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Of Brain Networks and Rhythms

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Habilitation à Diriger des Recherches

Université Claude Bernard Lyon 1

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Of Brain Networks and Rhythms

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CV

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EDUCATION

2009 **PhD in cognitive neuroscience**, *cum laude*, Université de Lyon, France

2005 **MSc in neuroscience**, graduated with distinction, Université de Lyon, France

CURRENT POSITION

2021-present **Co-leader of the Cophy team** (Computation, Cognition and Neurophysiology) at CRNL

2016-present **Tenured scientist at Inserm**

Lyon Neuroscience Research Center (CRNL), Lyon, France

PREVIOUS POSITIONS

2012-2017 **Senior Researcher/Post-doc/Visiting Researcher**

Donders Institute, Radboud University, Nijmegen, Netherlands

2010- 2012 **Post-doctoral research fellow**

Supervisor: Prof. Ole Jensen, Donders Institute, Radboud University, Nijmegen, Netherlands

Subject: Role of alpha oscillations in cognition

2005 - 2009 **PhD student**

Supervisor: Dr. Van Der Henst, L2C2, UMR CNRS 5304, Lyon, France

Subject: 1) Role of alpha oscillations in functional inhibition in reasoning tasks

2) Use of brain imaging to assess validity of psychological theories of reasoning

FELLOWSHIPS

2021-present **Labex Cortex Collaborative research grant** (co-PI with S. Ben Hamed & J. Mattout)

2017-present **ERC starting grant**

2016 **ATIP-AVENIR grant**

2010-2012 **Post-doctoral fellowship from the Fyssen Foundation**

INVITED TALKS

- Bonnefond M (2021) Role of alpha and gamma oscillations in anticipating and processing visual stimuli.** Universidad Nacional Autonoma de Mexico, Mexico
- Bonnefond M (2021) Role of alpha oscillations in anticipating and processing visual stimuli.** International Graduate School of Neuroscience, Ruhr University Bochum, Germany
- Bonnefond M (2021) Investigating the properties of slow and fast oscillations using a multimodal approach,** Université de Genève, Suisse.
- Bonnefond M (2020) Oscillatory dynamic of feedforward and feedback processing in the visual network.** Workshop 'Inter-areal communication and cognitive processes'. Marseille, France.
- Bonnefond M (2018) While waiting for the OPMs.** 20th anniversary of the MEG-EEG in Paris. Institut du cerveau et de la moelle épinière, Paris, France.
- Bonnefond M (2017) Investigating the role of nested oscillations in cognition.** Cortex conference. Institut des sciences cognitives, Lyon, France.
- Bonnefond M (2017) Sharpening attention through alpha and gamma oscillations.** Institut des Neurosciences de la timone. Marseille, France.
- Bonnefond M, Solis-Vivanco R, Jensen O (2017) Left prefrontal cortex controls alpha phase adjustment in anticipation of predictable stimuli.** Symposium 'top-down influences on perception and action: electrophysiological mechanisms'. Gent University, Belgium
- Bonnefond M, Solis-Vivanco R, **Jensen O (2016) Left prefrontal cortex controls alpha phase adjustment in anticipation of predictable stimuli.** Symposium 'The role of amplitude, phase, and rhythmicity of neural oscillations in top-down control of cognition'. 23rd annual meeting of the Cognitive Neuroscience Society, New York, USA
- Bonnefond M (2016) Evidence for top-down control of the phase of alpha oscillations.** Workshop on top-down control and transcranial manipulation of neuronal oscillations. Radboud University, Nijmegen, Netherlands.
- Bonnefond M (2014) Of frequencies and networks. Cross-frequency interactions in the healthy and pathological brain.** Lyon Neuroscience Research Center (CRNL), Dycog group, Lyon
- Bonnefond M & Jensen O (2014) Alpha activity as a mechanism to preserve working memory integrity.** *Symposium* 'Working memory 2014: 40 years on since Baddeley & Hitch'. **12th International Conference on Cognitive Neuroscience Brisbane, Australia**
- Bonnefond M & Jensen O (2013) An oscillatory mechanism for prioritizing processing.** *Symposium* 'Alpha oscillations and selective attention'. 12th NVP Winter Conference on Cognition, Brain and Behaviour, Egmond, Netherlands
- Bonnefond M & Jensen, O (2013) Top-down controlled alpha activity phasically disrupts gamma activity: Evidences from cross-frequency coupling analysis on MEG data.** *Symposium* 'Functional Mechanisms of Attention'. 43rd annual meeting of the Society for Neuroscience, San Diego, USA

- Bonnefond M (2012) Analysis of distributed phase locking factor: An alternative to coherence?** University of Amsterdam, Netherlands.
- Bonnefond M (2011) Psychophysiological interaction analysis for MEG data.** Workshop on functional connectivity. Radboud University, Nijmegen, Netherlands.
- Bonnefond M (2011) Alpha oscillations, functional inhibition and other MEG stories.** Workshop on magnetoencephalography. CERMEP, Lyon, France.
- Bonnefond M (2006) Neurobiology of memory and the effect of aging.** Centre Interdisciplinaire d'Ethique. Université Catholique de Lyon, France
- Bonnefond M (2005) Neurobiology of memory.** Université Catholique de Lyon, France

TEACHING

- Avr 2019-21 **Role of oscillations in information coding and inter-areal communication.** Université de Lyon, mention computational neuroscience, *MSc level*
- Oct 2020 **Intelligence In Silico. Biological vs Artificial Networks.** Université de Lyon, *MSc level*
- Nov 2017 **Role of oscillations in information coding and inter-areal communication.** Aix-Marseille Université, *MSc level*
- Nov 2017 **Rythmes et réseaux de la perception et la mémoire.** Université de Lyon, *MSc level*
- Aug 2015 **The role of brain oscillations in cognition.** Radboud Summer School, *MSc level*
- Aug 2013-14 **Neural oscillations: analysis & applications.** Donders Tool-kit of cognitive neuroscience, *Post-graduate level*
- May 2013-15 **The role of oscillations in cognition.** University of Amsterdam, *Undergraduate level*
- Feb 2011-13 **Introduction to Neuroimaging technics.** Radboud University, *Undergraduate level*
- May 2012-15 **MEG basics and analysis of oscillations.** Maastricht University, *MSc level*
- Sept 2011 **The role of alpha activity in cognition.** Radboud University, *MSc level*
- April 2010-11 **Hands on analysis of signal using Matlab.** University of Twente, *MSc level*
- 2008-10 **Workshops on Magnetoencephalography.** Lyon, *MSc and post-graduate levels*
- Oct-Dec 2007 **Introduction to neuroscience.** Université Catholique de Lyon, *Undergraduate level*

(CO-)SUPERVISIONS/COLLABORATIONS

J'ai commencé à superviser des étudiants lorsque j'étais doctorante. Déjà à l'époque, mon inspiration venait de mes anciens et actuels encadrants (principalement Nadine Ravel et Jean Baptiste Van der Henst) et plus tard j'ai continué à « voler » les idées de mon encadrant post-doc Ole Jensen. Je crois fermement que la supervision doit être adaptée à chaque étudiant(e) car ils peuvent avoir besoin de différents niveaux de soutien à différentes étapes du processus de recherche, de la conception de la tâche à la rédaction de l'article. Être

disponible pour que les étudiants frappent à votre porte et organiser régulièrement des réunions est également essentiel pour moi. Cependant, je crois aussi que l'un des meilleurs moyens d'apprendre sur le long terme est de faire des erreurs, d'essayer des choses par soi-même et d'être proactif et il existe en effet une importante littérature scientifique soutenant cette idée. De plus, je considère que mon expertise est importante pour prendre des décisions, mais je les considère aussi comme des collaborateurs avec des idées et des suggestions valables. Bien qu'il soit confortable d'être un expert dans le sujet de recherche de l'étudiant(e), j'aime aussi explorer de nouveaux domaines scientifiques, en prenant des risques avec elles et eux. Je veille cependant à mettre en place des collaborations solides qui leur apporteront le soutien nécessaire. Je pense aussi qu'il est essentiel de se soucier de l'avenir de ces étudiant(e)s, de ce dont ils ont besoin pour leur future carrière (suivre des cours spécifiques, éventuellement acquérir un diplôme supplémentaire etc...). J'ai fait de nombreuses erreurs d'encadrement par le passé et j'en ferai sans doute encore beaucoup (et je m'en excuse auprès des étudiant(e)s qui ont travaillé ou qui travailleront sous ma supervision) mais j'essaie toujours d'apprendre de ces erreurs.

En tant que nouvelle cheffe d'équipe (depuis début 2021, en co-direction avec Jérémie Mattout) et grâce à mes propres expériences d'encadrement, ainsi qu'au soutien de mes collègues de recherche de l'équipe Cophy et du CRNL, je me sens maintenant prête à assumer formellement la responsabilité de superviser de manière indépendante les doctorants.

(Senior) post-doctoral fellow	Maciej Szul	2020
	Rasa Gulbinaite	2018-2020
	Anne Kosem	2018-2020
	Fardin Afdideh	2018-2019
	René Scheeringa	2017-2019
	Solis-Vivanco Rodolfo	2014-2018
PhD student	Tommy Clausner	2018-now (FRM grantee- 4 th year)
	Maxime Ferez	2020-now
	Skujevskis Maris	2015-2017
	Jörn Horschig	2011-2014
	Vitória Piai	2011-2012
	Eelke Spaak	2011-2012
MSc student	Agnès Oros	2021-2022 (2 nd year)
	Cléa Michaud	2021-2022 (2 nd year)
	Tommy Clausner	2017-2018 (2 nd year)
	Cerise Massé	2017-2018 (1 st year)
	Jessy Deroche	2017-2018 (1 st year)
	Juliette Lenouvel	2017-2018 (1 st year)
	Floris de Vries	2013-2014 (2 nd year)
	Yagmur Gucluturk	2012_2013 (2 nd year)
	Suzanne Robic	2008_2009 (1 st year)
	Eve Fabre	2008-2009 (2 nd year)
	Marion Gougain	2008-2009 (1 st year)

Celine Vial	2007-2008 (1 st year)
Thomas Castelain	2007-2008 (2 nd year)

OUTREACH ACTIVITIES (CITIZEN SCIENCE)

En 2012, j'ai ajouté une nouvelle question de recherche à mon agenda : comment les couleurs affectent-elles l'attention et l'apprentissage ? Ce nouvel intérêt n'est pas venu de l'incitation d'une bourse ou de la lecture de la littérature scientifique mais de lycéens de Molins de Rei (Espagne), qui se demandaient si repeindre leurs salles de classe pouvait améliorer leurs apprentissages. Ils ont posté leur question dans une vidéo en ligne, qui a attiré l'attention d'un programme de science citoyenne (Ateliers des Jours à Venir <http://www.joursavenir.org/>). C'est ainsi que j'ai (avec le Dr Sescousse) été embauché par des lycéens grâce au financement de la Fondation de France. Nous les avons aidés à affiner leur question en fonction de la littérature scientifique existante et leur avons appris à construire un protocole et à effectuer des analyses statistiques. Les élèves ont réalisé une expérience à l'école et ont obtenu des résultats préliminaires intéressants qui constituent la base d'expériences réalisées par la suite à Lyon. Les étudiants ont partagé leur expérience avec d'autres jeunes dans un article publié dans *Frontiers for Young Minds* (Andújar et al. 2015), tandis que nous avons partagé notre expérience avec d'autres scientifiques dans une lettre publiée dans *Science* (Bonfond, et al. 2015) dans laquelle nous soulignons l'importance de ce type d'interactions pour le succès de l'avancement de la science et de la société. Trois étudiantes en master de l'Université Lyon 2 (Cerise Massé, Juliette Lenouvel et Jessy Deroche) ont mené une expérience ambitieuse au Lycée du Parc de Lyon en 2018, c'est-à-dire en milieu écologique. Nous n'avons pas trouvé d'effet des couleurs sur l'apprentissage contrairement à ce qu'affirmait un article paru dans *Science* quelques années auparavant. Nous prévoyons de poursuivre cette approche cette fois axée sur le rôle de la motivation et du choix dans les apprentissages (sujets que les élèves de Molins ont évoqués la première fois que nous nous sommes rencontrés) en impliquant des nouveaux lycéens ou même des élèves plus jeunes. Ce projet s'inscrit dans la lignée des initiatives actuelles d'amélioration des apprentissages à l'école avec l'originalité de partir des idées non pas de chercheurs ou d'enseignants mais de des apprenants eux-mêmes. Nous prévoyons de démarrer un nouveau projet dans une école défavorisée de Lyon dans les années à venir.

En décembre 2021, j'ai également été "capitaine" d'un événement Declics qui consistait à présenter la recherche en général et mes travaux en particulier à des lycéens à Lyon (Cité Scolaire Internationale). Avec un groupe plus large de chercheurs, doctorants et ingénieurs, nous avons ensuite discuté avec de petits groupes d'étudiants de la recherche notamment des enjeux qu'elle porte (intégrité scientifique, statistiques etc...) mais aussi de leur devenir et de la manière dont la méthodologie de recherche peut être appliquée au quotidien.

PUBLICATIONS

Topic: Oscillations

Submitted/In preparation

1. Ferez M., Bayle D., Noveck I., Van der Henst J.-B., Bertrand O., Mattout J., **Bonfond M.** (in prep.)
Overcoming a perceptual bias in reasoning: evidence for a role of alpha activity in inhibition.

2. Clausner T.*, Scheeringa R.*, Norris D., Jensen O., **Bonnefond M.** (in prep.) New vistas on computational roles of alpha and gamma rhythms. A laminar fMRI-EEG study.
3. Ferez M. Luther L., **Bonnefond M.** (in prep) Inhibition of the ventral attention network during a Stroop task.
4. **Bonnefond M.**, Jensen O. (in prep.) Computation roles of alpha rhythm: a critical review.
5. **Bonnefond M.**, Jensen O., Clausner T. (submitted) Visual processing by dynamic multiplexing and phase coding.

Published

6. Solis-Vivanco R., Jensen O., **Bonnefond M.** (2021) New insights on the ventral attention network: Inhibition and recruitment during a bimodal task. *Human Brain Mapping*.
7. Bonaiuto J.J., Afdideh F., Ferez M., Wagstyl K., Mattout J., **Bonnefond M.**, Barnes G.R., Bestmann, S. (2020). Estimates of cortical column orientation improve MEG source inversion. *Neuroimage* 216, 116862
8. Solis-Vivanco R., Jensen O., **Bonnefond M.** (2018) Top-down control of alpha phase adjustment in anticipation of temporally predictable visual stimuli. *Journal of Cognitive Neuroscience* 30(8):1157-1169
9. **Bonnefond M.**, Kastner S., Jensen O. (2017) Communication between brain areas based on nested oscillations. *eNeuro*. 4:ENEURO.0153-16.2017
10. Staresina B.P., Michelmann S.*, **Bonnefond M.***, Jensen O., Axmacher N., Fell J. (2016) Hippocampal pattern completion is linked to gamma power increases and alpha power decreases during recollection. *eLife*. 5, e17397
11. Staresina B.P.*, Bergmann T.O.*, **Bonnefond M.**, van der Meij R., Jensen O., Deuker L., Elger C.E., Axmacher N., Fell J. (2015) Hierarchical nesting of slow oscillations, spindles and ripples in the human hippocampus during NREM sleep. *Nature Neuroscience*. 18 (11), 1679
12. Horschig J., Smolders R., **Bonnefond M.**, Schoffelen J.M., Cools R., Denys D., Jensen O. (2015) Directed communication between nucleus accumbens and neocortex in humans is differentially supported by synchronization in the theta and alpha band. *PloS One*. 10 (9), e0138685
13. **Bonnefond M.** and Jensen O. (2015) Gamma activity coupled to alpha phase as a mechanism for top-down controlled gating. *PloS One*. 10 (6), e0128667
14. Jensen, O., **Bonnefond, M.**, Marshall, T. and Tiesinga, P. (2015) Oscillatory mechanisms of feedforward and feedback visual processing. *Trends in Neurosciences*. 38 (4), 192-194
15. Jensen O., Gips B., Bergmann T.O.*, **Bonnefond M.*** (2014) Coupled alpha and gamma oscillations prioritize visual processing. *Trends in Neurosciences*. 37 (7), 357-369
16. Kaplan R., Bush D.R, **Bonnefond. M.**, Bandettini P.A., Barnes G.R., Doeller C.F., Burges N. (2014) Medial Prefrontal Theta Phase Coordination of Spatial Memory Retrieval. *Hippocampus*. 24 (6), 656-665
17. Piai V., Roelofs A., Jensen O., Schoffelen J.M., **Bonnefond M.** (2014) Cortical dynamics of lexical activation and competition in overt picture naming. *PloS One*. 9 (2), e88674
18. Horschig J., Jensen O., Van Schouwenburg M.R., Cools, R., **Bonnefond M.** (2014) Alpha activity reflects individual abilities to adapt to the environment. *Neuroimage*. 89, 235-243
19. Jensen O. and **Bonnefond M.** (2013) Prefrontal alpha- and beta-band oscillations are involved in rule selection. *Trends in Cognitive Sciences*. 17(1):10–2

20. **Bonnefond M.** and Jensen O. (2013) The role of gamma and alpha oscillations for blocking out distraction. [Communicative and Integrative Biology](#). 6 (1), e22702
21. Jensen O., **Bonnefond M.** & VanRullen R. (2012) An oscillatory mechanism for prioritizing salient unattended stimuli. [Trends in Cognitive Sciences](#). 16 (4), 200-206
22. Spaak, E., **Bonnefond, M.**, Maier, A., Leopold, D.A. & Jensen, O. (2012) Layer-specific entrainment of gamma-band neural activity by the alpha rhythm in monkey visual cortex. [Current Biology](#). 22 (24), 2313-2318
23. **Bonnefond M.** and Jensen O. (2012) Alpha oscillations serve to protect working memory maintenance against anticipated distractors. [Current Biology](#). 22 (20), 1969-1974

Topic: Reasoning and other

24. **Bonnefond M.**, Castelain C., Noveck I., Van Der Henst JB. (2014) [Reasoning from transitive premises: An EEG study](#). [Brain and Cognition](#). 90, 100-108
25. **Bonnefond M.**, Kaliuzhna M., Van der Henst JB., De Neys N. (2014) Disabling conditional inferences: an EEG study. [Neuropsychologia](#). 56, 255-262
26. **Bonnefond M.** and Van Der Henst JB. (2013) Deduction electrified: ERPs elicited by the processing of words in conditional arguments. [Brain and Language](#). 124 (3), 244-256
27. **Bonnefond M.**, Noveck I., Baillet S., Cheylus A., Delpuech C., Bertrand O., Fournieret, P. & Van Der Henst JB. (2013) What MEG can reveal about reasoning: The case of if...then sentences. [Human Brain Mapping](#). 34, 684–697
28. **Bonnefond M.**, Van Der Henst JB., Gougain M., Robic S., Olsen M., Weiss O. & Noveck I. (2012) How pragmatic interpretations arise from conditionals: Profiling the Affirmation of the Consequent argument with reaction time and EEG measures. [Journal of Memory and Language](#). 67 (4), 468-485
29. Noveck I., **Bonnefond M.** & Van der Henst, JB (2011) A deflationary account of invited inferences. [Belgian Journal of Linguistics](#). 25 (1), 195-208
30. **Bonnefond M.** & Van der Henst JB. (2009) What's behind an inference? an EEG study. [Neuropsychologia](#). 47 (14), 3125-3133
31. Chevallier C., **Bonnefond M.**, Van der Henst JB. & Noveck I. (2009) Using ERPs to capture prosodic stress and inference making. [Italian Journal of Linguistics](#). 22 (1), 125-152
32. Desgranges B., Sevelinges Y., **Bonnefond M.**, Lévy F., Ravel N. & Ferreira G. (2009) Critical role of insular cortex in taste but not odor aversion memory. [European Journal of Neuroscience](#). 29 (8), 1654-1662

Topic: researchers-citizens collaboration

33. **Bonnefond M.**, Riboli-Sasco, L., Sescousse, G. (2015) Repainting citizen science. [Science](#). 350 (6260), 518-518
34. Andújar B., Campderrós G., García M., Marino M., Mas M., Narbona L., Pérez L., Rodrigo P., Velásquez A.J., Vilà J., Laguna D., Sescousse G., Flutre T, Riboli-Sasco L., **Bonnefond M.** (2015) Twenty tips for high-school students engaging in research together with scientists. [Frontiers for young minds](#). 3 (7)

General overview/Summary

Après avoir suivi, en master 1, un cours inspirant sur le rôle putatif des oscillations neuronales dans le codage de l'information (donné par le Pr Rémi Gervais à l'Université de Lyon 1), j'ai décidé de m'orienter vers ce domaine de recherche passionnant et prometteur. Le cours mémorable donné en master 2 par le Dr Olivier Bertrand sur les oscillations m'a définitivement convaincue de poursuivre dans cette voie.

