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# The role of brain oscillations in visual perception, attention and consciousness

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# THÈSE

**En vue de l'obtention du  
DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE  
Délivré par l'Université Toulouse 3 - Paul Sabatier**

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**Présentée et soutenue par  
Canhuang LUO**

Le 21 décembre 2020

**Le rôle des oscillations du cerveau dans la perception visuelle,  
l'attention et la conscience**

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**The role of brain oscillations in visual perception,  
attention and consciousness**

Canhuang Luo

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## ABSTRACT

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Oscillations are ubiquitous in the brain. A large body of literature has supported that brain oscillations are not a by-product of brain activities; in fact, they shape our perception by modulating cortical excitability and facilitating neuronal communications. Consequently, our visual perception, attention and maybe even consciousness wax and wane across time. However, the role of oscillations in these perceptual or cognitive functions is not entirely understood. For visual perception and attention, although the relationship between them and brain oscillations has been established, it is unclear where and how these brain oscillations are generated. As for consciousness, how the oscillations are involved in producing conscious perception remains unknown. These are the questions the current thesis attempts to address.

The thesis starts with brain oscillations in the most basic and best understood brain function – visual perception. It has been suggested that visual perception is an oscillatory process, sampling the world at the alpha frequency. Perceptual echoes are one demonstration of visual sampling. The echo is an impulse response function that oscillates at ~10 Hz in response to white-noise stimuli. While the temporal properties are gradually revealed, the origin of the echoes remains unclear. The first study set out to study the neural basis of perceptual echoes, and we found the echoes originate in the early visual cortex.

Next, we move on to attention. It has been shown that attention samples the environment at theta frequency. A monkey study suggests that the theta oscillation of attention may arise from competitive receptive field interactions of V4. To investigate if the mechanism can be generalized to humans, we replicate the behavioral experiment in humans.

Finally, in the last two studies, we examine brain oscillations in consciousness. Utilizing binocular rivalry, we first investigate if the perceptual echoes require consciousness. The results show that perceptual echoes can be elicited both when the stimulus is in consciousness and out of consciousness. Second, we investigate information flow during binocular rivalry and show an increased top-down beta and theta activities before perceptual switches.

In conclusion, the brain is a dynamic system in which the oscillations flexibly facilitate various brain functions by playing different functional roles.

## RESUME SUBSTANTIEL

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Le cerveau est un système dynamique, et les oscillations y sont omniprésentes. Bien qu'elles aient été initialement considérées comme un sous-produit produit par le cerveau, de nombreux neuroscientifiques ont réalisé la signification des oscillations et ont essayé d'établir le lien entre les oscillations et les fonctions cognitives.

L'une des théories permettant d'établir ce lien est celle des "cycles perceptifs" (VanRullen, 2016). L'idée est que si les activités cérébrales sont périodiques, il est naturel de considérer que la rythmicité des activités cérébrales se manifestera dans notre perception, conduisant à une perception oscillatoire. Cela peut sembler fou, car notre perception consciente semble si lisse, homogène et stable. Cependant, au cours des dernières décennies, des recherches considérables ont prouvé que les oscillations cérébrales donnent lieu à des "cycles perceptifs", montrant que la perception n'est pas continue; elle est plutôt "discrète" et oscillatoire, prenant des "instantanés" du monde comme une caméra. Notre perception stable, contre-intuitive, n'est qu'une illusion. Dans les cycles de perception, les oscillations cérébrales pourraient jouer un rôle d'"excitateur", en modulant périodiquement l'excitabilité des zones sensorielles du cerveau.

La conscience s'emballé et s'efface aussi comme les cycles de perception. Cependant, les oscillations cérébrales peuvent également jouer un autre rôle dans la conscience. La conscience est la fonction cognitive la plus complexe qui nécessite l'interaction de différentes fonctions cognitives, telles que le contrôle cognitif et la perception visuelle. Ainsi, il peut y avoir des communications entre différentes zones du cerveau pendant la perception consciente, et les oscillations cérébrales peuvent jouer un rôle de "communicateur".

Tous ces rôles d'oscillations permettent au cerveau de fonctionner efficacement. Même si la nature oscillatoire du cerveau est largement acceptée et que de plus en plus de scientifiques se sont lancés dans la recherche sur les oscillations cérébrales, il reste encore beaucoup de mystères. Quel est le mécanisme de génération des oscillations cérébrales qui se rapportent à une fonction perceptive ou cognitive spécifique? D'où viennent-elles dans le



cerveau? Comment sont-elles impliquées dans la perception consciente? Ce sont les principales questions que j'ai cherché à aborder au cours de mon doctorat.

Cette thèse se concentre sur la façon dont les oscillations neuronales sont impliquées dans trois fonctions perceptuelles ou cognitives fondamentales : la perception visuelle, l'attention et la conscience. Bien que j'aborde ces trois fonctions séparément, les expériences que je rapporte ici sont toutes basées sur des tâches visuelles.

### **Oscillations dans la perception visuelle**

Dès la fin du XIXe siècle, il a été proposé que la perception est discrète et que la perception visuelle discrète balaie l'environnement extérieur environ 10 fois par seconde (Whitlock, 2009).

L'un des premiers travaux démontrant la relation entre la perception visuelle discrète et la phase du rythme alpha est celui de Valera, Toro, John, & Schwartz Valera (1981). Les auteurs ont présenté deux flashes à déclenchement asynchrone à différentes phases alpha et ont demandé aux sujets de signaler s'ils n'avaient vu qu'un ou deux flashes. Les chercheurs ont constaté que les deux flashes qui apparaissaient au creux de la phase alpha étaient perçus comme un seul flash alors que les flashes apparaissant au sommet étaient perçus comme deux. L'étude suggère que la perception visuelle pourrait dépendre de la phase (c'est-à-dire du moment) des oscillations. Bien que la dépendance de la perception à la phase ne soit pas une idée nouvelle (see Nunn & Osselton, 1974), elle a fait l'objet de recherches approfondies ces dernières années (Busch, Dubois, & VanRullen, 2009 ; Dugué, Marque, & VanRullen, 2011 ; Fiebelkorn, Saalman, & Kastner, 2013 ; Hanslmayr, Volberg, Wimber, Dalal, & Greenlee, 2013), peut-être en raison des progrès de l'électrophysiologie et de la puissance de calcul. L'une des preuves les plus solides a été fournie par Busch et al. (2009). Ils ont demandé aux sujets de détecter des stimuli proches du seuil d'alerte lors de l'enregistrement de l'EEG, puis ont séparé les essais perçus et les essais non perçus en deux groupes. Après avoir calculé la cohérence de phase de l'activité EEG pour les deux groupes d'essais, ils ont constaté que, avant le début du stimulus, l'alpha et le thêta présentent des concentrations de phase différentes à des angles de phase différents dans les deux groupes d'essais. L'effet représente 16% de la variabilité de la performance de détection, ce qui est impressionnant compte tenu de la nature bruyante du signal EEG.

La perception visuelle discrète est également liée à la fréquence alpha. Comme mentionné ci-dessus, deux stimuli tombant à une phase spécifique de l'oscillation critique peuvent être perçus comme un seul. Logiquement, la phase est associée à la bande de fréquence de l'oscillation correspondante; lorsque la fréquence d'une oscillation critique est plus lente, les pics sont plus espacés. En d'autres termes, la fréquence pourrait déterminer le seuil des deux flashes à être perçus comme un seul. En adoptant un paradigme similaire à celui de Varela en 1981, Samaha and Postle (2015) ont découvert que la fréquence alpha individuelle peut prédire le seuil de fusion des deux flashes. Un alpha plus rapide est associé à une résolution temporelle plus élevée de la perception visuelle.

L'amplitude des oscillations cérébrales est liée à l'excitation et à l'inhibition de l'état du cerveau (Pfurtscheller, 2001). Lorsqu'un grand groupe de neurones se synchronise à la même fréquence, l'amplitude de cette fréquence augmente. La fluctuation de l'amplitude des oscillations en cours a été liée aux potentiels évoqués visuels et à la perception visuelle. Les données de plusieurs études suggèrent que l'état cortical (dynamique de l'activité neuronale continue) peut expliquer la variabilité de la réponse neuronale au stimulus à venir (Arieli, Sterkin, Grinvald, & Aertsen, 1996; Azouz & Gray, 1999; Van Der Togt, Spekreijse, & Supèr, 2005). L'augmentation de l'activité neuronale est liée à l'amélioration de la perception des stimuli. Ainsi, l'amplitude de l'activité en cours peut moduler la perception des stimuli. Une ligne de preuve suggère que la puissance du pré-stimulus alpha pourrait favoriser ou aggraver la sensibilité lorsque la puissance est faible ou élevée. Sur la base d'un seul essai, l'amplitude du pré-stimulus alpha est inversement corrélée au taux de détection des stimuli proches du seuil et du potentiel évoqué visuel (Ergenoglu et al., 2004). Dans le même ordre d'idées, on a constaté que l'amplitude alpha du pré-stimulus est en corrélation avec la perception consciente (Hanslmayr et al., 2007) et les tâches de discrimination (Roberts et al., 2014; Van Dijk et al., 2008). Ces résultats indiquent que la fluctuation de l'amplitude alpha est liée au niveau d'excitabilité du cortex visuel. Pour fournir une preuve causale de l'hypothèse selon laquelle l'amplitude alpha est un indice d'excitabilité corticale, Romei et al. ont (2008) induit une perception visuelle illusoire (phosphènes) avec la TMS et ont constaté que la probabilité de percevoir les phosphènes est liée à la puissance alpha pré-stimulus. Lorsque la puissance est élevée, la probabilité de percevoir les phosphènes est faible. Cependant, ces études ont surtout adopté une tâche de détection ; l'augmentation du taux de détection pourrait être due à une sensibilité accrue ou à un critère de réponse réduit. Dans ce dernier cas, les sujets ont tendance à répondre plus fréquemment. Par conséquent, le taux de

détection augmente. iemi y sus colegas (2017) doute l'idée d'une modulation de la sensibilité par la puissance alpha. Profitant de la théorie de la détection du signal, ils ont prouvé que la fluctuation de la puissance alpha avant le stimulus est associée au critère de détection plutôt qu'à la sensibilité.

Tous les éléments ci-dessus étayent la notion de cycles perceptifs, montrant que la perception visuelle est modulée par différentes caractéristiques des oscillations cérébrales. Bien que ces preuves montrent que l'état du cerveau avant le stimulus module la perception visuelle, aucune d'entre elles ne montre que le système visuel est oscillatoire pendant le traitement du stimulus. Peut-on trouver des cycles perceptuels après le stimulus? Et si la stimulation est continue plutôt qu'un seul flash? VanRullen et MacDonald (2012) ont présenté aux sujets un disque dont la luminance suit les séquences de bruit blanc (BB) pendant l'enregistrement de leur signal EEG. Après avoir fait une corrélation croisée entre le signal EEG et les séquences de luminance, ils ont constaté que la fonction de réponse impulsionnelle de sortie (IRF) au niveau des canaux occipitaux est un rythme alpha qui dure jusqu'à  $\sim 1$  seconde. Ces "échos perceptifs" de longue durée caractérisent non seulement les propriétés oscillatoires de la perception visuelle, mais suggèrent également que l'information visuelle est transportée dans le système visuel à travers le temps. Peut-être que l'information visuelle oscillante persistante est ce que le cerveau utilise pour cacher le traitement visuel discret réel et créer une perception lisse illusoire. Plus important encore, puisque les séquences BB sont à large bande et que la puissance de toutes les fréquences des séquences BB est égale, les échos reflètent les propriétés oscillatoires intrinsèques du système visuel. Contrairement à l'activité alpha permanente, qui est souvent liée au processus d'inhibition (Jensen et al., 1999; Klimesch, 1999), les échos perceptifs semblent jouer un rôle actif dans le traitement visuel.

Récemment, la dimension spatiale des échos a fait l'objet d'une étude. Les échos perceptifs ne sont pas une signature neuronale confinée aux canaux occipitaux ; au contraire, ils se déplacent des régions occipitales vers les régions frontales pendant la stimulation du réseau hydrographique (Lozano-Soldevilla & VanRullen, 2019). Les ondes progressives peuvent être modulées par l'attention. Lorsque l'on est attentif d'un côté du champ visuel, les échos émergent de l'hémisphère contra-latéral et se propagent vers les sites frontaux. Une autre étude a démontré que les échos et l'activité alpha se déplacent de manière anticipée lorsqu'il y a une entrée visuelle. Lorsque les yeux sont fermés, les ondes alpha vont dans la

direction opposée (Alamia & VanRullen, 2019). Bien que les études sur les ondes progressives montrent que le point de départ des ondes est le canal occipital, l'endroit exact où les échos sont générés dans le cerveau reste incertain. Le fait de répondre à cette question peut aider à démêler la signification fonctionnelle des échos et à mieux comprendre le mécanisme d'échantillonnage de notre système visuel. Jusqu'à présent, les échos n'ont été étudiés qu'à l'aide de l'EEG, qui ne peut offrir qu'une estimation grossière et imprécise de leur emplacement. Le chapitre 3 traitera de la manière dont nous combinons l'EEG et l'IRMf (enregistrées à des moments différents) pour localiser l'origine neuronale des échos perceptifs.

### **Des oscillations dans l'attention**

Il a été proposé que le centre de l'attention soit indivisible et unique (Posner et al., 1980; Treisman et Gelade, 1980). Pour traiter plusieurs objets dans une scène, l'attention doit se déplacer d'un objet à l'autre, et il a été prouvé que ce déplacement est rythmique (Buschman et Miller, 2009; Wolfe et al., 2011).

Il a été démontré que lors de l'observation libre, chaque saccade se produit ~200 ms, dans la gamme de la bande de fréquence thêta (Millan et al., 2008; Engbert & Mergenthaler, 2005). Cette rythmicité thêta se retrouve même dans les microsaccades lorsque les sujets fixent leurs yeux. L'attention fonctionne également de manière dynamique sans mouvements oculaires manifestes. Une étude psychophysique (VanRullen et al., 2007) a observé que l'attention échantillonne plusieurs éléments de manière séquentielle au niveau du thêta. Dans le même ordre d'idées, une étude (Dugué et al., 2015) utilisant une tâche de recherche visuelle difficile a montré que l'attention spatiale est allouée à chacun des stimuli périodiquement à ~7 Hz.

Pour examiner l'échantillonnage attentionnel au niveau comportemental, on utilise souvent une queue pour "réinitialiser" la phase de l'oscillation de l'attention. Le repère est généralement utilisé pour indiquer où les sujets doivent diriger leur attention. Lors de l'étude de l'attention oscillatoire, elle sert de référence temporelle; à partir de ce point, l'attention commence à se déplacer vers la cible indiquée. La réponse comportementale à la cible doit être une fonction d'oscillation de l'intervalle inter-stimulus entre le signal et la cible si l'attention est oscillatoire. Deux études (Landau & Fries, 2012; Fiebelkorn et al., 2013) ont utilisé un signal pour réinitialiser l'attention et ont exigé des sujets qu'ils s'occupent d'un ou deux objets. Ils ont trouvé que l'attention échantillonne chaque objet de manière séquentielle

à 4 Hz. Cependant, il y a un écart dans les fréquences rapportées par les études ci-dessus, certains trouvant des échantillons d'attention à  $\sim 7$  Hz, d'autres à 4 Hz. Il se pourrait que dans les études qui ont trouvé la fréquence la plus basse, l'attention ait été divisée en plusieurs objets (VanRullen 2016). Une étude (Holcombe et Chen, 2013) appuie directement cette interprétation; les sujets devaient suivre un, deux ou trois objets en mouvement sans mouvement des yeux. La fréquence temporelle de l'échantillonnage était de 7 Hz lors de la poursuite d'un objet, et la fréquence réduite à  $\sim 3$  Hz lors de la poursuite de trois objets.

Plusieurs études EEG et MEG ont établi un lien entre cet échantillonnage attentionnel et les oscillations cérébrales. Busch et VanRullen (2010) présentent des données qui suggèrent que la phase de pré-stimulus 8 Hz est prédictive de la performance de détection des cibles dans le lieu fréquenté. Une autre étude (Landau et al., 2015) a démontré que l'activité gamma indiquant le traitement d'un objet surveillé est modulée par la phase des oscillations de 4 Hz pendant la surveillance continue de deux objets. Cette étude étend également la compréhension de l'échantillonnage attentionnel étudié avec une réinitialisation externe en montrant que le mécanisme d'échantillonnage est un processus continu. Alors que de nombreuses études ont révélé la relation entre les oscillations thêta et l'échantillonnage attentionnel, on en sait peu sur la base neuronale et le mécanisme de génération de l'oscillation thêta.

Des oscillations thêta ont été observées dans le V4 et le cortex inférotemporel (IT) par plusieurs études (Lee et al., 2005; Rollenhagen et Olson, 2005; Sheinberg et Logothetis ; Nakamura et al., 1991). Une étude sur le macaque (Rollenhagen et al., 2005) a montré que le rythme thêta du cortex IT pouvait dépendre d'interactions compétitives entre les neurones sélectifs pour différents stimuli. L'étude a présenté deux stimuli aux singes, un objet dans la fovéa et un flaqueur en périphérie. Lorsque l'objet était présenté en présence du flaqueur ou vice versa, une forte oscillation de 5 Hz était déclenchée. Dans la même veine, une étude récente sur les singes (Kienitz et al., 2018) a enregistré l'activité neuronale dans V4 et a constaté que l'activité thêta émergeait dans l'activité multi-unité (MUA, activité enregistrée à partir d'un groupe de neurones) lorsqu'un objet était présenté dans le centre excitateur du champ réceptif, et qu'un autre objet était présenté dans l'environnement suppressif. Dans une tâche d'attention spatiale de la même étude, ils ont présenté aux singes un disque et des flancs de façon séquentielle, ce qui, selon le résultat de la première expérience, devrait évoquer une compétition neuronale et donner lieu à une oscillation thêta. Ensuite, la cible est apparue soit

dans les flaqueurs, soit dans les objets après un intervalle temporel aléatoire. Les singes ont été entraînés à déplacer rapidement leurs yeux vers la cible. Le temps de réaction a oscillé en fonction du moment où la cible est apparue, et plus intéressant encore, l'oscillation de réponse a été corrélée avec l'oscillation thêta enregistrée dans V4. Cette découverte délimite un mécanisme neuronal plausible pour l'échantillonnage attentionnel. Bien que cette conclusion soit convaincante, elle soulève également une question. Ce mécanisme s'applique-t-il également aux sujets humains? Le chapitre 4 est consacré à cette question.

### **Oscillations dans la conscience**

Les oscillations cérébrales servent à la conscience comme un rôle de communication. Dans les études sur le masquage, il a été prouvé que la perception consciente est en corrélation avec une synchronisation accrue des oscillations. Une étude a montré que la synchronisation gamma à longue distance est associée à la perception consciente des mots (Melloni et al., 2007). En plus de la synchronisation gamma, l'activité thêta est accrue dans les zones frontales lorsque les mots sont retenus en mémoire, ce qui indique que davantage de régions du cerveau sont impliquées dans la perception consciente par rapport à la perception non consciente. Dans une autre étude, la synchronisation bêta à longue distance a été trouvée lorsque les sujets percevaient consciemment les mots cibles (Gaillard et al., 2009).

La synchronisation des oscillations de la conscience a également été révélée dans des études employant des tâches de perception ambiguës. Une preuve a été fournie par des études utilisant la rivalité binoculaire. Chez les chats strabisme, le percept dominant évoque une plus grande synchronisation gamma que le percept supprimé, alors qu'il n'y a pas de différence dans la mise à feu des neurones des deux conditions (Fries et al., 1997), ce qui met en évidence la synchronisation des oscillations dans la formation de la perception consciente. Dans des études humaines utilisant la rivalité binoculaire, Doesburg et al. (2005) ont découvert que la synchronisation gamma augmentait avant que les sujets ne signalent les changements de perception, ce qui suggère que la synchronisation gamma est liée à l'émergence d'une perception cohérente. La synchronisation gamma liée aux changements de perception est également modulée à un taux thêta et cette synchronisation apparaît non seulement dans les régions activées, mais aussi entre ces régions (Doesburg et al., 2009). Ces résultats suggèrent que l'intégration à grande échelle est cruciale pour une perception consciente sans ambiguïté. Une autre source de preuves provient d'autres méthodes de perception ambiguë. En utilisant des stimuli audiovisuels, Hipp et al. (2011) démontrent que

la force de la synchronisation bêta et gamma à grande échelle est prédictive de la perception de stimuli audiovisuels ambigus et de l'intégration des informations auditives et visuelles.

Les études susmentionnées ont souligné l'importance des oscillations cérébrales dans la perception consciente. Parmi ces études, plusieurs études utilisant la rivalité binoculaire ont fait état d'intégrations à grande échelle reflétées par la synchronisation des oscillations cérébrales dans la perception consciente, confirmant l'opinion selon laquelle l'intégration interaréale est essentielle pour la conscience (Engel et Fries; 2016). Une autre preuve de la synchronisation provient d'une étude qui combine le marquage de fréquence et la rivalité binoculaire (Tononi et al., 1997). Le marquage de fréquence est une méthode qui permet de relier les stimuli à l'activité cérébrale correspondante afin de suivre quand et où les stimuli sont traités dans le cerveau. Lorsqu'on présente une cible oscillant à une fréquence donnée, les neurones qui répondent à cette cible ont tendance à se synchroniser à cette fréquence. Tononi et ses collègues (1997) ont montré deux stimuli qui scintillaient chacun à une fréquence différente. Ce faisant, ils ont pu suivre l'activité neuronale qui était en relation avec le percept dominant et le percept supprimé. Ils ont constaté que par rapport au percept dominant, la puissance de la fréquence liée au percept supprimé était de 50 à 85 % inférieure dans de nombreux canaux. Puisque la puissance de la fréquence marquée reflète les activités neuronales synchronisées en réponse à la cible (Tononi et al., 1998), les résultats suggèrent qu'il y a une synchronisation distribuée dans le cerveau pendant la perception consciente.

Le paradigme du marquage des fréquences est ici similaire à celui de la mesure des échos perceptifs ; tous deux relient l'activité cérébrale à la fluctuation des stimuli. Dans l'étude du marquage de fréquence, l'activité neuronale se synchronise en réponse aux stimuli dominants. En revanche, les résultats des échos perceptifs suggèrent qu'il existe un ensemble de neurones se synchronisant à 10 Hz pour permettre au cerveau d'échantillonner l'environnement de façon rythmique et active. La synchronisation qui sous-tend les échos perceptifs exige-t-elle que le cerveau soit conscient des stimuli? En d'autres termes, dans quelle mesure l'échantillonnage visuel à 10 Hz est-il automatique? C'est l'une des questions concernant les oscillations de la conscience que nous essayons d'aborder .

Il a été proposé que la synchronisation se fasse par un traitement descendant et ascendant (Engel et al., 2001; Engel et Fries, 2010). Dans le cas de la rivalité binoculaire, diverses données suggèrent que la rivalité est résolue à un niveau bas ou haut de la voie visuelle, puis se propage aux autres niveaux. Ces résultats indiquent donc qu'il pourrait y

avoir un traitement descendant ou ascendant qui est responsable de la transmission du signal de résolution. Cela soulève une question: Existe-t-il un flux d'information dirigé mis en œuvre par des oscillations contribuant à résoudre la compétition visuelle dans la rivalité binoculaire ? C'est la deuxième question liée aux oscillations de la conscience que nous voulons aborder.

## **Questions et cadre**

De toute évidence, de nombreuses preuves ont révélé la nature dynamique de nos fonctions cérébrales. Les oscillations cérébrales se manifestent dans les cycles de perception, bien que dans les fonctions cérébrales plus complexes telles que la conscience, les oscillations cérébrales soient impliquées d'une manière plus complexe (par exemple, la communication interaréale).

Comme nous pouvons le voir dans la revue de la littérature ci-dessus, la manière dont les oscillations cérébrales sont liées à l'échantillonnage visuel et attentionnel a été bien étudiée. Certaines études ont approfondi le rôle causal des oscillations cérébrales sur la perception visuelle et l'attention. Cependant, on ne sait pas encore d'où viennent ces oscillations liées à l'échantillonnage dans le cerveau ni comment elles sont générées. Ainsi, ce sont deux questions concernant la perception visuelle et l'attention que la présente thèse vise à aborder. Après avoir étudié les oscillations cérébrales dans la perception visuelle et l'attention, nous allons un peu plus loin pour étudier le rôle des oscillations cérébrales dans la conscience. C'est-à-dire que nous étudions comment les oscillations cérébrales sont impliquées lorsque le cerveau perçoit consciemment.

En matière de perception visuelle, les échos perceptifs, une démonstration des cycles perceptifs, caractérisent notre perception visuelle comme un processus cyclique et récurrent. Malgré le fait que de nombreuses propriétés des échos perceptifs ont été étudiées, le mécanisme sous-jacent n'est toujours pas clair. Une question importante reste à résoudre : quelle partie du cerveau génère ces échos ? Nous avons essayé de répondre à cette question au chapitre 3 par une expérience EEG-IRMf.

Les oscillations de l'attention sont un autre exemple de cycles perceptifs. Les preuves électrophysiologiques suggèrent que les oscillations de l'attention sont régies par un rythme thêta. Une étude sur les singes a cherché à explorer le mécanisme sous-jacent de ce rythme thêta, et ils ont découvert qu'il pourrait être généré par la compétition neuronale en V4



(Kienitz et al., 2018). Il est passionnant de constater que cette étude a permis de faire un progrès important dans la compréhension du mécanisme de l'oscillation de l'attention. Toutefois, il reste à vérifier si cette découverte peut être généralisée aux sujets humains. Pour l'examiner, nous avons reproduit l'expérience comportementale de l'étude sur les singes, comme nous l'avons vu au chapitre 4.

Dans une fonction cérébrale plus complexe comme la conscience, l'implication des oscillations cérébrales peut être plus compliquée, car la conscience est un processus cérébral qui nécessite une intégration à grande échelle de l'activité neuronale. L'intégration est réalisée par la synchronisation des oscillations cérébrales. La synchronisation de l'activité neuronale peut être reflétée par la puissance des oscillations neuronales. Pour évaluer si la synchronisation est essentielle pour l'échantillonnage visuel en perception consciente, nous avons adopté une tâche de rivalité binoculaire et examiné les échos perceptifs liés à la perception dominante et à la perception supprimée, détaillés au chapitre 5. La synchronisation de l'activité neuronale est soumise à un flux d'informations dirigé, tel que le traitement descendant et ascendant dans le cerveau. Pour traiter consciemment l'information visuelle, le cerveau a besoin d'une communication directe entre le cortex visuel qui envoie l'information sensorielle et les zones frontales qui délivrent des signaux modulateurs. Cependant, cette preuve fait défaut dans la rivalité binoculaire. Des études antérieures ont proposé que la résolution de conflits visuels ambigus dans la rivalité binoculaire nécessite une communication entre les zones de haut et de bas niveau. Nous proposons que la synchronisation des oscillations soit un candidat potentiel pour cette communication. Dans le chapitre 6, nous fournirons les preuves expérimentales correspondantes.

Toutes les questions auxquelles cette thèse vise à répondre sont résumées ci-dessous:

- 1 Quelle est la base neuronale des échos perceptuels? (Chapitre 3)
- 2 L'échantillonnage attentionnel découle-t-il du rythme thêta généré par la compétition visuelle? (Chapitre 4)
- 3 Les oscillations neuronales sont-elles responsables de la communication interzone dans la perception consciente? (chapitres 5 et 6)

La pierre angulaire de la présente thèse est constituée par les oscillations neuronales et leur rôle dans la perception visuelle, l'attention et la conscience. Le cadre des études

empiriques de la présente thèse suit les niveaux des fonctions perceptuelles ou cognitives du cerveau, c'est-à-dire de la fonction la plus ancienne et la plus fondamentale - la perception visuelle, à la fonction de niveau supérieur - l'attention et enfin, elle se terminera par la fonction la plus complexe - la conscience.

