of processing speed on various cognitive variables in normal aging (Salthouse, 1996). However, contrary to our expectations based on young participants, we did not observe a major influence of attentional variables on executive efficiency and some exploratory *post-hoc* analyses suggest that inhibition could be another important mediator. These results, particularly the relative contribution of processing speed and inhibition, have to be confirmed in further studies but suggest that the relationships between attention, processing speed, and executive functioning could be modified with age.

Notes

1. The alerting network comprises frontal and parietal areas and allows maintaining an alert state and a phasic reaction to a cued signal. The orienting network comprises the temporal parietal junction, the superior parietal lobe, and frontal eye field (Corbetta & Shulman, 2002) and allows selection of information. The executive control network comprises the anterior cingulate and lateral prefrontal cortex (Fan, Fossella, Sommer, Wu, & Posner, 2003; Fossella et al., 2002) and is responsible for cognitive and emotional auto-regulation.
2. Moreover, participants were also excluded from the study (a) if we did not possess at least three executive composite scores in older participants and at least four executive composite scores in young participants. This criterion was a little less severe for older participants because the sample was smaller; (b) if we did not have at least four measures assessing the attentional system; and (c) if we did not possess at least three measures assessing processing speed. Finally, if a participant did not have at least two different measures for a particular function, we decided not to compute the composite score on the function for this participant, what gave rise to four missing values.
3. Some studies have evidenced a certain influence of processing speed on inhibitory tasks in normal aging (De Ribaupierre, 1995; Hogge, Salmon, & Collette, 2008; Salthouse, 1992; Salthouse & Meinz, 1995; Verhaeghen & Cerella, 2002; Verhaeghen & De Meersman, 1998). This is the reason why many authors (De Frias, Dixon, & Strauss, 2006; Delaloye et al., 2009; Ludwig, Borella, Tettamanti, & De Ribaupierre, 2010) rightly prefer to adopt relative scores that control for individual differences—namely, baseline *processing speed* individual difference—in their analyses instead of simple difference score. However, the choice of score computation has to be done according to each study design. Given that we were interested in the mediation effect of processing speed between age and inhibition, we use simple difference score (MacLeod, 1991) to avoid to control for processing speed in our interference scores.
4. We have added the adjective “so-called” because we do not fully agree with this conceptualization tending to “merge” attention and executive concepts as being all attentional. Rather, we theoretically prefer to distinguish between attentional and executive functions.

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