Par conséquent, le sujet de l'un de mes stages de master portait sur la dynamique oscillatoire dans les réseaux de mémoire chez le rat (sous la direction de Nadine Ravel à l'Institut des sciences cognitives-Marc Jeannerod). Nous avons constaté que des oscillations lentes (< 25 Hz) étaient impliquées dans l'encodage et la récupération des informations olfactives. En raison d'une condition médicale, je me suis orienté vers la recherche humaine pour mon doctorat et j'ai rejoint le groupe des Drs. Van der Henst et Noveck travaillant sur le raisonnement (L2C2 ; Institut des sciences cognitives Marc Jeannerod ISCMJ Lyon). J'ai utilisé l'électroencéphalographie (EEG) et la magnétoencéphalographie (MEG) afin de (1) identifier la dynamique des étapes cognitives impliquées dans le raisonnement telles que les attentes probabilistes (section 1- Synthesis of past work) et (2) tester le rôle général des oscillations alpha (~ 10 Hz) dans l'inhibition active, dans le cas d'un raisonnement heuristique (section 2- Synthesis of past work). Pour étendre mes travaux sur la dynamique oscillatoire cérébrale sous-jacente au traitement de l'information et à la cognition, j'ai rejoint (avec une bourse Fyssen) le groupe du Prof. Jensen au Donders Institute (Nimègue, Pays-Bas). En utilisant une combinaison de techniques d'investigation cérébrale complémentaires, nous avons découvert de nouvelles propriétés des oscillations alpha jouant un rôle clé dans l'inhibition fonctionnelle (section 2 - Synthesis of past work).

Enfin, en parallèle de ce travail expérimental, j'ai apporté un certain nombre de contributions théoriques à mon domaine, notamment avec Ole Jensen (section 2- Synthesis of past work) et j'ai développé un nouveau cadre théorique concernant le rôle des oscillations dans le codage de l'information et la communication cérébrale (section 1-Framework and current project). Afin de tester les prédictions découlant de ce cadre théorique, j'ai développé un projet incluant des expériences utilisant l'IRMf laminaire-EEG combinées, de la magnétoencephalographie (MEG) haute résolution, de la stimulation transcrânienne (tACS) combinée à des flickers ainsi que des données d'électrophysiologie (laminaire) chez le singe (section 2-Framework and current project). Ce projet a été fortement impacté par la crise sanitaire (et également par un congé maternité) mais la quasi-totalité des données a été enregistrée et les analyses sont en cours. Je présente ici principalement les résultats de l'étude en IRMf-EEG combinée.

En parallèle, j'ai porté un regard plus critique sur les différents cadres théoriques existants dans la littérature sur les oscillations incluant ceux auxquels j'ai contribué. Notamment, une grande

question est de déterminer si les oscillations, du fait de certaines propriétés détaillées dans ce manuscrit, sont adaptées au traitement de l'information en milieu écologique. Dans la dernière section de ce manuscrit, je propose ainsi de nouvelles idées sur le rôle computationnel des oscillations ainsi qu'un projet visant à tester ces idées (section 3 – New Framework and future project).

Enfin en conclusion, je discute de la formidable synergie qu'il existe dans notre équipe Cophy, que je co-dirige avec le Dr Jérémie Mattout, et qui ouvre la voie à de nouvelles lignes de recherche. Notre force est de toujours proposer un versant théorique et un versant expérimental qui se complètent.

De manière plus générale, un aspect clé de mon travail est d'essayer de tester (1) la robustesse des résultats que nous avons observés soit en concevant des expériences visant à les reproduire partiellement, soit en collaborant avec des individus visant à concevoir des expériences similaires et (2) la validité des idées théoriques que j'ai contribué à développer.

Synthesis of Past work – Current Debate

1. M/EEG CAN PROVIDE UNIQUE INSIGHTS INTO THE MECHANISMS INVOLVED IN REASONING

1.1 GENERAL BACKGROUND

Deductive reasoning involves deriving a logically certain conclusion from premises. Consider a prototypical example, **Modus Ponens (MP)**, in (1) below:

- (1) **Major premise:** *If Claire sings then she dances* (If P then Q)
Minor premise: *Claire sings* (P)
Conclusion: *Therefore Claire dances* (Q)

The conclusion that Claire dances derives from the integration of the two premises. The mechanism underlying such reasoning has been intensively investigated in cognitive psychology but an important breakthrough has been made in the last few years with the use neuroimaging techniques such as functional magnetic resonance imaging (fMRI). In particular, fMRI has allowed to show that different types of reasoning rely either on spatial or verbal processing (Bonnefond & Van der Henst, 2009; Prado et al., 2011).

However, these approaches were based on techniques and analyses which did not allow (1) to separate the main steps (premises and conclusion) and substeps (e.g. integration of premises and anticipation of the conclusion inferred) of reasoning and (2) to detect cognitive mechanisms such as probabilistic expectations. We therefore used EEG and MEG to unfold these mechanisms in time during logical and **fallacious** reasoning such as the **Affirmation of Consequent (AC)**, in (2) below:

- (2) **Major premise:** *If Claire sings then she dances* (If P then Q)
Minor premise: *Claire dances* (Q)
Conclusion: *Therefore Claire sings* (P)

We investigated reasoning based on abstract (e.g. *If P then Q*; **section I.1**) and thematic (e.g. *If Claire sings then she dances*; **section I.2**) contents. We identified several event-related potentials (ERPs) of interest in the EEG experiments and I will focus in this report on one of them (a frontal ERP arising at 200ms), which indicated whether participants had expectations regarding the stimulus presented.

1.2 REASONING BASED ON ABSTRACT MATERIAL GENERATES NARROWED EXPECTATIONS

In a first EEG experiment (Bonnefond & Van der Henst, 2009), based on the use of letters, the major premise (e.g. *If P then Q*), the minor premise (e.g. *P*) and the conclusion (e.g. *Q*) were presented sequentially. The profile of the frontal ERP indicated that the processing of the major

premise *If P then Q* generated specific expectations regarding the minor premise *P* to be presented. In addition, the integration of the premises (i.e. the inference) also generated specific expectations about the conclusion to be presented *Q*. This experiment served as ground work for further EEG experiments that I conducted during my PhD and in which we tested predictions derived from theories of reasoning (Evans, 2006).

The second experiment was a typical example of how EEG can provide information about processes involved in reasoning (Bonnetfond et al., 2012) that neither behavior nor fMRI can provide. The profile of the frontal ERP clearly showed that even participants who eventually endorsed the fallacious inference AC (see example 2) did not expect the minor premise of the AC argument (*Q*), even though its likelihood of presentation was the same as the minor premise of the MP argument (see example 1). These findings suggest that conditional statements raise specific expectations about MP arguments among all participants. Moreover, this experiment allowed to **reproduce** the findings of the first experiment (Bonnetfond & Van der Henst, 2009) as the EEG profile observed in the MP argument was similar in both experiments.

In addition, we conducted an MEG experiment to investigate in details the substeps of the MP inference (see example 1). To that aim, we used visual shapes as minor premises and sounds as conclusions (Bonnetfond et al., 2013) in order to efficiently disentangle the processing of the minor premise in the visual cortex and the auditory anticipation of the conclusion in the auditory cortex. This experiment revealed distinct networks associated with the substeps of the inference during the minor premise processing including the integration of the premises in a fronto-parietal network (at 400-450 ms after the minor premise onset in figure 1) and the encoding/maintenance of the conclusion generated in working memory in the right medial frontal gyrus and auditory cortex (at 500-1500ms in figure 1). The fronto-parietal network revealed here is in line with the results of a meta-analysis of the fMRI data obtained during reasoning tasks (Prado et al., 2011). Therefore, this experiment provides a proof of principle that MEG can be a powerful tool to study the dynamics of reasoning as it combines a good spatial resolution with an excellent temporal resolution.

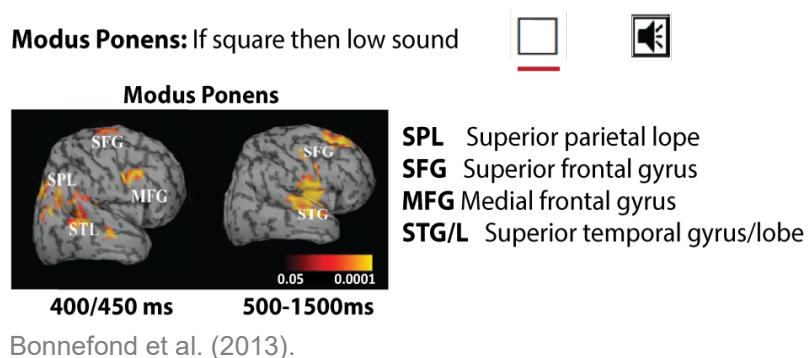


Figure 1. Dynamics of brain activation observed using MEG during the inference, i.e. during the processing of the minor premise (e.g. a square) of a Modus Ponens argument. T=0ms corresponds to the onset of the minor premise, i.e. the shape. Adapted from

1.3 REASONING BASED ON THEMATIC MATERIAL INCORPORATES THE LIKELIHOOD OF EVENTS

First, we were able to **replicate** the results of our first EEG experiment using thematic material (Bonfond & Henst, 2013). However, one specificity of thematic premises (e.g. *If Claire works then she passes her exams*) is that people might consider that the inference that *Claire passes her exams* given that she worked hard is not necessarily true as they will consider that additional elements (i.e. **disablers**) might prevent Claire's success (e.g. she was ill the day of the exam). Using EEG, we compared the processing of the conclusion for major premises associated with few versus many potential disablers (Bonfond, Kaliuzhna, et al., 2014). We showed that the conclusion preceded by a major premise with many potential disablers was less expected than the conclusion preceded by a major premise with few potential disablers. We interpreted this result as providing evidence that participants encoded the likelihood of the relation between the elements of the major premise, a mechanism predicted by the suppositional theory of Evans et al. (2006).

We pioneered the use of EEG/MEG in the field of reasoning, as such studies were not available when I started my PhD (Bonfond, Castelain, et al., 2014). This work has been influential in the field and has since been **reproduced** by many groups (e.g. Blanchette & El-Dereby, 2014).

2. UNRAVELING THE ROLE OF OSCILLATIONS IN COGNITION

2.1 GENERAL BACKGROUND

One central question in neuroscience is how brain areas become engaged in a task and interact. One proposition is that this is achieved through functional connectivity set up by synchronized neuronal activity in task-relevant regions oscillating at the **gamma** (30-100Hz) frequency (Fries, 2005, 2015a). During my PhD and my post-doctoral work, I worked on a complementary hypothesis which is that functional disengagement of task-irrelevant regions is just as important as the engagement of task-relevant regions. This disengagement serves to optimally direct the flow of information by blocking irrelevant regions, and has been proposed to occur through **alpha** oscillations (8-13 Hz) (Jensen & Mazaheri, 2010; Klimesch et al., 2007). Specifically, we conjectured

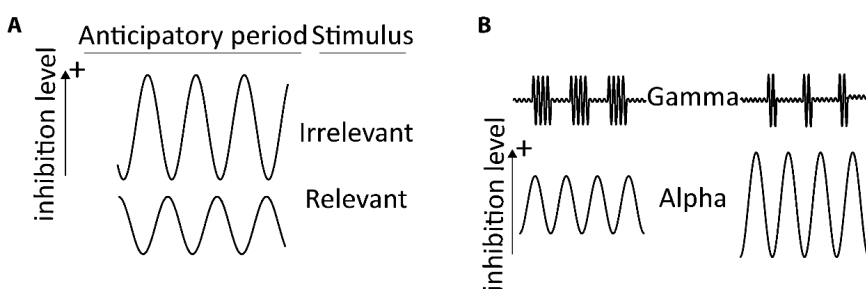


Figure 2. Main hypotheses tested in my PhD/Post-doctoral work (A) Hypothesis 1: Both the phase and magnitude of alpha oscillations are adjusted in anticipation of a predictable irrelevant or relevant item. **(B) Hypothesis 2:** Alpha

magnitude increase is associated with an alpha phase-specific gamma magnitude decrease.

that high alpha magnitude reflects disengagement and as such predicts performance in high-level cognitive tasks (section 2.2). Moreover, alpha oscillations are expected to reflect pulses of inhibition every ~100ms. This leads to two hypotheses: **(1)** the phase of alpha oscillations –and not just their magnitude (Thut et al., 2006a)– could be adjusted in anticipation of a predictable stimulus, in order to optimize its processing (when relevant) or suppress its processing (when irrelevant). More precisely, visual alpha oscillations would be in their excitable phase when relevant information reaches the visual cortex, and in their inhibition phase when this information is irrelevant. **(2)** Gamma oscillations should be coupled to alpha oscillations and their magnitude should decrease during the inhibition phase of alpha oscillations (i.e. the phase associated with the pulse of inhibition) when alpha magnitude increases (figure 2B and section 2.4).

2.2 ALPHA OSCILLATIONS ARE INVOLVED IN HIGH LEVEL COGNITIVE TASKS

Although alpha oscillations had been shown to be modulated in anticipation of stimuli in attentional tasks, it remained unknown whether they were similarly modulated in high level cognitive tasks and how this modulation was top-down controlled.

The last experiment of my PhD aimed at studying the role of alpha oscillations in functional inhibition using MEG and a reasoning task that induces a perceptual bias known as the “matching bias”. This bias leads people to reject any conclusion (e.g. *a J in a circle*) whose items are not “matched” to those presented in a preceding rule (e.g. *If there is a J then there is not a square*, which is compatible with the conclusion *a J in a circle*). In order to correctly perform the task, participants have to overcome such a perceptual bias. An fMRI study has shown that this process can be accounted for in terms of functional inhibition of the visual cortex by a prefrontal area (Prado and Noveck 2007). Using MEG, we showed that this inhibition was correlated with an increase of alpha magnitude in the visual cortex. Moreover, we revealed that posterior alpha magnitude was inversely correlated with gamma oscillations in the dorsolateral prefrontal cortex (Bonfond et al., Human Brain Mapping Conference 2010; Ferez et al. in prep.). During my post-doc at the Donders Institute, we further showed using MEG that fluctuations in alpha magnitude predict individual differences in detecting the implicit statistical properties of a task (Horschig et al., 2014).

2.3 BOTH ALPHA MAGNITUDE AND PHASE ARE ADJUSTED IN ANTICIPATION OF STIMULI

The first experiment of my post-doc (Bonfond & Jensen, 2012, 2013) aimed at determining whether both alpha magnitude and phase are under top-down control and help to maintain relevant information in working memory (WM). We designed a WM task in which a memory set of 4 consonants was presented to the participants followed by a memory probe. In the retention interval, we presented either weak (a symbol) or strong (a letter) distractors (figure 3A). Importantly, the strength and onset of the distractor were predictable across trials. We found that alpha magnitude in visual areas was increased and its phase was adjusted in anticipation of strong compared to weak

distractors (figure 3B & C), so that the processing of strong distractors would be optimally suppressed. This interpretation was in line with an additional analysis showing that trials in which the pre-distractor phase was opposite to this overall adjusted phase presented longer reaction times (RT) to the probe (figure 3D).

The literature on the link between alpha power and distractor processing suppression in WM, memory encoding but also attention, tasks is rich. Many studies has confirmed a tight relation between the two (Park et al., 2014, 2014; Payne et al., 2013). However, and very interestingly, many studies have also found contradictory or null findings (Sghirripa et al., 2021), e.g. during working memory tasks in particular when the distractors are strong (in terms of set size for example) and remain on the screen. For instance, in a WM task, Schroeder, Ball, & Busch (2018), alpha power decreases with the number of distractors presented on the screen which might either be related to a failure to inhibit them or an alternative mechanism. The current debate regarding the link between alpha oscillations and functional inhibition in general is discussed in detail in section 2.6.