Dans le **chapitre 3**, je me concentre sur l'une des oscillations liées à la perception visuelle - les échos perceptifs. Plus précisément, l'objectif de l'étude est de localiser la source neuronale des échos perceptifs. Afin de comprendre pleinement les échos perceptifs, nous devons savoir d'où ils proviennent dans le cerveau. Cependant, la résolution spatiale de l'EEG est faible. L'un des moyens possibles d'étudier l'origine neuronale des échos de perception est de mener une étude IRMf-EEG pour mettre en relation le signal EEG des échos de perception avec les signaux BOLD (même si ceux-ci sont enregistrés à un moment différent). Bien que les zones du cerveau qui sont en corrélation avec les échos perceptifs ne soient pas nécessairement l'endroit exact où les échos perceptifs sont générés, le résultat peut réduire l'emplacement potentiel. La connaissance de l'origine neuronale pourrait permettre de comprendre comment les échos perceptifs sont générés et leur rôle fonctionnel.

Au **chapitre 4**, je passe à un autre niveau de la fonction cognitive: l'attention. De nombreuses études sur l'attention ont révélé que l'attention oscille à la fréquence thêta, et le signal EEG en bande thêta est associé à l'échantillonnage de l'attention. Cependant, le mécanisme sous-jacent de cette oscillation de l'attention reste inconnu. Une étude sur le singe a révélé que la rythmicité thêta pourrait provenir de la compétition neuronale des neurones V4 lors de la présentation de stimuli au centre et à l'extérieur d'un champ réceptif des neurones V4. Cette rythmicité thêta est en outre corrélée avec la rythmicité comportementale lors d'une tâche de recherche visuelle. Cependant, il n'est pas certain que les résultats puissent être généralisés à l'homme. L'étude actuelle a pour but de reproduire l'expérience comportementale de l'étude sur les singes chez les sujets humains.

Dans le **chapitre 5**, j'étudie comment la perception consciente module les échos perceptifs. Des études antérieures suggèrent que la synchronisation des oscillations cérébrales est essentielle à la perception consciente. L'apparition d'échos perceptifs doit exiger que les neurones sous-jacents se synchronisent à 10 Hz. Cette synchronisation aura-t-elle lieu lorsque les sujets ne percevront pas consciemment les cibles? D'autre part, les échos perceptifs ne sont pas encore bien compris. Des études antérieures ont montré que l'amplitude des échos perceptifs est modulée par l'attention. Puisque l'attention est étroitement liée à la conscience,

les échos perceptifs nécessitent-ils de la conscience? La rivalité binoculaire offre une grande opportunité d'étudier les échos perceptifs dans différentes conditions de conscience (dominante et supprimée). Dans l'étude actuelle, deux plaques de gabor dont la luminance suit des séquences aléatoires de bruit blanc ont été montrées aux deux yeux des sujets. En conséquence, nous avons pu faire une corrélation croisée du signal EEG avec les séquences dominantes et les séquences supprimées pour obtenir des échos perceptuels dominants et des échos supprimés. Ensuite, nous avons analysé les propriétés de puissance et d'ondes progressives de ces échos. En outre, l'étude peut également répondre à une autre question: quelle quantité d'informations visuelles peut survivre dans le cerveau si elles ne sont pas perçues consciemment?

Le **chapitre 6** continue avec les oscillations neuronales de la conscience. Une question non résolue dans la rivalité binoculaire est de savoir à quel niveau la rivalité est résolue. Les preuves existantes suggèrent qu'elle pourrait se produire à plusieurs niveaux de la voie visuelle, ce qui indique qu'il pourrait y avoir un processus descendant ou ascendant contribuant à la résolution de l'ambiguïté visuelle. Comme indiqué précédemment, l'une des principales fonctions des oscillations cérébrales est la communication. Ainsi, les oscillations neuronales sont de bons candidats pour une communication potentielle à haut et bas niveau. Pour étudier cela, nous avons enregistré des signaux EEG pendant que les sujets effectuaient une tâche de rivalité binoculaire, puis nous avons analysé la directivité des oscillations pendant la rivalité binoculaire en utilisant des ondes progressives et des mesures de causalité de Granger.

## **Résultats et discussion**

De nombreuses recherches ont montré que le traitement visuel est un processus discret, et ce traitement d'échantillonnage discret est généralement associé à des oscillations alpha. L'étude des échos perceptifs décrit la propriété temporelle de l'échantillonnage visuel pendant un traitement visuel soutenu. Bien que les échos soient un rythme de fréquence alpha, ils présentent un profil de réponse différent de celui de l'alpha dans certaines tâches. Afin d'étudier dans quelles régions du cerveau les échos perceptifs sont générés, nous avons réalisé une expérience EEG-FMRI (chapitre 3). Contrairement aux études EEG/IRMF simultanées, dans notre étude, les sujets ont effectué la même tâche lors d'une session EEG et d'une session IRMF séparément. Nous avons d'abord mesuré les échos lors de la séance d'EEG, puis nous avons utilisé les échos comme modèle pour reconstruire le signal EEG en

effectuant une convolution avec les séquences BB lors de la séance d'IRMf. Nous avons ensuite utilisé l'EEG reconstruit pour créer des régresseurs pour l'analyse en IRMf. Nous avons trouvé une activité étendue dans V1 et V2 qui pourrait être responsable de la génération des échos.

Au chapitre 4, nous avons reproduit l'expérience comportementale d'une étude sur les singes, qui visait à déterminer si l'activité thêta est générée par la compétition neuronale dans V4 lorsqu'un objet se présente dans le centre excitateur et l'environnement suppressif (Kienitz et al., 2018). Avec l'étude sur le singe, notre étude vise à étudier le mécanisme sous-jacent du rythme thêta de l'échantillonnage attentionnel. Nous avons obtenu des résultats similaires avec l'étude sur le singe; le temps de réaction saccadé fluctue à la fréquence thêta. Les phases de l'oscillation du rythme thêta dépendent de l'ordre d'un objet et de deux flancs présentés aux sujets, dont on suppose qu'ils provoquent des oscillations thêta dans le cerveau. Nos résultats soutiennent l'hypothèse que le rythme thêta de l'échantillonnage attentionnel peut être dérivé de la compétition des neurones V4.

Dans le chapitre 5, nous avons utilisé un paradigme de concurrence binoculaire pour étudier les échos perceptifs évoqués par le stimulus dominant ainsi que par le stimulus supprimé. Nous avons découvert que l'amplitude alpha des échos était plus importante dans la condition dominante que dans la condition supprimée. En outre, chaque condition a montré autant d'ondes de fuite par l'analyse des ondes progressives. L'amplitude des ondes alpha était plus grande dans la perception consciente, ce qui reflète peut-être le fait que plus de neurones sont synchronisés. Cela peut également impliquer que l'échantillonnage visuel en perception consciente est plus efficace (par exemple, le traitement est plus exhaustif) en raison du plus grand nombre de neurones impliqués. Cependant, les échos perceptifs n'ont pas entièrement disparu dans l'état supprimé, ce qui suggère que la génération d'échos perceptifs ne nécessite pas nécessairement l'implication de la conscience. Ce résultat démontre en partie l'importance de la communication entre les neurones par une meilleure synchronisation dans l'échantillonnage visuel perceptif conscient. De façon surprenante, la quantité d'ondes progressives était aussi importante dans la condition supprimée que dans les conditions dominantes et de contrôle. Selon des recherches antérieures, il y a plus de régions de haut niveau impliquées dans la perception consciente (Dehaene and Changeux, 2011), comme les lobes frontaux, qui n'apparaissent pas dans nos résultats. D'autres méthodes sont nécessaires pour étudier plus avant ce flux d'informations, et la causalité de Granger pourrait être un bon

candidat. Notre deuxième étude sur la conscience (chapitre 6) a abordé plus en détail la communication entre les régions en perception consciente.

Au chapitre 6, nous avons cherché à savoir s'il y a un flux d'informations dans la rivalité binoculaire, tel que reflété par les oscillations. Tout d'abord, nous avons montré que l'amplitude des oscillations alpha et bêta dans la rivalité binoculaire ainsi que dans la condition de contrôle, suit un schéma similaire, c'est-à-dire que l'amplitude ne reflète pas le traitement unique qui peut être nécessaire pour résoudre une perception ambiguë dans la rivalité binoculaire. La puissance accrue de ces deux oscillations est présente tant qu'il y a une perception stable ou claire. Nous avons en outre appliqué la causalité de Granger et constaté une augmentation de l'activité bêta descendante avant les commutations perceptives dans la rivalité binoculaire.

Les quatre études de cette thèse traitent du rôle des oscillations dans le cerveau sous l'angle de trois fonctions perceptuelles et cognitives : la perception visuelle, l'attention et la conscience. En tant qu'"excitateur", les oscillations cérébrales modulent la perception visuelle et l'attention de telle sorte que notre cerveau échantillonne les informations visuelles de façon rythmique. Les deux premières études (chapitres 3 et 4) visent à étudier l'origine neuronale et le mécanisme de génération des oscillations liées à ces échantillonnages visuels et attentionnels. Nous avons découvert que les échos perceptifs, les oscillations liées à l'échantillonnage visuel, pouvaient provenir des premières zones visuelles ; et les oscillations thêta, le modulateur sous-jacent de l'échantillonnage attentionnel, pouvaient provenir de la compétition visuelle des neurones V4. En tant que "communicateur", les oscillations cérébrales permettent d'échanger des informations entre les zones du cerveau par le biais de la synchronisation. Les deux dernières études (chapitres 5 et 6) démontrent que la communication et le flux d'informations entre les zones pourraient être associés à la perception consciente. Dans l'ensemble, le cerveau est un système dynamique dans lequel les oscillations facilitent de manière flexible diverses fonctions cérébrales.

# 1 CHAPTER 1. LITERATURE REVIEW

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## 1.1 GENERAL INTRODUCTION

If you stare at the cube in (Figure 1-1 A) long enough, you will see that it is changing periodically. Sometimes the left-lower corner is in the front, but sometimes the right-upper corner switches to the front. No matter how hard you try to maintain one perception, the switch is unavoidable. As you may notice, it is not that the image is changing; it is your brain itself that changes over time. This phenomenon strongly demonstrates that our perception and our brain activities are fluctuating.

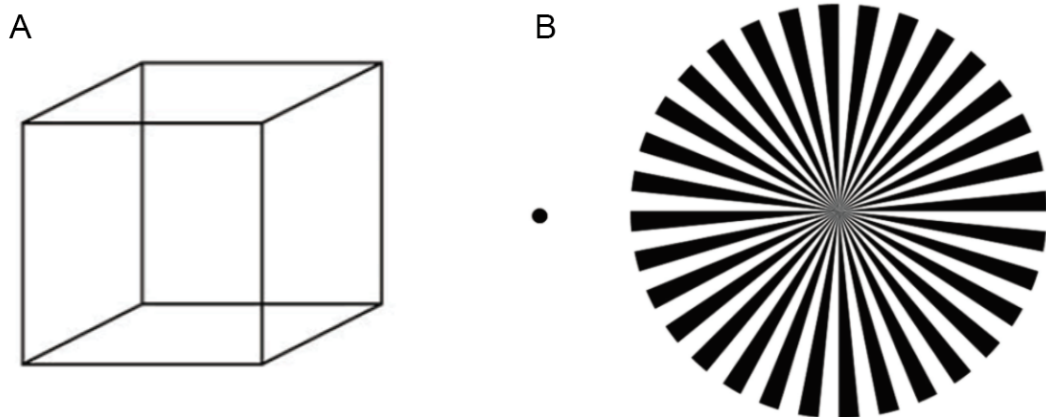


Figure 1-1 (A) Necker cube. When looking at the cube, the perception of its morphology continuously changes, sometimes the inside bottom-left corner comes out to the front. (B) Flickering wheel illusion. When fixating at the dot on the left and attend to the wheel on the right, the center of the wheel flickers about 10 time a second adapted from (Sokoliuk & VanRullen, 2013).

The brain is a dynamic system, as demonstrated by the Necker cube in Figure 1-1 A. And oscillations are one of the main components of brain dynamics. Oscillations are ubiquitous in the brain. Although they were initially considered a by-product produced by the brain, many neuroscientists realized the significance of the oscillations and tried to establish

the link between the oscillations and cognitive functions. One of the theories for establishing this link is "perceptual cycles" (VanRullen, 2016). The idea is that if brain activities are periodic, it is natural to consider that the rhythmicity of brain activities will manifest in our perception, leading to oscillatory perception. It might sound surprising, as our conscious perception seems so smooth, seamless and stable. However, in the last decades, considerable research has revealed that brain oscillations give rise to "perceptual cycles", showing that perception is not continuous; instead, it is "discrete" and oscillatory, taking "snapshots" of the world as a camera. Our stable perception, counterintuitively, is just an illusion. Some special visual conditions allow you to experience the "oscillatory perception". If you fixate your eyes on the black dot in (Figure 1-1 B) and pay attention to the wheel on the right, you can see the wheel's center is flickering about ten times a second (Sokoliuk & VanRullen, 2013). In perceptual cycles, brain oscillations might play an "exciter" role, periodically modulating the excitability of the sensory areas of the brain.

Consciousness also waxes and wanes like perceptual cycles. However, brain oscillations might also play another role in consciousness. Consciousness is probably the most complex cognitive function that requires the interaction of different cognitive functions, such as cognitive control and visual perception. Thus, there might be communication between different brain areas during conscious perception, and brain oscillations can serve as a "communicator" role.

All these roles of oscillations allow the brain to work effectively. Even though the oscillatory nature of the brain is gradually accepted and more and more scientists have dived into researching brain oscillations, there are still plenty of mysteries. What is the generation mechanism of the brain oscillations that relate to a specific perceptual or cognitive function? Where do they come from in the brain? How are they involved in conscious perception? These are the main questions I sought to address during my Ph.D.

The backbone of the current thesis is brain oscillations. Hence, I will start with neural oscillations in the literature review. This thesis focuses on how neural oscillations are involved in three fundamental perceptual or cognitive functions: visual perception, attention and consciousness. Although I discuss these three functions separately, the experiments I report here are all based on visual tasks. This is why I introduce the biophysics of visual perception, which will also help discuss attention and consciousness. In each section of visual perception, attention and consciousness, I will first take a brief detour to describe some

background, and then I will go back to the main story – the role of brain oscillations in these functions.

Let us begin with brain oscillations.

## **1.2 BRAIN OSCILLATIONS**

Brain oscillations can be measured with various electrophysiology tools such as Electroencephalography (EEG). The history of brain oscillations started in 1929 when Hans Berger (Berger, 1929) observed an EEG wave that oscillates at  $\sim 10$  Hz, which is now the most well-known brain wave, the alpha rhythm. Since then, more and more brain oscillations have been observed and investigated. That said, not all oscillations can be readily seen by visual inspection due to the amount of noise in EEG and the mixture of oscillations at different frequencies. Alpha is an exception; it is large enough to be easily seen from electrodes at occipital areas when subjects close their eyes and relax. While for observing the other frequencies, some signal processing methods such as Fourier transform are required.

### **1.2.1 Characteristics of oscillations: frequency, amplitude, phase.**

Like any other oscillations, the characteristics of brain oscillations comprise the frequency, amplitude and phase. Frequency is the speed of oscillations or the duration of a cycle of an oscillation. The unit of frequency is “Hertz” (Hz). Hz describes the number of cycles in one second (in Figure 2, if  $T = 1$ , the oscillation in the plot is 1Hz). Higher frequency means more cycles in one second and faster speed. Amplitude is how strong an oscillation is, and power is the square of the amplitude. These two terms are interchangeable in the current thesis. Brain oscillations are subject to the  $1/f$  power law (Ouyang et al., 2020); that is, frequency is inversely proportional to power (Figure 1-3); low frequency tends to have a higher power. Phase depicts the timing or location within a cycle of a wave (Figure 1-2). For instance, the phase of  $\pi/2$  is at the peak of the sine wave in Figure 1-2.



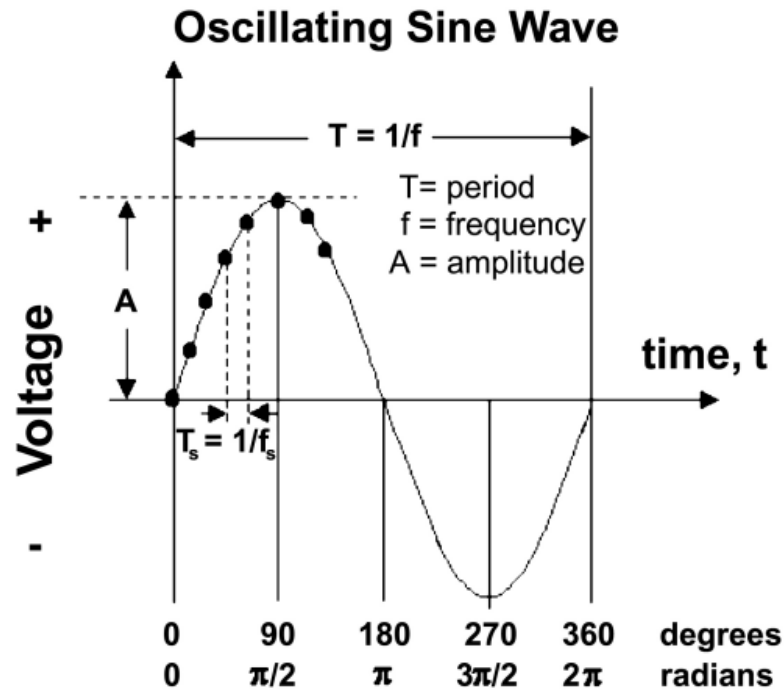


Figure 1-2. One cycle of a sine wave. (By National Institute of Standards and Technology (NIST) - National Institute of Standards and Technology (NIST) [1], Public Domain, <https://commons.wikimedia.org/w/index.php?curid=49393371>)

### 1.2.2 The main frequency bands of oscillations in the brain

Usually, frequencies are grouped into different bands (Figure 1-3) (Buzsáki & Draguhn, 2004), which are typically linked with different cognitive functions. Most studies in human focus on the delta (2~4 Hz), theta (4~7 Hz), alpha (7~13 Hz), beta (13~30 Hz) and gamma (30~100 Hz) bands. Here, I give a brief introduction to the main frequency bands (theta, alpha and beta) that are related to the four studies in the thesis.

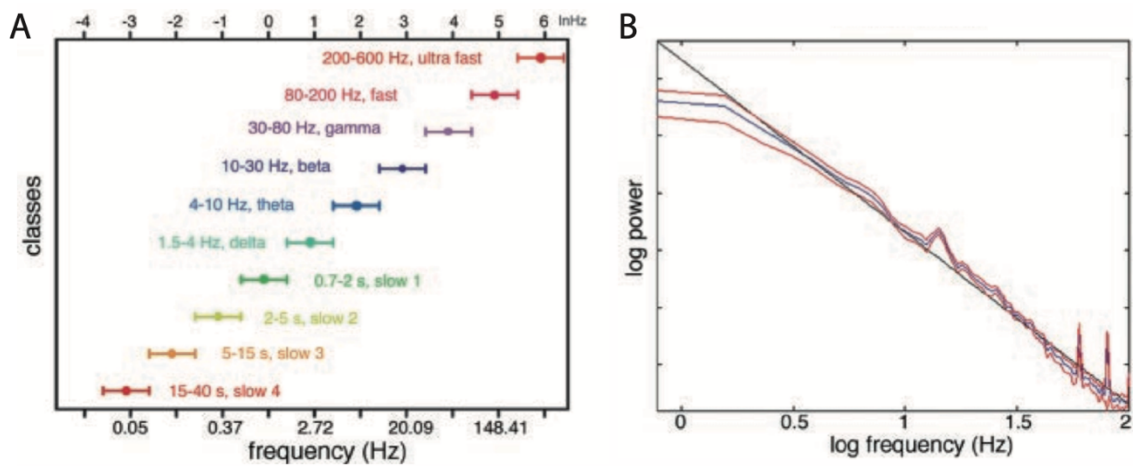


Figure 1-3 (A) Frequencies are grouped into different bands. (B) Brain oscillations follow  $1/f$  power law. Reproduced from Buzsáki & Draguhn (2004)

### Theta oscillations

Many insightful findings regarding theta oscillations come from the multi-electrode recording of rats. The well-known functional role of the theta rhythm recorded in the rat hippocampus is the phase coding of the hippocampal place cells; more specifically, the firing of place cells is locked to the hippocampal theta phase activity (Wilson & McNaughton, 1993). The place cells contain information regarding the environment where the rats explore. When a rat moves in the place field (area coded by place cells), each place cell tends to fire progressively at an earlier and earlier phase of the theta activity. This phenomenon is named “theta phase precession” (O’Keefe & Recce, 1993).

In human intracranial studies, theta oscillations are associated with working and long-term memory (Kahana et al., 2001; Tesche & Karhu, 2000). In EEG and MEG studies, theta oscillations are most prominent at the frontal midline (FM) (Mitchell et al., 2008). The FM theta activity has been linked to working memory, as it has been found to increase with memory load in working memory tasks (Gevins & Smith, 2000; Jensen & Tesche, 2002; René Scheeringa et al., 2009). The FM theta has also been related to error-processing (Michael X Cohen & Van Gaal, 2013). The FM theta activity increases after subjects make wrong responses in a go/no-go task in which subjects need to respond quickly when a go signal appears and not to respond when there is a no-go signal.

In this thesis, the role of theta oscillations in the brain is associated with attentional sampling, as discussed in section 1.4.3.

### **Alpha oscillations**

Alpha was once considered as an “idle” rhythm whose power increases when subjects are relaxing or not doing tasks. However, this notion has been challenged recently. Accumulating evidence suggests that alpha is related to “active inhibition.”

A piece of early evidence against the idling notion of alpha is a study in which subjects were required to shift attention between vision and hearing. When attention was directed to hearing, the posterior alpha decreased (Adrian, 1944) (Figure 1-4, A). Another line of evidence disproving the idling notion is from working memory studies, in which memory demand increase is accompanied by alpha increases (Figure 1-4, B) (Jensen et al., 1999; Wolfgang Klimesch, 1999). On the other hand, the inhibition hypothesis has gained support from working memory and attention studies. In a working memory study, distracting information was presented during the retention period during which subjects were required to keep the targets in memory (Bonnefond & Jensen, 2012). When doing the task, the subjects could anticipate the arrival of the upcoming distractors. The results showed that alpha power increased prior to the arrival of the distractors, suggesting alpha power increases in order to filter out the distracting information (Figure 1-4, C). In addition to the working memory study findings, attention experiments have observed that when subjects attend to the left side, the alpha power in the right hemisphere decreases (Worden et al., 2000).

All in all, the alpha studies mentioned above suggest that alpha is an inhibitor. In the current thesis, we can see a different role of alpha. That is, alpha is closely linked with the discrete sampling of visual perception, as discussed in section 1.3.2.

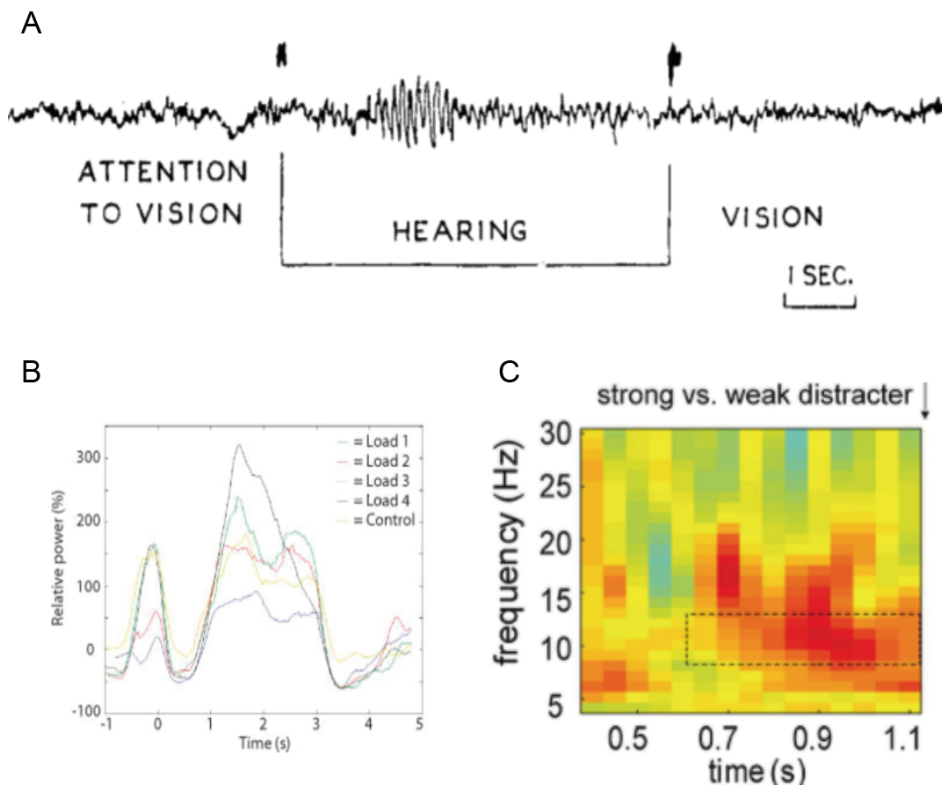


Figure 1-4 (A) In an attention study by Adrian (1944), subjects were required to attend to visual or auditory stimuli. Alpha increased when the subjects attended to the auditory stimuli, decreased when they attended to the visual stimuli. (reproduced from Adrian 1944) (B) Time course of alpha power in a working memory task (Tuladhar et al., 2007). Alpha systematically decreased as the memory load increased. (reproduced from Tuladhar et al., 2007) (C) In a working memory task, distracters were presented during the memory retention period. Alpha power increased before the arrival of the distracter. (reproduced from Bonnefond & Jensen, 2012)

## Beta oscillations

The role of beta oscillations is elusive. Some studies link beta with the motor system (Baker, 2007). Electrophysiology studies have shown that beta oscillations might be responsible for transmitting information between the motor cortex and muscles. (Baker, 2007; Kilner et al., 2000; van Elswijk et al., 2010). A review paper holds a different opinion. They proposed that beta oscillations are associated with “status-quo”, maintaining the current cognitive or sensorimotor state (Engel & Fries, 2010). However, a recent paper proposes that beta oscillations are related to reactivating the latent representation (Spitzer & Haegens, 2017). The key supporting evidence is a transcranial magnetic stimulation (TMS) study in

which unattended memory was pushed into an active state by TMS pulses. The reactivated item could only be decoded from beta activity, suggesting beta underlies the reactivation process.

### **1.2.3 The functions of brain oscillations**

Now we know what brain oscillations are, and there are different frequency bands being associated with specific cognitive functions. One might ask why these oscillations are important and how they work to produce or facilitate our perceptual and cognitive functions.