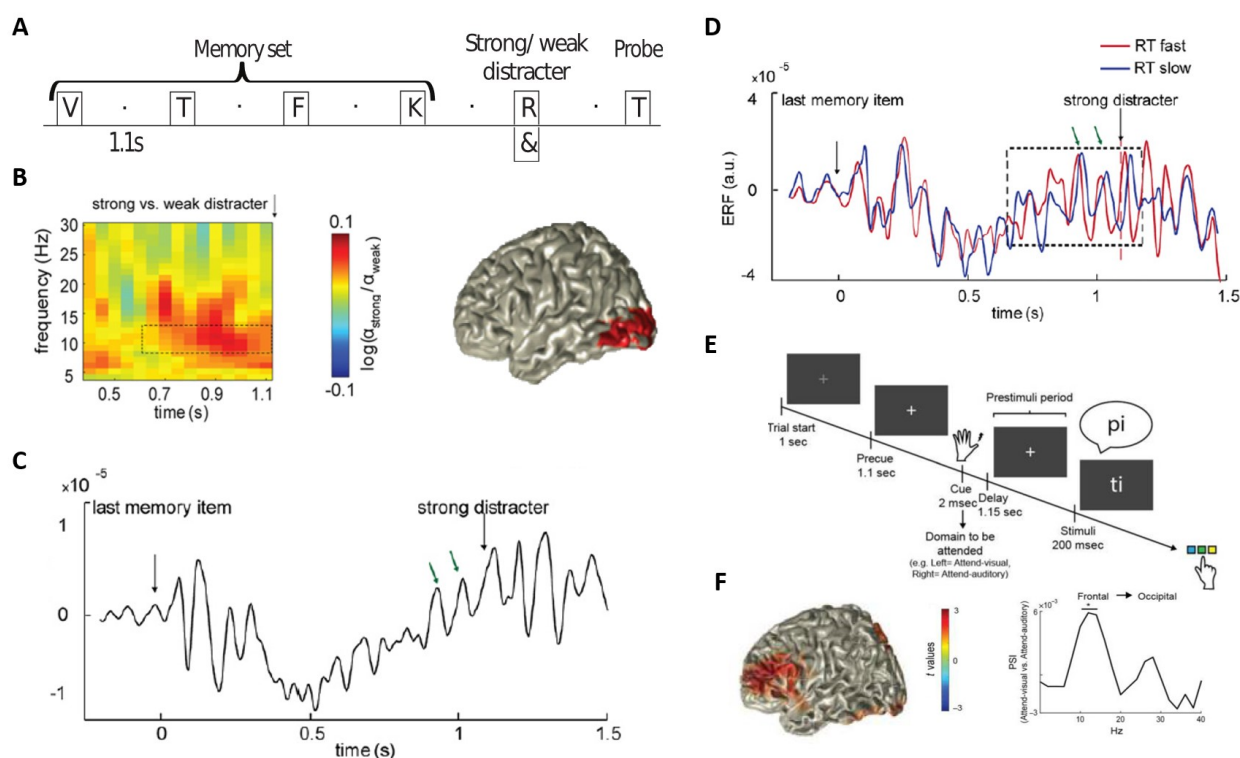


Figure 3. Adjustment of alpha magnitude and phase in anticipation of distracting stimuli. (A) Working memory task. Participants had to indicate whether a probe was part of the previously presented memory set of 4 letters. In the retention interval a ‘weak’ (a symbol) or ‘strong’ (a consonant) distractor was presented. **(B)** (left) Time frequency representation (TFR) showing higher alpha magnitude in anticipation of strong compared to weak distractors (right) This effect was localized in visual areas, including the left temporal cortex. The arrow indicates the distractor onset. **(C)** Event related field (ERF) within a region of interest in the left temporal area. This figure illustrates that alpha cycles appears prior to the strong distractor indicating that the phase of these oscillations was coherent across trials. **(D)** ERF in fast and slow RT to the probe. This figure illustrates that the alpha phase observed in slow trials differs from the overall adjusted alpha phase. Adapted from Bonnefond and

Jensen (2012). (E) Bimodal attention task. A somatosensory cue indicated which sensory domain to attend (visual or auditory). After a constant delay of 1.15s, congruent or incongruent visual and auditory stimuli were simultaneously presented to the subjects who had to indicate with a button press which type of stimulus ('pi', 'ti' or 'ki') was presented in the attended domain. (F) (left) High alpha phase locking value was observed in anticipation of the relevant visual stimulus in both visual and left frontal areas (right) phase slope index results indicated that the frontal alpha activity was leading visual alpha activity. Adapted from Solís-Vivanco, Jensen and Bonnefond (2018)

Interestingly, the phase adjustment also remains an open issue as it has been replicated by two groups (Cravo et al., 2015; Samaha et al., 2015; see also Harris et al., 2018) but not by another one (van Diepen et al., 2015). Therefore, we designed an attentional task to specifically test the hypothesis of the alpha phase adjustment (Solís-Vivanco et al., 2018). In this experiment, a somatosensory cue indicated which sensory domain to attend, i.e. the visual or the auditory domain. Following a constant delay (1.15s), a visual and an auditory stimulus (the consonants 'pi', 'ti', 'ki' which does not have meaning in Dutch) were simultaneously presented (figure 3E). This design was particularly challenging for the alpha phase adjustment hypothesis as the constant duration to detect for the brain was between a somatosensory cue and visual and auditory stimuli and the design was not rhythmic as in the first experiment. We observed stronger alpha phase adjustment in anticipation of relevant than in anticipation of irrelevant visual stimulus in the visual cortex (figure 3F). The increase phase adjustment could not be attributed to a larger signal to noise ratio (SNR) as the magnitude of alpha oscillations was weaker in that condition. **The adjusted phase was moreover associated with faster RT and stronger stimulus induced gamma oscillations than the opposite phase.** We therefore **confirmed the result of the first experiment** using a different design aiming at challenging this hypothesis. However, alternative mechanisms could not be completely ruled out by this last experiment such as the fact that the somatosensory cue could generate an evoked activity in the visual domain as it has been observed in the auditory to visual domain (Romei et al., 2012). However, this is unlikely as this evoked activity emerges later in our study than in Romei' study (0.75 to 1.15s after the somatosensory stimulus compared to a no delay effect) and depend on the attention state. Another design manipulating the time predictability of the target stimulus, as it was initially planned, would however be better appropriate to definitely rule out this hypothesis (but see also Samaha et al., 2015). More importantly, it is crucial to put the necessity of such phase adjustment for optimizing sensory processing into perspective, as it relies on predicting the timing of a stimulus with a ~50ms resolution. The question is then in which natural condition could it occur? Most of the situations requiring such a subtle time prediction are linked to a motor output, e.g. during ping pong or when the time of the stimulus processing is controlled by a motor action such as saccades. Further studies are required to determine whether alpha oscillations anticipatory adjustment can be used in similar situations (see Grabot et al., 2019; Kononowicz et al., 2020 showing an interesting link between alpha-beta coupling and the precision of temporal representations). However, our main

interest in these experiments was to show that **the phase of alpha oscillations was internally controlled**, a mechanism crucial for setting-up inter-areal communication (see section 3). In line with that idea, we further showed that alpha activity in the left (dorsolateral) prefrontal cortex was leading posterior alpha activity (figure 3F; see also supplementary material of Bonnefond & Jensen, 2012 presenting similar results which, however, did not reach significance level).

2.4 ALPHA PHASE AND GAMMA MAGNITUDE ARE COUPLED AND ANTI-CORRELATED

Previous work had indicated the existence of cross-frequency coupling between alpha and gamma oscillations in humans during rest (Osipova et al., 2008) but it remained to be understood how this interaction was implemented between the layers of the cortex as well as to get insights into the magnitude relationship between the two frequency bands (hypothesis 2 in figure 2).

In collaboration with David Leopold (National Institute of Mental Health, USA), we re-analyzed laminar recordings in visual area V1 of awake monkeys previously showing prominent alpha activity in deep cortical layers (Maier et al., 2010). We showed that (1) alpha oscillations in deep layers were specifically coupled to gamma oscillations in superficial layers (figure 4A) and (2) gamma magnitude decreased when alpha magnitude increased, mainly during the trough of alpha activity (Spaak et al., 2012a).

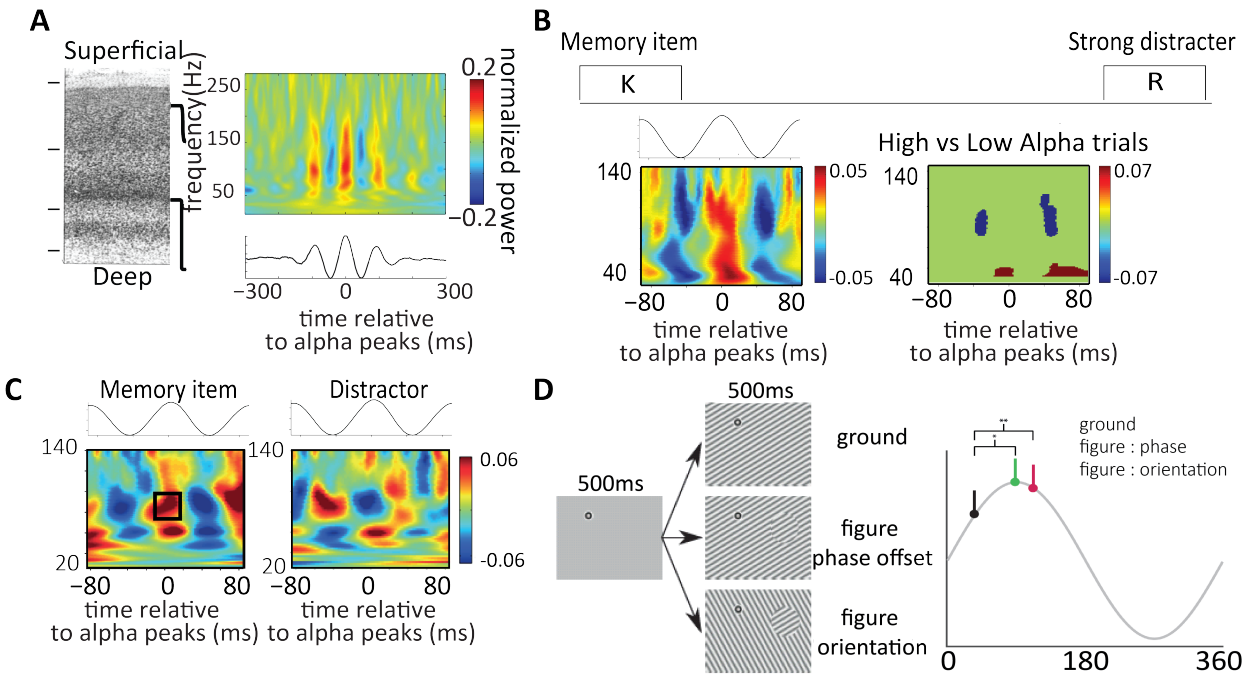


Figure 4. Coupling between alpha phase and gamma magnitude. (A) Time Frequency Representation (TFR) of normalized magnitude in superficial layers for epochs time-locked to the peaks of the deep alpha rhythm. (B) **Left:** TFR of power for epochs time-locked to alpha peaks. **Right:** contrast of the peak-locked TFR for high versus low alpha power trials. (C) Peak-locked TFRs during memory item and distractor processing

indicate a different preferred phase for stimulus induced gamma. (D) Preliminary results from an EcoG study using a figure ground task. These results in V3 of two participants showed that the gamma induced by the figure or ground did not occur during the same alpha phase. Adapted from Spaak et al. (2012), Bonnefond & Jensen (2015) and Gutteling et al. (in prep.).

In order to test whether the above negative correlation between alpha and gamma magnitude could be observed during a cognitive task in humans (and not just during rest in monkeys), we performed further analyses on the previously described WM/MEG data (figure 3A). We found that alpha phase was coupled to gamma oscillations in anticipation of distracting stimuli, and that the higher the alpha magnitude, the lower the gamma magnitude at the trough of alpha activity (figure 4B; Bonnefond & Jensen, 2015). We further showed that gamma magnitude is maximal at different alpha phases during the memory item and processing of the distractor. This is consistent with a theoretical idea we had previously proposed, suggesting that gamma oscillations associated with a stimulus occur at different alpha phase according to its relevance (Jensen, Gips, Bergmann, & Bonnefond, 2014; see also figure 3D; but see section 3).

2.5 ALPHA/BETA OSCILLATIONS ASSOCIATED WITH INHIBITION IN THE VENTRAL ATTENTION NETWORK

Most results presented above were found in the occipito-parietal cortex. A remaining question was whether similar effect could be found in other networks. Interestingly, several studies have reported a decrease of the BOLD signal in the right ventral attention network (including the temporo-parietal junction, the inferior and the medial frontal gyri) during goal-oriented tasks such as attentional tasks (for reviews, see Corbetta et al., 2008; Corbetta & Shulman, 2002). As this attention network has been associated with the detection of, relevant, but unattended stimuli, this decrease was interpreted as reflecting the inhibition of this network in order to prevent the processing of distracting information during these tasks. We therefore hypothesized that this network would be inhibited, as reflected by an increased power in the alpha band, after the processing of the cue in the bimodal task introduced in Solís-Vivanco et al. (2018; see figure 3E). We found an increase in the high alpha-low beta band (10-20Hz) in the right attentional network during the delay following the cue processing compared to the delay before the cue (figure 5A). This effect was correlated across subjects with a lower sensitivity to distractors (figure 5B). These results provided the first evidence that inhibition in the ventral network was associated with alpha oscillations although the frequency range encompassed the beta band (Solís-Vivanco et al., 2021). We replicated this effect in a cue-based Stroop task (figure 5C; Ferez et al., in prep.). The frequencies associated with functional inhibition might therefore differ across networks (see also Haegens et al., 2014).

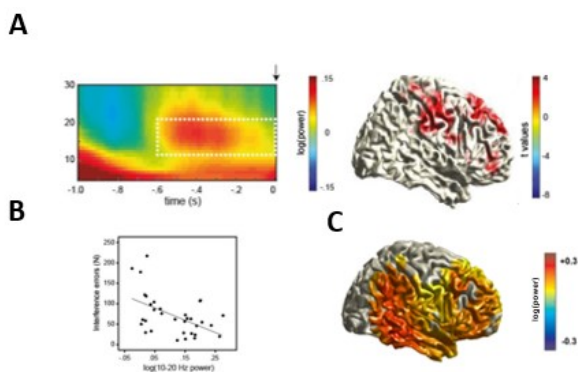


Figure 5. Increase of high alpha-low beta amplitude before stimulus onset. (A) (left) TFR showing higher alpha/beta magnitude during the post-cue delay (before stimulus onset) compared to the pre-cue period over right sensors during the task presented in figure 3D (right) this increase was localized over the right temporo-parietal junction and the right and middle frontal gyri (B) Higher power in this frequency band was associated with less interference errors (i.e. errors corresponding to the report

of the stimulus presented in the unattended domain) across subjects ($p=0.004$) (C) Similar results (10-20Hz) were observed post-cue in a feature attention task similar to a Stroop task with a cue indicating whether to attend to the word or the color of the ink in each trial.

2.6 CURRENT DEBATE REGARDING THE ROLE OF ALPHA OSCILLATIONS

The putative role of alpha oscillations in functional inhibition has been challenged lately (Antonov et al., 2020; Foster & Awh, 2019; Gundlach et al., 2020; Noonan et al., 2016, 2018; Slagter et al., 2015; van Moorselaar et al., 2021). In particular, whether alpha amplitude is increased to protect perceptual and working memory processes from distractors is still unclear. I present briefly here a review of the observed link between pre-stimulus alpha oscillations and perception. I will then present studies showing how they are modulated by attention in different brain networks. Finally, I will discuss the context in which alpha increase might be specifically observed. This section will be further developed in a paper (Bonfond et al. in prep.).

2.6.1 Ongoing alpha oscillations impacts perception and early event related components

First, a large body of literature shows that spontaneous prestimulus alpha (and surrounding frequencies) amplitude influence visual processing, e.g. it impacts both the probability of reporting near-threshold stimuli and of reporting the presence of stimuli while they were absent (i.e. change of the criterion parameter as defined in the signal detection theory). More precisely, lower alpha amplitude, is associated with an increase of the criterion as well as of early (50-75ms) stimulus evoked potentials (C1; Iemi et al., 2019; Zazio et al., 2021). It has therefore been suggested that alpha decrease/increase would be associated with an increase/decrease of the baseline sensory excitability respectively (see Samaha et al., 2020).

Similarly, to amplitude changes, alpha phase has been shown to influence visual stimulus processing, e.g. the detection of near-threshold stimuli or the reaction times to supra-threshold stimulus as well as early visual evoked components (Harris et al., 2018; Dou et al., 2021; Zazio et al., 2021; see VanRullen, 2016 for a review). Only a handful of papers did not find an effect of alpha

phase on perception (e.g. Bompas et al., 2015; Ruzzoli et al., 2019). Recently, Dou et al. (2021) and Fakche et al. (2022) showed that posterior alpha phase impacted more the early evoked component and the likelihood of perceiving TMS-induced phosphenes when alpha power was strong (additional analyses ruled out the signal-to-noise ratio as an explanation). These results were in line with the alpha-inhibition hypothesis, i.e. the alpha amplitude increase would be associated with stronger pulses of inhibition (see figure 2). These results show that alpha power and phase can impact perception and early evoked components indicating that they modulate excitability in the **early visual cortex**.

However, as mentioned above, there is currently a debate as whether alpha oscillations are modulated, in particular whether alpha power increase, during (spatial and feature) attention and working memory tasks. Also, the source localization of these modulations and how they relate to the excitability of the visual cortex or perception is highly discussed (Antonov et al., 2020; Zhigalov & Jensen, 2020).

2.6.2 Alpha decrease/increase in attention and memory tasks

Although many studies have studied alpha lateralization during **covert spatial attentional** tasks, i.e. following a cue indicating which side to attend, some of these studies did not report (via a contrast with baseline) whether the lateralization was driven by the contralateral (to the attended side) alpha decrease, the ipsilateral alpha increase or both (Barne et al., 2020; Heideman et al., 2018; Horschig et al., 2014; Zhigalov & Jensen, 2020; Zumer et al., 2014).

However, many studies have reported a **contralateral (to the attended side) decrease of alpha amplitude** in anticipation of targets (Capilla et al., 2014; Dombrowe & Hilgetag, 2014; Gould et al., 2011; Grent-'t-Jong et al., 2011; Ikkai et al., 2016; Jongen et al., 2006; Kelly et al., 2009; Rihs et al., 2007; Rihs et al., 2009; Thut et al., 2006; Trenner et al., 2008; Voytek et al., 2017; Wildegger et al., 2017; Worden et al., 2000; Wyart & Tallon-Baudry, 2008; Yamagishi et al., 2005, 2008) which was often (12 of the 18 studies mentioned here) correlated with accuracy and reaction times (e.g. Capilla et al., 2014a; Thut et al., 2006b). The link between the effect of alpha oscillations on criterion in detection tasks as described above and the effect observed on sensitivity (as indexed by an improved accuracy) in attention tasks remains however to be understood (Samaha et al., 2020). In **spatial somatosensory, feature or cross-modal attention tasks**, an alpha decrease related to the anticipation and processing of relevant feature has been reported as well (Bollimunta et al., 2008; Diepen & Mazaheri, 2017; Foxe et al., 1998; Fu et al., 2001; Mazaheri et al., 2014; Solis-Vivanco et al., 2018; van Diepen et al., 2015; Haegens et al., 2012a; Haegens, Luther, et al., 2011).

Ipsilateral alpha increase has been also been reported in **spatial attention studies** (Antonov et al., 2020; Capilla et al., 2014b; Frey et al., 2014; Green et al., 2017; Gundlach et al., 2020; Gutteling

et al., 2021; Ikkai et al., 2016; Kelly et al., 2006a; Rihs et al., 2007, 2009; Sauseng et al., 2009; Siegel et al., 2008; Wildegger et al., 2017; Zhigalov & Jensen, 2020; see figure 6). According to the alpha inhibition related theories (Foxye & Snyder, 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007), it has been, in particular, suggested that **alpha increase would be related to the protection of perception and/or working memory processes from distractors**. In line with that, most of these studies presented distractor on the unattended side (9/13) and one of them had placeholders all the trials long even in the unattended side. Gutteling et al. (2021) further reported a link between alpha modulation with perceptual load (related to the degree of noise of the target) and the behavioral distractor interference. They also reported that alpha increased with the strength of distractors under the high target load condition only (figure 6D). Using a retro-cue visual attention paradigm with clearly dissociated target/distractor positions, Rösner et al. (2020) showed a distractor-related alpha increase following the retro-cue presentation. Such increase was also correlated with behavior, i.e. stronger alpha power was related to weaker interference effect. In **spatial somatosensory and auditory tasks**, many studies have reported an alpha increase (compared to baseline) over ipsilateral sensory areas in presence of distractors (e.g. Haegens et al., 2012; Wöstmann et al., 2019) while no increase (compared to baseline) was observed in absence of distractors (Haegens, Handel, et al., 2011). A link between alpha increase and discrimination performance was reported in Haegens et al. (2012) and Wöstmann et al. (2019). In a retro-cue spatial auditory task, Klatt et al. (2020) also found a clear distractor-related alpha increase. Alpha increase has further been reported in irrelevant areas in **feature/cross-modal attention tasks** (Bollimunta et al., 2008; Diepen & Mazaheri, 2017; Gomez-Ramirez et al., 2011; Mazaheri et al., 2014; Snyder & Foxye, 2010) and working memory tasks in presence of distractors (Bonnefond & Jensen, 2012; Payne et al., 2013; Sauseng et al., 2009) and was also correlated to performance.

2.6.3 The debate regarding the link between alpha increase and gain modulation

From the results presented above, we could draw the conclusion that alpha oscillations, in all the sensory domains studied, are modulated in both anticipation of targets (alpha decrease) and distractors (alpha increase) to optimize relevant information and suppress the processing of distractors respectively.

However, whether **alpha oscillations are related to active inhibition/gain modulation in particular in covert attention tasks** remains debated (e.g. Antonov et al., 2020; Foster & Awh, 2019).

Specifically, here, we highlight three points that need to be discussed:

First, some studies **did not report any alpha increase** even in presence of distractors (Dombrowe & Hilgetag, 2014, 2014; Gould et al., 2011; Grent-'t-Jong et al., 2011; Kelly et al., 2009; Thut et al., 2006b; Trenner et al., 2008; Voytek et al., 2017; Worden et al., 2000; Wyart & Tallon-Baudry, 2008). In addition, when, instead of cueing the target position, Noonan et al. (2016) cued the distractor position, they did not report a clear contralateral (to the distractor position) alpha increase. Finally, some **studies did not report an additional modulation from distractor strengths** in somatosensory attention task (Haegens et al., 2012b), retrocue based visual attention task (Rösner et al., 2020b), retro-cue based spatial working memory task (Poch et al., 2018), and Sternberg-like working memory task (Sghirripa et al., 2021).

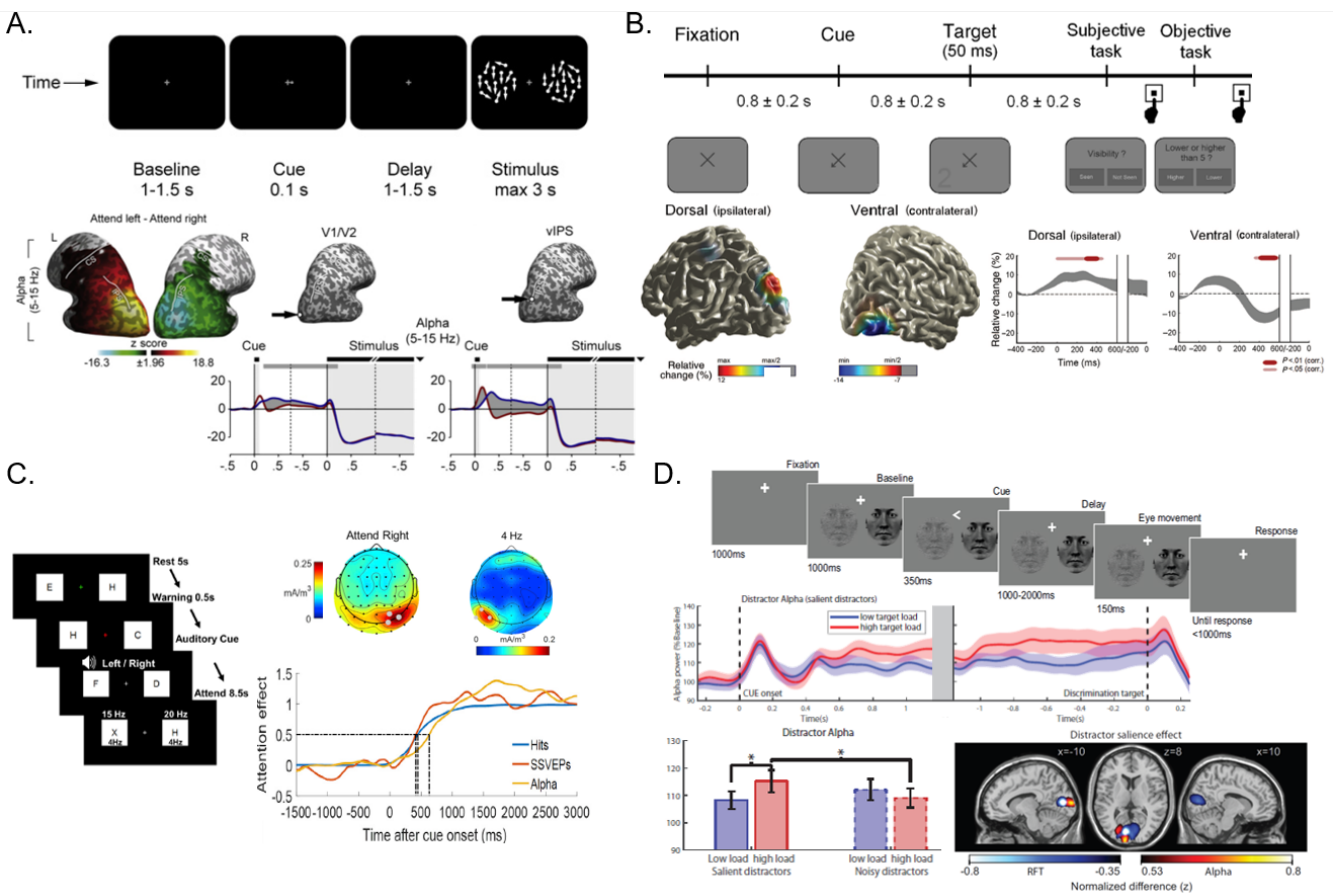


Figure 6. Alpha power increase in different visual attention tasks. **A.** In a MEG attention task involving moving dots, an ipsilateral (to the attended side) alpha increase over V1/V2 and IPS was observed. From Siegel et al. (2008) **B.** In a MEG attention task involving the detection and discrimination of a letter (with no distractor on the unattended side), an alpha decrease was observed in the contralateral (to the attended side) temporal cortex while an earlier alpha increase was observed over the ipsilateral parietal cortex. **C.** In an EEG attention task involving rhythmical visual stimuli (letters), an ipsilateral alpha increase was observed over parietal electrodes while the activity evoked by the rhythmical stimuli (steady state evoked potentials; SSVEPs) was observed over temporal electrodes. In addition, the time course (and the amplitude) of these activities were not

related, the alpha increase occurring later than the SSVEPs modulation (or performance) by attention, i.e. it could not be the cause of the modulation. **D.** In an attention task involving noisy and salient faces as target (high and low load trials respectively) and distractors (noisy and salient distractors), alpha power contralateral to distractors was stronger in the high load condition than in the low load, and higher in the salient than noisy distractors trials only in the high load condition. The source localization of the alpha modulation originated in the occipital cortex but did not overlap with the distractor-related SSVEPs.

Second, the source localization of the alpha increase has rarely been performed, only some MEG studies have attempted to localize it. **If alpha increase was related to a gain control mechanism, in particular a protection of relevant processes from distractors, it should be observed in early sensory areas or in feature specific areas.** However, the sources found in visual spatial tasks were relatively heterogenous.

Many studies have found the increase in early or feature-relevant sensory areas. The alpha increase observed in an attention task with moving dots (on both sides) by Siegel et al. (2008) originated in V1/V2 and the parietal cortex (figure 6A; see also Wildegger et al., 2017). The source of the alpha increase in Gutteling et al. (2021) was found just outside the calcarine extending in the fusiform area while the activity generated by the rhythmical distractor was found in V1 (figure 6D). Using fMRI-EEG, Green et al. (2017) showed that the ipsilateral occipital alpha increase observed using an attention discrimination task was correlated negatively with the BOLD signal in the ipsilateral cortex and positively with the ipsilateral pulvinar. Alpha increase has also been found in early sensory areas in somatosensory and auditory spatial tasks. Haegens et al. (2012) showed that the ipsilateral increase was located in the somatosensory cortex. They also revealed a posterior alpha increase (not lateralized) in the visual cortex which was also linked to performance. Interestingly, Wöstmann et al. (2019), showed that the distractor related alpha increase was located in parietal, posterior temporal, and frontal lobe regions, it was actually more in frontal regions than the target related alpha decrease. In a feature-attention task, Snyder and Foxe (2010) further reported alpha increase in feature-specific (motion and color) streams (dorsal and ventral). In a working memory task, the distractor related increase was reported in the occipital and left temporal cortex (specialized in processing letters) in a Sternberg-like task using letters (Bonnefond & Jensen, 2012).

Other studies have reported an increase over the parietal cortex. Capilla et al. (2014a) used MEG and an attention task without distractors. They localized the contralateral alpha decrease in the temporal cortex but the relatively short lived ipsilateral alpha increase in the parietal cortex (figure 6A). Zhigalov & Jensen (2020) used a an attention task with flickering faces and houses (one on each side in each trial) also found that the alpha modulation originated from the parietal cortex while the target/distractor SSVEPs originated in the early occipital cortex. The authors of this last study suggested that this parietal alpha increase could reflect the gating of the information in higher order regions rather than the gain modulation in early visual regions.

In addition to early sensory and parietal areas, alpha/beta increase has been observed in the ventral attention network during attention tasks (Solís-Vivanco et al., 2021) when the post-cue and pre-cue periods were contrasted. In addition, the higher the increase the lower the behavioral interference from distractors in this task (see also Ferez et al. in prep.).

Finally, four studies tested the link between alpha oscillations and excitability using EEG or MEG and steady-state visual evoked potentials (SSVEPs), i.e. activity generated by visual stimulations at a given frequency (Antonov et al., 2020; Gundlach et al., 2020; Gutteling et al., 2021; Zhigalov & Jensen, 2020). They reported that the ipsilateral alpha increase was not related, in amplitude and latency (and space as mentioned above), to both the attended and non-attended SSVEP (figure 6C and D).

2.6.4 The why, when and where of alpha oscillations

The questions that can be derived from the results presented above are in which context alpha oscillations increase and what is the origin of this increase as well as the mechanism behind (figure 2).

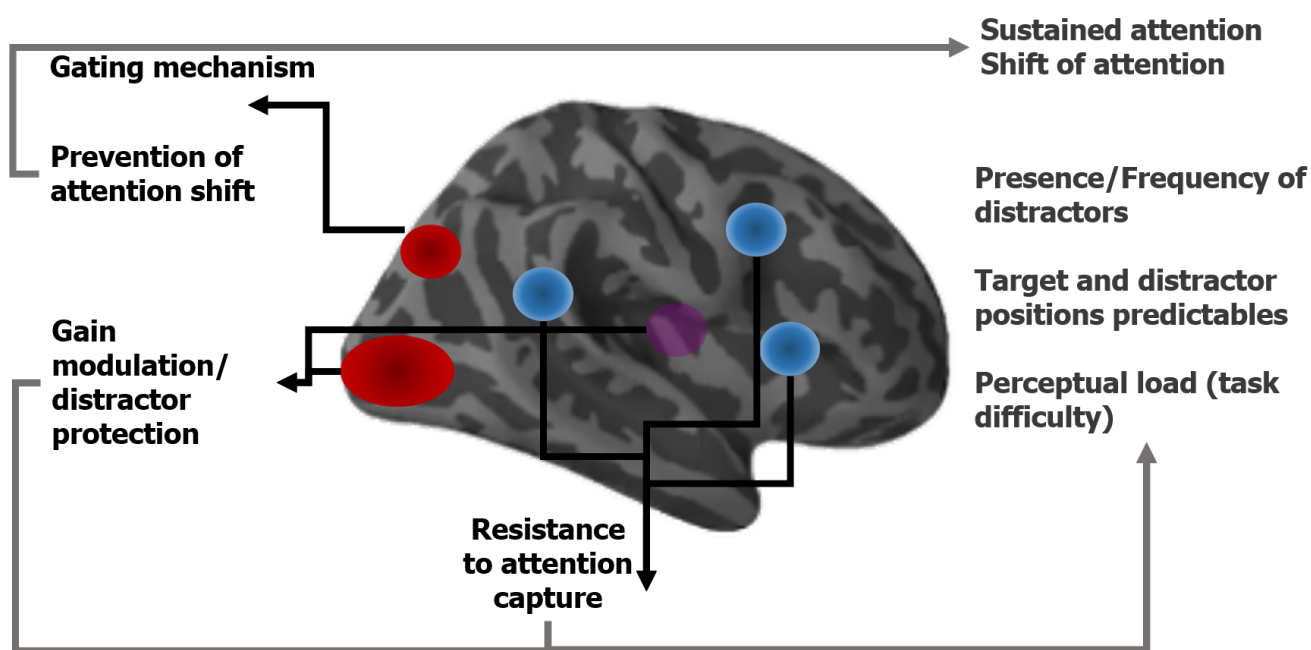


Figure 7. The where and why of alpha power increase. Brain sources (colored circles) of alpha increase, experimental context (in grey) promoting this increase and corresponding mechanisms (in black). Red circles correspond to the occipito-temporal and parietal sources. Blue circles correspond to the ventral attention network. The purple circle corresponds to the thalamus.

2.6.4.1 Experimental contexts promoting alpha increase

Three, non-fully independent, experimental contexts seem to influence the presence of alpha increase:

First, **alpha increase seems often modulated by the presence of distractors, albeit not necessary by the strength of distractors** (Haegens et al., 2012; Poch et al., 2018; Rösner et al., 2020b; Sghirripa et al., 2021; but see below). As reported in Haegens et al. (2012) and Van Diepen et al. (2017), the presence of distractors can lead to an increase of alpha power compared to an experiment without distractors reflecting a general state change due to a general context change. This effect could be compatible with the expectation suppression mechanism mentioned in Noonan et al. (2018) and van Moorselaar & Slagter (2020) and supported by several behavioral studies. It has been shown that distractor suppression might depend on the statistics of the environment. Suppression occurs when frequent distractors are presented at the same position during a task (e.g. Vatterott & Vecera, 2012) and not when their position is indicated on a trial basis (Bogaerts et al., 2022; Noonan et al., 2016). This is in line with predictive processing models in which statistical regularities of the environment are used to limit the processing of the less informative stimuli (Friston, 2005; Friston, 2019; Rao & Ballard, 1999). According to Noonan et al. (2018), this effect would therefore result from inhibition processes within the sensory (visual, somatosensory or auditory) hierarchy. It has been suggested that this suppression mechanism could occur via synaptic changes and would manifest during the processing of distractors via specific evoked potentials (e.g. van Moorselaar & Slagter, 2020). The examples discussed above as well as two studies which specifically studied the effect of repeated distractor position in visual search tasks (Wang et al., 2019; Zoest et al., 2021) indicate, however, that **alpha increase could be involved**. Moreover, an important parameter in these models is the precision weighting, i.e. the expectation about the precision of the incoming input. Such precision weighting has been associated with pre-stimulus alpha oscillations in e.g. the auditory cortex (Sedley et al., 2016). Accordingly, the processing of the distractor (and the prediction error it produces) could be down-regulated via anticipatory high alpha power compared to targets. However, Noonan et al. (2016) and Moorselaar et al. (Moorselaar & Slagter, 2019; van Moorselaar et al., 2020, 2021) did not observe a preparatory alpha increase in similar tasks. It might be due to specific designs, but the studies performed by Moorselaar et al. encompassed many experimental manipulations performed in. One possible explanation could be that the distractor and target positions were better separated in the Zoest et al. (2021) and Wang et al. (2019) as either target or distractor would appear specifically on the vertical line or on the horizontal line relative to the fixation cross. In Noonan et al. (2016) and Moorselaar et al. (2019, 2020, 2021), the target could occur on the same side as the distractor and alpha decrease in anticipation of targets could possibly alter the detection of the alpha increase (but see Moorselaar & Slagter, 2019). Also, as discussed in the next section, in Noonan et al. (2016) and Moorselaar et al. (2020), the distractor can

catch the attention and slow down the process but does not compete with the target at the decision level (different features not associated with a competing response). This might also be a crucial point promoting alpha increase. Finally, the timing of the distractor was predictable in these experiments (it was not in Zoest et al., 2021; but see Wang et al., 2019), although unlikely, the inhibition could rely on alpha phase adjustment rather than alpha power (see Bonnefond & Jensen, 2012; Samaha et al., 2015; Solís-Vivanco et al., 2018; see outstanding questions). However, as suggested by the authors of this study, another mechanism based on synaptic plasticity, in particular in context with very low irregularities, could be at play.