#### **Neuronal communication**

Effective and flexible neuronal communication is essential for performing complex cognitive functions. The Communication-through-coherence (CTC) hypothesis (Fries, 2005, 2015) has provided a neuronal communication mechanism to account for this efficient and flexible signal routing in the brain (Figure 1-5). The fundamental idea is that the oscillation phase modulates and aligns the excitability of groups of neurons, therefore creating specific moments of the phase cycle that allow these neurons to receive and send the signal to each other most effectively. The phase not only modulates the excitability of the output of neurons but also their sensitivity for input. Hence, when an output neuron group and an input neuron group are phase-coherent, their excitability windows match each other; thereby, information can be exchanged efficiently (Figure 1-5) (Fries, 2005, 2015). This hypothesis has received support from intracranial recordings and MEG/EEG studies. MEG studies have shown that the coherence of oscillations across areas can facilitate behavioral performance (Gross et al., 2004). Intracranial recording in cats reveals that coherence of gamma band activity, rather than the neuronal firing rate, correlates with conscious perception (Fries et al., 1997). In short, oscillations can facilitate neuronal communication by aligning the activity of neurons to the same phase.

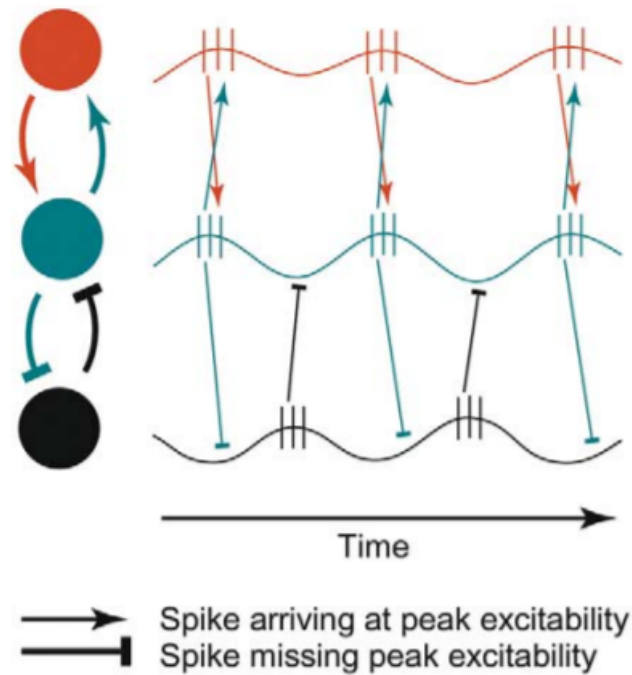


Figure 1-5 Illustration of communication through coherence. The spikes of the red and green cells are phase-locked such that the information they send to each other can arrive at the peak excitability, which allows for effective communication. The green cell and the black cell are not synchronized; hence, the information sent from both cells will miss the optimal moment of excitability to arrive. Adapted from (Fries, 2005)

### Excitability modulation

Brain oscillations modulate cortical excitability. This hypothesis was first proposed by Bishop in 1932 (Bishop, 1932) and was supported by an abundance of empirical evidence from intracranial recordings, EEG and MEG studies over the years. In intracranial recordings, it has been shown that the oscillations of local field potential are correlated with neuronal spike rate (Montemurro et al., 2008). Another study showed that the synaptic activity responded differently when a stimulus appeared at different phases of delta oscillation (Lakatos et al., 2005). In a concurrent EEG-fMRI study, the researchers presented simple visual stimuli to subjects and recorded their EEG and fMRI BOLD signal (the details about EEG and fMRI will be introduced in Chapter 2) at the same time, which allowed them to investigate the relationship between neural oscillations and BOLD signal in response to the stimuli. They focused on the alpha frequency band. Since the timing when visual stimuli appeared was random, the stimuli could arrive at different phases of the alpha. They found

that the BOLD response is strong when the stimuli appeared at the trough of the alpha activity and weak when they were displayed at the peak of the alpha. In short, brain oscillations might reflect or modulate the excitability of neurons such that there is a specific phase that can facilitate neural processing. As we will see in the oscillations in visual perception and attention (sections 1.3.2 and 1.4.3), the oscillatory sampling might stem from this excitability mechanism.

### **Phase coding of brain oscillation**

It has been hypothesized that another important function of brain oscillation is to carry information. Many studies have demonstrated that sensory information is encoded in the phase of brain oscillations (Kayser et al., 2009; Montemurro et al., 2008; O’Keefe & Recce, 1993; Vinck et al., 2010). For example, Kayser et al. (2009) used mutual information analysis to quantify the amount of information encoded in power and phase of neural oscillations. They found the phase contained more information about the stimuli than the power. Furthermore, a working memory study in monkeys shows that neuron spikes carry most of the information of memorized objects at specific phases (Siegel et al., 2009). In a facial expression categorization experiment, Schyns, Thut, & Gross (2011) analyzed the contribution of power, frequency and phase for coding cognitive task information and found that phase contains most of the information. They further demonstrate the “multiplexing” property of brain oscillations, that is, different frequencies of neural oscillations codes different information.

In this section, I have introduced neural oscillations, the characteristics, the functional role, as well as the generation mechanism of the oscillations. Now we have the basic knowledge about neural oscillations; we can go further to see how the oscillations play a role in our visual perception, giving rise to “discrete” perception.

## **1.3 VISUAL PERCEPTION AND NEURAL OSCILLATIONS**

Despite the obvious familiarity of our vision, we remain in many ways ignorant of how it functions. Every day, we wake up, open our eyes; naturally and effortlessly, we start to use

our vision. Visual perception is fast. For instance, we can recognize various things quickly, identifying our friends in a group of strangers within a second. Our vision works extremely fast and seems to require minimal or no effort. Vision is also flexible and robust. No matter how we see an object from different angles, for example, seeing a computer from its front, its top or even its bottom, we can easily recognize that it is a computer. By contrast, the most powerful computer vision algorithms fails to recognize a picture when only a small amount of noise or distortion is added (Akhtar & Mian, 2018). How does visual perception achieve this feat? What operates behind the eyes? The main focus of this section is the oscillations in visual perception, but it would be helpful first to introduce the neural structure that produces visual perception. Therefore, before discussing the oscillatory properties of visual perception, I will briefly introduce the visual pathway.

### **1.3.1 Biophysics of Visual perception**

#### **Retina**

The retina is the “gate” of visual information, which receives light reflected by objects in our environment. The retina for humans is like a lens for cameras. The light first arrives in a layer of photoreceptor cells called rods and cones, where the light energy is transformed into electrochemical energy to be further transmitted into the neural system. The connection between the retina and the brain is made up of ganglion cells. Through these cells, electrical visual information is delivered mainly via two pathways. Most (90%) of the optic fibers project to the geniculostriate pathway, through the relay center in the thalamus - LGN, to the striate cortex (Figure 1-6)(Banich & Compton, 2018). This pathway is responsible for our conscious perception because the information of fine-grained object features and colors goes through this way and finally into our consciousness. The other main pathway starting from the retina is the tectopulvinar path, which is in charge of fast motion and coarse visual information, enabling humans to react quickly to the environment. Since the tectopulvinar path is not relevant to our studies, I mainly talk about the geniculostriate pathway.

#### **Lateral Geniculate Nucleus**



The Lateral Geniculate Nucleus (LGN) is the connector of the retina and the primary cortex. It also has been known as a relay center of the Thalamus. It receives bottom-up input from the retina and top-down feedback from the primary visual cortex (Sillito et al., 2006) . The LGN has six layers, and each layer receives the signal from a single eye, which means the information of two eyes will not merge in LGN. LGN has a retinotopic organization, meaning the cells in LGN are spatially mapped with ganglion cells in the retina. As the LGN is higher in the hierarchy compared to the retina, the cells in LGN get input from a set of cells from the retina. In other words, the receptive field of the cells in LGN is larger than the cells in the retina.

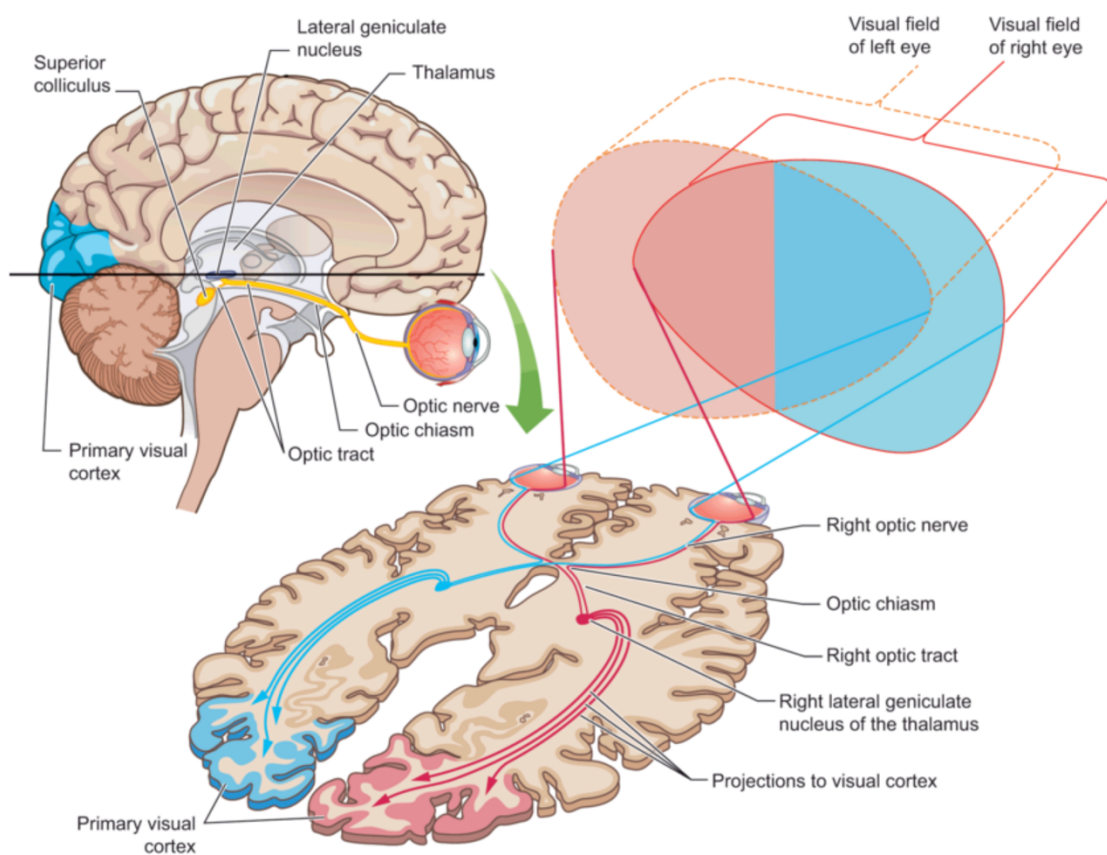


Figure 1-6. The visual pathway shown in sagittal (top left) and axial (bottom right) view. The pathways that are responsible for the left and right visual fields are depicted in red and blue. The visual information of both sides enters the retina, advances along the optic tract, passes LGN and arrives at the contra-lateral primary visual cortex. (Figure reproduced from Banich & Compton, 2018)

## Primary Visual Cortex

Once the visual information has passed the LGN, it arrives at the cortex's first station- primary visual cortex, called V1 or “striate cortex” because stripes on the V1 are obvious in anatomical slices. V1 processes the signal from LGN and sends the output to the higher visual hierarchy.

V1 is also an area where the information from the two eyes starts to merge. That means in V1, both monocular neurons and binocular neurons coexist. As we will see in the Chapter on consciousness, at what level the binocular rivalry (alternating perception while two eyes are viewing dissimilar images) is resolved is still a mystery. Could it happen at a very early stage, such as a monocular level, or at a higher stage, after the monocular information from two eyes is combined (Tong et al., 2006)?

The visual information is processed in a hierarchical fashion in the visual pathway. Higher-order areas process more abstract information about visual objects, while the lower-order areas like V1 and LGN process the physical properties of objects. The neurons in V1 are tuned for orientation, spatial frequency and contrast. Beyond the primary visual cortex, visual information is transmitted to extrastriate areas (V2, V3 and V4). The function of V2, V3 are not well understood so far. V2 shares some properties with V1. V2 cells are selective for orientation, and motion, color and stereoscopic disparity to some extent (Boynton & Hegdé, 2004). V2 cells are also modulated by some more complex patterns, such as combinations of orientation (Anzai et al., 2007) and illusory contours (Von der Heydt et al., 1984). As for V3, V3 neurons are involved in multiple aspects of visual processing, such as color, orientation and binocular disparity (Felleman & Van Essen, 1987); V3 neurons are also selective for different aspects of stimulus motion, such as speed and direction (Felleman & Van Essen, 1987; Gegenfurtner et al., 1997). V4 is rather complex. V4 neurons exhibit a wide range of receptive field preferences. V4 might be related to color vision (Zeki, 1983), shape (Essen & Zeki, 1978; Mountcastle et al., 1987; Schein et al., 1982) and attention (Chelazzi et al., 2011; Moran & Desimone, 1985).

### **Dorsal and ventral pathway**

The visual information departing from the primary cortex, through extrastriate areas, enters two distinct visual pathways, the dorsal pathway (“where stream”) and the ventral pathway (“what stream”) (Milner & Goodale, 2008; Mishkin et al., 1983). The dorsal

pathway starts from the primary visual cortex and stretches into the parietal lobe. In contrast, the ventral pathway goes through the occipitotemporal cortex until the anterior part of the inferior temporal gyrus. These two pathways are known for their distinct functional characterizations: The dorsal pathway processes the information of object location to guide action, while the properties of objects, such as shape, size and orientation, pass through the ventral pathway.

We have just finished going through the spatial arrangement of the visual system; this can give us an overview of how visual information flows in the visual system. Next, we will start our main topic: the temporal dimension of the visual system - oscillations in visual perception.

### **1.3.2 Oscillations in visual perception**

As early as the late 19th century, it had been proposed that perception is discrete and that discrete visual perception scans the external environment approximately 10 times per second (Whitlock, 2009). Although many studies have been conducted since then, especially in the mid to late 20th century, in an attempt to prove the existence of discrete visual perception, those studies could not provide decisive evidence due to technical and experimental paradigm limitations. Therefore, I will present here the more recent literature. On the other hand, the concept of discrete vision was associated with alpha waves soon after their discovery, due to the close frequency of the estimated visual samples and alpha waves (Adrian & Yamagiwa, 1935). So far, most studies support this view. The phase, frequency, and amplitude of alpha, however, are all related to discrete visual perception - we thus discuss these correlations separately. The literature review of section 1.3.2 is inspired by (VanRullen, 2016, 2018).

#### **Phase and visual perception**

One of the earliest works demonstrating the relationship between discrete visual perception and the alpha rhythm phase is by Valera, Toro, John, & Schwartz (1981). The authors presented two flashes with asynchronous onset at different alpha phases and asked

the subjects to report if they saw only one flash or two. The researchers found that the two flashes that appeared at the trough of alpha were perceived as one flash while the flashes appearing at the peak were perceived as two. The study suggests that visual perception might depend on the phase (i.e., timing) of oscillations. Although the phase-dependence of perception is not a new idea (see Nunn & Osselton, 1974), it has been extensively researched in recent years (Busch et al., 2009; Dugué et al., 2011; Fiebelkorn et al., 2013; Hanslmayr et al., 2013), possibly due to the advancement of electrophysiology and computational power. One of the strongest lines of evidence was provided by Busch et al., (2009). They required subjects to detect near-threshold stimuli while recording EEG and then separated the perceived trials and the unperceived trials into two groups. After the phase coherence of EEG activity was computed for both trial groups, they found that, before the stimulus onset, the alpha and theta exhibit different phase concentrations at different phase angles in the two trial groups. The effect accounts for 16% of the variability in detection performance, which is impressive considering the noisy nature of the EEG signal.

### **Frequency and visual perception**

Discrete visual perception is also related to alpha frequency. As mentioned above, two stimuli falling at a specific phase of the critical oscillation can be perceived as one. Logically, the phase is associated with the frequency band of the corresponding oscillation; when the frequency of a critical oscillation is slower, the peaks are further apart. In other words, the frequency might determine the threshold of the two flashes to be perceived as one. Adopting a similar paradigm as Varela in 1981, Samaha and Postle (2015) found that the individual alpha frequency can predict the two-flash fusion threshold. Faster alpha is associated with a higher temporal resolution of visual perception.

### **Amplitude (power) and visual perception**

The amplitude of brain oscillations is related to excitation and inhibition of the brain state (Pfurtscheller, 2001). When a large group of neurons synchronizes at the same frequency, the amplitude of this frequency increases. The fluctuation of the amplitude of ongoing oscillations has been linked to visual evoked potentials and visual perception. Data

from several studies suggest that the cortical state (dynamics of the ongoing neural activity) can account for the variability of the neuronal response to the forthcoming stimulus (Arieli et al., 1996; Azouz & Gray, 1999; Van Der Togt et al., 2005). The increase of neuronal activity is related to enhancement of stimulus perception. Thus, the amplitude of the ongoing activity can modulate stimulus perception. One line of evidence suggests that prestimulus alpha power might promote or worsen sensitivity when power is low or high. On a single-trial basis, the prestimulus alpha amplitude is inversely correlated to the detection rate of near-threshold stimuli and visual evoked potential (Ergenoglu et al., 2004). Along the same line of thought, the prestimulus alpha amplitude was found to correlate with conscious perception (Hanslmayr et al., 2007) and discrimination tasks (Roberts et al., 2014; Van Dijk et al., 2008). These findings indicate that the fluctuation of alpha amplitude is linked to the excitability level of the visual cortex. To provide causal evidence for the hypothesis that alpha amplitude is an index of cortical excitability, Romei et al. (2008) induced illusory visual perception (phosphenes) with TMS and found that the probability of perceiving phosphenes is related to prestimulus alpha power. When the power is high, the chance of perceiving phosphenes is low. However, these studies mostly adopted a detection task; the detection rate increase could be due to increased sensitivity or decreased response criterion. In the latter case, subjects tend to respond more frequently. As a result, the detection rate increase. Iemi and colleagues (2017) cast doubt on the idea of alpha power modulating sensitivity. Taking advantage of signal detection theory, they proved that the fluctuation of prestimulus alpha power is associated with the detection criterion rather than sensitivity.

## **Perceptual echoes**

All the evidence above supports the notion of perceptual cycles, showing that visual perception is modulated by various characteristics of brain oscillations. Although this evidence shows that pre-stimulus brain state modulates visual perception, few studies show the visual system is oscillatory during stimulus processing. Can we find perceptual cycles post-stimulus? What if the stimulation is continuous rather than a single flash? VanRullen and MacDonald (2012) presented to subjects a disc whose luminance follows white-noise (WN) sequences while recording their EEG signal. After doing cross-correlation between the EEG signal and the luminance sequences, they found that the output impulse response function (IRF) at occipital channels is an alpha rhythm that lasts up to ~1 second (Figure 1-

7). These long-lasting “perceptual echoes” not only characterize the oscillatory properties of visual perception but also suggest that visual information is carried in the visual system across time. Perhaps the lingering oscillating visual information is what the brain uses to hide the actual discrete visual processing and create the illusory smooth perception. More importantly, since the WN sequences are broadband and the power for all frequencies in the WN sequences are equal, the echoes are reflecting the intrinsic oscillatory properties of the visual system. Contrary to the ongoing alpha activity, which is often linked with the inhibition process (Jensen et al., 1999; Wolfgang Klimesch, 1999), perceptual echoes seem to play an active role in visual processing.

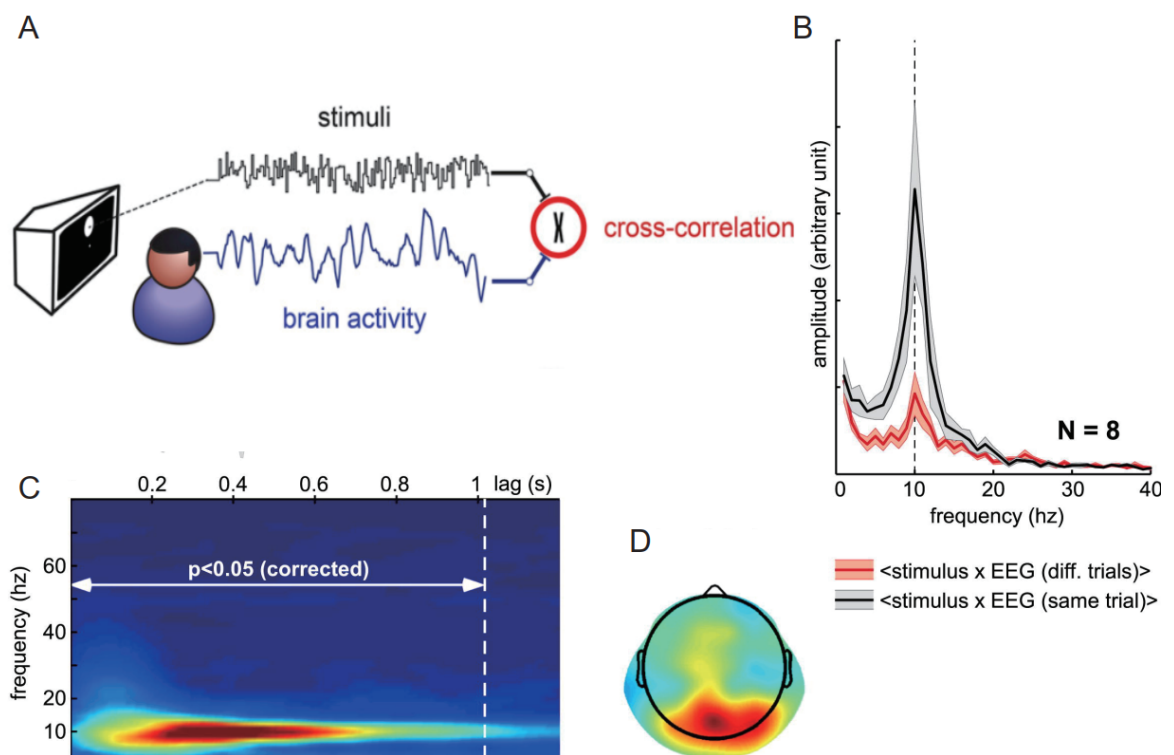


Figure 1-7 Perceptual echoes measurement procedure and the properties of the echoes. (A) A subject is viewing a disc whose luminance fluctuates randomly with the EEG signal being recorded. For calculating the echoes, the random luminance sequences will be cross-correlated with the corresponding EEG signal, and the output coefficients are the echoes. Figure adapted from (Alamia & VanRullen, 2019) (B) Frequency spectrum of perceptual echoes averaged across eight subjects measured by VanRullen and Macdonald (2012). (C) Time-frequency representation of perceptual echoes; the echoes last up to 1 second. (D) Topography of the echoes. The echoes are prominent at occipital electrodes. Figure adapted from (VanRullen and Macdonald, 2012)

The echoes share several features with ongoing alpha oscillations. Not only do the amplitude and frequency of the echoes correlate with the ongoing alpha, but they are located in similar channels (Fig. 1-7 D). Interestingly, they also exhibit different profiles in a spatial attention task. When subjects attend to one of the objects presented in the left and right visual fields, the alpha power decreases in the contralateral hemisphere and increases in the ipsilateral hemisphere. Conversely, the opposite effect was observed for echoes. Echo power increased in the contralateral hemisphere and decreased in the ipsi-lateral hemisphere because subjects attended to the left or right side of the visual field.

Recently the spatial dimension of the echoes has come under study. Perceptual echoes are not a neural signature confined to the occipital channels; instead, they travel from occipital regions to frontal regions during WN stimulation (Lozano-Soldevilla & VanRullen, 2019). The traveling waves can be modulated by attention. When attending to one side of the visual field, the echoes emerge from the contra-lateral hemisphere and propagate to the frontal sites. Another study demonstrated that the echoes and the alpha activity travel in a feedforward fashion when there is visual input. When eyes are closed, the alpha waves go in the opposite direction (Figure 1-8) (Alamia & VanRullen, 2019). Although the traveling waves studies show that the waves' starting point is occipital channels, the exact location in the brain where the echoes are generated remains unclear. Addressing this question could help unravel the functional significance of the echoes and further our understanding of the sampling mechanism of our visual system. Up to date, the echoes have only been investigated using EEG, which can only offer a rough and inaccurate estimation of the echoes' location. Chapter 3 will discuss how we combine EEG and fMRI (recorded at separate times) to locate the neural origin of perceptual echoes.

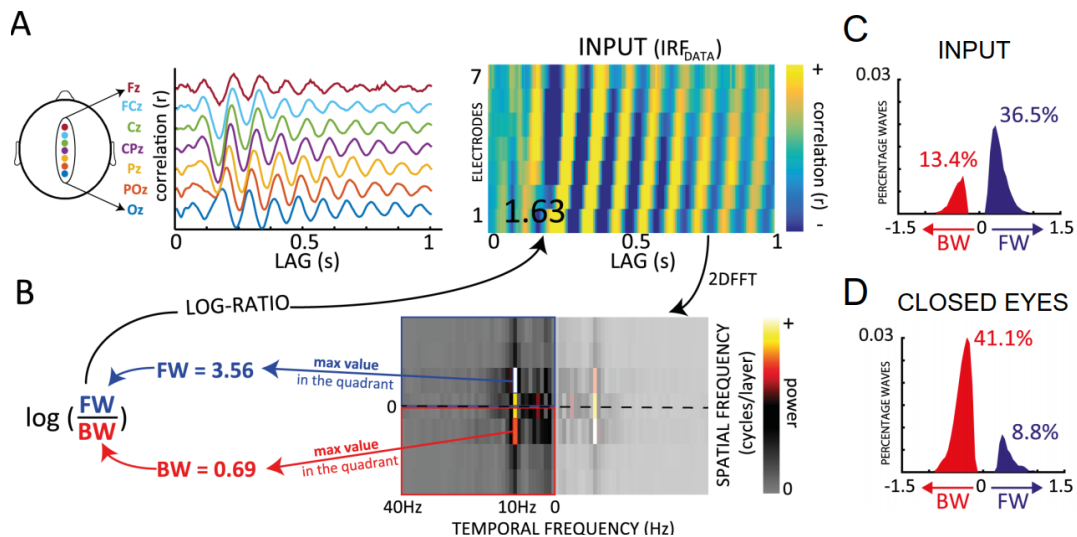


Figure 1-8 In Alamia and VanRullen’s predictive coding model paper (2019), They showed that there are more forward traveling waves of alpha during visual stimulation and more backward during eyes-closed. (A) Traveling waves can be seen by stacking perceptual echoes from the mid-line electrodes. The waves can be represented as a 2-dimensional image. (B) The direction and the frequency of the waves can be quantified by applying 2D Fourier transform on the 2D wave image. (C) and (D) The authors found more forward waves than backward waves when there is visual input, and the opposite pattern in the eyes-closed condition. Reproduced from (Alamia & VanRullen, 2019)

Thus far, we have learned that our visual perception is subject to periodic brain activities, exhibiting a temporal oscillatory property. However, oscillatory processes do not only exist in the low-level brain functions. When we explore the world using our “camera” (visual perception), the exploratory process controlled by our attention also follows a certain rhythm, as we will see below.

## 1.4 ATTENTION AND NEURAL OSCILLATIONS

### 1.4.1 Attention and the paradigms

Before we dive into the oscillations in attention, let us briefly learn what attention is and the research paradigms to study attention and the underlying neural networks.



We are using our attention all the time. For instance, when we are looking for our friends in a bar, when we are focusing on writing and when our attention is captured by a car accident. Attention is a flexible function. It can be “bottom-up”, e.g., captured by a “car accident”; it can also be “top-down”, e.g., looking for a friend in the crowd (Connor et al., 2004). In the first case, attention allows us to notice salient things, such as something that signals danger. In the latter, voluntary attention enables us to focus on one thing. Thanks to attention, the brain resources can concentrate on one target, and therefore we are not swamped by the information surrounding us.