Second, in addition to this contextual effect, **possibly longer anticipatory period (>1s) or trials with sustained attention on one side** (and multiple target/distractors) could favor alpha increase related to sustained attention (see below; Antonov et al., 2020; Frey et al., 2014; Green et al., 2017; Gundlach et al., 2020; Gutteling et al., 2021; Ikkai et al., 2016; Rihs et al., 2007; Siegel et al., 2008; Wildegger et al., 2017). We discuss below, the possible source of and hence mechanisms behind this effect.

Finally, **anticipating the target and associated distractor position, in particular in difficult tasks** seem to be a major component. Already, in behavioral task (at the exclusion of the statistical learning tasks discussed above), distractor suppression occurs only when (1) the presence or not of distractors is indicated to the subjects and (2) when the target position can be anticipated and is predictive of the distractor position (Leber et al., 2016; Noonan et al., 2018). Noonan et al. (2018) suggested that this inhibition would result from secondary inhibition following the top-down modulation of areas related to the processing, i.e. inhibition would arise from biased competition at the lower level and not be as selective as the target facilitation (widespread inhibition). The **perceptual load theory** initially proposed by Lavie (2005) is in line with a link between target processing and distractor filtering. The idea behind this theory is that observers are able to efficiently filter out distractors only when the perceptual load is high. Gutteling et al. (2021) aimed at testing this theory and as discussed above found higher contralateral to the distractor alpha increase in the high than in the low load condition and a higher alpha for high distractors than for low distractors trials specifically in the high load condition. A behavioral benefit of the alpha increase was only found in the high load condition regardless of the distractor noise level. The results from this study are therefore in line with the perceptual load theory and the idea developed in Noonan et al. (2020). Most studies did not manipulate the perceptual load, it is therefore difficult to determine whether the interpretation of the results presented above could be revised in the light of this theory. We here, however, suggest that perceptual load could be a strong predictor of the presence or absence of alpha increase (and of a link with filtering out efficiently the distractors) over occipital areas. Some discrepancies observed between tasks could be driven by the perceptual load.

2.6.4.2 Source origin of the alpha increase and associated mechanism

The source localization of the effects observed is crucial to understand the mechanisms at play in the different contexts. **Many studies reported an alpha increase over the occipital areas** (see above) in line with a gain modulation of the early visual cortex to protect from distractors.

However, as mentioned above; many studies have reported that alpha increase originated in **the parietal cortex**. Zhigavlov & Jensen (2020) suggested that this parietal increase reflected a gating mechanism downstream the early visual regions as opposed to a gain mechanism in the early visual cortex. Alternatively, we suggest that it could reflect an inhibition process preventing attention shifts to the unattended side. This could be particularly important in these studies as covert attention was maintained on the same side for several seconds (see also Antonov et al., 2020; Gundlach et al., 2020). In case of change of attention over trials (without flickers), a relatively short post-cue increase over ipsilateral parietal cortex could also occur to implement the shift (Capilla et al., 2014b). This is in line with a tACS study indicating that stimulation at 10Hz over the left parietal cortex induced a leftward bias in reaction times as compared to sham (Schuhmann et al., 2019). This parietal origin and the associated mechanism would explain the absence of link between alpha and SSVEP amplitude and time course in Antonov et al. (2020), Gundlach et al. (2020) and Zhigalov & Jensens (2020). Alpha increase observed in EEG studies without distractors could also reflect such a process (e.g. Grent-'t-Jong et al., 2011). Furthermore, it is possible that the authors of these three studies did not observe an occipital alpha increase because the rhythmical stimulations prevented the detection of alpha oscillations in early visual regions (see also Samaha et al. 2020 for a discussion of this issue). This interpretation is in line with the absence of alpha power decrease contralateral to the attended side in these studies while it has been observed in many more classical studies (see above). Even in Guttelling & al. (2021), the alpha increase contralateral to distractor was observed in occipital and temporal areas (including the fusiform) but outside the early visual regions in which SSVEPs modulation was observed. This could reflect a gating mechanism as suggested by the authors or a technical issue preventing the early sensory alpha modulation. Possibly the use of flickering stimuli might not be ideal to determine the link between alpha modulation and cortical excitability (see below for an alternative).

Additionally, in many studies, it is also possible that the inhibition is implemented at the **thalamus** level and was not detected using EEG/MEG (Hughes et al., 2004; Hughes & Crunelli, 2005; Lopes da Silva et al., 1974). fMRI studies have indeed shown that attention modulation can be observed in the lateral geniculate (LGN) using fMRI (Kastner et al., 2004, 2006; Schneider & Kastner, 2009).

An additional hypothesis is that alpha/beta increase over the **ventral attention network** (Solís-Vivanco et al., 2021) is involved in protecting the processing of the target from the capture of attention by distractors in many tasks but the relevant contrast was not performed in most of the studies.

2.6.4.3 Future direction and predictions

In conclusion, while the link between alpha oscillations and functional inhibition has been seriously challenged lately (e.g. Antonov et al., 2020; Foster & Awh, 2019; van Moorselaar & Slagter, 2020), it cannot definitely be ruling out. Carefully designed experiments could allow to understand more specifically in which context, which brain regions and therefore to which mechanism it is associated alpha increase occur.

It is possible that synaptic change might be the mechanism underlying distractor suppression in task with implicit learning of the distractor position and low demand of flexibility (Noonan et al., 2016; van Moorselaar & Slagter, 2020). However, in more flexible conditions (with a cue validity or a distractor position certainty below 100%), we predict an alpha increase in sensory regions, possibly reflecting a gain change (or a change of precision weighting), in presence of distractors with an expected spatial position either manipulated with the context or predicted indirectly by the target position.

We further state that the perceptual load is a major predictor of the presence/need for a sensory alpha increase. It is further possible that the level of competition between the distractor and the target at the decision level might play a role, the stronger the competition, the higher the alpha in sensory regions. For instance, in Zhigalov & Jensen (2020), the target was a circle which appeared in 20% of the trials (and in 5% of the trials on the unattended side) on a face or a house. As the relevant target and even more the distractors were rare in this task, the alpha increase over parietal areas could be enough to maintain attention on the attended side. In Gutteling et al. (2020), the participants had to indicate the eyes movements of the attended face, but an eye movement also occurred on the unattended face (figure 6D). In this specific case, the attended and unattended stimuli compete at the level of decision and could explain the alpha increase in sensory regions. Future work is needed to specifically test this effect.

The link between alpha modulation and gain change with attention should probably not be studied using rhythmical stimuli and might rather be highlighted by analyzing the link between pre-stimulus alpha power and stimulus evoked C1 (see the properties of such stimuli in e.g. Dou et al., 2021; lemi et al., 2019). To determine whether expecting features of the distractors would also reflect in specific increase of alpha oscillations in groups of neurons coding for these features, it is important to separate feature and space, i.e. manipulating features that are not mainly coded in early visual regions (e.g. faces, words). Interestingly, Gutteling et al. (2020) used faces in their experiment and found an alpha increase up to the fusiform area.

Finally, the alpha increase in contralateral parietal cortex observed in many studies (e.g. Capilla et al., 2014a; Zhigalov & Jensen, 2020) should be observed in sustained attention task and could be

correlated with the fluctuations of performances. This increase is also expected but should be short-lived during switches of attention side.

Also, the alpha/beta profile over the ventral attention network and whether it prevents the capture of attention by distractor – and how - should be specifically studied in these attentional tasks.

2.6.5 Open questions

In addition to or instead of alpha power increase, resistance to distractors could be implemented via changes in the brain connectivity set-up in the alpha-band (or in another frequency) leading to a decreased communication between higher order and lower order regions associated with the processing of the distractor (Bosman et al., 2012; Chapeton et al., 2019; Pascucci et al., 2018). The link between alpha and gamma locally could further be altered (Pascucci et al., 2018). Therefore, not only alpha power but also connectivity should be studied.

Can alpha oscillations power gradually increase following to the need for inhibition e.g. from weak to strong distractors? If so, it might be hard to determine the mechanisms behind. In the case of the stronger alpha power for strong distractors in Bonnefond et al. (2012), it seems to rather be due to an alpha increase in the left temporal cortex in addition to the occipital cortex, i.e. more neurons seem involved.

While studies using simple detection (of near-threshold stimuli or TMS-induced phosphenes) tasks found a stronger effect of phase when alpha power is high, some studies reported a lower alpha phase effect for the unattended stimuli (supposedly associated with a stronger pre-stimulus alpha power than attended stimuli (Busch & VanRullen, 2010; but see Harris et al., 2018). Another discrepancy between ongoing and attention-modulated alpha power is that the former has been strongly associated with change in criterion but not in sensitivity (discrimination performance) while the later has been associated with change in sensitivity (see Samaha et al., 2020). It is possible that the brain region in which the modulation was observed influences the results. Using MEG, to obtain good spatial resolution, and both discrimination and detection tasks in attention studies could help disentangle the effects observed in the different experiments.

Furthermore, the role of alpha oscillations during stimulus processing and not only in anticipation remain to be fully addressed (van Kerkoerle et al., 2014a). Alpha increase might not only result in higher inhibition but could be a mechanism impacting the stability of visual representation (see van Moorselaar & Slagter, 2020). Very importantly, cognition is tightly linked to action and recent papers further discuss how alpha oscillations could link action, in particular saccades, to visual perception (Jensen et al., 2021) by regulate how long to look at a given target and how fast to saccade to a next (Popov et al., 2021). Oculomotor behavior should therefore be carefully manipulated and analyzed during attention and memory tasks.

In addition to alpha power increase, the existence of a phase adjustment in anticipation of target or distractors with a predictable timing in order to optimize or suppress their processing is still debated with three studies reporting an effect (Bonnefond & Jensen, 2012; Samaha et al., 2015; Solís-Vivanco et al., 2018; see also Harris et al., 2018) and one which did not (Diepen et al., 2015). Also, whether alpha frequency can be top-down modulated according to the instructions of the task requiring e.g. to integrate (slow frequency) or dissociate (faster frequency) two stimuli (Wutz et al., 2018) needs to be further addressed.

We discussed the role of alpha oscillations in sensory gain modulation but their role in motor inhibitory control (Burle et al., 2016) has also been studied (Bönstrup et al., 2015; Hummel et al., 2002; Sauseng et al., 2013). Whether motor inhibition is always associated with alpha increase is remains to be determined.

Finally, it is possible that slower rhythms, in particular in the theta frequency band, instead of alpha oscillations, are modulated by attention and protect against perceptual and memory processes against distractors (Fiebelkorn et al., 2018; Spyropoulos et al., 2018; see last section).

2.7 THEORETICAL WORK: PHASE CODING AND BRAIN COMMUNICATION

The results presented above also led to the development of different theoretical frameworks. Indeed, while a massive amount of data is collected in cognitive neuroscience, there is a strong need for identifying canonical neural mechanisms. I contributed to the development of such theoretical frameworks for studying the role of alpha oscillations beyond inhibition, i.e. in coding and transferring information in the brain (Jensen et al., 2012, 2014). In particular, in my last manuscript (Bonnefond et al., 2017), I attempt to reconcile and expand several frameworks (Fries 2015, Jensen and Mazaheri 2010, Klimesch, et al. 2007) including ours (Jensen et al., 2012, 2014). I will develop the main ideas of this framework in this section along with the current project allowing to test for the predictions derived from this framework. I will then present a new framework developed recently (Bonnefond, Jensen and Clausner, under review) and the associated project.

Framework, Current Project

1. FRAMEWORK: ROLE OF SLOW AND FAST OSCILLATIONS IN BRAIN COMMUNICATION

Beyond the role of alpha oscillations in protecting perceptual/memory processes from distractors, we suggest that it could be involved in brain communication.

The brain can be seen as a mosaic of local networks of neurons specialized in specific computations whose outputs need to be transferred to other specialized local networks for cognition and adaptive behavior to emerge. Along the visual hierarchy in the ventral stream, neurons are sensitive to increasing parts of the visual field resulting from converging feedforward pathways. Feedforward pathways are often associated with feedback pathways which are consequently diverging (figure 8 A). More generally, converging and diverging pathways are ubiquitous in the brain so that the external and internal processing as well as the output behavior are adaptable. As a consequence of this dissociation between anatomical and functional connectivity, the information computed by brain regions has to be flexibly routed through the fixed anatomy of the brain according to the behavioral context or the internal state. Even though this is a core mechanism of the brain, it is still unknown how such routing, or so-called specific inter-areal communication, occurs. Neuronal oscillations are a strong candidate to support such context-dependent routing (Akam & Kullmann, 2014).

Two main frameworks have proposed routing of information based on oscillations. In the example shown in figure 8A, two pools of neurons **a** and **b** are connected to a third pool of neurons **c**. The communication has to be specific from **a** to **c**. The '**communication through coherence**' (CTC; Fries, 2005, 2015) hypothesis suggests that two pools of neurons interact via the alignment of the excitable phase of their local oscillations. This would allow the excitable phase of neurons in **c** to be aligned with synaptic input from neurons in **a**. This framework initially focused on gamma oscillations (>30 Hz, but see Bastos, Vezoli, & Fries, 2015; Fries, 2015) which have been associated with active stimulus processing (Bertrand & Tallon Baudry, 2000; Jensen et al., 2007; Jerbi et al., 2009; Lachaux et al., 2005; Tallon-Baudry et al., 1999). Fries and colleagues proposed that CTC is established by oscillations in neurons in pool **a** entraining neurons in pool **c** at the gamma frequency. This mechanism also implies that interregional synchronization among the neurons in **a** is stronger than in **b**. This is achieved by a top-down drive boosting the synchronization in region **a**. As a consequence, the neurons in **c** are entrained by **a** rather than **b**, thus dynamically strengthening the functional connectivity. The second framework, the '**gating by inhibition**' (GTI) (Jensen & Mazaheri, 2010) suggests that the routing is achieved via the inhibition of irrelevant pools of neurons, set-up through high alpha oscillations (~10Hz) which have been shown to be internally-generated and linked to pulses of inhibition (Foxye & Snyder, 2011; Klimesch et al., 2007). In this way, the information is

constrained to run only through relevant nodes of the network (**a** and **c** in figure 8A) in which the inhibition would be released via a decrease of the magnitude of alpha oscillations.

Even though these frameworks have been extremely helpful, one important shortcoming is that they account for distinct parts of the literature. In particular, CTC does not clearly address the specific issue of diverging routes where gamma oscillations in one pool of neurons will entrain all the pools it is connected to (but see Fries, 2015 for the specific case of the feedback pathway). GTI does not elaborate on the role of gamma oscillations in inter-areal communication -in particular the coherence in the gamma band- nor does it consider synchrony in the alpha-band as a potentially crucial mechanism for communication. Finally, none of these hypotheses proposes a clear mechanism of interaction between internally- and stimulus-driven oscillations, nor do they clearly propose an implementation of these interactions at the microcircuit level (but see Bastos et al., 2015; Fries, 2015). This is why we think there is a crucial need for these frameworks to be unified and extended. **As mentioned in the last section, it is likely that some of the oscillations (e.g. gamma and beta) mentioned here are not per se oscillations, e.g. they are not sustained, but we still use this term in this section to more easily ground this work within previous frameworks (but see last section).**

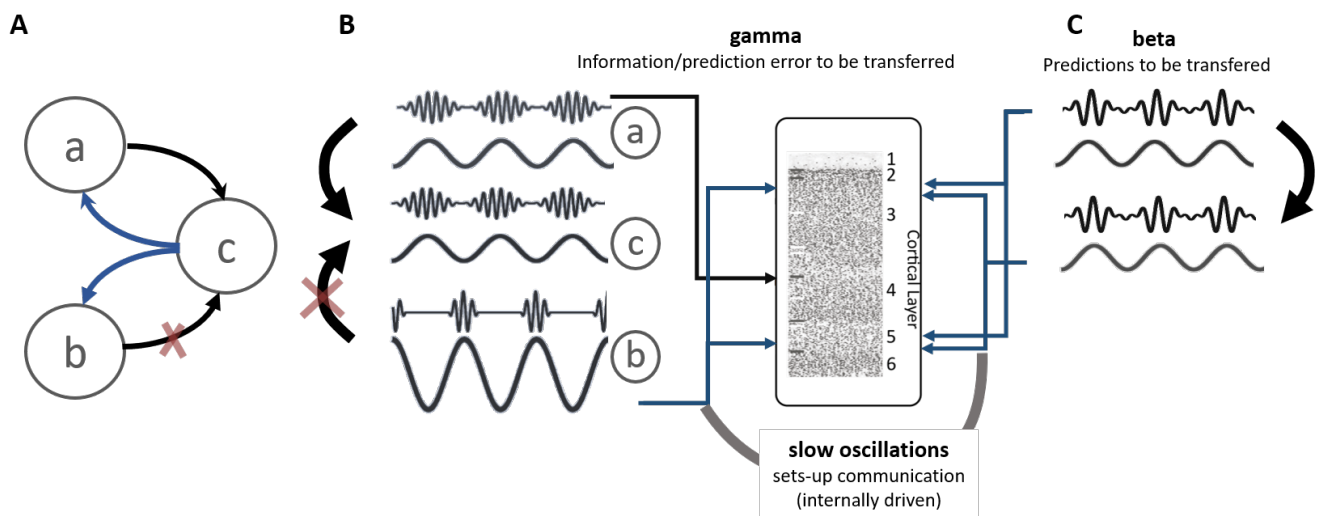


Figure 8. Communication based on nested oscillations (A) a and b neurons in V1 process different stimuli of the environment. Pools of neurons in IT process specifically each of the stimuli but some neurons are involved in the processing of both stimuli (c). **(B)** (left) Example in which the stimulus processed by a is attended while the stimulus processed by b is ignored. The communication from a to c has to be specific. Internally-driven alpha oscillations are expected to be low and in synchrony in a and c while they are expected to be high in b and possibly in anti-synchrony with c. Stimulus-driven, alpha-nested gamma oscillations (possibly carrying prediction error) in a can then specifically entrain gamma oscillations in c. (right) The cortex is organized in layers of neurons that receive input from lower or higher order areas. Alpha/beta and gamma oscillations are prominent in supragranular/infragranular layers and granular/supragranular layers respectively. **(C)** Like gamma in the feedforward direction, predictions regarding the (ongoing or upcoming) stimuli would be carried from higher order to lower order regions in beta bursts nested within alpha oscillations.

The general framework

In order to address the above listed limitations of current models, we introduced a general framework for inter-areal communication based on the nesting of oscillations at different frequencies (see Bonnefond et al., 2017 for details; figure 8). As previously mentioned, many pathways are convergent in the brain. For instance, the processing of two stimuli next to each other will involve overlapping neuronal representations in IT (figure 8A, B). We can consider here two pools of neurons in V1 (**a** and **b**) processing a subpart of two distinct stimuli and targeting a partly similar pool of neurons in IT (**c**). We here propose that:

(1) The context-specific communication between pools of neurons is not set-up by gamma oscillations directly (as proposed by CTC) but by an internally-generated (via feedback mechanisms) slow oscillation (SO) which we expect to be alpha oscillations in the visual network. This is achieved via two mechanisms:

(a) a modulation of SO magnitude (as in GTI for alpha oscillations)

(b) a modulation of the inter-areal SO synchrony

For instance, if you attend the stimulus processed by **a** and ignore the stimulus processed by **b** next to it (figure 8):

- Alpha magnitude will be relatively low (**low inhibition level**) in **a** and **c**. Moreover, the alignment of the excitable phase of alpha oscillations in **a** and **c** (**in synchrony**) will set-up the coupling.
- Alpha magnitude will be high (**high inhibition level**) in **b**. In an extreme case scenario, the alignment of the shortened phase of excitability in **b** to the phase of non-excitability in **c** (**anti-synchrony**) will set-up the decoupling. **Interestingly, another way of limiting the communication is the presence of a difference in frequency between b and c.**

(2) The information about the stimulus is carried out by the stimulus-induced gamma oscillations (60-80Hz). Very importantly, these gamma oscillations are nested within the SOs.

- In **a**, the low magnitude of alpha oscillations allows for a longer duty cycle, i.e. a longer time-window for gamma oscillations to occur during the high excitability phase of alpha oscillations. As the high excitability phase of alpha oscillations will be aligned between the two relevant pools of neurons, gamma oscillations in V1 will **then** be able to entrain gamma oscillations in IT as they are expected to control the timing of the spikes sent from V1 to IT (Fries, 2015a). As a consequence, gamma oscillations in **a** and **c** will be correlated.
- In **b**, the high magnitude of alpha oscillations will reduce the duty cycle, i.e. the gamma oscillation duration. The anti-synchrony of alpha oscillations in V1 and IT will prevent gamma oscillations in IT to be entrained by gamma oscillations in V1. Alternatively, the phase lag between **b** and **c** could just delay the occurrence of gamma oscillations in **c** compared to the gamma oscillations transferred from

a. Consequently, a phase coding of the different information received by IT could be set-up within IT alpha cycles with the most relevant information being processed first.

(3) The framework aims at introducing a general principle that governs interactions within any network regardless of the frequency of the prominent SOs in this network, which can e.g. be theta oscillations (4-8Hz) as in the memory network.

(4) The interaction between internally-generated SOs and stimulus-driven gamma oscillations is expected to be implemented at the microcircuit level.

(5) **This framework can be embedded within the predictive coding scheme** which supposes that perception results not only from the input from our senses but relies as well on expectations (prior predictions). More precisely, this scheme proposes that the brain is a statistical organ generating predictions, with a certain level of confidence, about the state of the world. These predictions are then tested against sensory evidence (deviation between prediction and input is termed *prediction error*) to generate a percept which allows to update the prediction. Based on the literature, we suggest that **predictions** would be encoded, by **beta oscillations (15-25 Hz)** in cells in the deep layers of the cortex receiving feedback projections (Bastos, Vezoli, Bosman, et al., 2015; Sedley et al., 2016). **Confidence** in such prediction would be encoded by **alpha oscillations (8-12Hz)** in deep or superficial layers receiving feedback connections, similarly to the role of alpha amplitude presented in the general framework (figure 8). **Prediction error** would be encoded by **gamma oscillations (>30Hz)** in superficial layers from which feedforward connections originate. **The transfer of top-down prediction (feed-back direction) and bottom-up prediction error (feedforward direction)** will be set-up by (1) local nesting within alpha oscillations of beta (Grabot et al., 2019) and gamma oscillations (e.g. Bonnefond & Jensen, 2015b) respectively and (2) **alpha band synchronization as described in figure 8b (figure 8c)**. Prediction and prediction error would be expressed in an iterative manner, repeating in different alpha cycles, allowing to build, refresh, prioritize, consolidate or update it. The specific layers involved in the different roles of alpha, i.e. communication of predictions and information/prediction errors and attention/precision weighting-related local modulation of excitability, needs to be further specified. The stronger receptive field of the superficial layer anatomical connectivity (Markov et al., 2014) is a good candidate for setting up the communication via alpha synchronization while alpha in the deep layers could be involved in attention (less specific at least for the irrelevant pools of neurons)/precision weighting processes (see also section 3; new framework). The interaction between predictions related beta and the input would occur within the cortical column and would lead to the prediction error-related gamma (Bastos, Vezoli, Bosman, et al., 2015).

(6) The framework has other implications, e.g. regarding other frequencies such as theta oscillations (but see last section) and interactions between networks with different SOs or the impact of alpha power on gamma frequency. This is developed in a new opinion paper (see last section).

Some results in the literature already provide evidence that such a mechanism could be implemented. For instance, Saalmann et al. (2012, 2018) used a paradigm in which monkeys were cued to covertly attend a location (among 6 locations) in order to subsequently determine whether a target was presented at that location. During the delay between the cue and the stimulus presentation, the alpha-band coherence between V4 and the infero-temporal area TEO was higher when the attended location was part of the receptive field of these visual areas than when it was not. Moreover, gamma coherence between V4 and TEO was also observed. In addition, some studies in humans using EEG and intracranial EEG have linked alpha coherence to network shaping and the transfer of gamma oscillations between the nodes of the network (Chapeton et al., 2019; Palva & Palva, 2007; Pascucci et al., 2018).

Predictions

In the visual network, the frameworks presented above result in the following specific predictions:

(1) Stimulus-driven (or/and prediction-error related) gamma oscillations and prediction-related beta oscillations are controlled by internally-generated alpha oscillations. Cross-frequency coupling between alpha and gamma oscillations has mainly been reported during rest (Roux et al., 2013; Spaak et al., 2012b). The decrease of alpha power during stimulus processing constitutes a challenge for applying cross-frequency coupling analyses due to the decrease of the signal-to-noise ratio. However, a few recent studies (Berman et al., 2014; Seymour et al., 2017; Voytek et al., 2010), including one of my studies (Bonfond & Jensen, 2015b), reported coupling between alpha and gamma oscillations during stimulus processing. These results need to be extended to other nodes of the brain networks.

Addressing the question of the coupling between alpha and beta oscillations is more challenging given that the frequency of beta oscillations might be close to the harmonics of alpha oscillations and we might observe spurious coupling. However, new model-based methods for detecting cross frequency coupling might help disentangling the two phenomenon (Tour et al., 2017) Grabot et al. (2017) recently showed such coupling during a timing task. A side question is to determine to what extent beta oscillations observed in the visual networks are true oscillations or beta burts (one cycle) such as observed in somatosensory and motor cortices and hypothesized to results from activity in different layers (Sherman et al., 2016; Shin et al., 2017). It is consistent with the duration of the duty cycle (the excitable phase) to observe one cycle of beta oscillations.

More generally, the directionality of the different coupling observed, i.e. which oscillation controls the other, was not analyzed and thus remains to be tested (but see Jiang et al. 2015).

(2) Synchrony of alpha oscillations between relevant areas predicts inter-areal correlation/synchrony of gamma and beta oscillations. The synchrony within these frequency

bands (alpha, beta and gamma oscillations) observed during several cognitive processes (Bastos, Vezoli, Bosman, et al., 2015; Bosman et al., 2012; Pollok et al., 2007; van Kerkoerle et al., 2014b) constitutes promising preliminary evidence supporting this prediction.

(3) Local alpha magnitude and/or frequency in irrelevant areas and anti-phase synchrony between irrelevant and relevant areas will be associated with less inter-areal correlation of gamma oscillations. The high alpha magnitude and or frequency observed in irrelevant regions during attentional and memory tasks, as shown in many experiments (e.g. Capilla et al. 2014; Kelly et al. 2006; Foxe et Snyder 2011; Snyder et Foxe 2010) including in my own work (Bonfond & Jensen, 2012, 2015b; ElShafei et al., 2018; Horschig et al., 2014), as well as the observation of anti-synchrony in the brain during cognitive tasks (Dotson et al., 2014), provide preliminary support in favor of this prediction. This prediction might be specific to stimulus-induced gamma oscillations as the brain might prevent spurious prediction to disturb the relevant predictions by other mechanisms, e.g. by preventing the generation in the first place.

(4) Alpha oscillations are locally modulated.

To allow communication between two specific pools of neurons, alpha oscillations must be modulated at a fine spatial scale. The framework proposes that alpha oscillations are differently modulated in pools of neurons **a** and **b** (so that the communication is specific between **a** and **c**). This should be the case even if the stimuli processed by **a** and **b** are close to each other in the retinotopic space. **This results in the hypothesis that alpha oscillations must be modulated locally.** However, it is a pervasive idea in the literature that alpha oscillations in the visual network are modulated more globally, at least at the hemispheric level (Thut et al., 2006b). I want to challenge that view and show that alpha can be modulated at the receptive field level (and possibly at the stimulus representation level but this is not a strong requirement of the framework). Some recent data provided promising evidence that alpha can be modulated locally (e.g. Harvey et al., 2013).

(5) Alpha oscillations are under top-down control

It has been proposed that alpha oscillations are controlled via feedback activity from higher order regions (van Kerkoerle, et al. 2014) or via subcortical and fronto-parietal regions (Marshall, et al. 2015, Saalman, et al. 2012) but there is no consensus in the literature. In any case, if alpha synchrony is set-up through feedback pathways from higher order regions, the diverging nature of these pathways implies that another mechanism is needed to account for the specific synchrony from **c** to **a** in figure 8. The pulvinar, which is connected to **a**, **b** and **c** (Saalman & Kastner, 2011), is a good candidate for such a mechanism. The role of the feedback pathway and extra-regions in setting up both alpha power and synchrony remains to be tested. Another candidate is the claustrum due to its connection to the entire brain (Dillingham et al., 2017).

(6) Alpha/beta oscillations should be mainly observed in feedback related cortical layers while gamma oscillations should be observed in feedforward related layers.

SOs such as alpha oscillations control stimulus-driven gamma oscillations within the microcircuit of brain areas. The framework proposes that stimulus-driven gamma oscillations are nested within internally-generated SOs but it remains to be understood how this interaction is implemented in the brain. In particular, it is crucial to understand how these oscillations interact within the microcircuit. Importantly, alpha oscillations have been shown to be strong in supragranular and infragranular layers of visual areas which receive (context-related) input from higher order brain regions. Gamma oscillations, on the other hand, have been shown to be strong in granular/supragranular layers (van Kerkoerle et al., 2014a) which receive (stimulus-related) input from lower-order brain areas. This result in the hypothesis that alpha oscillations in supragranular and/or infragranular layers control stimulus-induced gamma oscillations in the granular and supragranular layers of microcircuits. Surprisingly, there is only scarce evidence of a coupling between alpha and gamma oscillations between layers in monkey recordings, and this evidence is often restricted to resting periods (e.g. Spaak et al. 2012). Moreover, the directionality of the effect, i.e. which oscillation controls the other, has not been tested so far (but see Jiang et al., 2015).

2. PROJECT

In order to test the validity of these framework, we need a multi-level approach allowing to either zoom out up to the whole brain level to observe within- and between-network interactions, or to zoom in down to the microcircuit. We therefore used an original multimodal and transversal approach, including four recording techniques in humans and two in monkeys.

All these techniques have advantages and drawbacks, and only their combination allows for optimal testing of the predictions of the framework. In particular, fMRI will be used in order to optimize the spatial sensitivity of EEG and MEG.

This general goal is divided into four axes:

2.1 AXIS 1: COMMUNICATION THROUGH NESTED SLOW AND FAST OSCILLATIONS

In this axis, we tested the predictions regarding how internally-driven SOs magnitude and inter-areal synchrony promote/prevent the transfer of information/prediction error and predictions carried by gamma and beta oscillations. We started by setting up 3 experiments to test these predictions in different networks and at different spatial resolution levels. More precisely, we tested these predictions:

(1) In the entire visual network using MEG in combination with fMRI. 43 participants were enrolled in this experiment which included 7 lab visits (inclusion session; (f)MRI session; EEG session; 4 MEG sessions) We took advantage of the good spatial resolution of fMRI to determine in each participant, the optimal stimulus categories and positions increasing the likelihood of separating the different visual areas when performing source localization using MEG. The step 2 consisted in using the stimuli selected in three tasks manipulating either spatial visual attention and prediction (paradigm manipulating the predictability of upcoming stimuli implicitly) or feature attention (figure 9 A and C).

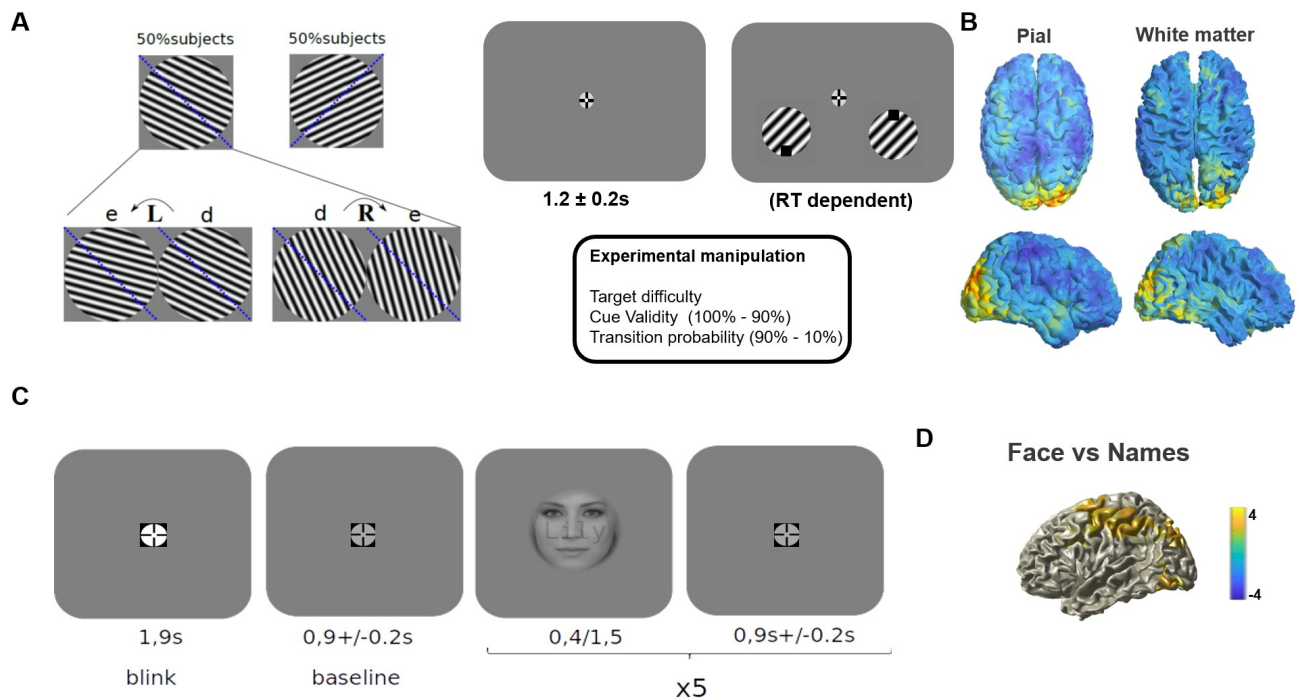


Figure 9. Designs and preliminary results (A) Stimuli used in two tasks. Participants had to determine whether the gratings presented on the attended side were oriented clockwise to the left or the right of a given diagonal. These stimuli were used in three sessions during which they were either presented alone (no distractor) or with a distractor on the other side. Leftward and rightward oriented stimuli had two levels of difficulty (determined by the angle with the diagonal). We further manipulated explicitly the cue validity and implicitly (in two sessions) the transition probability between stimuli (counterbalanced across subjects), i.e. to what extent a given stimulus (e.g. easy leftward) is predicted by the previous stimulus (e.g. difficult rightward) **(B)** Preliminary results showing stronger gamma power in response to gratings in Pial surface (“superficial layer” compartment) than in white matter surface (“deep layer”) in three participants **(C)** Feature attention task. Names on top of faces were presented. In each block, participants were asked to either determine the likely gender of the names or of the faces **(D)** Source localization of the anticipatory alpha amplitude difference in the “attend face” than in the “attend name” condition. Stronger alpha power was observed over the left visual word form area and the parietal cortex. The alpha power difference observed over the motor cortex is driven by a stronger desynchronization in the “attend name” condition associated with faster reaction times.

We expected further to test the predictions up to the laminar level as we developed (at the local neuroimaging center Cermep with Claude Delpuech, Denis Schwartz and Sébastien Daligault) a setting, involving individual headcasts to limit head movements and supine position, to obtain high resolution MEG (2 to 3 layers) (Bonaiuto et al., 2018a).