Attention is one of the most important topics in neuroscience. “Spotlight” is often used as a metaphor for attention. When this spotlight is directed to an external or internal object, the processing of this object will be enhanced (Moran & Desimone, 1985). For studying attention in the laboratory, two classical paradigms are often used, spatial orienting (Posner et al., 1980) and visual search (Treisman & Gelade, 1980) (Figure 1-9). In the spatial orienting paradigm, a cue is presented to indicate where the attention should be allocated. After the cue appears, the target might or might not appear at the cued location. Next, the behavioral performance for the trials of the valid cue (target appears at the cued location) and the invalid cue (target does not appear at the cued location) are calculated separately. Logically, the corresponding behavioral performance should be higher in valid cue trials compared to the invalid ones. For example, when subjects are required to detect a near-threshold target that could appear at cued and uncued locations, detection rate for the cued location will be higher than the uncued location because more attention is directed to the cue. The other paradigm is visual search. In visual search paradigms, the target (for example, the green T in Figure B) is presented together with a group of distractors (for example, letter L and blue T). The searching difficulty depends on the number of distractors and the similarity between the target and the distractors. The target is relatively more salient in some conditions than the others, for example, when the target color is different from distractors. Figure B is a relatively difficult condition, in which the target green T shares both the color and shape with the distractors. When doing a visual searching task, subjects need to pay attention to the stimuli that share the same feature with the one they are instructed to search. The searching difficulty can be measured by how much time they take to search the target or how many times they find the wrong target. Various tasks are derived from these two classical paradigms. The behavioral response could be overt eye movement; in this case, the saccadic reaction time is usually estimated by measuring the duration when the eye leaves the fixation

and arrives at the target. The tasks could also be applied to measure covert attention, which is directing attention without moving eyes. One way to measure covert attention is to present near-threshold targets at the cued location and measure the detection rate.

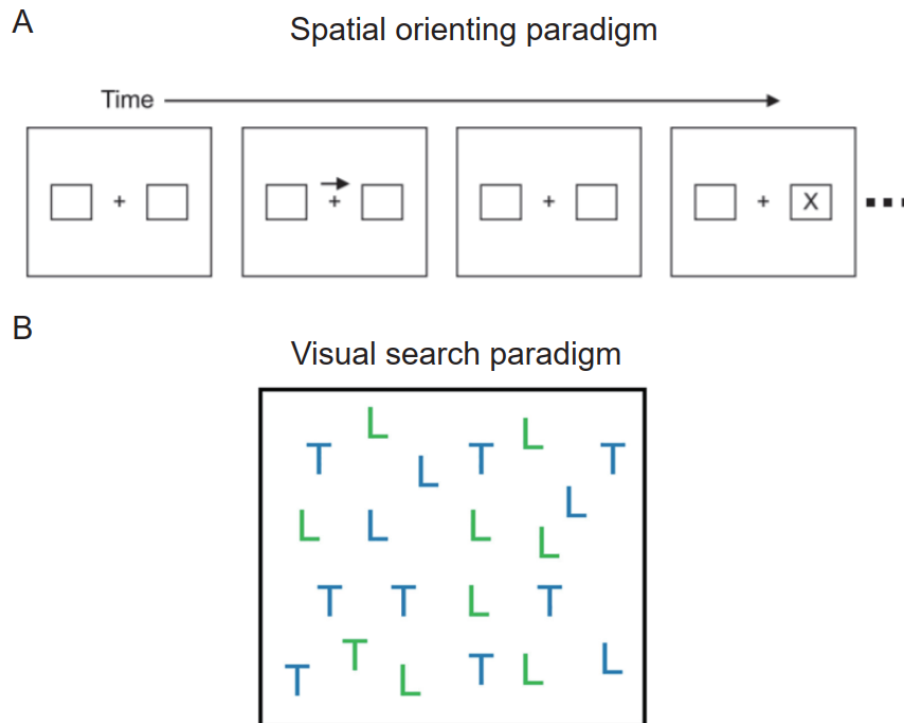


Figure 1-9 A) The target (X) might appear in the left box or the right. After a trial starts, an arrow appears to indicate the possible location where the target might appear. Figure adapted from (Mayer et al., 2004) B) An example of visual search paradigm. Searching for the green T is difficult because the distractors (green L and blue T) share the same features with the green T. Figure adapted from (Buschman & Kastner, 2015).

## 1.4.2 Attention networks

Attention involves large-scale neural networks (Chica et al., 2013) (Figure 1-10). When performing a visual attention task, a distributed dorsal fronto-parietal network comprising superior parietal lobule (SPL), intraparietal sulcus (IPS), the frontal eye field (FEF) and the supplementary eye field (SEF), is activated (Kastner & Ungerleider, 2000) together with occipital regions. This network has been identified with a variety of visual attention tasks (Kastner & Ungerleider, 2000). The fronto-parietal network selectively sends the modulatory signal to the low-level sensory areas, enhancing the neural processing to the task-relevant or

attended object (Kastner et al., 1999; Moore & Armstrong, 2003). In other words, the fronto-parietal network conveys top-down signals to bias the stimulus selection to form the neural representation in the visual cortex (Beck & Kastner, 2009). In support of the top-down modulatory role of the fronto-parietal network, Kastner et al. (1999) found that when subjects were expecting a stimulus in peripheral location, the signals in frontal and parietal areas increase more than in the visual cortex. The frontal and parietal areas might modulate the signal in the visual cortex in the absence of visual stimulation via a top-down process. Moreover, a physiology study in monkeys (Moore & Armstrong, 2003) showed that the electrical stimulation in FEF enhances the response of the topographically corresponding location in V4.

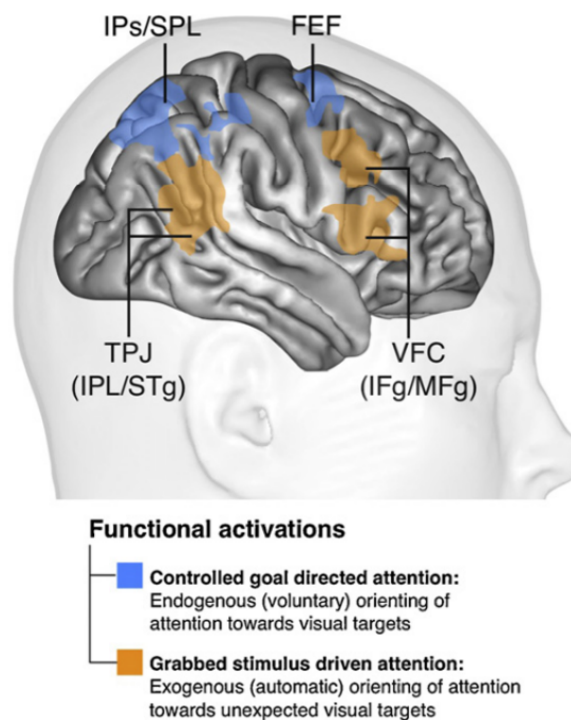


Figure 1-10. The fronto-parietal network associated with attention. TPJ and VFC are temporo-parietal junction and ventral frontal cortex respectively. Figure adapted from (Chica et al., 2013).

### 1.4.3 Oscillations in attention

It has been proposed that the spotlight of attention is indivisible and unique (Posner & Petersen, 1990; Treisman & Gelade, 1980). To process multiple objects in a scene, the

spotlight has to move from object to object, and this shifting has been proven to be rhythmic (Buschman & Miller, 2007; Wolfe et al., 2011).

It has been shown that during free viewing, each saccade occurs  $\sim 200$ ms, in the range of the theta frequency band (Engbert & Mergenthaler, 2005; Otero-Millan et al., 2008). This theta rhythmicity can even be found in microsaccades when subjects are fixating their eyes. Attention also operates dynamically without overt eye movements. A psychophysics study (VanRullen et al., 2007) observed that attention samples multiple items sequentially at the theta range. Along the same line, a study (Dugué et al., 2015) utilizing a difficult visual searching task showed that spatial attention is allocated to each of the stimuli periodically at  $\sim 7$  Hz.

For examining the attentional sampling on the behavioral level, a cue is often used to “reset” the phase of the attention oscillation. The cue is typically used to indicate where the subjects should direct their attention. When studying oscillatory attention, it serves as a time reference; from that time point attention starts to shift to the cued target. The behavioral response to the target should be an oscillation function of the inter-stimulus-interval between the cue and the target if attention is oscillatory. Two studies (Fiebelkorn et al., 2013; Landau & Fries, 2012) used a cue to reset attention and required subjects to attend to one or two objects. They found that attention samples each object sequentially at 4 Hz. However, there is a discrepancy in the frequencies reported by the above studies, some finding attention samples at  $\sim 7$  Hz, some finding 4Hz. It could be that in the studies which found the lower frequency, attention was divided into multiple objects (Figure 1-11) (VanRullen, 2016; VanRullen & Dubois, 2011). A study (Holcombe & Chen, 2013) lends direct support to this interpretation; Subjects were required to track one, two or three moving objects covertly. The temporal frequency of sampling was 7 Hz while tracking one object, and the frequency reduced to  $\sim 3$  Hz while tracking three.

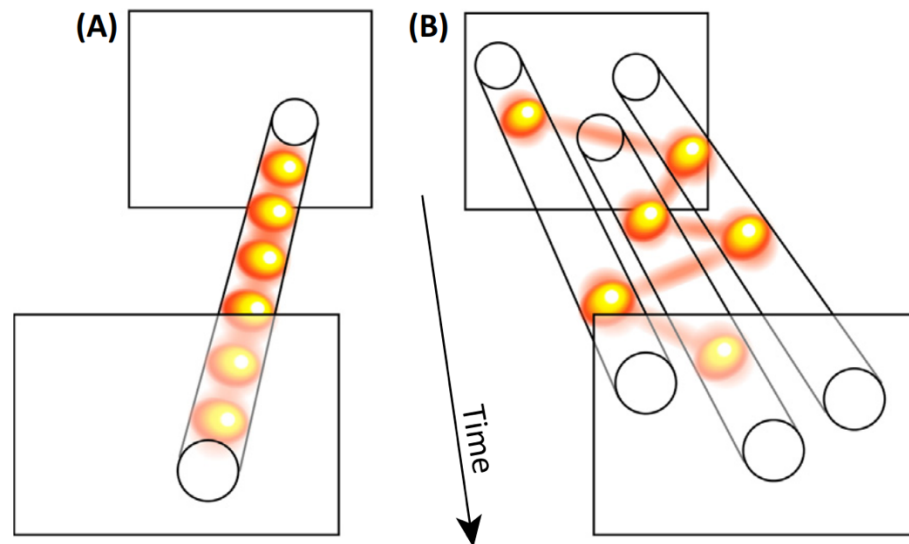


Figure 1-11 (A) When there is only one object to be attended, attention samples the same object rhythmically. (B) When there are more objects that need to be monitored, attention jumps from object to object, thus the sampling for each object reduces. Adapted from (VanRullen & Dubois, 2011)

Several EEG and MEG studies have linked this attentional sampling to brain oscillations. Busch and VanRullen (2010) present data that suggests the phase of pre-stimulus 8 Hz is predictive of the detection performance for targets in the attended location. Another study (Landau et al., 2015) demonstrated that gamma activity indicative of processing an attended object is modulated by the phase of 4 Hz oscillations during continuous monitoring of two objects. This study also extends the understanding of the attentional sampling investigated with external reset by showing that the sampling mechanism is an ongoing process. While many studies have revealed the relationship between theta oscillations and attentional sampling, little is known about the neural basis and the generation mechanism of the theta oscillation.

One possible neural source of the attentional theta rhythm is the underpinning fronto-parietal network of attention. An intracranial recording study by Helfrich et al. (2018) showed that the hit rate (detection rate) of subjects in an attention task exhibited a theta rhythm. They further demonstrated that the behavioral oscillations were correlated with the theta oscillation in electrodes implanted in the attention network (Figure 1-12), indicating the attentional sampling at theta frequency might originate from the attention network.

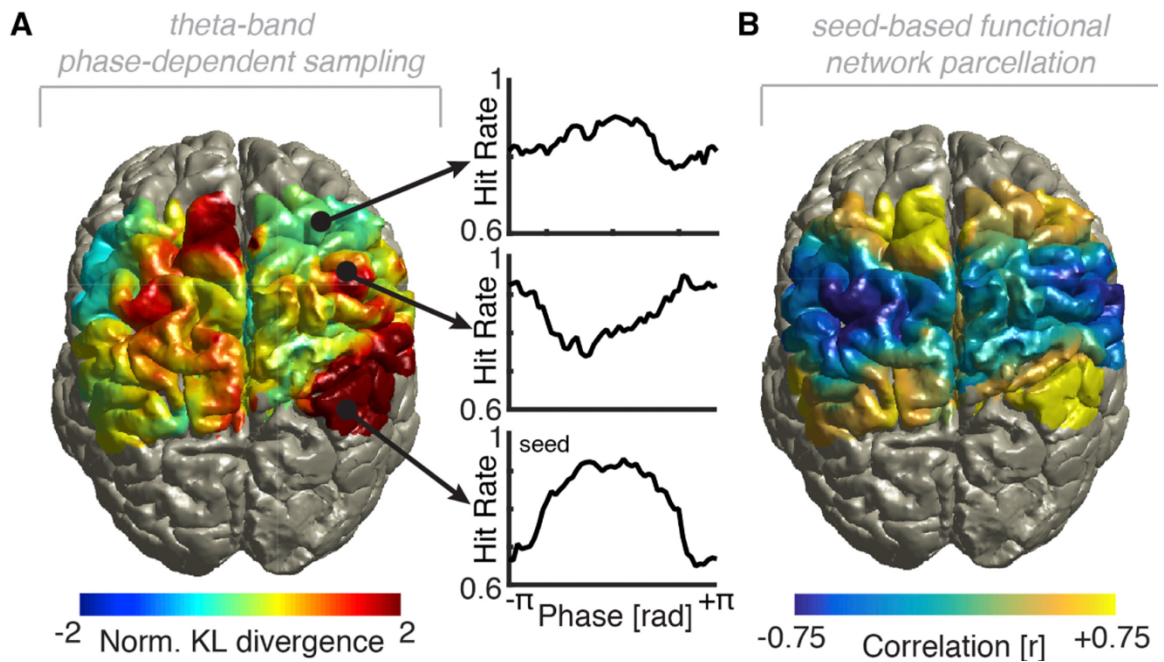


Figure 1-12 Dynamical attention network underlying attentional sampling shown by Helfrich et al.(2018) (A) They analyzed if phase of the theta oscillation in multiple areas modulated the hit rate. The plot describes the phase modulation across the attention network. Left: topographical illustration of the areas contributing to rhythmic sampling. Right: frontal regions (top), sensorimotor regions (center) and parietal regions (lower) which contributed for rhythmic attentional sampling. (B) The brain areas correlated with the behavioral theta rhythm. Frontal and parietal areas have the same preferred phase for optimal perception. Figure adapted from (Helfrich et al., 2018)

The attention network is not the sole source for theta oscillations. The theta rhythm has also been observed in V4 and inferotemporal cortex (IT) by other studies (Lee et al., 2005; Nakamura et al., 1991; Rollenhagen & Olson, 2005; Sheinberg & Logothetis, 1997). A study in macaque (Rollenhagen & Olson, 2005) found that the theta rhythm in IT might depend on competitive interactions of the neurons selective for different stimuli. The study presented two stimuli to the monkeys, an object in the fovea and a flanker in the periphery. When the object was presented in the presence of the flanker or vice versa, a strong 5Hz oscillation was elicited. In the same vein, a recent monkey study (Kienitz et al., 2018) recorded neuronal activity in V4 and found that theta activity emerged in the multi-unit activity (MUA, activity recorded from a group of neurons) when an object was displayed in the excitatory center of the receptive field, and another object was presented in the suppressive surround. In a spatial attention task of the same study (Figure 1-13), they presented a disk and flankers sequentially

to the monkeys, which, according to the result of the first experiment, should evoke neuronal competition and give rise to theta oscillation. Then, the target appeared either in the flankers or in the objects after a random temporal interval. The monkeys were trained to saccade to the target. The saccadic reaction time oscillated depending on when the target appeared, and more interestingly, the response oscillation was correlated with the theta oscillation recorded in V4. This finding delineates a plausible neural mechanism for attentional sampling. While the finding is compelling, it also raises a question. Does this mechanism also apply to human subjects? Chapter 4 is dedicated to addressing this very question.

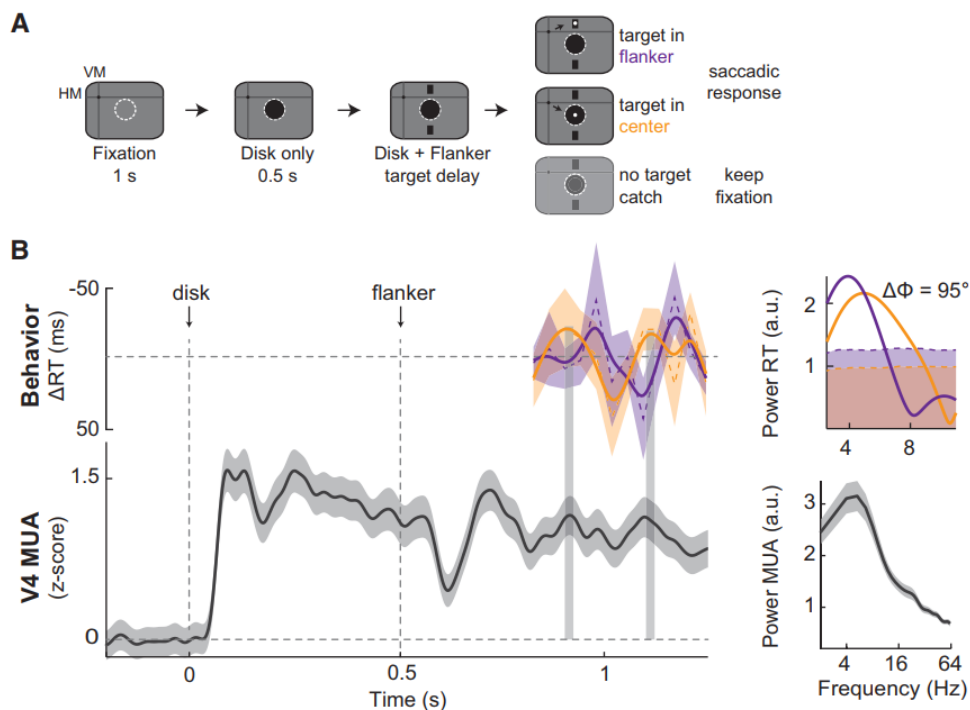


Figure 1-13 The task and the results of the second experiment in (Kienitz et al., 2018). (A) task design, a disk was presented first, then a flanker was added in the presence of the disk. The monkeys needed to saccade to the target which could appear either in the flanker or in the center of the disk. (B) Upper: time courses of response time (RT). RT to the target in disc is in orange, and RT to the target in flanker is in purple. Bottom: time courses of MUA signal. The shaded bar highlights the MUA and the RT are phase-locked. Right: spectra of RT and MUA show that the peak of power is in the theta band. Adapted from (Kienitz et al., 2018).

So far, this section has focused on attention. I have introduced the typical paradigms for studying attention, the neural basis of attention, the brain oscillations related to attentional

sampling and the possible mechanisms for attentional sampling. One possible mechanism for attentional sampling has been proposed by a study in monkeys (Kienitz et al., 2018) showing the theta rhythm might result from the neuronal competition of V4 neurons. One related question is whether this mechanism can be generalized to human subjects, which is one of the questions I focus on in this thesis. The following section will discuss consciousness.

## **1.5 CONSCIOUSNESS AND NEURAL OSCILLATIONS**

Unraveling the mystery of consciousness is an ultimate goal for many psychologists and neuroscientists. Consciousness has different meanings. Consciousness can refer to a conscious state, such as out of consciousness (coma, sleep) and conscious (awake). It could also mean conscious content or conscious perception, for example whether you are aware of a stray dog on the road. In the current thesis, we focus on conscious content (or conscious perception). For assessing conscious perception empirically in the laboratory, the current commonly accepted method is to measure the “reportability” of the target, for instance, “if you are conscious of something, you are able to report it” (Dehaene & Changeux, 2011). In this section, I start with the typical paradigms for studying conscious perception, then I will review one of the paradigms - binocular rivalry in more detail. After that, I will return to the mainline of the thesis: oscillations in consciousness.

### **1.5.1 Paradigms for studying conscious perception**

How does a bunch of physical matter - the brain - generate subjective experience? To answer this question, we need to find which parts of the brain give rise to consciousness, which is equivalent to searching for the neural correlates of consciousness (NCC). To investigate NCC, the widely accepted strategy is to compare the neural activity of two conditions in which one is conscious while the other is not, which is known as “contrastive analysis” (Baars, 1993). By adopting contrastive analysis, searching for NCC can be restated as a more pragmatic experimental question: what neural activity only appears during conscious perception but is absent in non-conscious perception? Many tools can serve to answer this question. Two commonly used paradigms are backward masking and ambiguous perception. The former manipulates the visibility of the target using backward masks so as to



create conditions in which one target can be consciously perceived and the other cannot (Ruhnau et al., 2014). The shorter the inter-stimulus interval between the backward mask and the target, the less visible the target is. With the masking paradigm, researchers can study what neural responses are relevant for conscious perception while keeping conscious and non-conscious perception under similar visual conditions. In ambiguous perception paradigms, subjects are usually required to see a bistable image such as the Necker cube described at the beginning of the introduction. This type of image triggers visual ambiguity even if the images stay unchanged. The brain resolves the ambiguity every few seconds and leaves only the dominant percept in consciousness and the other suppressed. One promising and popular ambiguous perception task widely used to study consciousness is binocular rivalry, since endorsed by Crick and Koch(1998). Binocular rivalry is a fascinating phenomenon that has evoked a huge amount of interest for many years. As we used binocular rivalry in two of our studies (Chapters 5 and 6), I will briefly review the binocular rivalry literature.

### **1.5.2 Binocular rivalry - a tool for studying neural correlates of consciousness**

When two different images are presented to two different eyes, the perception of the two images alternates in consciousness. The image in consciousness is dominant, while the other is suppressed. This perception switches every few seconds as if the two image representations were competing, hence the term "binocular rivalry" (Fig. 1-14). Dominant and suppressed perceptions provide an ideal condition for one to compare the brain activity associated with the two perceptions separately, consistent with the principles of comparative analysis. It is interesting to note that during binocular rivalry, the physical input is constant, hence, the only thing that modulates conscious perception must be brain activity (Crick & Koch, 1998, 2003; Rees et al., 2002).

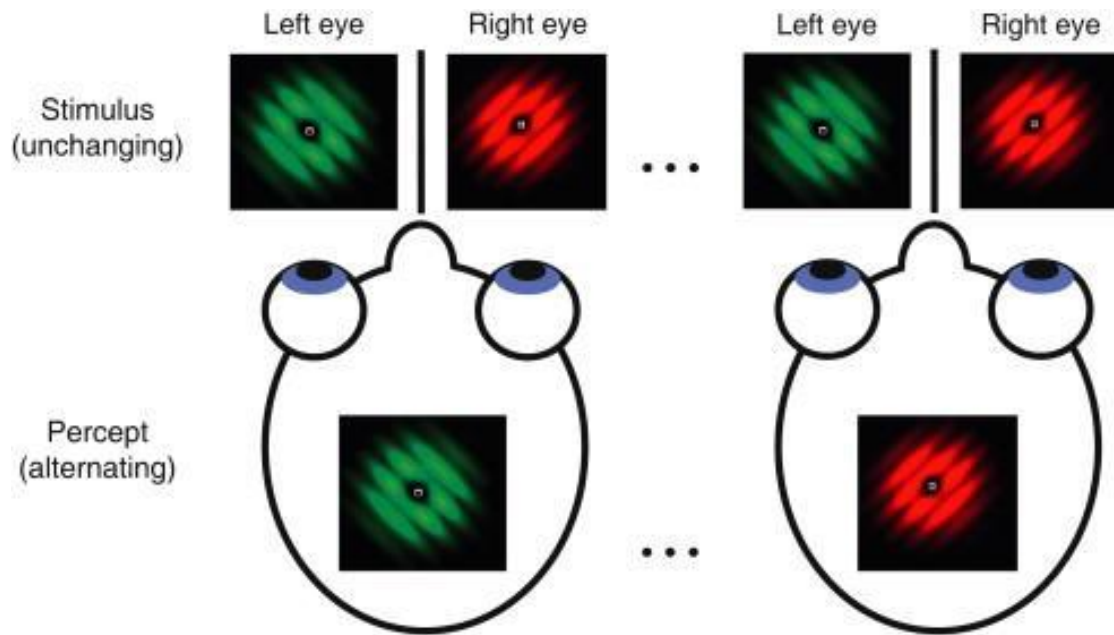


Figure 1-14 Illustration of binocular rivalry. One green gabor and one red gabor are displayed to two eyes and remain constant, the percept alternates over time, the green gabor is perceived for a short period, then the red is perceived. Reproduced from (Clifford, 2009).

### What is competing in binocular rivalry?

The information of an image needs to travel a long way after it has been converted to electrical activity at the retina until it is finally consciously perceived. During binocular rivalry, the dissimilar monocular visual information from both eyes competes or fuses (during transition) at a specific level of the visual pathway. It is tempting to think that visual rivalry happens at monocular areas, since the images that subjects see are shown to two eyes separately. Previously, there was a debate regarding where binocular rivalry is resolved. One group of researchers believed that binocular rivalry is resolved at an early stage of the visual pathway, resulting from mutual inhibition between monocular neurons in the primary visual cortex (V1) (Blake, 1989) and LGN (Wunderlich et al., 2005). This view receives evidence from studies by (Tong & Engel, 2001) and (Polonsky et al., 2000). By using fMRI, they found that the neural activity in monocular areas of V1 changes with the perception over time. The stronger evidence is provided by (Blake et al., 1980; Lee & Blake, 2004). Blake et al. (1980) swapped the stimuli that were in the dominant and the suppressed perception, the

suppressed stimulus became dominant. The result suggests that the competition is from monocular neurons, regardless of stimulus content.

However, a contradicting view considers that the competition might arise from the neural representation of the two images being viewed, called pattern competition. Supporting this view, an ingenious study broke the coherency of two stimuli and replaced them by complementary patchworks of intermingled rivalrous images and showed subjects the patchwork images (Figure 1-15). The subjects tended to see one of the two coherent images by grouping the patchworks that belonged to the same image, even though they were presented to different eyes (Kovacs et al., 1996). Furthermore, electrophysiology experiments in monkeys show that the proportion of neurons firing with the conscious perception increases at higher levels of processing (Logothetis et al., 1996; Logothetis & Schall, 1989).

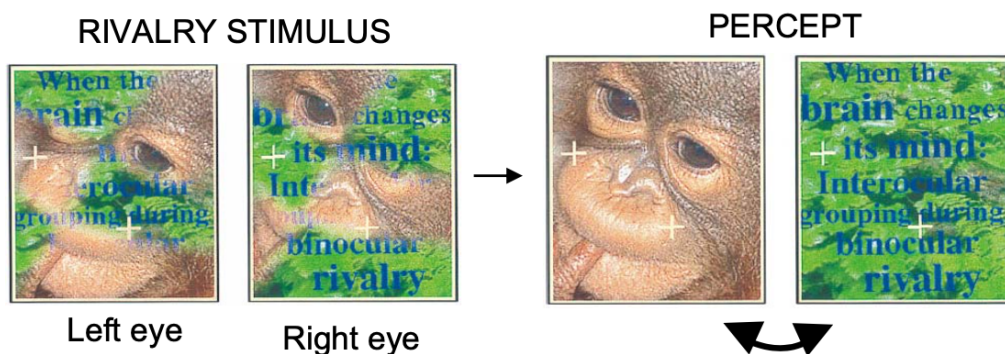


Figure 1-15 The patchwork images used in Kovacs et al. (1996). The patchworks from the two images are complementary since they are cut from two coherent meaningful images as shown on the right. When the patchwork images are shown to different eyes of a subject, the subject will see the images on the right. Figure adapted from (KOVAcS et al., 1996)

The studies above suggest that the rivalry (or competition) occurs at different visual processing levels. To reconcile the two distinct sets of evidence, a hybrid view has emerged (Tong et al., 2006), as detailed below.