The main expected outcome is to demonstrate that internally-generated alpha power/synchrony promotes or prevents the transfer of predictions (carried by beta oscillations) and information/prediction error (carried by gamma oscillations) between visual areas. We further expect that this promotion vs. prevention of information transfer is prepared via alpha synchrony vs. anti-synchrony already during the anticipation of (relevant and irrelevant) visual stimuli. As such, we expect that this mechanism will predict behavioral performance. We expect to be able to determine the role of the fronto-parietal network and of the pulvinar in setting up this communication using various connectivity methods (Battaglia & Brovelli, 2020; Brovelli et al., 2004, 2017). According to the framework, we should further observe that alpha power increases are associated with shorter gamma duration (Bonfond & Jensen, 2015a; Spaak et al., 2012b). In addition, a 3-4Hz rhythm, related to micro-saccades or not, to be coupled to gamma (Bosman et al., 2009) as well as alpha oscillations and to predict performance. We here expect that the alpha-gamma coupling will be nested within the slower rhythm. Finally, gamma frequency has been shown to be a more reliable marker of change of attention, with an increase of frequency with attention, than gamma power change (Fries, 2015b). We further expect that alpha oscillations set-up the level of excitability and as such influence gamma frequency which has been proposed to depend on excitatory input drive (Lowet et al., 2015). We will further adopt a **modelling** approach (Bayesian learning models) to further investigate the computational role of oscillatory activity. Beyond learning mechanisms (between trials), we want to test computational hypothesis at a finer grain (within trials) to reveal the neurophysiological implementation of perceptual inference. In particular, we will explore the possible relationship between oscillatory cycles (e.g. in the alpha band) and iterative gradient descents in (variational) Bayesian inference (Deco et al., 2008).

The preprocessing steps were particularly demanding given the number of trials (over 1600 trials per condition for the 43 participants). **The preliminary results** show that attended stimuli, as expected, induce a decrease of alpha amplitude together with an increase of gamma amplitude in all tasks. We further were able to discriminate deep and superficial layers for gamma induced by gratings in three participants (figure 9B). Furthermore, attending the face in the feature attention task is associated with an alpha increase over the left temporal cortex, the visual word form area (figure 9D), which was further associated with faster reaction times in line with a functional inhibition role of alpha oscillations (see section 2.6 in section - synthesis of the past work). Interestingly, we did not find (so far) an increase of alpha amplitude over the FFA in the “attend name” condition (or in any other area). Interestingly, overall reaction times were slower in the “attend face” condition than in the “attend

name” condition indicating a larger difficulty in the former. This could relate to the perceptual load hypothesis developed in section 2.6 regarding the role of alpha oscillations in inhibition. Here, a higher perceptual load in the “attend face” condition could be associated with a stronger need for inhibition. The stronger salience of the name (in the middle of the screen) could also explain these results. However, even in the name condition, we found an effect of congruence (faster reaction times for face-name congruent than incongruent trials) indicating that the face was distracting in the “attend name” condition too.

(2) In two visual areas with a receptive field precision level in monkey. This experiment allow to zoom-in down to the cortical level in monkeys and to get a receptive field level resolution (compared to the area level resolution in MEG) and will be based on electrode array LFP recordings in areas V1 and V4 of two monkeys performing two tasks involving a modulation of attention during stimulus processing (data were provided through a collaboration with the group of Pieter Roelfsema (Amsterdam, Netherlands; van Kerkoerle, et al. 2014).

In these experiments, we will analyze in each region of interest the anticipatory and stimulus-related directional cross-frequency coupling between SOs and beta and gamma oscillations, using a state-of-the-art approach. We will develop a method inspired by two papers (Jiang et al., 2015; Voytek et al., 2015) to assess the causal relationship between inter-areal alpha phase difference and inter-areal gamma correlation. We expect to demonstrate that internally-generated alpha power/synchrony promote or prevent the transfer of information (carried by gamma oscillations) between visual areas at the receptive field level. The analyses are ongoing and preliminary results reproduce what is presented in Van Kerkoerle et al. (2014).

2.2 AXIS 2: IMPLEMENTATION OF THE INTERACTION BETWEEN OSCILLATIONS AT THE MICROCIRCUIT LEVEL

This axis will aim at determining the implementation of the **interaction between SOs and gamma oscillations within the microcircuit**, i.e. between the layers of the cortex. Importantly, alpha oscillations have been shown to be strong in superficial and deep layers of visual areas which receive (context-related) input from higher order brain regions. Gamma oscillations, on the other hand, have been shown to be strong in middle/superficial layers which receive (stimulus-related) input from lower-order brain areas. **These observations lead to the hypothesis that alpha oscillations in superficial and/or deep layers control stimulus-induced gamma oscillations in the middle/superficial layers of microcircuits.** Surprisingly, there is only scarce evidence of a coupling between slow and gamma oscillations between layers, (Lakatos et al., 2005; Spaak et al., 2012b). Moreover, the directionality of the effect, i.e. which oscillation controls the other, has not been not tested so far. We will determine using the directional CFC method whether deep and/or superficial

alpha oscillations control stimulus-induced middle/superficial gamma oscillations. We will test how attention affects the coupling between the two oscillations. If alpha oscillations are associated with pulses of inhibition, I specifically expect that an increase in alpha power will be associated with a phase-specific (i.e. the phase of the pulse of inhibition) gamma power decrease.

It will be based on (1) the analysis of data from multi-site microelectrodes in V1 of two monkeys (data also provided by the group of Pieter Roelfsema) performing attention tasks and (2) the analysis of the laminar data we expect to obtain from high resolution MEG mentioned above.

The main expected outcome is to show that infragranular and/or supragranular alpha oscillations control stimulus-driven gamma oscillations in granular/supragranular layers.

We will further try to determine in which layer (the micro-saccade related or not) 3-4Hz rhythm occurs and whether it is coupled to alpha and gamma oscillations. This will help to integrate such a rhythm in the framework (see last section). We will also investigate whether the behavior of alpha oscillations in infragranular and supragranular layers can be differentiated in terms of task/stimulus-dependent power modulation and how these two layers interact during baseline and during stimulation.

The analyses are ongoing and preliminary results also reproduce what is presented in Van Kerkoerle et al. (2014).

2.3 AXIS 3: SPATIAL RESOLUTION OF ALPHA AND GAMMA OSCILLATIONS

To allow communication between two specific pools of neurons, alpha oscillations must be modulated at a fine spatial scale.

The framework proposes that alpha oscillations are differently modulated in pools of neurons **a** and **b** (so that the communication is specific between A and C). This should be the case even if the stimuli processed by **a** and **b** are close to each other in the retinotopic space. **This results in the hypothesis that alpha oscillations must be modulated locally.** However, it is a pervasive idea in the literature that alpha oscillations in the visual network are modulated more globally, at least at the hemispheric level. I wanted to challenge that view and show that alpha can be modulated at the receptive field level (and possibly at the stimulus representation level).

In the present study, we used high-resolution fMRI-EEG such approach for the first time focusing over the visual cortex while participants were presented with left or right oriented gratings (figure 1 a, B). We were able to extract feature specific BOLD signals in voxels encompassing three compartments associated with deep, middle and superficial cortical layers in V1, V2 and V3 regions. Very interestingly, we showed that negative BOLD signals (compared to baseline) also partially exhibited feature specificity.

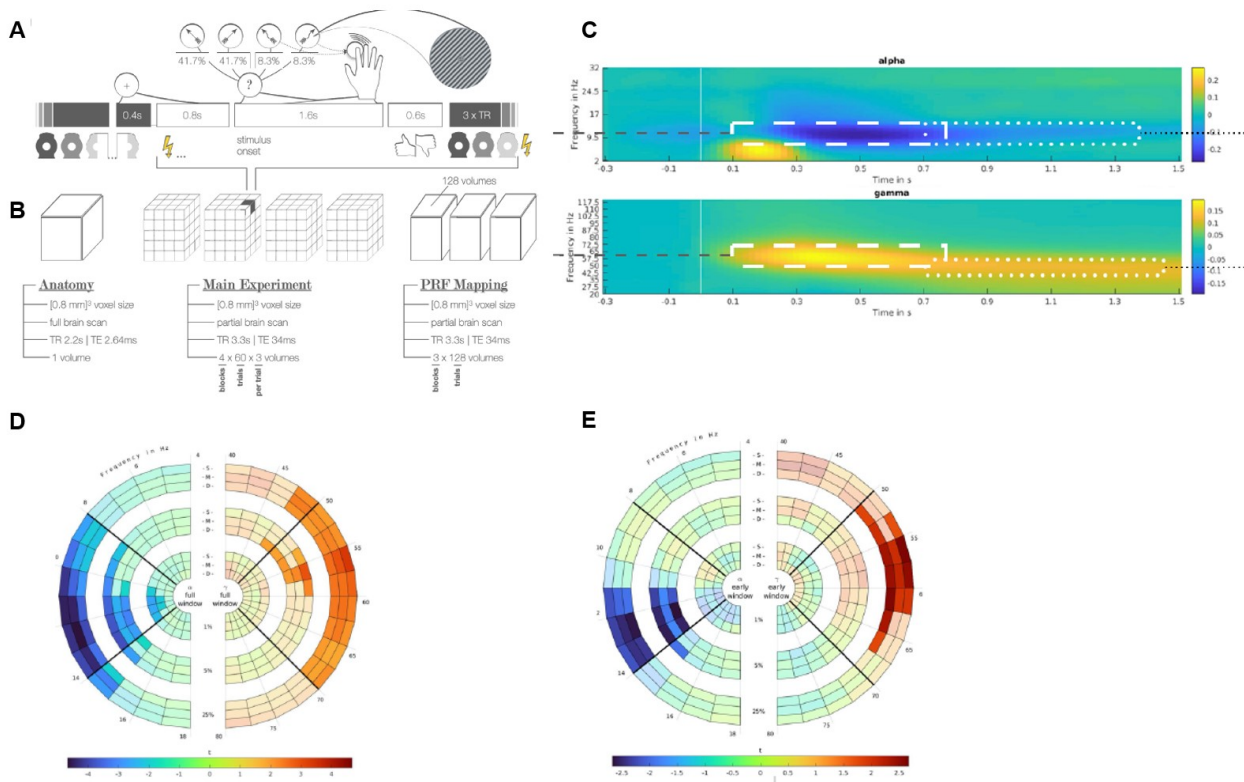


Figure 10. Feature specificity of alpha and gamma oscillations (A) fMRI-EEG paradigm. We used an interleaved fMRI sequence to allow artefacts free periods of EEG recordings. Participants were centrally presented with left and right gratings and were asked to press a button when the grating presented was composed of sine waves (16.6% of the trials) (B) Parameters used for the anatomical scan, the main fMRI experiment and the retinotopy task. (C) Time frequency results in the visual cortex (LCMV beamformer). The presentation of the stimulus (white line) was associated with a decrease of alpha amplitude and an increase of gamma amplitude. (D) (E) Alpha and gamma correlation with BOLD change in voxels activated by the gratings in the 1%, 5% and 25% most activated voxels (number of voxels considered are different in different studies, we decided to present three sizes of voxels groups for transparency reasons) (F) Contrast of the correlation between orientation specific voxels and corresponding alpha and gamma signal.

We found that stimulus induced alpha and gamma oscillations in the visual cortex (figure 10C) were (negatively and positively respectively) correlated with the stimulus induced BOLD signal (broad frequency band; figure 10D). Alpha is negatively correlated with the BOLD signal, in line with the idea that the higher the alpha amplitude, the lower the excitability and hence the BOLD signal (Scheeringa et al., 2011). Both feature specific alpha and gamma oscillations were correlated with the BOLD signal observed in feature-specific voxels but in a narrower frequency band. It is particularly interesting for alpha oscillations given the feature-specific frequency is not the frequency that is the most modulated by stimulus presentation (figure C). An even more interesting results is that alpha oscillations in this frequency band were also correlated with the feature-specific **negative** BOLD signal. This could indicate that alpha oscillations in this frequency band are involved in both increasing the excitability of stimulus specific groups of neurons (alpha decrease) and inhibit other

groups of neurons (alpha increase). This would be in line with the low modulation of this frequency band by the stimulus observed in the EEG data (figure 10C). Further analyses are currently performed to determine whether the correlation between alpha oscillation and positive and negative BOLD are independent. The laminar specificity observed here is in line with the laminar profile of both alpha and gamma oscillations in Van Kerkoerle et al. 52014).

These results could indicate that alpha oscillations could be feature specific as predicted by the framework.

2.4 AXIS 4: CAUSAL ROLE OF ALPHA SYNCHRONY

This axis will aim at testing whether inter-areal synchrony of alpha oscillations is a necessity for perception, i.e. whether it plays a **causal role** in our ability to perceive our environment. More specifically, the aim of this axis is to show that the (anti-)synchrony in the alpha band is a crucial mechanism for setting-up inter-areal communication that generates visual perception. We will use simultaneous MEG, transcranial alternating current stimulation (tACS) and visual flickering stimuli. tACS will be used to entrain alpha oscillations in early visual regions of the visual cortex (Vossen et al., 2015) while flickering face stimuli will be used to entrain alpha oscillations in the fusiform face area (FFA). We will create two conditions of interest in which alpha oscillations will be in synchrony or in anti-synchrony between the low-level visual areas and the FFA and will test whether subtle face changes in the visual field of interest are less well detected in case of anti-synchrony. We have already performed the behavioral task, a mooney face detection task, using flickering faces to determine whether FFA can be entrained. The results did not indicate that FFA could be entrained (the behavioral performance was not rhythmical following the end of the stimulation). We have however adapted the task and started to record new data.

Towards a new framework

The frameworks presented (and the projects) above suffer from several limits. First, they might not be adapted to ecological situation which imply to deal with a volatile environment. Second, they do not consider recent results indicating that some oscillations reported in the literature might not be, per se, 'oscillations', i.e. they are not sustained and do not exhibit a sinusoidal shape (Cole & Voytek, 2017). The framework presented in the next section attempt to address these points.

New Framework and future project

1. FRAMEWORK: VISUAL PROCESSING OF BY DYNAMIC MULTIPLEXING AND PHASE CODING

The complexity of the environment we are operating in requires a highly flexible brain mechanism for adaptable behaviour to emerge. The large repertoire of frequencies and shapes of neuronal oscillations, which index rhythmical changes of excitability, could be ideal to implement such flexibility in neural systems. However, such computational role of oscillations is highly debated. Many theories have proposed that sustained oscillations would play a crucial role in sensory processing and brain communication (Fries, 2015c). Our own previous theoretical framework, which is the basis of the ERC-funded project presented above, has put forward the idea that slow oscillations are instrumental in setting up network communication. However, most of these theories have been developed from data obtained in the lab, i.e. in simplified settings. They might not be suited to more ecological settings. However, we here propose that **(1) the fluctuations of excitability associated with oscillations could actually be particularly relevant to organize processing in real-life situations in which the flow of information is way more important than in lab settings BUT (2) sustained oscillations could actually be detrimental for efficient processing in these complex, settings** (Bonfond, Jensen & Clausner, under review in Progress in Neurobiology).

More specifically, we suggest that **possibly non-sinusoidal and highly dynamic, fluctuations of excitability in specific frequency bands would be good candidates to organize the neuronal dynamics processing of complex visual information in naturalistic contexts**. We further propose that **multiplexing**, where numerous information streams share a common neural substrate and rely on the interconnection of rhythmical activity at multiple frequencies, might be crucial for actively extracting information from complex visual scenes. Finally, **We suggest that these oscillations at different frequencies adapt very rapidly, e.g. with a change in wave-form (oscillations are not expected to be perfectly sinusoidal; e.g. see Cole & Voytek, 2017), amplitude and frequency, to match the specific computational needs that emerge in a complex dynamic environment, and therefore allow the system to be highly flexible**.

Precisely, we suggest that each cycle of fluctuations in the alpha-band (7-14Hz) would be involved in the processing of single objects by visual areas (Womelsdorf et al., 2012) (figure 11a). Furthermore, these alpha fluctuations would be nested within slower fluctuations of excitability (1-6Hz) and **could vary in frequency or shape within one cycle of the lower frequency**. The slow activity would thus be involved in organizing multiple objects processing (figure 11b). Finally, (micro-) saccades would be tightly linked to these oscillations. In line with Fiebelkorn et al. (2018), we suggest that significant shift of attention (e.g. between hemifields; Gaillard et al., 2020), overt following microsaccades (Lowet et al., 2018) or covert through saccades, could occur during a specific phase of slow fluctuations, the phase in which less information is processed or during which predictions are

formed (figure 1b). Many circumstantial evidences already exist in favor of this framework. For instance, Alpha oscillations have been shown to be related to temporal integration/fusion of two consecutive stimuli (e.g. Samaha & Postle, 2015), with artificial feature binding (e.g. Zhang et al., 2019), as well as with attentional sampling of single space position or object (e.g. Fiebelkorn et al., 2018; Gaillard et al., 2020; Senoussi et al., 2019). Delta and theta oscillations (1-6Hz) have been associated with attentional sampling of multiple space position or objects (e.g. Fiebelkorn et al., 2018; Helfrich et al., 2018; Huang & Luo, 2020). Furthermore, a coupling between delta-theta and alpha rhythms have been observed at the behavioral (Bellet et al., 2017; Fiebelkorn et al., 2013; Song et al., 2014) and at the neural level (Gomez-Ramirez et al., 2011; Halgren et al., 2018; Helfrich et al., 2018; Wilson & Foxe, 2020). The paper also discusses the role of the attentional aperture (in line with what is considered as an object at each given time) and how the framework relates to brain communication and predicting coding (see Bonnefond, Jensen and Clausner, under review and figure 11 for more details). Our framework indeed suggests interactions between predictions and stimulus processing over the delta-theta and alpha cycles.

2. PROJECT

The first axis will test the hypothesis that, deep cortical layer, fluctuations in the alpha-band could allow to group several elements of an object to form a coherent representation while simultaneously chunking the processing of these elements along its phase. The specific frequency and shape of the oscillation involved would depend on the nature of the object processed and on cognitive demand.

The second axis will allow to test whether slower frequencies would organize the processing and active exploration of multiple objects, each processed within an alpha cycle, along its phase. Again, the frequency and shape of the oscillations required would dynamically evolve with the complexity of the scene processed and cognitive demand. We will use high resolution magnetoencephalography (MEG), a recent method we further developed within the context of the ERC starting grant, and advanced connectivity analyses (Battaglia & Brovelli, 2020) and modelling. Additionally, methodological development will be necessary to follow rapid changes of frequencies and shapes of the oscillations involved.