### Model of Binocular rivalry

The alternation of the percepts seems unpredictable. It is still unclear what triggers perceptual switches in binocular rivalry, and why and where the rivalry is resolved. The most common account for this is that the neural representations of the two stimuli compete with each other. The neural representation of the dominant stimulus inhibits the neural representation of the other. Gradually, the inhibition becomes weaker due to adaption and neural noise and eventually the perception switches. Reciprocal inhibition between the neurons that code the information of the two competing percepts has long been proposed as the mechanism of binocular rivalry (Fox & Rasche, 1969), developed by many other researchers (Arrington, 1993; Kalarickal & Marshall, 2000; Lago-Fernández & Deco, 2002; Laing & Chow, 2002; Lehky, 1988; Lumer, 1998; Matsuoka, 1984; Noest et al., 2007; Stollenwerk & Bode, 2003; H. R. Wilson, 2003) and integrated in models of binocular rivalry as an essential element (e.g., Tong et al., 2006).

To reconcile the contradicting findings concerning where the resolution of rivalry happens, Tong and colleague (2006) proposed a model comprising inhibitory connections, lateral excitatory connections and feedback connections. Based on the hybrid view of binocular rivalry (i.e., competition can occur in both higher and lower level areas), inhibition in binocular rivalry can be divided into two types: competition between monocular neurons and pattern-selective competition. Monocular neuronal competition occurs primarily in the regions responsible for monocular processing such as LGN and part of V1). Pattern-selective competition, on the other hand, occurs mainly in the regions after binocular fusion. To account for binocular competition at each level of the visual pathway, the model introduces inhibitory connections at different levels (Figure 1-16 A). The authors point out that in this model, monocular competition is also involved in pattern selection. When monocular cells from both eyes are processing similar stimuli, such as a grating in the same direction, monocular neurons will facilitate information fusion via the excitatory connections between monocular neurons, but if the visual information is very different, monocular neurons will inhibit each other. Excitatory connections promote the integration both in the low-level monocular areas and the high-level areas (Figure 1-16 B). The patchwork grouping study by KOVACS et al. (1996) can be explained by these lateral excitatory connections. In addition, to account for top-down effects in binocular rivalry, such as the effect of attention, top-down excitatory connections were added to the model (Figure 1-16 C). Different excitatory connections are activated depending on the region being affected by attention. For instance, when paying attention to the monkey patchworks (Figure 1-15), the top-down connections

can facilitate the fusion of information from the neurons representing the monkey to integrate the monkey picture.

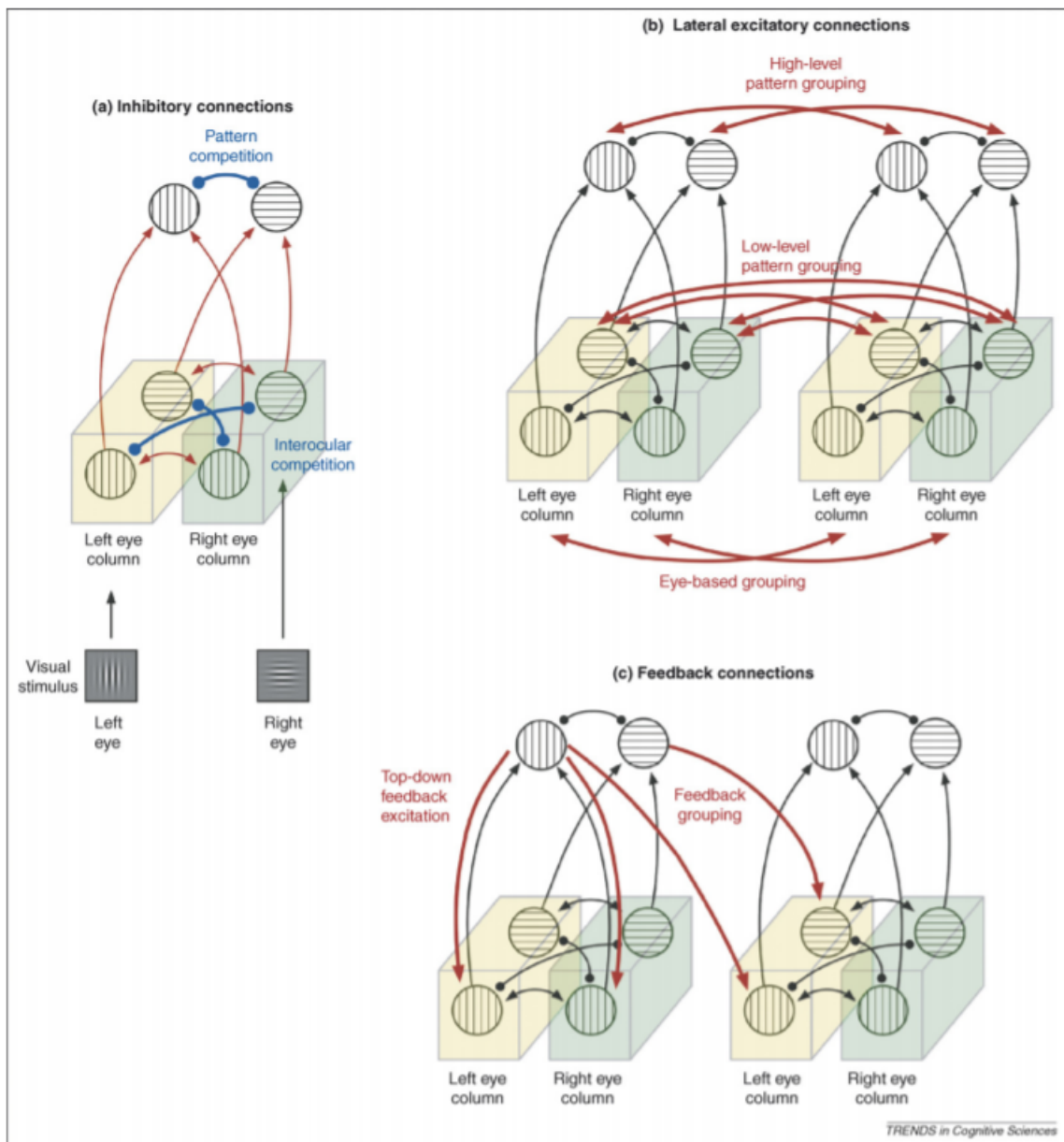


Figure 1-16 Schematic illustration of a hybrid rivalry model by Tong et al. (2006). Lines with filled circles represent inhibitory connections; lines with arrows represent excitatory connections. (a)

Adapted from (Tong et al., 2006)

### 1.5.3 Oscillations in consciousness

According to the “contrastive analysis”, the NCC can be investigated by comparing the neural activity of conscious perception and non-conscious perception. In visual studies using a near-threshold stimulus, subjects are aware of the visual stimuli under specific brain states (e.g., subjects’ detection rate is low when pre-stimulus alpha power is high). Thus, in these studies, there are trials of both conscious and non-conscious perceptual conditions. This kind of study is in accord with the principle of contrastive analysis. The studies in support of “discrete perception” reviewed in section 1.3.2 are exactly such studies. To a certain extent, these studies demonstrate that oscillations affect consciousness by modulating cortical excitability. Oscillatory conscious perception has also been found using the masking paradigm (Mathewson et al., 2012); rhythmic stimuli were used to entrain alpha oscillations. After the entrainment, a target preceding a mask was presented after random stimulus-onset asynchrony. The study found that the visual awareness of the target was phase-locked to the entrained oscillation, suggesting that the subjects only consciously perceive the target at a specific phase of alpha.

Apart from causing oscillatory conscious perception, brain oscillations also serve consciousness in a communication role. In masking studies, conscious perception has been proved to correlate with increased synchronization of oscillations. One study showed long-range gamma synchronization is associated with conscious perception of words (Melloni et al., 2007). In addition to the gamma synchronization, theta activity is enhanced in the frontal areas when the words are retained in memory, indicating more brain regions are involved in conscious perception compared to non-conscious perception. In another study, long-range beta synchronization has been found when subjects consciously perceived the target words (Gaillard et al., 2009).

Synchronization of oscillations in consciousness has also been revealed in studies employing ambiguous perception tasks. One line of evidence has been provided by studies using binocular rivalry. In strabismic cats, the dominant percept evokes more gamma synchronization than the suppressed percept, whereas there is no difference in the firing of neurons of the two conditions (Fries et al., 1997), highlighting synchronization of oscillations in forming conscious perception. In human studies using binocular rivalry, Doesburg and colleagues (2005) uncovered that gamma synchrony increased before subjects reported the switches of perception, suggesting that the gamma synchrony is related to the emergence of

coherent perception. The perceptual switching related gamma synchronization is further shown to be modulated at a theta rate and such synchronization appears not only in the activated regions but also between these regions (Doesburg et al., 2009). These results suggest that large-scale integration is crucial for unambiguous conscious perception. Another line of evidence is from other ambiguous perception methods. Using audiovisual stimuli, Hipp, Engel and Siegel (2011) demonstrate that the strength of large-scale beta and gamma synchrony is predictive of the perception of ambiguous audiovisual stimuli and integration of auditory and visual information.

The above-mentioned studies have stressed the importance of brain oscillations in conscious perception. Of these studies, several studies utilizing binocular rivalry reported large-scale integrations reflected by synchronization of brain oscillations in conscious perception, confirming the view that interareal integration is essential for consciousness (Engel & Fries, 2016). Further evidence supporting the synchronization view comes from a study which combines frequency tagging and binocular rivalry (Tononi et al., 1998). Frequency tagging is a method to link stimuli with the corresponding brain activity in order to track when and where the stimuli are processed in the brain. When presenting a target oscillating at a given frequency, the neurons that respond to this target tend to synchronize at this frequency. Tononi and colleagues (1998) displayed two stimuli that each flickered at a different frequency. By doing this, they could track the neural activity that was in relation to the dominant and the suppressed percept. They found that compared to the dominant percept, the power of the frequency relating with the suppressed percept was 50-85% lower in many channels. Since power of the tagged frequency reflects the synchronized neuronal activities in response to the target (Tononi et al., 1998), the findings suggest that there is a distributed synchronization across the brain during conscious perception.

The frequency tagging paradigm here is similar to the paradigm for measuring perceptual echoes; both of them link the brain activity with the fluctuation of the stimuli. In the frequency tagging study, the neural activity synchronizes in response to the dominant stimuli. In contrast, the findings of perceptual echoes suggest that there is an ensemble of neurons synchronizing at 10 Hz to enable the brain to sample the environment rhythmically and actively. Does the synchronization underlying perceptual echoes require the brain to be conscious of the stimuli? In other words, how automatic is the 10 Hz visual sampling? This is one of the questions regarding the oscillations in consciousness we attempt to address.

It has been proposed that synchronization is mediated by top-down and bottom-up processing (Engel et al., 2001; Engel & Fries, 2010). While in binocular rivalry, various evidence suggests that the rivalry is resolved at either a low level or a high level of the visual pathway, and then propagates to the other levels. These findings, therefore, indicate that there might be a top-down or bottom-up processing that is responsible for conveying the resolving signal. This raises a question: Is there a directed information flow implemented by oscillations contributing to resolving the visual competition in binocular rivalry? This is the second question related to oscillations in consciousness we aim to address.

In the consciousness section, I've reviewed the methods to study conscious content/conscious perception, binocular rivalry, and oscillations in consciousness. To end the review on consciousness, I've introduced two questions this thesis attempts to answer: 1) Do perceptual echoes require consciousness? 2) Is there any directed information flow reflected by oscillations responsible for unambiguous conscious perception in binocular rivalry?

## **1.6 QUESTIONS OF THE THESIS**

Thus far, I have introduced the basics of brain oscillations and the related literature on the oscillations in visual perception, attention and consciousness. Evidently, an abundance of evidence has revealed the dynamic nature of our brain functions. Brain oscillations manifest themselves in perceptual cycles, albeit in the more complex brain functions such as consciousness, brain oscillations are involved in a more complex manner (e.g., interareal communication).

As we can see from the literature review above, how the brain oscillations are related to visual and attentional sampling has been well investigated. Some studies further investigated the causal role of brain oscillations on visual perception and attention. However, where these sampling-related oscillations come from in the brain and how they are generated are not yet understood. Thus, these are two questions concerning visual perception and attention the current thesis aims to address. After investigating the brain oscillations in visual perception and attention, we go a step further to study the role of brain oscillations in consciousness.



That is, we study how brain oscillations are involved when the brain is consciously perceiving.

In visual perception, perceptual echoes, one demonstration of perceptual cycles, characterized our visual perception as a cyclic, recurrent process. In spite of the fact that many properties of perceptual echoes have been investigated, the underlying mechanism is still not clear. One important question that remains to be addressed is which part of the brain generates these echoes? We tried to answer this question in Chapter 3 with an EEG-fMRI experiment.

Another example of perceptual cycles is attention oscillations. Electrophysiological evidence suggests that attention oscillations are governed by a theta rhythm. A monkey study set out to explore the underlying mechanism of this theta rhythm, and they found it might be generated by neuronal competition in V4 (Kienitz et al., 2018). It is exciting that this study has made an important advance in understanding the mechanism of attention oscillation. However, it remains to be tested whether this finding can be generalized to human subjects. To examine this, we replicated the behavioral experiment of the monkey study, as discussed in Chapter 4.

In a more complex brain function like consciousness, the involvement of brain oscillations can be more complicated, as consciousness is a brain process that requires large-scale integration of neural activity. The integration is achieved by synchronization of brain oscillations. Synchronization of neuronal activity can be reflected by the power of neural oscillations. To assess if synchronization is essential for visual sampling in conscious perception, we adopted a binocular rivalry task and examined the perceptual echoes related to the dominant percept and suppressed percept, detailed in Chapter 5. The synchronization of neural activity is subject to directed information flow, such as top-down and bottom-up processing in the brain. To process visual information consciously, the brain requires directed communication between the visual cortex which sends sensory information and the frontal areas which deliver modulatory signals. However, this evidence is lacking in binocular rivalry. Previous studies proposed that resolving ambiguous visual conflicts in binocular rivalry requires communication between high-level and low-level areas (Leopold & Logothetis, 1999). We propose that the synchronization of oscillations is a potential candidate for this communication. In Chapter 6, we will provide the corresponding experimental evidence.

All the questions this thesis aims to answer are summarized below:

- (1) What is the neural basis of perceptual echoes? (Chapter 3)
- (2) Does attentional sampling arise from the theta rhythm generated by visual competition? (Chapter 4)
- (3) Are neural oscillations responsible for inter-area communication in conscious perception? (Chapters 5 and 6)

This chapter has given a general introduction and has raised the questions. It is now necessary to introduce the research approaches and the framework of the paper.

## 2 CHAPTER 2. GENERAL APPROACH AND FRAMEWORK OF THE THESIS

### 2.1 EEG

Electroencephalography (EEG) was used in three of my studies in this thesis (Chapter 3, 5, 6). EEG is a non-invasive recording method to record the electrical signal of the brain on the scalp (Figure 2-1). Since the EEG signal is recorded on the scalp, it is susceptible to the contamination of various noise and artifacts, such as eye blinks and movements, heartbeats, facial muscle movement, and the noise coming from the environment. Compared with these noises, the brain's electrical activity is tiny. Nevertheless, EEG is an ideal tool to study neural oscillations. It allows us to record brain activity in a very fine time scale because its temporal resolution is very high. However, the spatial resolution of EEG is very low (Figure 2-1).

In chapter 3 and chapter 5, we used EEG to measure perceptual echoes. In chapter 6, we recorded EEG signals and then analyzed the information flow with traveling waves analysis and granger causality analysis.

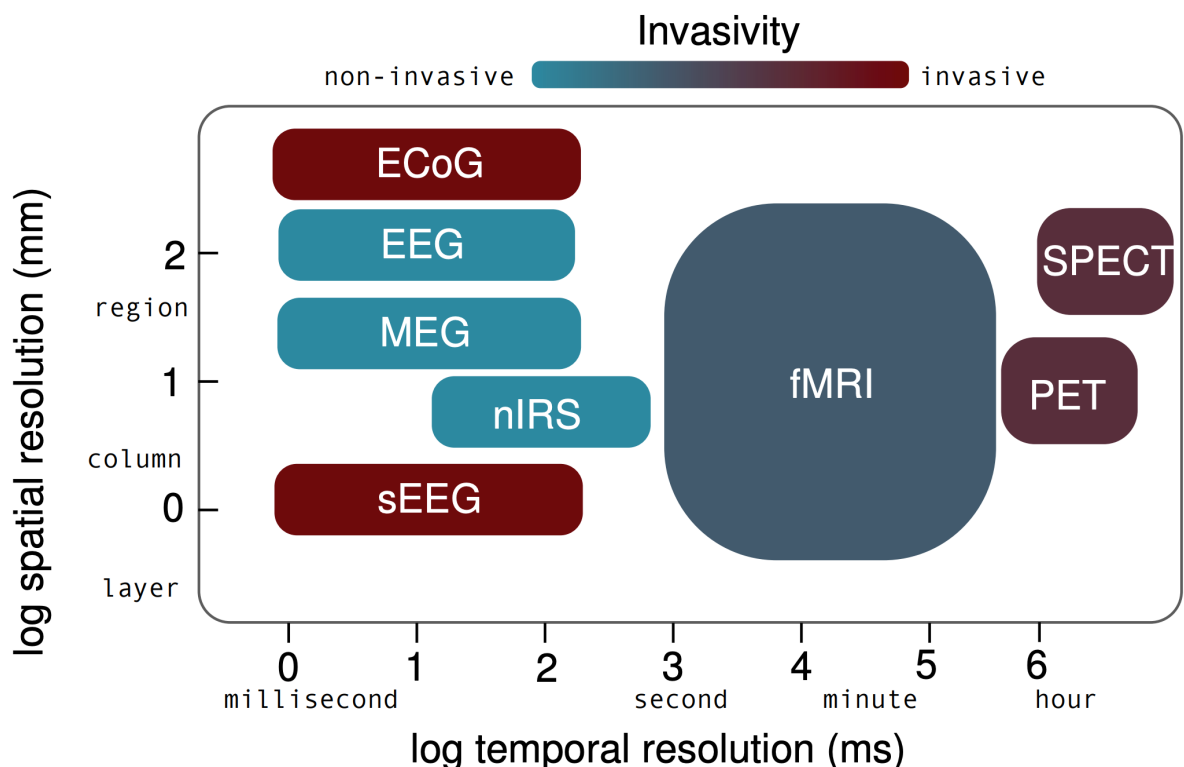


Figure 2-1. EEG has very high temporal resolution but low spatial resolution. fMRI is the opposite. Adapted from (Pedregosa-Izquierdo, 2015).

## **2.2 fMRI**

In contrast to EEG, Functional magnetic resonance imaging (fMRI) is a tool to study “where” something happens rather than “when” something happens in the brain, due to its high spatial resolution but low temporal resolution. fMRI measures the blood-oxygen-level-dependent (BOLD) signal, which reflects the change of relative level of oxyhemoglobin and deoxyhemoglobin. This change is due to the blood releasing oxygen to the neurons that are firing (Kahn et al., 2011).

## **2.3 COMBINATION OF EEG AND fMRI**

To obtain high temporal and spatial resolution concurrently, we will naturally think that combining EEG and fMRI could be a good solution. However, this presents a number of challenges. There are several ways to combine EEG and fMRI. The most common way is to run a concurrent EEG-fMRI experiment, meaning recording EEG and fMRI simultaneously. The problem is that the EEG signal will be influenced by MRI significantly. Besides, the fMRI signal will also be impaired by EEG caps. Several groups have observed signal loss in brain images when recording EEG signal in MRI (Bonmassar et al., 2001; Iannetti et al., 2005; Krakow et al., 2003; Mullinger et al., 2008; Negishi et al., 2008; Stevens et al., 2007). Other than that, fMRI artifacts will lead to false correlation (Greenlee et al., 2016; Huster et al., 2012).

In chapter 3, we attempt to localize the neural basis of perceptual echoes. Therefore, we combined EEG and fMRI—recorded at separate times—to obtain high temporal resolution and high spatial resolution signals.

## 2.4 FRAMEWORK OF THE THESIS

The cornerstone of the current thesis is neural oscillations and their role in visual perception, attention and consciousness. The framework of the empirical studies in the current thesis follows the levels of perceptual or cognitive functions of the brain, that is, from the earliest and most basic function – visual perception, to the higher-level function - attention and finally, it will end with the most complex function – consciousness.

In **Chapter 3**, I focus on one of the oscillations related to visual perception – perceptual echoes. More specifically, the goal of the study is to localize the neural source of perceptual echoes. In order to fully understand perceptual echoes, we must know where they come from in the brain. However, the spatial resolution of EEG is low. One of the feasible ways to study the neural origin of perceptual echoes is to run an fMRI-EEG study to relate the EEG signal of perceptual echoes with the BOLD signals (even if those are recorded at a different time). Although the brain areas that correlate with perceptual echoes might not necessarily be the exact location where the perceptual echoes are generated, the result can narrow down the potential location. Knowing the neural origin could pave the way for understanding how the perceptual echoes are generated and their functional role.

In **Chapter 4**, I move on to another level of cognitive function – attention. Many attention studies have revealed that attention oscillates at theta frequency, and the theta band EEG signal is associated with attentional sampling. However, the underlying mechanism of this attention oscillation remains unknown. A monkey study has found that the theta rhythmicity might come from the neuronal competition from V4 neurons when presenting stimuli in the center and the surround of a V4 neuron receptive field. This theta rhythmicity is further correlated with the behavioral rhythmicity during a visual search task. However, it is unclear if the results can be generalized to humans. The current study set out to replicate the behavioral experiment of the monkey study in human subjects.

In **Chapter 5**, I investigate how conscious perception modulates perceptual echoes. Previous studies suggest that synchronization of brain oscillations is essential for conscious perception. The emergence of perceptual echoes must require underlying neurons to synchronize at 10 Hz. Will this synchronization occur when subjects are not consciously perceiving the targets? On the other hand, perceptual echoes are not well understood yet. Previous studies have shown that the amplitude of perceptual echoes is modulated by

attention. Since attention is tightly linked with consciousness, do perceptual echoes require consciousness? Binocular rivalry offers a great opportunity to study perceptual echoes in different conscious conditions (dominant and suppressed). In the current study, two gabor patches whose luminance follows white-noise random sequences were shown to subjects' two eyes. Accordingly, we could cross-correlate the EEG signal with both the dominant sequences and the suppressed sequences to obtain dominant perceptual echoes and suppressed echoes. Then we analyzed the power and traveling wave properties of these echoes. Additionally, the study can also answer another question: how much visual information can survive in the brain if it is not consciously perceived?

**Chapter 6** continues with neural oscillations in consciousness. One unsolved question in binocular rivalry is at what level the rivalry is resolved. The existing evidence suggests that it could happen at multiple levels of the visual pathway, which indicates there might be a top-down or bottom-up process contributing to the resolution of visual ambiguity. As stated before, one of the main functions of brain oscillations is communication. Thus, neural oscillations are good candidates for potential high-low level communication. To investigate this, we recorded EEG signals while subjects were performing a binocular rivalry task, then we analyzed the directionality of oscillations during binocular rivalry by using traveling waves and granger causality measures.

### **3 CHAPTER 3. fMRI SIGNATURES OF PERCEPTUAL ECHOES IN EARLY VISUAL CORTEX**

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This chapter contains an original manuscript under review: Canhuang Luo\*, Saskia Brüers\*, Isabelle Berry, Rufin VanRullen and Leila Reddy. " fMRI signatures of perceptual echoes in early visual cortex." \*Co-first author with Saskia Brüers.

#### **3.1 ABSTRACT**

The visual Impulse Response Function (IRF) can be estimated by cross-correlating random luminance sequences with concurrently recorded EEG. It typically contains a strong 10Hz oscillatory component, suggesting that visual information reverberates in the human brain as a “perceptual echo”. The neural origin of these echoes remains unknown. To address this question, we recorded EEG and fMRI in two separate sessions. In both sessions, a disk whose luminance followed a random (white noise) sequence was presented in the upper left quadrant. Individual IRFs were derived from the EEG session. These IRFs were then used as “response templates” to reconstruct an estimate of the EEG during the fMRI session, by convolution with the corresponding random luminance sequences. The 7-14Hz (alpha) envelope of the reconstructed EEG was finally used as an fMRI regressor, to determine which brain voxels co-varied with the oscillations elicited by the luminance sequence, i.e., the “perceptual echoes”. The reconstructed envelope of EEG alpha was significantly correlated with BOLD responses in V1 and V2. Surprisingly, this correlation was visible outside, but not within the directly (retinotopically) stimulated region. We tentatively interpret this lack of alpha modulation as a BOLD saturation effect, since the overall stimulus-induced BOLD response was inversely related, across voxels, to the signal variability over time. In conclusion, our results suggest that perceptual echoes originate in early visual cortex, driven by widespread activity in V1 and V2, not retinotopically restricted, but possibly reflecting the propagation of a travelling alpha wave.

Keywords: perceptual echo, alpha, EEG, fMRI, oscillation, traveling wave

#### **3.2 INTRODUCTION**

Visual information is not fleeting, but instead “echoes” in our visual system in an oscillatory fashion (VanRullen & Macdonald, 2012). When subjects are presented with random luminance sequences (white noise, WN) while concurrently recording the electroencephalography (EEG) signal, an impulse response function (IRF) can be calculated by cross-correlating the WN sequences with the corresponding EEG. The resulting IRF contains a strong  $\sim 10$ Hz component that can last up to one second, suggesting that the brain processes and carries visual information over time at  $\sim 10$ Hz. This phenomenon has been called the “perceptual echo” (Ilhan & VanRullen, 2012; VanRullen & Macdonald, 2012).

The IRF is highly correlated with resting-state and ongoing EEG alpha in both amplitude and frequency, and both signals are most prominent in posterior regions (VanRullen & Macdonald, 2012). Despite the fact that they share the same frequency range and topographical location, the alpha-band EEG signal in response to the WN sequences (IRF or “perceptual echo”) does not necessarily correspond to the ongoing EEG alpha activity; in fact, the two signals can even sometimes be dissociated and there are important functional differences between them. Ongoing alpha activity has long been considered to play an inhibitory role in sensory areas (Bonnefond & Jensen, 2012; Jensen & Mazaheri, 2010; Kizuk & Mathewson, 2017; Klimesch et al., 2002; Sadaghiani & Kleinschmidt, 2016), whilst the IRF suggests that the visual system actively processes and retains information over time (Ilhan & VanRullen, 2012; VanRullen & MacDonald, 2012). For instance, in a spatial attention task, contralateral alpha amplitude decreased when subjects attended to the left or right side of the screen, while on the contrary the IRF was enhanced by contralateral attention (VanRullen & MacDonald, 2012).

The IRF has been associated with various visual phenomena. For instance, the IRF is thought to play a role in the triple flash illusion: when subjects are presented with two flashes in succession, they sometimes report seeing a third flash (Bowen, 1989). This illusion could be explained as the superposition of oscillatory impulse response functions to the two visual flashes, coming in alignment to create a third (illusory) percept (Bowen, 1989; Gulbinaite et al., 2017). In addition to the temporal dimension of the IRF, recent studies from our group have investigated its spatial dimension. Lozano-Soldevilla and VanRullen (2019) showed that the IRF propagates from occipital to frontal areas as a travelling wave when WN sequences are presented in the upper visual field. Alamia and VanRullen (2019) further demonstrated that when there is visual input, both the IRF and the alpha propagate from posterior channels



to frontal channels, whereas when subjects close their eyes, the alpha travels in the opposite direction. The forward and the backward propagations have been postulated (Alamia & VanRullen, 2019) to represent feedforward and feedback signals in the framework of predictive coding (Rao & Ballard, 1999). However, despite this progress in understanding the spatial propagation of the IRF under different conditions, its neural origins remain unknown. One of the above studies (Lozano-Soldevilla & VanRullen 2019) attempted to perform EEG source localization of the IRF travelling waves, but the outcome was ambiguous, i.e., compatible with both a large-scale propagation across multiple brain regions, or a localized propagation within a restricted region, e.g., an occipital sulcus. The aim of the current study was to use fMRI to identify the neural source of the IRF.

We conducted an EEG-fMRI study to localize the neural source of the IRF (Figure 1). Instead of concurrently recording EEG and fMRI, which often leads to artifacts and spurious correlations (Greenlee et al., 2016; Huster et al., 2012), we recorded EEG and fMRI in two separate sessions. In both sessions, a disk whose luminance followed a random (white noise) sequence was presented in the upper left quadrant. Subjects (N=20) detected a rare near-threshold target embedded in the disk. Individual IRFs were derived from the EEG session by cross-correlating WN sequences with the corresponding EEG signal. These IRFs were then used as “response templates” (Brüers & VanRullen, 2017) to reconstruct an estimate of the EEG during the fMRI session by convolution with the random luminance sequences presented in the fMRI session. Finally, we used the alpha envelope of the reconstructed EEG as fMRI regressors to determine which brain voxels co-vary with the oscillations (i.e., the “perceptual echoes”) elicited by the luminance sequence. In a second step, we investigated other frequency bands (delta: 2-4 Hz, theta: 4-8 Hz, beta: 14-20 Hz). As described below, we found that the reconstructed envelope of EEG alpha (but not other frequencies) was significantly correlated with BOLD responses in V1 and V2.

### **3.3 METHOD**

#### **3.3.1 Subjects**

22 subjects (10 females, 1 lefthanded, age range 20-43, mean age 28.73) took part in the study after a medical interview, and giving written informed consent. In total 20 subjects completed the experiment; two subjects failed to come back for one or both experimental sessions after being included. The EEG session was systematically conducted before the fMRI session. Of the 20 subjects, 14 subjects finished the two sessions in one week, 4 subjects in 2 weeks and the remaining 2 subjects in 3 weeks. This study was approved by the ethics “Comité de Protection des Personnes Sud-Méditerranée I” (N°2016- A01937-44).

### 3.3.2 Stimuli

In both the EEG and the fMRI sessions, a disc (subtending  $2^\circ$  of visual angle) whose luminance followed a random (white noise) sequence was presented on a black screen, in the upper left quadrant, at 5 degrees of visual angle from fixation. We used a smaller visual stimulus than in our previous studies (VanRullen & Macdonald, 2012; Ilhan & VanRullen, 2012; Brüers & VanRullen, 2017; Lozano-Soldevilla & VanRullen, 2019; Alamia & VanRullen, 2019) because in pilot experiments we noticed widespread reflections of the display light onto the inner surface of the MRI scanner bore, which resulted in diffuse rather than localized stimulation. The smaller size of 2 degrees allowed us to minimize this reflection artifact. PsychToolbox (Kleiner et al., 2007) for MATLAB (MathWorks, Natick, MA) was used to display the WN sequences. Subjects were required to fixate the center of the screen during the task and detect a near threshold lighter disk (i.e., a target) surrounded by a darker annulus. This target disk lasted 1 frame and was embedded in the white-noise disk. The fixation point was  $0.1^\circ$  of visual angle.

Using a staircase procedure on the first 100 targets presented (i.e., about 30 trials), we manipulated the visibility of the targets by changing the contrast between the outer (darker annulus) and inner (lighter disk) parts to achieve a contrast at which subjects perceived the target on about 50% of trials. The resulting contrast was kept constant for the remainder of the session. The perceptual threshold was computed for each session independently using the quest function (Pelli & Watson, 1983).

Because of differences in computer setup, the stimuli presented in the EEG and the fMRI recording sessions were not identical in terms of temporal frequency. In the EEG session, the CRT monitor had a refresh rate of 160 Hz, giving the WN sequences a flat power spectrum

between 0 and 80Hz. During the fMRI session, the projector used had a maximum presentation rate of 60 Hz, which meant the WN sequences had a flat power spectrum between 0 and 30 Hz (still well above the temporal resolution of the BOLD activity). The maximal luminance of the stimulus was 114.7 cd/m<sup>2</sup> in the EEG session, and 827.9 cd/m<sup>2</sup> in the fMRI session.

### **3.3.3 Experimental protocol**

Each subject completed one EEG and one fMRI session (Figure 1, step 1 and 2). The EEG session was composed of 8 runs of 48 WN sequences, each sequence lasting 6.25s. The fMRI session consisted of 12 runs. Each run was composed of 7 random luminance sequences, each lasting 30 seconds, with an inter-trial-interval of 12 seconds.

### **3.3.4 EEG recording, preprocessing, extraction of IRF and regressors**

During the EEG session, the EEG signal was recorded using a 64-channel BioSemi EEG system with 4 extra ocular electrodes monitoring the horizontal and vertical oculograms. Signals were digitized at a sampling rate of 1024 Hz.

EEG pre-processing was performed using the EEGLAB toolbox (Delorme & Makeig, 2004) and customized Matlab scripts. Bad channels were interpolated when needed. EEG data were down-sampled to 160 Hz to facilitate the cross-correlation with the stimuli. Notch filtering (47~53 Hz) was applied to remove artifacts. EEG data were then referenced to the average and separated into epochs of -0.25s before to 6.5s after the stimulus onset. Baseline correction was performed using the pre-stimulus signal. Furthermore, epochs containing ocular and movement related artifacts were rejected. On average 6.97% (SD = 5.57%) of epochs have been excluded (on average 353 epochs left) and the worst subject had <20% of epochs removed. The IRFs were extracted by doing a cross-correlation between the standardized pre-processed EEG epochs and the standardized corresponding WN sequences (VanRullen & MacDonald, 2012) (Figure 1, step 1). The IRF was cut from lags -0.2 to 1.5s, resulting in 1.7s long IRFs.

The IRFs were then used to reconstruct the EEG signal corresponding to the WN sequences in the fMRI session (Figure 1, step 2). First, the IRFs were down-sampled to 60 Hz to match the presentation rate of the WN sequences in the scanner. The reconstructed EEG was computed by convolving the IRF (from 0 to 1.5s) (from the EEG session) with the exact WN sequences used in the fMRI session. Previous experiments have shown that this method can provide a reliable estimate of EEG activity in the alpha-band (Brüers & VanRullen, 2017). Brüers and VanRullen (2017) adopted a 10-fold cross-validation approach. On each validation, the IRF was computed from 90% trials and the remaining 10% trials were used to reconstruct EEG, which was then correlated with the real EEG. In spite of the noisy nature of EEG signals and the single-trial level estimation, the correlation between the reconstructed alpha and the real alpha was still compelling (mean  $r = 0.163$ ,  $t(19) = 8.21$ ,  $p = 1.14 \cdot 10^{-7}$ , 95% CI for  $r$ : 0.121–0.204). Because signal envelopes were strongly correlated across EEG electrodes, we decided to only use one electrode for each subject. For each subject and each frequency band, we chose the electrode with maximum IRF power in the “IRF area” for that frequency band—defined as the electrode with strongest IRF power, on average across all subjects, in the “late” part of the IRF where “echoes” are typically visible (from 250ms to 1250ms), together with the 8 surrounding electrodes. For example, for the alpha band, the “IRF area” was centered on POz, and also included electrodes P1, PO3, O1, Oz, Pz, P2, PO4, O2. The central electrodes for the delta, theta and beta bands were Cz, CPz and O1 respectively.

The reconstructed EEG was filtered in 4 frequency bands: delta = 2-4 Hz, theta = 4-8, alpha = 7-14 Hz, beta = 14-20 Hz (Figure 1, step 3). The absolute value of the Hilbert transformed data was taken as the envelope. This envelope of the reconstructed EEG signal was then used as a regressor of the BOLD activity (Figure 1, step 4). Finally, the regressors were ‘clipped’ by removing 4s at the beginning and 2s at the end of each trial to remove any systematic filtering artefacts, which could have led to spurious correlations. The clipping length was longer at the beginning, in order to avoid onset transients at the beginning of the envelope and at the beginning of the BOLD response.

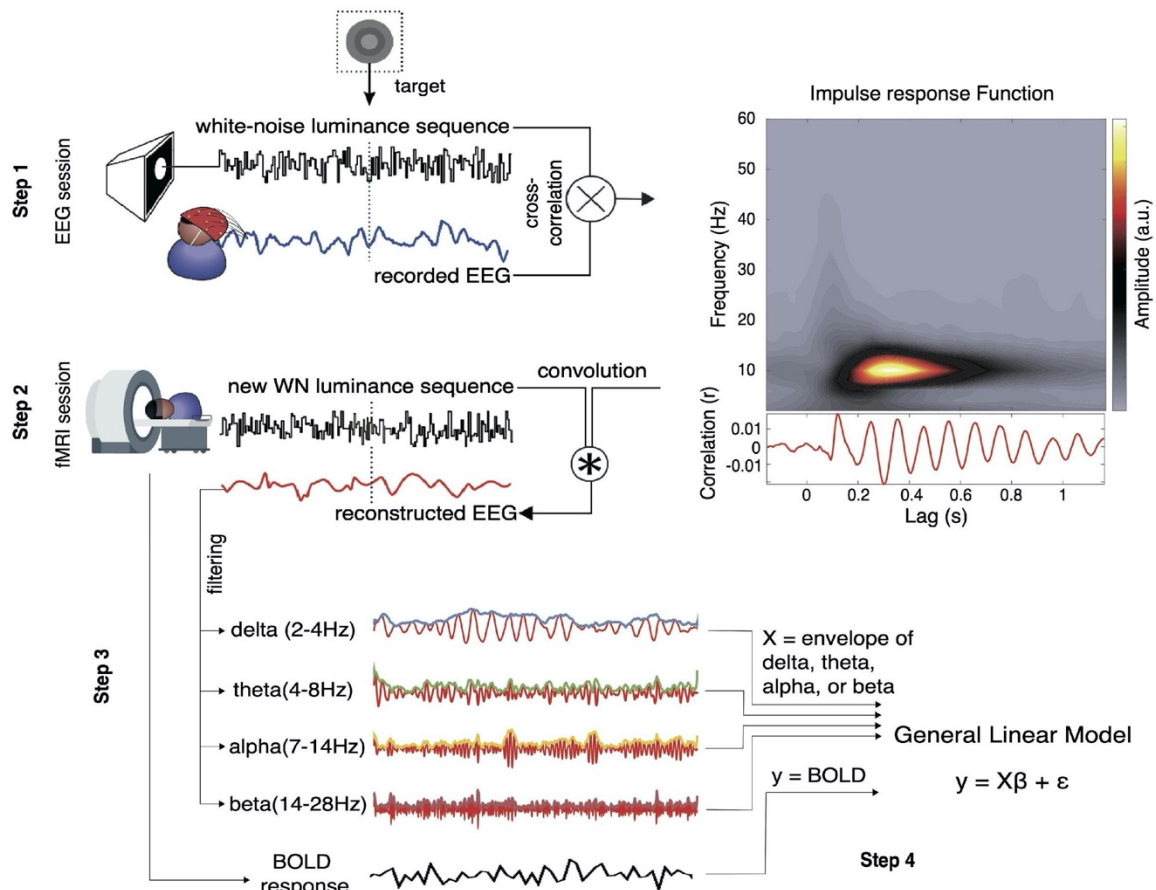


Figure 1. Data collecting and processing steps. Step 1) In the EEG session, we recorded EEG signals and computed the IRF by cross-correlating the EEG and the WN luminance sequences. The IRF time frequency transform (on channel POz) averaged across subjects, and the IRF of one representative subject are shown on the right of the figure. Step 2) We reconstructed an estimate of EEG signals during the fMRI session by convolving this IRF with the WN luminance sequences used in the MRI scanner. BOLD fMRI signals were also recorded. Step 3) We filtered the reconstructed EEG into four frequency bands. Step 4) Finally, we used the envelopes of the filtered EEG as BOLD regressors for the GLM.

### 3.3.5 fMRI recording and preprocessing

In the fMRI session, data were collected in a 3T Philips (Amsterdam, The Netherlands) ACHIEVA scanner with a 32-channel head coil. High resolution anatomical images were recorded from each subject at the beginning of the scanning: 170 sagittal slices were acquired

with a voxel size of 1mm<sup>3</sup>, a repetition time (TR) of 8.13ms, and a time to echo (TE) of 3.74ms. Functional images were acquired in the transverse plane using a gradient-echo pulse sequence (TE = 35 ms, TR = 2000 ms). 39 slices were acquired (80 \* 80 image matrix, 240 \* 240 FOV, with 3 mm<sup>3</sup> voxels) to cover the whole brain. Data analysis was performed with FreeSurfer and the FreeSurfer Functional Analysis Stream (FS-FAST) (<http://surfer.nmr.mgh.harvard.edu>) and custom Matlab scripts. Pre-processing followed the FS-FAST processing stream. All images were motion corrected (using AFNI with standard parameters), slice-time corrected, intensity normalized and smoothed with a 3-mm full-width at half maximum Gaussian kernel.

### ROI definition

In a first analysis we used a GLM to define functional regions of interest (ROIs) based on voxels that were responsive to the visual stimulus. Two types of functional ROIs were defined accordingly: group functional ROIs and individual functional ROIs. The GLMs were performed in the Freesurfer average brain space with the contrast of visual stimulation blocks versus the inter-trial-intervals for each subject. The GLM fitted the hemo-dynamic response (HRF) with a gamma function ( $\delta = 2.25$ ,  $\tau = 1.25$ ) and modeled the drift with an order 1 polynomial. At the time of the analysis, we used an older version of the FS-FAST software, in which this gamma function was the default model for fitting the hemodynamic response. Note, however, that we also replicated our main analysis using the canonical HRF, and the results did not show any significant difference. For all other parameters of the GLM we used the default settings from FS-FAST.

A group analysis was performed to define significant clusters using this contrast. We used a voxel-wise  $p$  of 0.001, and a cluster-wise  $p$  of 0.0005 to define the visual clusters at the group level.

We also defined three functional ROIs at the individual-subject level, in V1, V2 and in extrastriate areas outside of V1 and V2. For each anatomical region, we found the connected cluster containing the most significant voxels (lowest  $p$ -value), then increased the cluster-forming  $p$ -value threshold gradually until a preset number of voxels was reached. By doing this, we obtained a ROI in V1, with approximately 100 voxels (R1-100). Likewise, we applied the same method in V2 to define R2-100, and in the areas outside of V1 and V2 to define R3-100. (See Figure S1 for the results of corresponding ROIs with 50 and 200 voxels)

### Analysis of BOLD modulation by alpha envelope in the ROIs

We next analyzed whether BOLD activity in the ROIs was modulated by the alpha envelope. To determine which ROIs co-varied with the alpha envelope of the reconstructed EEG, we performed a first-level GLM for each subject in the FreeSurfer average brain space. The amplitude envelope in the alpha band was used as a parametric regressor and motion parameters were included as nuisance regressors. The GLM was performed separately for these regressors. The HRF was modeled as a gamma function (delay = 2.25, tau = 1.25) and the drift was modeled with an order 2 polynomial. To test the statistical significance of alpha modulation in each ROI, we performed a one sample t test using  $\beta$  estimates of all voxels in the ROIs defined from the ROI definition analysis above.

### Whole brain analysis of BOLD modulation by the alpha envelope

A group level GLM was applied to test the correlation between the BOLD activity and the reconstructed EEG alpha envelope in the whole brain defined by the FreeSurfer atlas. Specifically, a one sample group mean analysis was conducted using the `mri_glm-fit` command (with the `-osgm` flag) in FreeSurfer to test whether the beta values of each voxel from each subject's GLM were significantly higher than 0 over the group. The runs with high variance were de-weighted (with the `-wls cesvarpct` flag). We used a voxel-wise p of 0.05 as the threshold to visualize the voxels that were significantly modulated by the alpha envelope.

### Correlating ROI BOLD activity with voxel-wise response variance

In subsequent analyses, we investigated the relationship between response variability of voxels in V1 and V2 (R1 and R2 included) during visual stimulation and the level of the BOLD response in each voxel (this analysis was intended to evaluate the possibility of a saturation effect in strongly activated voxels which could have masked alpha-related fluctuations). To quantify the variability of each voxel, we calculated the standard deviation (SD) of the percent signal change (PSC) within a fixed time window (5 - 28 seconds for each trial, same time window as the time window used to define the regressors). For each voxel, the preprocessed BOLD time series of each trial was extracted and converted to PSC by dividing the BOLD signal by the prestimulus baseline (6 seconds). The SD of the PSC was calculated across time per trial and further averaged across trials, runs and subjects. To estimate the level of the BOLD response in each voxel, we used the T value of the stimulus-

on vs. stimulus-off contrast for each voxel. Finally, we calculated the correlation between the T value and the SD of the PSC across voxels.

#### Correlating the BOLD activity in V1 and V2 with other frequency envelopes

Finally, we tested if other frequencies significantly correlated with the BOLD in V1 and V2. As done for the alpha-band envelope, for each subject we used the delta, theta and beta envelopes as parametric regressors and performed separate first level GLMs for each regressor. Motion parameters were used as nuisance regressors. The HRF and the drift were modeled using the same function as above. We next performed a one sample t-test to test whether the  $\beta$  estimates of all the voxels in V1 and V2 from these first level GLMs were significantly higher than 0, and a nonparametric permutation test to determine if the  $\beta$  estimates of any frequency were higher than those of the other frequencies.

### **3.4 RESULTS**

We first determined the voxels that were activated by the stimulus, by contrasting stimulus on versus off periods. A group level analysis revealed two clusters of activity in the right hemisphere: cluster one (C1, Figure 2, left) was located in the lingual gyrus below the calcarine fissure, and extending towards the fusiform gyrus ( $p < 0.05$  corrected, MNI coordinates:  $x = 21.9, y = -79, z = -8.3$ ). The second cluster (C2, Figure 2, right) of activity was found in the lateral occipital gyrus ( $p < 0.05$  corrected, MNI coordinates:  $x = 41.3, y = -72.6, z = -0.5$ ). There was no corresponding cluster in the left hemisphere, since the stimulus was lateralized to the left. These two clusters C1 and C2 were considered as group functional regions-of-interest (ROIs). In addition to these two ROIs, we defined three other group functional ROIs by considering the overlap of C1 and C2 with the Freesufer-atlas based definitions of V1 and V2: R1 and R2, the intersection of C1 with V1 and V2 respectively, and R3, which were the voxels in C1 that were not in V1 or V2. Additionally, Freesufer-atlas based V1 and V2 were defined as anatomical ROIs. (Figure 2). Finally, we defined functional ROIs at the individual-subject level (with a pre-determined voxel number: 100 voxels) in V1, V2 and in extra-striate areas outside of V1 and V2. As some voxels shared the same p-value, the selection of the most significant voxels did not always return the exact number of



expected voxels. Across subjects, the regions actually contained  $103.1 \pm 5.1$  voxels (R1, mean $\pm$ sd),  $109.4 \pm 17.7$  voxels (R2) and  $111.2 \pm 12.2$  voxels (R3).

Since alpha is the main frequency component in the IRF, we first used the 7-14Hz (alpha) envelope of the reconstructed EEG as a regressor in the fMRI analysis to determine which ROIs co-vary with the perceptual echoes induced by the white-noise luminance sequence. In order to test the significance, we conducted a t-test and a permutation test. For the permutation test, we created 2000 surrogates by shuffling the alpha envelopes of all the trials for each subject and performed the first-level GLM on the shuffled data. P values of the mean coefficients were computed from the percentile within the permuted null distributions. In the pre-defined group-level functional ROIs (C1, C2, R1, R2 and R3) we found that BOLD activity was not significantly modulated by the alpha envelope of the reconstructed EEG (Figure 3A, middle). The mean coefficient of R1, R2, R3, C1 and C2 was close to 0, with large inter-subject variability (t-test against 0: R1  $t(20) = -0.0734$ ,  $p = 0.9422$ , R2  $t(20) = 0.3510$ ,  $p = 0.7295$ , R3  $t(20) = 0.1249$ ,  $p = 0.9019$ , C1  $t(20) = 0.1748$ ,  $p = 0.8631$ , C2  $t(20) = 0.4264$ ,  $p = 0.6746$ . Permutation test: R1  $p = 0.5400$ , R2  $p = 0.4900$ , R3  $p = 0.5000$ , C1  $p = 0.4800$ , C2  $p = 0.4300$ ). Likewise, the individual-level functional ROIs were insignificant, even though the alpha envelope modulation of R1-100 was visibly higher than in the other functional ROIs (Figure 3A, left) (t-test against 0: R1-100  $t(20) = 1.1484$ ,  $p = 0.2650$ , R2-100  $t(20) = 0.1195$ ,  $p = 0.9061$ , R3-100  $t(20) = -0.4706$ ,  $p = 0.6433$ . Permutation test: R1-100  $p = 0.1400$ , R2-100  $p = 0.5200$ , R3-100  $p = 0.7500$ ). Besides, the individual functional ROIs with 50 voxels and 200 voxels also did not show significant alpha modulation (Figure S1). However, the mean coefficients for V1 and V2 were significantly higher than 0 in both hemispheres (Figure 3A, right). The corresponding statistical tests revealed: for Right V1, t-test against 0:  $t(20) = 2.3976$ ,  $p = 0.0269$ , mean = 0.0072, 95% CI = 0.0009 – 0.0135. Permutation test:  $p = 0.01$ , 95% CI = -0.0060 – 0.0054; Right V2, t-test against 0:  $t(20) = 2.2400$ ,  $p = 0.0372$ , mean = 0.0058, 95% CI = 0.0004 - 0.0111. Permutation test:  $p = 0.02$ , 95% CI = -0.0050 – 0.0051; Left V1, t-test against 0:  $t(20) = 2.7072$ ,  $p = 0.0140$ , mean = 0.0081, 95% CI = 0.0018 – 0.0143. Permutation test:  $p = 0.01$ , 95% CI = -0.0056 – 0.0061; Left V2, t-test against 0:  $t(20) = 2.2635$ ,  $p = 0.0355$ , mean = 0.0057, 95% CI = 0.0004 - 0.0110. Permutation test:  $p = 0.02$ , 95%, CI = -0.0048 – 0.0047. The t-tests and permutation test for V1 and V2 were conducted using all voxels in V1 and V2. In agreement with these findings, a whole-brain analysis revealed wide-spread BOLD activity modulation by the alpha envelope bilaterally in V1 and V2 (Figure 3B).

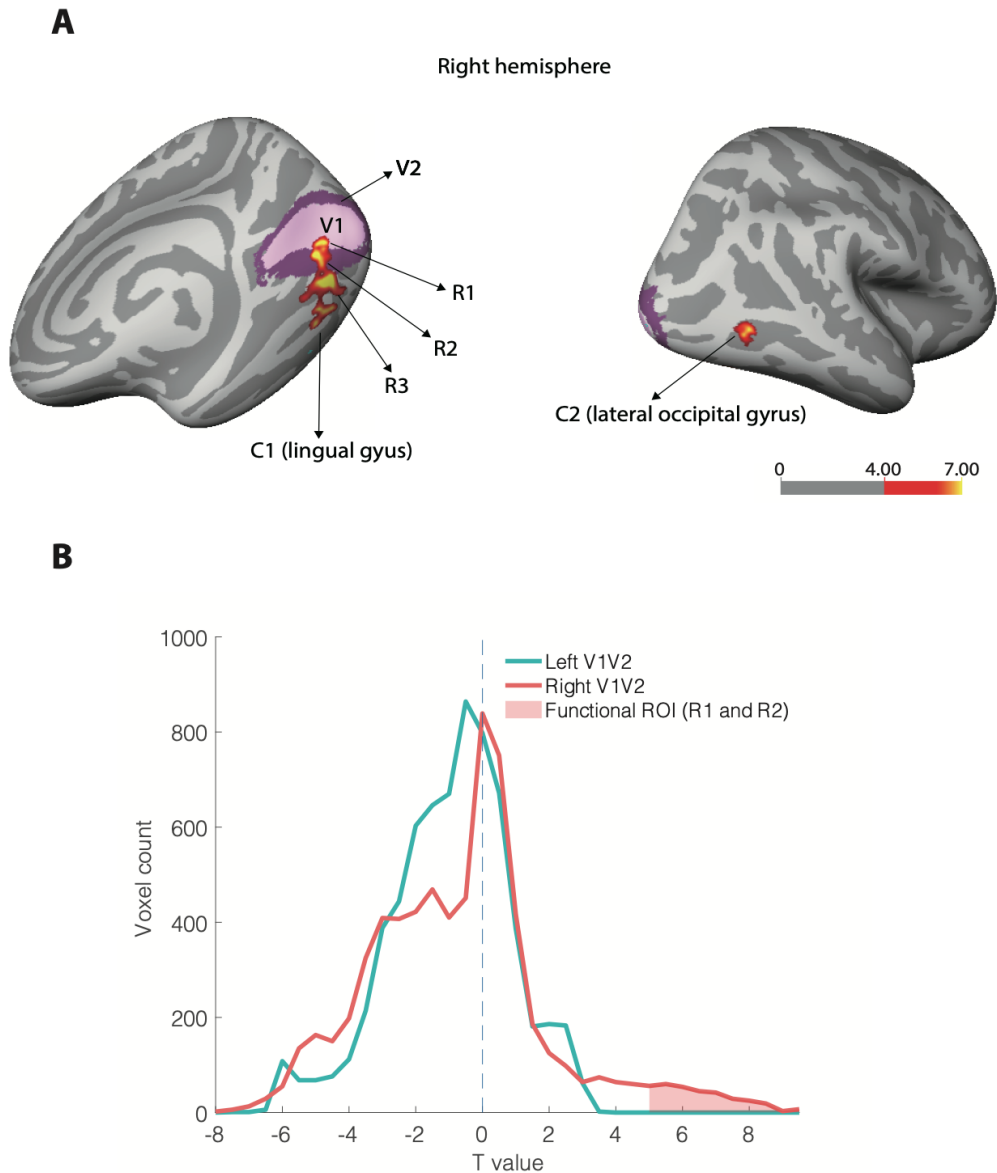


Figure 2. A) Group level retinotopic activation in early visual areas of the right hemisphere. The light purple represents the location of the primary visual area (V1) and the darker purple represents the location of the secondary visual area V2, which were extracted with the Freesurfer atlas. Statistical analysis at the group level revealed 2 clusters of retinotopic activity in response to the stimulus (red/yellow): cluster one (C1) on the left is located below the calcarine sulcus (MNI coordinates:  $x = 21.9, Y = -79, Z = -8.3$ ) with partial overlap with V1 and V2, and cluster 2 can be seen in the right panel, possibly corresponding to lateral occipital cortex (LOC). R1, R2 and R3 were defined as:  $R1 = V1 \cap C1$ ,  $R2 = V2 \cap C1$ ,  $R3 = C1 - (V1 \cup V2)$ . Color bar represents  $-\log_{10}$  of p value of F-test against 0. B) Distribution of t-values (voxel count) for the contrast between stimulus-periods and fixation-periods. The functional ROI was defined as  $t > 5$  (red shaded area), and only includes right-hemisphere voxels (as expected, since the stimulus is located in the left hemifield). In both Left and Right V1-V2 voxels, there is a significant trend towards negative values: 63% and 55% of voxels (respectively) had

negative stimulus responses, and this proportion was significantly larger than 50% (binomial test,  $p < 10^{-10}$  in both cases).