Finally, the long-term objective (discussions are still ongoing) of the third axis will be to build deep/spiking neural networks able to extract relevant information from visual scene to determine whether fluctuations of excitability (but not sustained oscillations) are used by this network to perform the task. **This project will therefore provide both theoretical and methodological insights into the dynamics underlying visual processing in ecological settings.**

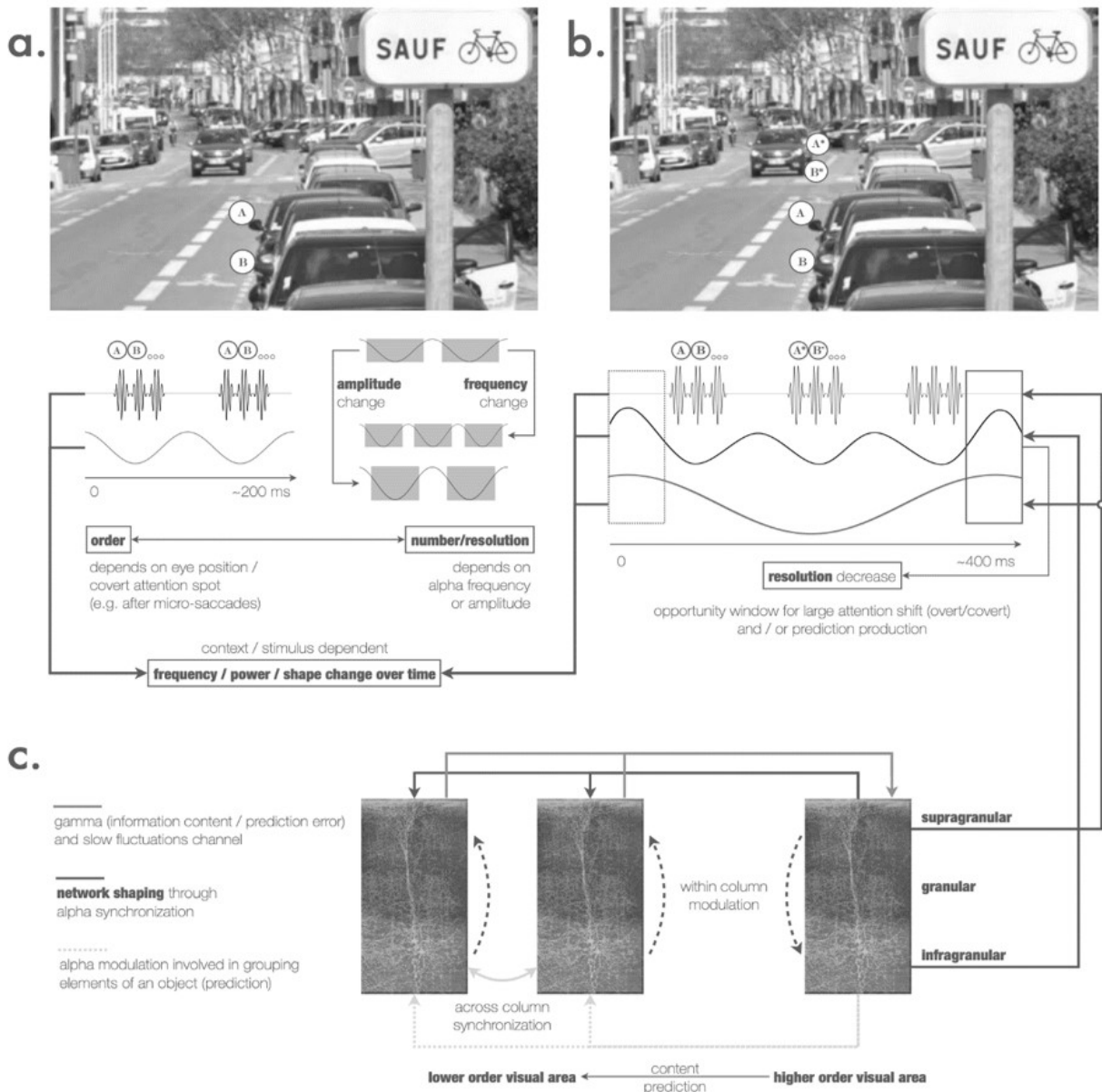


Figure 11. Flexible oscillatory multiplexing and phase coding allows for processing single and multiple objects. **a.** Imagine you are biking, and cars are parked on your right, you may have to consider that e.g. the door of one car could open or that this car could get out of its parking spot, you will then have to sample and process the door and the tires of the car. These different elements might be processed (e.g. in the gamma band) at different phases along alpha oscillations. The frequency of the gamma oscillations might be different for the different objects according to saliency, contrast or attention level. Many parameters (such as the number of the elements sampled) might depend on overt/covert attention and/or alpha frequency/amplitude. This mechanism would be at play for integrating (within an alpha cycle) the different elements of an object while taking into account the specificity of each element (segregation process). (inset) As alpha activity is hypothesized to be associated with pulses of inhibition, an increase in amplitude or frequency would decrease the duration of excitability (duty cycle) within a cycle. **b.** In case of multiple objects needed to be sampled, here an additional car on the road, a slower rhythm, at theta frequency, would organize the sampling of the different stimuli along its cycle. The alpha-gamma coupled fluctuations associated with sampling and processing one object would further be nested within the excitable phases of the theta rhythms. Alpha amplitude is expected to

be stronger, associated with a lower resolution of visual processing, during the peaks of theta oscillations (“bad” theta phase). Such a phase would be associated with a stronger likelihood of large (potentially towards the other hemifield) attention shift (and possibly generation of prediction about upcoming stimuli on the fovea). Very importantly, these oscillations, at both frequencies, are not expected to be sinusoidal, their shape, similarly to their amplitude or frequency, might even change with e.g. context to allow flexibility of processing. The very short bursts of gamma oscillations occurring during the troughs of alpha oscillations with high amplitude (during theta peaks) are not depicted for the sake of the clarity of the figure. **c. Brain communication and predictions.** Distinct alpha oscillations would allow for setting up network communication (in receptive field superficial cortical layers) and grouping the processing of different elements (in deep cortical layers and involving across columns synchronization within a given level of the hierarchy). Between layer connectivity in the alpha band would allow for brain communication and grouping of elements to influence each other (prediction process; see section 5) for the integrated visual information to be transmitted to higher level of the hierarchy. Visual elements would then be processed in the superficial layer gamma band (or spike timing) and nested within alpha oscillations to be transferred to the relevant regions across the visual hierarchy. Finally, superficial slow fluctuations, delta-theta, would control the timing of/organize the processing of each object. Prediction regarding the context of the stimuli would be passed down to the level below and would be compared to the incoming stimuli. In that case, gamma oscillations could result from the comparison between the prediction and the sensory input.

2.1 AXIS 1: FLUCTUATIONS IN THE ALPHA-BAND ARE INVOLVED IN INTEGRATING THE DIFFERENT ELEMENTS OF AN OBJECT WHILE SIMULTANEOUSLY ORGANIZING THE PROCESSING OF THESE ELEMENTS ALONG THEIR PHASE

The first objective of this project is to test whether alpha band fluctuations are related to the processing of one object (say a car) and its elements (e.g. tire and door). In addition, we aim to test whether the processing of the different elements of a single object, as indexed by high-frequency oscillations (>40Hz), is organized along the phase of these alpha fluctuations with the most relevant/salient element processed first in the cycle. Such phase coding has been observed in humans and animals during spatial navigation and memory (Bahramisharif et al., 2018; Belluscio et al., 2012). One paradigm, using electroencephalography, will be used to test these hypotheses. Two abstract elements (with different contrast or flicker frequency to generate separable signals) will be presented in each hemifield with a caching in the centre and the participants will have previously learned whether these elements belong to the same or different objects. We predict that the alpha phase in the two hemispheres will be coherent with a zero-phase lag only in the one object condition and from the moment the participants remember these elements belong to one object. Alternatively, phase coherence would be high in both conditions, but the 2 elements could be processed, as assessed by gamma oscillations, within a cycle when they belong to one object and in two successive cycles when they belong to different objects. However, as the goal is to determine whether fluctuations in the alpha band are crucial to process objects, the next experiment will use **naturalistic**

stimuli with a cache in the centre that could be processed either as a single object or two objects according to the context (e.g. one bench in a park, two chairs in a house)

The second objective will be (1) to determine whether alpha frequency changes with stimulus complexity and task demand in particular in deep cortical layers as predicted by the framework (Bonnefond, Jensen & Clausner, submitted) and papers on temporal integration of information (Wutz et al., 2018); (2) whether alpha fluctuations in superficial layers set-up brain communication as also predicted by the framework (see also Bonnefond et al., 2017b). We will use high precision MEG which consist in limiting head movements (using headcasts) within the MEG helmet and the use of adapted source localization methods to obtain a spatial resolution up to cortical layers (Bonaiuto et al., 2018b). We have already used this approach in the context of our ERC project presented above with excellent preliminary results and we will continue our ongoing collaboration with James Bonaiuto (ISCMJ, Lyon), one of the pioneers of this method (Bonaiuto et al., 2018b) and Denis Schwartz, head of the MEG center and member of the CoPhy team. The task will consist in different types of stimuli with increasing complexity and in different categories (abstract, faces etc...). We will further manipulate task demand with the instruction emphasizing on processing more or less details of an object. We expect deep layer alpha frequency (1) to decrease with the increase of stimulus complexity/task demand in order to integrate more information and (2) to be under control of fronto-parietal regions (Fiebelkorn et al., 2018). We further expect the superficial alpha to be involved in setting up brain communication. In addition to adapted source localization, we will use Dynamical Causal Modelling (DCM) to model out between areas/layers interactions along the visual hierarchy.

2.2 AXIS 2: SLOW FLUCTUATIONS ALLOW FOR ORGANIZING THE PROCESSING AND EXPLORATION OF MULTIPLE OBJECTS

Our framework predicts that slower fluctuations of excitability (1-6Hz) could be involved in organizing the sampling of multiple objects in each cycle. Each object of the scene would be sampled and processed, within alpha cycles, at different phases of this slow fluctuation (phase coding; figure 1b). This phase coding does not require a sustained oscillation at a given frequency similarly to the phase coding observed in the hippocampus of bats (Bush & Burgess, 2019). In fact, in the case of visual scene processing, a rapid adaptation of frequency might be necessary given the complexity of information to be processed over time and the regular change of cognitive demand (see Brookshire, 2021 for a discussion regarding the analyses currently performed in the field).

We will perform high-precision MEG during a task involving multi-item processing in more natural, while controlled, settings (each stimulus processing could be tracked in the visual system through manipulation with imperceptible flickering for instance). Participants will e.g. be in a parking and will be asked to “walk” through (button press to move) the parking looking for their car (target

detection). They will be allowed to do saccades or not (e.g. they have to focus on the center because they're watching a turbulent young kid walking in front of them). The scenes will involve a mixture of highly (e.g. cars) and weakly distracting objects (e.g. bikes). Additionally, we will manipulate predictions through past experiences with similar settings or difficulty of the task using noisy environment (e.g. lack of light). We will perform modelling of behavior, adapted source localization, DCM and effective connectivity analyses to test all the predictions from the framework. More importantly, we will develop specific tools to track rapid changes in frequencies/shape of fluctuations.

2.3 AXIS 3: ARTIFICIAL NEURAL NETWORKS: ARE FLUCTUATIONS OF EXCITABILITY USED BY THESE NETWORKS TO EXTRACT INFORMATION FROM SCENES?

The objective of WP3, which needs much further discussions with our collaborators, is to use deep and spiking neural network models (DNN/SNN) to attempt to determine whether the fluctuations mentioned in WPs1/2 are necessary or improve performances in a system with similar constraints to the neural system (mainly the convergence of information that creates bottleneck issues). These networks will be trained to perform the WP1/2 tasks in a similar way to the participants. We have recently started to work on these neural networks in collaboration with Christian Wolf (INSA Lyon) who is an expert on DNN.

The first objective will be to determine whether similarities can be observed between brain fluctuations observed at each hierarchical level of the visual system and response of in each layers of the trained DNN. These simulated data will be compared to real MEG data obtained in WP1/2 at different levels of the visual hierarchy (and in different cortical layers). Convolution layers can be used to learn and apply different filter kernels to process images and thus are often used for object recognition. Using fMRI, it has been shown that “knowledge” representation in the different layers of DNNs during a visual categorization task mimics the one in humans along the visual cortical hierarchy (Güçlü & van Gerven, 2015). However, to date, it has not been studied how brain fluctuations at different frequency bands (and their interactions) relates to DNNs, which would be an important milestone for understanding the computational role of brain fluctuations. This paper used DNNs to mimic the brain's signals given certain tasks (correlating brain and network activity at certain depths) and investigated afterwards how much structural or event related (time resolved) correspondence can be found between the two systems. In a similar way we expect structural similarities between the DNN and the time-frequency data in each visual brain area to be revealed. Importantly, we will add “feedback connections” to our DNN (recurrent network) to emulate feedback processes such as attention or predictions (Pang et al., 2021).

The second objective would be, since most DNNs inherently lack the time domain, to attempt to transfer this approach to a more biologically plausible SNN. However due to the inherently difficult

training phase of SNNs we could coarsely apply the learned weights from the DNN training phase to a similarly constructed SNN, such that the trained structure is preserved. By doing so, the learned processing structure could be investigated in a time resolved manner. This is however a very challenging project. Another possibility would be to add, biologically plausible, time delays between the layers of a DNN (including feedback pathways).

One related question is whether fluctuations of excitability are a byproduct or naturally emerge as an optimal way of processing information, due to the flexibility they allow. More precisely, we assume that the SNN performance will increase with further training, and fluctuations will be used to enhance this process while sustained oscillations should not be observed. This would provide evidence in favor of (non-sustained) oscillations possibly being a mechanism selected by evolution for animals and humans to evolve in a dynamic environment, supporting an effective feature selection and input processing.

Conclusion and opening

Ecrire ce mémoire a été plus difficile qu'anticiper car chaque partie amenait plus de questions que de réponses. Cela m'a au moins permis de me rendre compte que les dix prochaines années seront sans doute bien occupées.

Il y a tant à faire et les nouvelles avancées technologiques rendent tout cela encore plus excitant. Notre équipe, Cophy, s'investit beaucoup dans ces développements, notamment en ce qui concerne l'amélioration de la localisation de source en MEG/EEG (Lecaigard et al., 2021; cf projet section 2) ou encore l'intelligence artificielle (section 3). Un excellent exemple concerne le développement de la MEG portable basée sur les fameux magnétomètres à pompage optique (ou Optical Pumped Magnetometers ; OPMs). Nous utilisons déjà cette technique dans l'équipe à travers une collaboration avec la startup Meg4Health créée par Mathieu LePrado et Etienne Laby du CEA. Les OPMs à Hélium 4 créés par cette startup ont des propriétés remarquables car (1) contrairement aux OPMs alcalins, ils fonctionnent à température ambiante (2) ils ont une bande passante de plus de 2 kHz (3) ils permettent de mesurer selon 3 axes et (4) leur sensibilité est en cours d'amélioration (pour atteindre $20\text{ft}/\text{Hz}^{1/2}$). Cette collaboration est gérée par Denis Schwartz (membre de Cophy) et Sébastien Daligault de la plateforme MEG du centre d'imagerie de Lyon (Cermep). Grâce à un financement de la région, nous avons déjà pu enregistrer les données de 10 participants (durant des tâches visuelles, motrices, somatosensorielles et auditives), sur 30 prévus, avec un prototype de 5 capteurs (un prototype de plus de 30 capteurs est prévu d'ici un an). Le labex cortex a par ailleurs permis le recrutement d'un post-doctorant qui devrait commencer au mois d'avril. Son travail consistera (1) à évaluer toutes les possibilités de ces OPMs, (2) à comparer leurs performances aux OPMs alcalins et (3) à mettre en place une pipeline d'analyses des sources utilisant les données obtenues sur les 3 axes.

Sur le plan théorique et expérimental, il y a beaucoup de projets en cours de développement dans l'équipe Cophy. Cette équipe combine de nombreuses compétences théoriques et méthodologiques complémentaires. Jérémie Mattout, Christina Schmitz et François Lecaigard apportent leurs compétences concernant la modélisation en lien avec les cadres théoriques sur les processus prédictifs et leurs altérations dans certaines pathologies comme l'autisme. Anne Kösem, quant à elle, apporte ses compétences en matière de prédictions temporelles notamment dans le cadre du langage. Le langage est un formidable exemple de collaborations au sein de Cophy. Il a été démontré que le langage avait une composante rythmique (Kösem & van Wassenhove, 2017) et que notamment être exposé à un rythme musical au préalable impacte les performances grammaticales (Chern et al., 2018; Fiveash et al., 2021). Cependant, le langage présente également de nombreuses irrégularités notamment liées aux propriétés de chaque langue. L'étude du langage s'inscrit donc bien dans le modèle présenté dans la dernière section avec des adaptations lentes et rapides des fluctuations d'excitabilité à différentes fréquences. Ces adaptations seraient grandement influencées par les mécanismes prédictifs locaux (rythme de la parole, sémantique, audio-visual interaction ; see

van Wassenhove et al., 2005) et plus globaux liées aux statistiques de chaque langue (Kösem, Lecaigard, Mattout, Bonnefond, in prep.).

Par ailleurs, notre équipe a un fort intérêt pour les applications cliniques notamment les troubles attentionnels, l'autisme ou même le coma. Un projet de très longue haleine visera à tester les modèles présentés en sections 2 et 3 en situation clinique et à déterminer s'ils peuvent permettre d'identifier les marqueurs neuronaux précoces de certains troubles neurologiques et psychiatriques. Les troubles des rythmes cérébraux pourraient être un marqueur précoce de la maladie d'Alzheimer et une stimulation directe ou indirecte (via des flickers) pourrait ralentir la progression de la maladie (cf Iaccarino et al., 2016 pour un exemple chez l'animal). Par ailleurs, une communication inter-zone altérée (à la fois hyper- et hypo-communication) est supposée être impliquée dans de nombreux troubles, y compris les acouphènes (De Ridder et al., 2014) et la schizophrénie (Stephan et al., 2009). Un excellent exemple est également la douleur chronique en absence d'atteinte périphérique. Nous souhaitons d'abord tester si les prédictions des modèles présentés dans ce manuscrit s'applique dans le cas spécifique du traitement de la douleur qui implique des réseaux cérébraux étendus pour traiter les aspects sensoriels, émotionnels et cognitifs de la douleur (Peyron et al., 2000). Nous prévoyons de manipuler le niveau d'attention vers les stimuli douloureux dans une expérience MEG. Ensuite, nous prévoyons d'examiner si l'hyper-communication entre le noyau accumbens et le cortex orbitofrontal qui a été observée chez les patients souffrant de maux de dos (Baliki et al., 2012) est mise en place par une synchronie alpha/gamma élevée et si elle pourrait être normalisée via une stimulation cérébrale spécifique (ou liée à un stimulus).

Beaucoup de projets en perspective donc et qui montrent bien la belle dynamique que l'on a au sein de Cophy dont je suis ravie de faire partie.

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