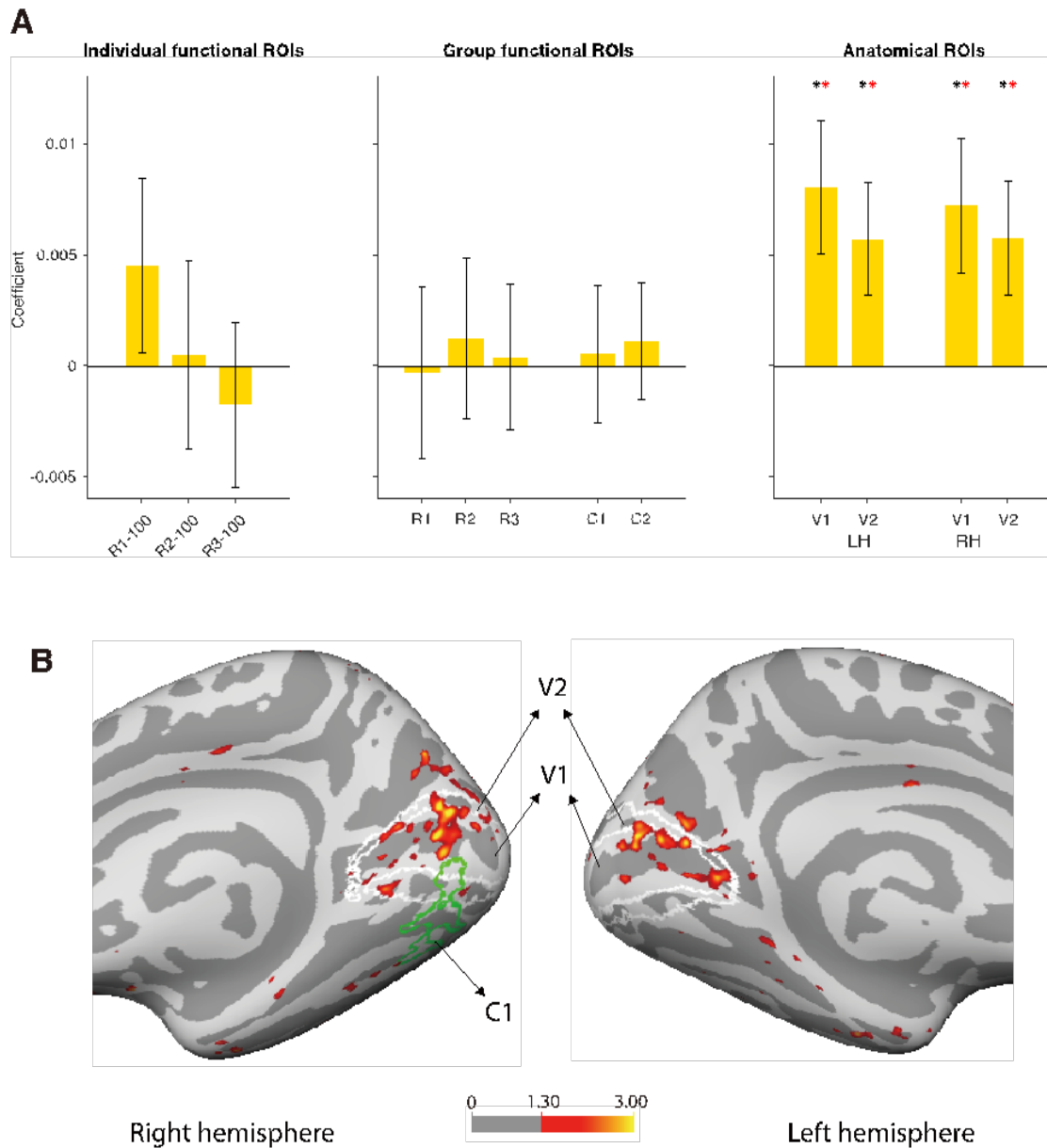


Figure 3. A) Beta weights of modulation of BOLD activity by the alpha envelope of the reconstructed EEG in the regions of interest. Bars represent mean  $\pm$  s.e.m across subjects. No individual-level (left) or group-level (middle) functional ROIs were significantly modulated by the perceptual echoes. In contrast, BOLD activity in bilateral V1 and V2 (anatomical ROIs) was significantly modulated by the alpha component of the reconstructed EEG (right). The black asterisks represent significant difference against 0, t-test across subjects ( $N=20$ ,  $p < 0.05$ ). The red asterisks indicate the coefficient is

significantly higher than the null hypothesis distribution of the surrogates (non-parametric test). B) Whole brain analysis of regions correlated to fluctuations in the alpha power envelope in the right and left hemispheres. The activations extend well beyond the stimulus responsive regions of interests (C1 outlined in green) into V1 and V2 (outlined in white). The significant voxels computed from the group-level GLM are shown in red/yellow at a threshold of  $p < 0.05$  ( $-\log_{10}(0.05) = 1.3$ ). The color bar represents  $-\log_{10}$  of p value of F-test against 0. Note that no significant negative correlations of BOLD with alpha envelope were observed in visual areas (and only few sparsely distributed negative correlations over the rest of the brain), hence the color scale only displays positive correlations.

These results indicate that the reconstructed envelope of EEG alpha was significantly correlated with BOLD responses in V1 and V2. Surprisingly however, this correlation was visible outside, but not within the directly (retinotopically) stimulated region (C1). This leaves two important issues to address: first, the absence of alpha modulation in the stimulus-responsive ROI, where we could have naturally expected it; second, the presence of alpha modulation in unstimulated regions of visual cortex, reaching as far as the opposite hemisphere. We tentatively interpret the first issue as a consequence of signal saturation, and the second as a signature of wide-spread inhibition, as detailed below.

First, we hypothesized that the lack of alpha modulation in the stimulus-responsive ROI (C1) may reflect saturation in these voxels by the continued presence of the visual stimulus. As a result of this saturation effect, we hypothesized that these voxels would not be susceptible to the smaller and rapid modulations in the luminance of the stimulus. In other words, over the group of voxels, we would expect voxels that have high levels of response (e.g., those within the retinotopically stimulated regions) to have lower response variability (since they would not be modulated by the random changes in stimulus luminance). In contrast, voxels that are modulated (possibly indirectly) by the luminance changes but not saturated by stimulus presentation, would show larger signal variability, but a lower BOLD response. In other words, over the group of voxels, we expected a negative correlation between the BOLD response and signal variability of voxels in V1 and V2. To test this hypothesis, we analyzed the relationship between the SD of PSC (a measure of signal variability) and the T value of the stimulus-on vs. stimulus-off contrast (a measure of BOLD response) of each voxel in V1 and V2. The SD of the PSC of each voxel in V1 and V2 (as explained in the Methods Section) was averaged across trials, runs and subjects. The results showed that the T value was negatively correlated with the SD of PSC ( $r = -0.1538$ ,  $p < 0.01$ ).

In other words, as predicted, the overall stimulus-induced BOLD response was inversely related, across voxels, to the signal variability over time. This is compatible with the notion that signal saturation prevented us from observing alpha amplitude fluctuations in the retinotopic regions of interest (C1 and C2).

Second, we turned to the observation of widespread alpha-IRF modulations across V1 and V2, bilaterally in both hemispheres. One possible interpretation could be that it was stimulus-dependent inhibition, rather than excitation, outside of the stimulus-responsive ROI that led to the widespread alpha-IRF modulations by routing information. To explore this possibility, we first looked into the distribution of stimulus-related BOLD activity across early cortex (V1-V2), that is, the contrast between stimulus periods and fixation periods (Figure 2B). We found indeed, in addition to a number of voxels with high t-values in the right hemisphere ( $t > 5.0$ , corresponding to our ROI), a general shift of the distribution towards negative BOLD activations. This negative trend was significantly present in both left and right V1-V2, even though the stimulus was lateralized (63% and 55% voxels in left V1-V2 and right V1-V2 respectively had negative responses to stimuli, binomial test:  $p < 10^{-10}$  in both cases). This is compatible with broadly distributed inhibition outside of the stimulus region. Even though such inhibition could happen without any relation to the stimulus fluctuations, the fact that the many voxels in the same broad region also show positive correlation with the reconstructed EEG envelope hints at a possible functional relation between neural inhibition and alpha IRF propagation. The existence of such a relation is further supported by two observations: first, there is a weak but significant negative correlation across voxels between the t-value of stimulus response and the t-value of the alpha IRF modulation ( $r = -0.018$ ,  $p < 0.04$ ); second, the voxels that were most significantly modulated by the alpha IRF (voxels mapped in Figure 3B) tended to have negative t-values for stimulus response (54.4% negative values,  $p = 0.0001$ , binomial test).

Finally, we asked if activity in V1 and V2 was exclusively modulated by alpha, or if other frequency bands also modulated the BOLD signal. We implemented separate GLMs with the envelopes of the reconstructed EEG filtered in the delta, theta, alpha and beta bands as regressors for the BOLD activity. The results, shown in Figure 4, revealed that the coefficients from these other frequency bands were not significantly higher than zero (V1 and V2: delta  $t(20) = 1.1142$ ,  $p = 0.2791$ , theta  $t(20) = 1.0316$ ,  $p = 0.3152$ , alpha  $t(20) = 2.5357$ ,  $p = 0.0202$ , beta  $t(20) = -0.1720$ ,  $p = 0.8653$ ). A nonparametric permutation test was

conducted to determine if IRF-dependent BOLD modulations at any frequency were higher than for the other frequencies. Surrogates were computed by shuffling the correlation coefficients across all frequency bands in single-subject data for each anatomical ROI (left V1, left V2, right V1 and right V2), then averaging across subjects and ROIs. The 95% and 99% CI as well as the p-values were taken from the null distribution composed of these surrogates (Permutation test: delta  $p = 0.6000$ , theta  $p = 0.4200$ , alpha  $p = 0.0020$ , beta  $p = 0.9800$ ).

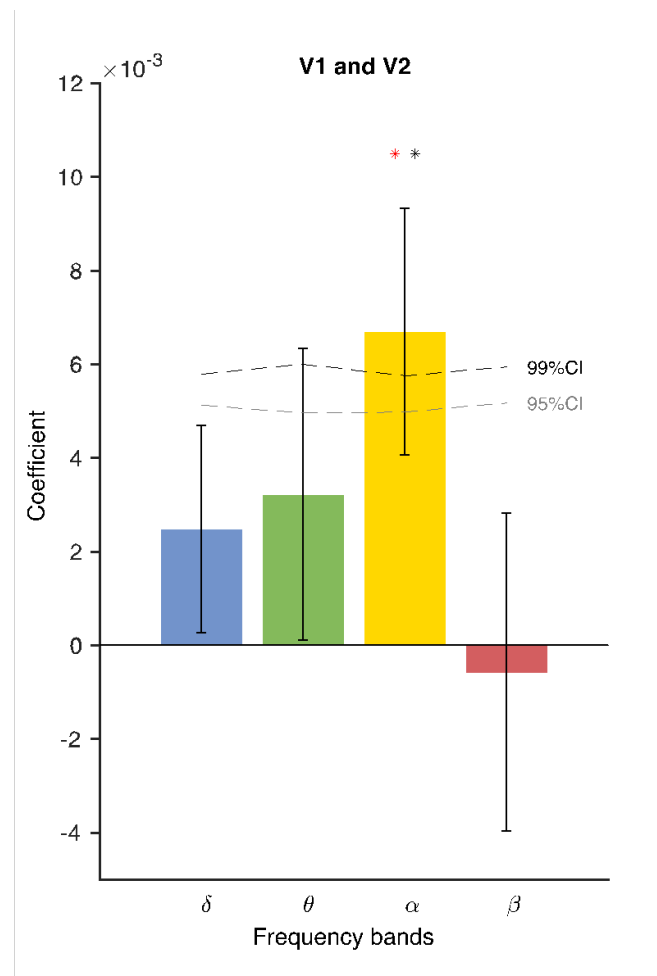


Figure 4. Coefficients of the modulation of BOLD activity by the reconstructed EEG envelope of delta, theta, alpha and beta band frequencies. The bars represent the mean, and the error bars represent the standard error of the mean across subjects. The black asterisk represents significant difference against 0, t-test across subjects ( $N = 20$ ,  $p < 0.05$ ). The red asterisk indicates the coefficient is significantly higher than the 95th percentile of the null hypothesis distribution (non-parametric test against other frequencies). This figure shows that the BOLD activity is only modulated by alpha envelope. The gray and black dash lines indicate the 95% and 99% CI of the null distribution.

### 3.5 DISCUSSION

In this study, we conducted an EEG-fMRI experiment to investigate the neural basis of the IRF. We first measured the IRF of each subject in the EEG session. We then reconstructed an estimate of the EEG signal by convolving the IRF with the stimuli presented in the fMRI session. The envelopes of reconstructed EEG signals in the theta, alpha, beta and gamma bands were taken as regressors for the GLM. We found that the envelope of the EEG alpha, but not the other frequencies, was positively correlated with BOLD activity in V1 and V2, but surprisingly not with activity in the retinotopically stimulated regions. We hypothesize that the lack of effect in the retinotopically stimulated ROIs might be due to a saturation effect by the visual stimulus.

The activations found in early visual areas (Figure 3) are in line with the observation that the IRF is a visual response, strongest in posterior regions (VanRullen & MacDonald, 2012). Intriguingly, large-scale activations were found in left V1 and V2, i.e., in the hemisphere that was not directly stimulated (Figure 3B). Let us first consider the possibility that subjects may have directly perceived the stimuli in their right visual field. This could have occurred for example because of unwanted eye movements, or possibly because of stimulus illumination reflecting off of the inner walls of the MRI. To avoid this second possibility, we had elected to use smaller stimuli than in our previous studies (2 degrees vs. 7 degrees in VanRullen & Macdonald, 2012 and subsequent studies). To avoid the first possibility, we instructed subjects to fixate in the center of the screen, and avoid unnecessary eye movements. The circumscribed stimulus-related activations in relatively small sub-regions of V1 and V2 of the right hemifield when contrasting stimulus-on and stimulus-off periods (Figure 2) suggest that subjects successfully maintained fixation and that the stimulus position was spatially restricted, as intended. If subjects had made systematic eye movements or if the stimulus had been reflected at distant positions, we would have expected instead a broader pattern of stimulus activations, possibly extending to the other hemifield. Hence, the alpha-envelope induced activations in the left hemisphere (Figure 3B) appear to be due to IRF propagation across hemispheres. This would be consistent with previously reported findings that the IRF propagates as a traveling wave (Alamia & VanRullen, 2019; Lozano-Soldevilla & VanRullen, 2019). In particular, the study by Lozano-Soldevilla and VanRullen (2019) pointed out that the propagation of the IRF to lateralized WN sequences follows

retinotopic rules such that it can travel from contra-lateral to ipsi-lateral regions, in agreement with the current results.

It is reasonable to compare our results with those of EEG-fMRI studies of the generators of the alpha rhythm, because of the relation between the IRF and the alpha rhythm—even though the current understanding of alpha generators is incomplete. The EEG alpha power was found to be negatively correlated with BOLD activity in occipital cortices in both resting-state studies (de Munck et al., 2007; DiFrancesco et al., 2008; Goldman et al., 2002; Gonçalves et al., 2006; Laufs, Kleinschmidt, et al., 2003; Laufs, Krakow, et al., 2003; Moosmann et al., 2003) and during task performance (Scheeringa et al., 2009; Scheeringa et al., 2016; Zumer et al., 2014). On the contrary, we found the IRF envelope to be positively correlated with V1 and V2 BOLD signals. The common neural basis (early visual areas) together with the opposite activation profiles (i.e., opposite correlations with the BOLD) indicate that the IRF and the EEG alpha rhythm might share neural pathways, but serve distinct functional roles in the brain.

The results of the present study suggest that the IRF in response to left-visual field stimuli might have originated from one or multiple starting points in the right early visual cortex (V1, V2), from which it spread over much of the early visual cortex. The activation at the origin could not be directly measured, presumably because of BOLD saturation effects, however its propagation to distant parts of the visual cortex, including the opposite hemifield, was readily visible. It is plausible that this propagation of IRF oscillations to distant parts of the visual cortex may be associated with stimulus-dependent inhibition of non-task-related regions, though this conclusion may require further confirmation. Our findings are of importance for further studies to locate the origin of the IRF more precisely. For example, future studies could specifically record the IRF in V1 and V2 using intracranial recordings during different visual tasks, to better understand where and when the IRF appears, and how it propagates to other parts of the visual cortex.

In conclusion, our study found BOLD activations whose time course was related to the IRF envelope in the early visual cortex. The widely spread activation might be due to the propagation of (possibly inhibitory) IRF traveling waves (Lozano-Soldevilla & VanRullen, 2019; Alamia & VanRullen, 2019). Our study advances our knowledge of the spatial properties of the IRF by narrowing down its neural basis, therefore paving the way



for future studies to precisely localize the generator(s) of the IRF and deepen our understanding of its functional relevance.

## **Another sampling: from visual perception to attention.**

We now know that the echoes might come from early visual areas, which is not surprising since alpha or the echoes are mostly observed at the occipital electrodes. Unlike visual sampling demonstrated by perceptual echoes, attentional sampling exhibits lower oscillatory frequency and might entail more distributed brain areas (see section 1.4.3 oscillations in attention). Theta oscillations have been observed in multiple regions, such as V4, IT, and the attention network. According to the hypothesis of perceptual cycles, these theta oscillations may be the source of the theta rhythm of attentional sampling. For unraveling the neural mechanism of attentional sampling, it is important to establish the link between neural activity and behavioral performance. As mentioned in the introduction, a monkey study found that visual competition can lead to theta activity in V4, which correlates with the oscillation of saccadic RT. Here we further investigate if the visual competition gives rise to attentional sampling at theta band in humans.

## 4 CHAPTER 4. ATTENTION SAMPLING ARISES FROM NEURAL COMPETITION

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This chapter contains the original manuscript that appeared as: Chota, S. \*, Luo, C. \*, Crouzet, S. M., Boyer, L., Kienitz, R., Schmid, M. C., & VanRullen, R. (2018). Rhythmic fluctuations of saccadic reaction time arising from visual competition. *Scientific reports*, 8(1), 1-7. \*Co-first author with Samson Chota.

### 4.1 ABSTRACT

Recent research indicates that attentional stimulus selection could be a rhythmic process. In monkeys, neurons in V4 and IT exhibit rhythmic spiking activity in the theta range in response to a stimulus. When two stimuli are presented together, the rhythmic neuronal responses to each occur in anti-phase, a result indicative of competitive interactions. In addition, it was recently demonstrated that these alternating oscillations in monkey V4 modulate the speed of saccadic responses to a target flashed on one of the two competing stimuli. Here, we replicate a similar behavioral task in humans (7 participants, each performed 4000 trials) and report a pattern of results consistent with the monkey findings: saccadic response times fluctuate in the theta range (6 Hz), with opposite phase for targets flashed on distinct competing stimuli.

### 4.2 INTRODUCTION

Many exploratory actions such as eye movements reveal a specific rhythmicity upon closer inspection. During overt saccadic exploration of the visual field, saccades occur approximately every 200 ms i.e., at 5 Hz (Hogendoorn, 2016; McLelland et al., 2016; Otero-Millan et al., 2008). Moreover, even in the absence of eye movements, target detection rates have been shown to vary as a function of the cue-target interval at a similar frequency. It has been proposed that these behavioral fluctuations emerge from rhythmic attentional processes in the theta range (Fiebelkorn et al., 2013; Holcombe & Chen, 2013; Landau & Fries, 2012; Song et al., 2014; VanRullen et al., 2007). Spatial covert attention paradigms have suggested that multiple objects in the visual field are rhythmically and sequentially sampled and that these attentional sampling rhythms are related to brain oscillations in the 4-8 Hz range (Busch & VanRullen, 2010; Crouzet & VanRullen, 2017; Dugué, Marque, et al., 2015). In addition, causal evidence was provided by Dugué, Marque and VanRullen (Dugué et al.,

2011) who used non-invasive brain stimulation, demonstrating that stimulus processing is vulnerable to disturbances via single TMS pulses at constant intervals in the theta range.

In a recent study, Kienitz et al. linked theta oscillations in macaque V4 to an attentional sampling process (Kienitz et al., 2018). V4 has been previously related to attention, e.g. via lesion studies (DeWeerd et al., 1999). Furthermore, sporadic theta oscillations have been measured in V4 as well as in inferotemporal cortex when the animals were viewing a single stimulus (Lee et al., 2005; Nakamura et al., 1991; Sato et al., 1980; Sheinberg & Logothetis, 1997; Tamura & Tanaka, 2001); when two stimuli were shown together, the competition between them resulted in intricate theta-band oscillatory phase relations between the corresponding IT neural responses (Rollenhagen & Olson, 2005). Building on these findings, Kienitz et al. (Kienitz et al., 2018) showed that the presence of two visual objects, one in the excitatory center ("object") and one in the inhibitory surround ("flanker") of a V4 neuron's receptive field (RF), resulted in theta-rhythmic multi-unit-activity (MUA). Furthermore, they showed that the saccadic reaction times to targets presented in either of the two stimuli were subject to similar fluctuations at 3-6 Hz. Most importantly, the phase of both RT time-series and MUA oscillations depended on the order of display onset between the object and flanker stimuli. The authors demonstrated that these theta-rhythmic fluctuations emerge from competitive receptive field interactions, and could at least partially underlie the rhythmic attentional sampling of multiple objects observed in numerous human studies (Busch & VanRullen, 2010; Crouzet & VanRullen, 2017; Dugué, McLelland, et al., 2015).

In the current study, we investigate this question in human subjects, using a behavioral spatial attention paradigm directly inspired by this monkey study (Kienitz et al., 2018). A central disk object and two bar flankers were presented in the periphery with asynchronous sequential onset (500 ms SOA), and remained on the screen while participants maintained fixation. After a varying SOA following the second stimulus onset, a target was presented either in the central object or the flankers. The subjects were instructed to perform a saccade to the target. Reaction times was investigated as a function of the SOA between the second stimulus and the target. As found in monkeys, the analysis of RT time-series revealed an oscillation at approximately 6 Hz; furthermore the phase of this oscillation was dependent on both the initial stimulus order (object- or flanker-first) and on the location of the target (object or flanker).

## 4.3 MATERIALS AND METHODS

### 4.3.1 Participants

Seven volunteers (aged 19-25, 3 females, all right-handed) with normal or corrected to normal vision participated in the experiment. Informed consent forms were signed before the experiment. The experiment was carried out in accordance with the protocol approved by the Centre National de la Recherche Scientifique ethical committee and followed the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Stimuli were presented at a distance of 50 cm with a cathode ray monitor (1280×1024 resolution, 85 Hz refresh rate) using the Psychophysics Toolbox (Brainard, 1997) running in MATLAB (MathWorks). Eye movements were recorded and monitored online using an EyeLink 1000 Desktop Mount (SR Research). A 9-point calibration was performed before each block of trials. Throughout the Methods section we will explicitly note the differences with the monkey study by Kienitz et al. (Kienitz et al., 2018). If no mention is provided, task parameters at hand were kept identical. Stimuli consisted of a fixation dot (central black dot, diameter=0.3°; [0.07° in Kienitz et al. 2018]), the object (a black disk in the lower right part of the screen, 2° diameter, positioned 4° right and 2° down from fixation center [in Kienitz et al. 2018 the disk was positioned, within the RF of a V4 neuron]) and the flankers (two bars above and below the disk, height=1°, width=0.25°, 1° gap between disk and each bar) (Fig. 1). Stimuli were presented on a gray background.

After a pseudo-random (400-800 ms [1000 ms in Kienitz et al. 2018]) interval during which participants maintained central fixation, the first stimulus of the sequence, either the Object or the Flankers, appeared. We introduced a variable delay in this pre-stimulus interval to counteract potential attentional effects that could be introduced by the predictability of the stimulus onset. The second stimulus (the Flankers if the Object was presented first and vice versa) was added to the display 500 ms later [Object was always presented first in Kienitz et al. 2018]. After another variable SOA (250 to 1250 ms, in steps of 12 ms [0 to 750 ms, in steps of 37.5 ms in Kienitz et al. 2018]) a small target (0.2° diameter white dot) then appeared for a single frame (12 ms [8.3 ms in Kienitz et al. 2018]), either in the center of the upper flanker or the center of the disk object. In one out of 16 trials ([1 out of 3 in Kienitz et al. 2018]), no target was presented (catch trials). This reduction in the number in catch trials still allowed us to reliably control for non-target related saccades.

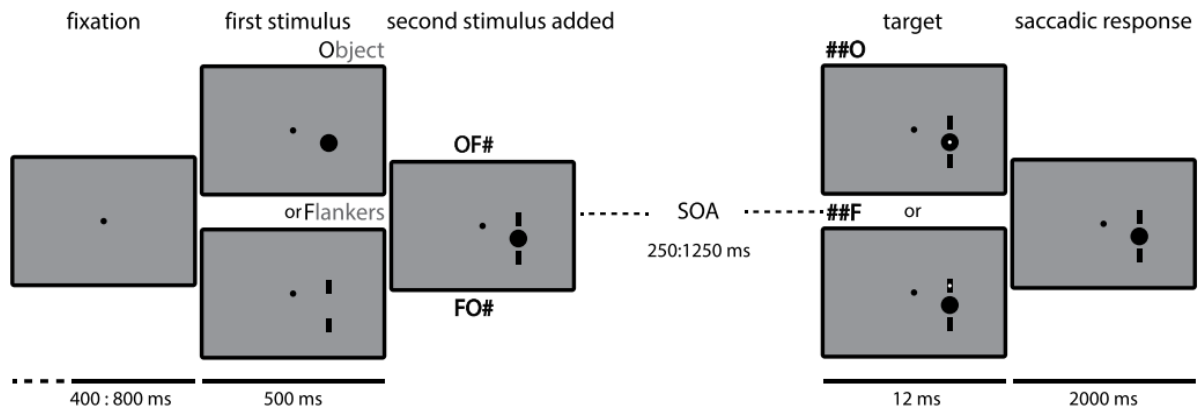


Figure 1. Experimental Protocol. Trials started with a fixation period during which participants maintained fixation for a variable delay between 400 to 800 ms. Following the fixation period the first stimulus (object or flanker) was presented for 500 ms after which a second object (flanker if object first (OF#) and vice versa (FO#)) was added. After a variable SOA of 250 to 1250 ms (in steps of 12 ms) a target was presented for 12 ms, either in the center of the object (##O) or in the flanker (##F). Participants were instructed to respond to the target with a saccade towards the stimulus in which it appeared

For consistency and clarity we will now refer to the four possible (non-catch) trial types as the conditions: OFO, OFF, FOO, FOF, where the 1st letter denotes the first stimulus onset (O for object, F for flanker), the 2nd letter corresponds to the second stimulus presented (identical notation), and the third to the stimulus in which the target appeared (identical notation) (See upper part of Fig. 2).

The timing of the target relative to the onset of the second stimulus (so-called stimulus onset asynchrony or SOA), was drawn from a uniform distribution with 85 steps from 250 to 1250 ms (corresponding to the refresh rate of the screen). The SOA tested on each trial was optimized online to equalize the number of trials obtained for each of the 85 SOA conditions: if a trial was not valid (see below), the same SOA value was more likely to be tested again.

The luminance of the target was adapted separately for each condition using a QUEST procedure (Pelli & Watson, 1983) so that each participant's detection performance remained around 90%. We chose the 90% threshold in order to collect sufficient trials that could be entered in our analysis and at the same time require participants to pay attention. Because of

the high number of trials, involving multiple sessions over several days, the luminance value defined by the QUEST procedure was adapted dynamically, based only on the last 40 trials.

Participants had to respond to the target by performing a saccade towards it. A saccade was considered valid if it landed in one of two  $2^\circ$  square boxes centered respectively on the object and upper flanker. Only valid saccades were included for further analysis. Reaction times (RT) were defined as the time between target onset and the time at which the eye position left a fixation region of  $1^\circ$  radius around the fixation point. Saccade durations were defined as the interval between the eye leaving the fixation region and the eye landing on one of the two boxes centered on the object or flanker. To encourage participants to respond as fast as possible, online RT measurement were used and a message saying “TOO SLOW” was displayed if the RT of a given trial was above  $2.5*SD$  from average (the average was calculated based only on valid trials (see below)). The experiment was stopped automatically when a participant obtained 4000 valid trials (split in blocks of 64). A trial was considered valid if (1) a target was presented, (2) the participant made a valid saccade to the correct location and (3) the RT was not an outlier (limits corresponding to  $2.5*SD$ , updated online after each trial by considering all previous trials, even non-valid ones).

#### **4.3.2 Data Analysis**

During preprocessing, we removed all trials in which the saccade duration was above 70 ms, or the luminance value selected by the QUEST was outside the  $2.5*SD$  limits (across all luminance values tested). For the RT analysis, we considered only trials in which a target was present (15 out of 16 trials) and the saccade was made to the correct location. This resulted in the inclusion of 72.67% of all trials on average ( $\pm 5.62\%$  standard error of mean across subjects).

To increase the number of trials per bin, SOA values were binned in groups of 3 (resulting in a change of effective sampling frequency from 85 Hz to 28 Hz). We validated in a separate re-analysis (not detailed here) that the exact position of the bin limits did not affect any of our findings. All the results were analyzed based on the binned SOA values. Single-trial RT values were then aggregated for each condition and SOA bin, outliers were removed (values outside 2.5 SD around average), and averages computed to obtain RT time-series (average RT as a function of SOA) for each of the 4 types of sequences (OFO, OFF, FOO, FOF) and each subject.

We observed a strong negative trend in the RT time-series: early SOAs resulted in much slower RTs for most subjects. We attribute the slow RT decrease to the hazard rate although an additional forward masking effect could contribute to the early RT's (200 ms). To minimize the influence of these factors, RT time-series were de-trended using a second order polynomial (as is commonly done in most previous studies investigating oscillations of behavioral measures)

### **4.3.3 Frequency Analysis**

RT time-series were analyzed in the frequency domain using both FFT and Hilbert methods. The 28 SOA values over a one second window allowed for a Nyquist frequency of 14 Hz. The complex FFT coefficients were squared to obtain oscillatory power at each frequency (Figs 2C,D and 3C,D).

## **4.4 RESULTS**

In the current experiment we investigated these fluctuations in a target detection task in humans, directly mirroring one part of the monkey study by Kienitz et al. (Kienitz et al., 2018). We presented a first stimulus, to which a second one was added (Fig. 1). A target was then presented in either of the two objects with many possible SOA's, spanning a 1000 ms interval in 12 ms steps. The participant was instructed to make a saccade to the target as fast as possible. We analyzed the reaction times as a function of the variable SOA. The dense temporal sampling of the target interval allowed us to quantify these behavioral modulations using frequency decomposition methods (Fourier and Hilbert transforms).

### **4.4.1 Fluctuations in RT time-series**

To investigate rhythmic fluctuations in behavior, we performed a frequency analysis on the RT time-series for each condition separately. Although the average time courses (Fig. 2A, B) do not show evident oscillations (possibly due to small differences in phase or frequency across subjects), the power spectra revealed a dominant oscillation at around 6 Hz for all conditions (Fig. 2C, D). To test if the observed peak at this specific frequency could be due to chance, we created 2000 surrogates by shuffling the 28 SOA-bin labels within subjects and within conditions and recalculating the power spectra. P-values were computed as the percentile of the mean power values within the bootstrapping distribution. This allowed us to test the null-hypothesis that all frequencies share similar power content. Both main data as well as the surrogates were de-trended. For all four conditions the observed spectral peak at 6



Hz proved to be significantly higher compared to the surrogate distribution (Fig. 2C, D; FOO:  $p = 0.0045$ , OFO:  $p = 0.0012$ , OFF:  $p < 0.0005$ , FOF:  $p = 0.0255$ ). We observed additional significant peaks at 11 Hz (FOO:  $p = 0.043$ ), 7 Hz (FOF:  $p = 0.0185$ ), 14 Hz (OFF:  $p = 0.0095$ ) as well as 1 Hz (OFF:  $p = 0.003$ ; FOF:  $p = 0.021$ ). As these additional effects were not consistent across the four conditions, we did not explore them further. The 6 Hz spectral peak, however, was present in all four conditions. Notably, the likelihood of all four conditions showing a significant peak at the same frequency would be extremely small under the null hypothesis: if the probability of one given frequency exceeding the statistical threshold is 0.05, then the likelihood of this event happening 4 successive times at the same frequency is  $14$  (frequencies)  $\times$   $0.054$  (conditions) =  $0.0000875$ , i.e.,  $p < 0.0001$ . We found no significant effect of stimulus sequence on the number of saccades during catch trials.

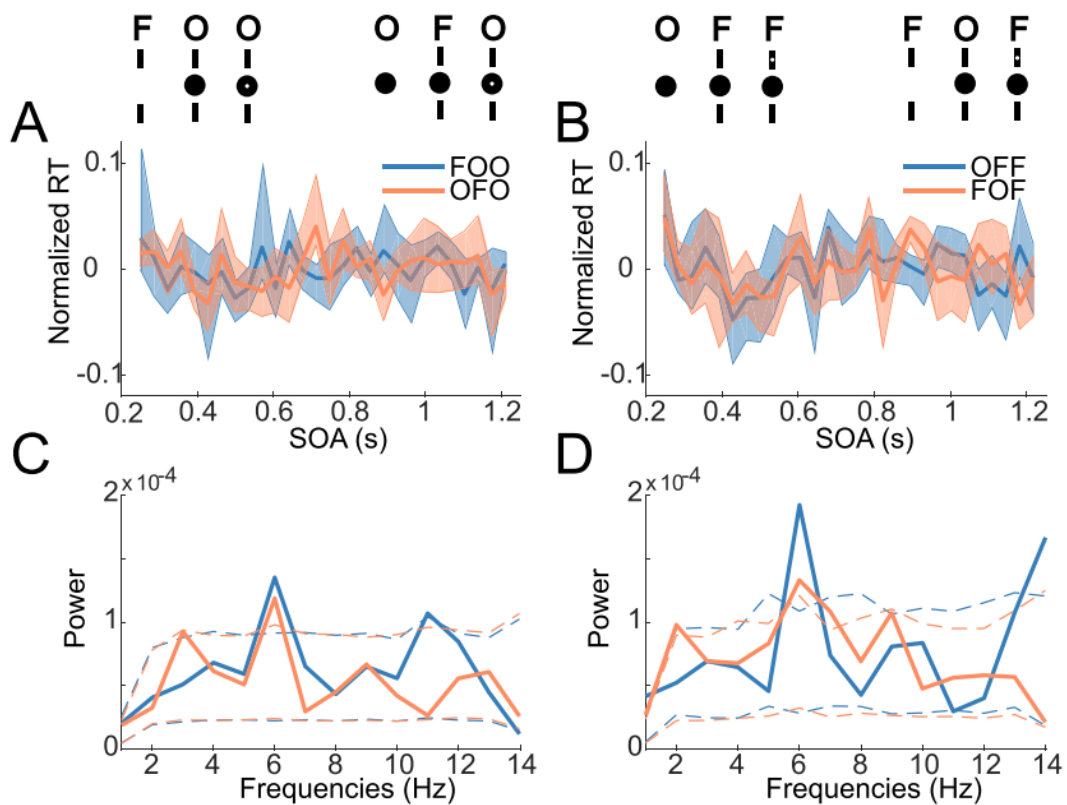


Figure 2. Analysis of RT fluctuations for each condition. The four conditions are illustrated at the top for reference; they vary based on the order of presentation of the stimuli (Object-first or Flanker-first) as well as the site of target presentation (Object, Flanker). (A, B) RT time-series averaged across subjects (error bars indicate bootstrapped 95% CI) for each of the four conditions, grouped according to the site of target presentation (Object in A, Flanker in B). (C, D) Average power spectrum across subjects for each of the four conditions (grouped as previously). Dotted lines indicate the

bootstrapped 95% confidence interval under the null hypothesis that all frequencies have similar power. We observed a significant peak at 6 Hz for all four sequence types.

#### 4.4.2 Opposed sequences reveal anti-phasic RT fluctuations

The spectral analysis illustrated in Fig. 2 reveals that all 4 experimental conditions display significant 6 Hz oscillations in behavioral RT time courses. Do all 4 oscillations share the same phase, or does the phase differ depending on task factors? In order to analyze potential differences in the phase of the observed oscillations, we subtracted the RT time-series of conditions that had identical target locations. These conditions differed only in the history of object and flanker presentation times. Stimulus competition normally begins when the second object appears on the screen; according to the idea of rhythmic attention sampling, this competition would initially be biased towards the second object (the last one to appear), then attention would move on to sample the first, and rhythmically alternate between them on subsequent cycles (Fiebelkorn et al., 2011; Rollenhagen & Olson, 2005; VanRullen, 2013; VanRullen & Dubois, 2011). In other words, the phase of attention sampling (and thus the phase of behavioral RT oscillations, for a fixed target location) should be opposite for Object-first and Flanker-first sequences. Such an anti-phasic relationship should be visible as an elevated peak in the power spectrum of the difference in the RT time-series. Conversely, if oscillations for the two conditions shared the same phase, the subtraction should reduce the amplitude of the 6 Hz spectral peak.

As expected according to the rhythmic attention sampling idea, we observed an enhanced spectral peak at 6 Hz for both time-course subtractions (Fig. 3), indicating that the experimental conditions shared a frequency-specific oscillatory component, however with opposite phase for the two stimulation sequences. For both comparisons, the amplitude of the 6 Hz peak in the subtraction was higher than that measured in either of the original signals (compare values in Fig. 3A, B with those in Fig. 2C, D), which is compatible with an anti-phase, but not an in-phase relation between the stimulation sequences. The significance of the 6 Hz peak (FOO minus OFO:  $p < 0.001$ , OFF minus FOF:  $p < 0.001$ , Bonferroni corrected) was confirmed by comparing it to a null hypothesis distribution, calculated by randomizing a subset of the target SOAs within subjects and between opposing sequences (FOO and OFO, OFF and FOF) 2000 times. The number of reaction times that were taken as the subset was determined by the total number of reaction times recorded for that specific SOA during the

experiment, resulting in an identical number of trials per SOA in the original and randomized datasets. This method revealed an additional significant peak at 3 Hz ( $p < 0.001$ ) for the FOO minus OFO condition, however markedly smaller than the peaks at 6 Hz.

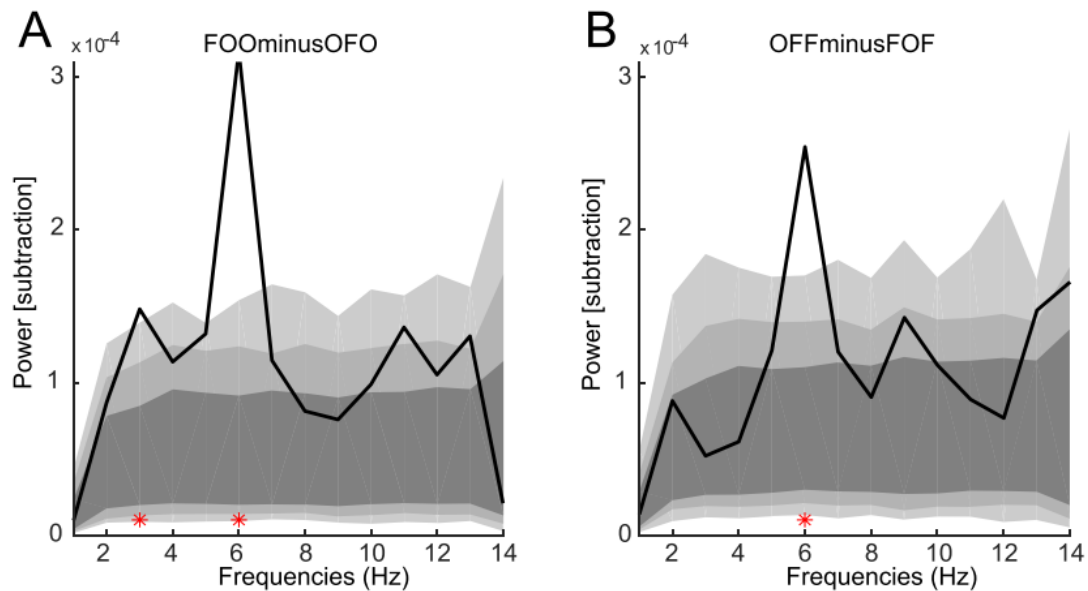


Figure 3. Frequency Analysis of the difference in RT time series between conditions with identical target location (FOO vs. OFO in A, OFF vs. FOF in B). Light grey areas indicate the bootstrapped 99.9% CI (99% in darker grey, 95% CI in darkest grey). Red dots indicate frequencies with significantly higher power compared to a null hypothesis distribution calculated by randomizing the SOAs within opposing sequences.

## 4.5 DISCUSSION

Our experimental paradigm was based on previous primate studies that investigated the oscillatory responses to competing stimuli (Rollenhagen & Olson, 2005; Kienitz et al., 2018). The paradigms used in these previous papers were as follows: A sequence of three stimuli was presented, Object followed by Flanker, or vice versa, followed by a target that could appear either in the Object or in the Flanker (Fig. 1). Firing responses of V4 and IT neurons selective for either of the stimuli (Object, Flanker) were recorded. The authors observed that firing rates oscillated at 4-5 Hz following stimulus presentation. Furthermore, if the neuron's "preferred" stimulus was presented second, the same oscillation was observed but in anti-phase (compared to the condition with "preferred" stimulus first). These oscillations were present but significantly weaker when only one stimulus was presented (even when it was the neuron's preferred stimulus). Finally, the Kienitz et al. (2018) study further revealed direct

behavioral correlates of these oscillations, whereby rhythmic fluctuations of saccadic reaction times accompanied the firing rate oscillations. Altogether, these findings imply that the competition between visual neurons coding for distinct neighboring objects in the visual scene is modulated at around 4-5 Hz. The authors suggested that this modulation of competition might reflect a rhythmic attentional sampling mechanism, initiated by the sequential presentation of the two competing objects.

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An increasing number of studies have reported rhythmic fluctuations in perceptual performance. In the specific case of spatial attention, when multiple objects are presented on the screen, attention seems to alternately switch between the attended objects (Dugué et al., 2011, 2016; Dugué, McLelland, et al., 2015; Fiebelkorn et al., 2013; Landau & Fries, 2012; Macdonald et al., 2014; VanRullen, 2013; VanRullen et al., 2007). This alternation is assumed to be instantiated by a sequential attentional sampling process that leads to behavioral oscillations that are out of phase for the different attentional targets. A crucial element in the investigation of attentional processes is the relationship between behavior and neuronal processes. While it is difficult to investigate theta oscillations measured from single

cells in humans, there are a number of electrophysiological EEG/MEG studies successfully relating theta rhythmicity in the human brain to attention. Busch and VanRullen (Busch & VanRullen, 2010) investigated pre-stimulus oscillatory activity, by contrasting trials in which target detection was successful to unsuccessful trials. They found that the pre-stimulus phase in the theta band was predictive of stimulus detection, however only for attended stimuli, indicating that attentional sampling operates at around 7 Hz. Landau et al. (Landau et al., 2015) reported that pre-target gamma-band activity was modulated at 4 Hz when two stimuli were presented on the screen. Furthermore this modulation was predictive of task performance and provided important evidence for the hypothesis that the presentation of a relevant stimulus resets an ongoing attentional mechanism. These findings are especially relevant in the context of our study, since it is based on the assumption that the behavioral performance fluctuations are a result of a phase reset of an ongoing attentional oscillation by the stimulus onsets in the display sequence.

The above mentioned studies indicate that the pre-stimulus phase of theta oscillations can predict performance (Busch & VanRullen, 2010; Dugué, McLelland, et al., 2015; Hanslmayr et al., 2013). This raises the question of how ongoing and evoked (phase-reset) theta oscillations interact to influence task performance. Insight can be provided by the findings of Dugue et al. (Dugu'e et al., 2015): In their EEG experiment on visual search they observed pre-stimulus theta phase opposition between successful and unsuccessful search trials, together with stronger post-stimulus theta phase-locking as well as higher post-stimulus theta amplitude for successful compared to unsuccessful trials. This suggests that the pre-stimulus theta phase was indicative of both the post-stimulus EEG signal and of task performance; to account for this relation between pre- and post-stimulus oscillations, they assumed that the presentation of a stimulus only leads to a partial phase reset of ongoing theta oscillations.

While our paradigm, closely resembling Kienitz et al. (Kienitz et al., 2018), was mostly concerned with covert attention, it remains unclear how our findings would translate to overt attention. Would we observe similar periodic fluctuations when observers are free to explore the visual scene? Interestingly eye movements occur approximately every 200-300 ms even in absence of a task, i.e. during free exploration (Otero-Millan et al., 2008). This rhythmicity is preserved if a target detection task is performed, in which participants can explore the visual scene freely (Hogendoorn, 2016). A crucial piece of evidence in the study by

Hogendoorn is the fact that the phase of the behavioral oscillation did not change as a result of the saccade, indicating that the saccades may have been executed as part of an underlying attentional oscillation. One interpretation of these results is thus that a unique theta-rhythmic sampling mechanism could underlie both overt and covert forms of spatial attention.

Kienitz et al. (Kienitz et al., 2018) suggested that center surround interactions between neighboring stimuli in V4 might facilitate attentional stimulus selection. The fact that the excitatory center of V4-neurons found by Kienitz et al. (2018) showed maximal responses for stimuli measuring 2° of visual angle certainly restricts the conclusions that can be drawn in terms of larger objects or of wider distances. It is thus an open question how the brain could instantiate attentional selection among objects that are further spread across the visual field. Would this interaction still arise in V4, or in hierarchically higher areas with larger receptive field sizes spanning larger distances? It has been shown that similar behavioral competition can result in anti-phase theta-band rhythmic attentional sampling between two stimuli presented in opposite hemi fields (Fiebelkorn et al., 2013; Landau & Fries, 2012; VanRullen et al., 2007), and that corresponding neural correlates can be observed in visual cortex (based on MEG source reconstruction) (Landau et al., 2015). The precise neural source of this large-scale rhythmic attentional sampling, however, remains to be determined by direct electrophysiological experiments.

Our paradigm used 3 stimuli (one object and 2 flankers) of which 2 (the object and one flanker) were behavioral significant. It would therefore be highly interesting to investigate how attention behaves if the number of potential target positions is extended beyond 2. Similar experiments have been conducted by Holcombe and Chen (Holcombe & Chen, 2013) as well as Macdonald et al. (Macdonald et al., 2014). They suggest an attentional sampling mechanism with limited capacity, such that multiple objects are sampled less and less frequently with increasing numbers of objects. We intend to investigate this matter in future experiments.

In conclusion we provided new evidence for a sequential attentional sampling mechanism in the theta range (6 Hz) in humans. Our findings support those of Kienitz et al. (Kienitz et al., 2018), and demonstrate similar behavioral patterns in monkeys and humans. Our conclusions provide further insight into how the brain resolves potential competition by using attentional mechanisms to rhythmically select relevant stimuli.

## **Switching roles: oscillations as a communicator in conscious perception**

Using a similar paradigm as Kienitz et al. (2018), the current study reveals theta rhythm in human saccadic RT, confirming that attentional sampling might be generated by visual competitions. Thus far, we have discussed the oscillations in visual perception and attention. The underlying alpha and theta activity require ensembles of neurons synchronizing at the same frequency, hence leading to perceptual sampling. Synchronization of neurons can facilitate neuronal communication (Fries, 2005, 2015). A more considerable amount of local and inter-area communication has been found in conscious perception compared to unconscious perception (Melloni et al., 2007). Can we still observe perceptual echoes, a potential driver of visual sampling, when subjects are not consciously perceiving the stimuli? In the next chapter, we will employ binocular rivalry to answer this question.

## 5 CHAPTER 5. CONSCIOUS PERCEPTION MODULATES PERCEPTUAL ECHOES

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This chapter contains the original manuscript that appeared as: Canhuang, L., VanRullen, R., & Alamia, A. (2020). Conscious perception modulates perceptual echoes. *bioRxiv*.

### 5.1 ABSTRACT

Alpha rhythms (~10Hz) in the human brain are classically associated with idling activities, being predominantly observed during quiet restfulness with closed eyes. However, recent studies demonstrated that alpha (~10Hz) rhythms can directly relate to visual stimulation, resulting in oscillations which can last for as long as one second. This alpha reverberation, dubbed Perceptual Echoes (PE), suggests that the visual system actively samples and processes visual information within the alpha-band frequency. Although PE have been linked to various visual functions, their underlying mechanisms and functional role are not completely understood. In the current study, we investigated whether conscious perception modulates the generation and the amplitude of PE. Specifically, we displayed two colored Gabor patches with different orientations on opposite sides of the screen, and using a set of dichoptic mirrors we induced a binocular rivalry between the two stimuli. We asked participants to continuously report which one of two Gabor patches they consciously perceived, while recording their EEG signals. Importantly, the luminance of each patch fluctuated randomly over time, generating random sequences from which we estimated two impulse-response functions (IRFs) reflecting the perceptual echoes generated by the perceived (dominant) and non-perceived (suppressed) stimulus respectively. We found that the alpha power of the PE generated by the consciously perceived stimulus was comparable with that of the PE generated during monocular vision (control condition), and significantly higher than the PE induced by the suppressed stimulus. Moreover, confirming previous findings, we found that all PEs propagated as a travelling wave from posterior to frontal brain regions, irrespective of conscious perception. All in all, our results demonstrate that conscious perception modulates PE, suggesting that the synchronization of neural activity plays an important role in visual sampling and conscious perception.



## 5.2 INTRODUCTION

The alpha rhythms [8-12 Hz] is the most prominent oscillation in the human brain, and the first one to be described in human electrophysiological recordings (Berger, 1933). It involves most of the cortical regions, but it is most dominant in occipital and parietal areas. Its origin can be related to different processes: some studies pointed at the closed-loop interaction between cortical and thalamic regions, the latter acting as alpha pacemakers (Bollimunta et al., 2011; Lopes da Silva et al., 1973, 1980), but recent evidence indicated uniquely cortical mechanisms as responsible for its generation (Halgren et al., 2019). Just like distinct sources can produce alpha-band rhythms, similarly these alpha band oscillations are likely to serve different functions. On the one hand, alpha oscillations have been shown to strongly but negatively correlate with task demand and increasing attention, hence their presumed involvement in inhibitory functions (Gazzaley & Nobre, 2012; Jensen & Mazaheri, 2010; Klimesch, 2012). On the other hand, alpha waves have been related to information processing, such as the temporal parsing of sensory information (Klimesch et al., 2007) or the perception of visual stimuli (VanRullen, 2016). Regarding the latter, electrophysiological recordings demonstrate that visual stimuli reverberate in visual cortical areas around 10Hz, producing what has been dubbed as perceptual echoes (VanRullen, 2016; Vanrullen & MacDonald, 2012).

Perceptual echoes (PE) are best observed by cross-correlating a non-periodic flickering stimulus, for example a disk whose luminance randomly varies over time, with the EEG signals recorded in occipital and parietal regions. The cross-correlation provides an Impulse Response Function (IRF) which describes the brain response to each stimulus transient. Such response reveals a clear oscillation in the alpha-band whose duration can last for as long as one second. A recent study ascribed the mechanisms generating the echoes to the interactions between brain regions within a predictive coding framework (Alamia & VanRullen, 2019). However, whether PE are a by-product of cortical interactions or serve some specific cognitive function remains unclear. Experimental studies demonstrated that PE are enhanced when repetitions are embedded in the visual sequence, suggesting that they could reflect a role in regularity learning (Chang et al., 2017), whereas other evidence show that attended stimuli generate larger echoes than unattended ones, suggesting that attention allocation plays a role in modulating PE amplitude (Vanrullen & MacDonald, 2012). In addition, PE have been characterized as travelling waves that propagates from occipital to

frontal regions, thus including a spatial component that may reflect the hierarchical processing of visual information along the visual system (Alamia & VanRullen, 2019; Lozano-Soldevilla & VanRullen, 2019).

All these findings indicate that PE are relevant to different functional roles in visual information processing, suggesting that they may reflect some fundamental mechanism in cortical processing. In this study we take one step further in this direction by exploring whether PE are modulated by conscious perception. In order to address this question, we tested a pool of participants within a Binocular Rivalry design, in which two different stimuli are shown separately to each eye, generating a rivalry that is resolved with the perception of only one of the two stimuli. In this experiment, a green and a red Gabor patch, respectively tilted by  $\pm 45^\circ$ , were displayed on the left and right side of the screen. We employed a dichoptic mirrors setup to project each stimulus separately to each eye. Importantly, the luminance of each stimulus varied over time in a random, non-periodic way, generating two flickering luminance sequences. Participants were instructed to continuously report which colored Gabor patch was being perceived throughout the experiment, thus defining two sequences corresponding to the dominant and suppressed stimuli. Here, we aimed at computing the echoes by cross-correlating the EEG recordings with each sequence, in order to assess whether the generation and amplitude of PE is modulated by conscious perception.

### **5.3 METHODS**

Participants and statistical power analysis. We estimated the number of participants via a statistical power analysis based on previously published data investigating PE in binocular vision (Brüers & VanRullen, 2017). We determined the effect size as equal to 1.7, computed as the mean alpha power difference between the actual echoes and the ones obtained after shuffling the temporal sequences (i.e., surrogate echoes, see below). Setting the power level to 0.90 and the statistical threshold at 0.05, that effect size requires a number of participants equal to 4. However, considering that we based our effect size estimates on binocular vision (i.e., both eyes fully perceiving the same stimulus), and we aimed at computing echoes in condition of monocular vision and binocular rivalry, we tripled the estimate, including a final number of 12 participants (7 female, mean age 26, SE=0.9). All participants had normal or corrected-to-normal vision and gave written consent before the first session of the experiment, in accordance with the Declaration of Helsinki. This study was carried out in accordance with the guidelines for research at the “Centre de Recherche Cerveau et

Cognition” and the protocol was approved by the committee “Comité de protection des Personnes Sud Méditerranée 1” (ethics approval number N° 2016-A01937-44).

**Experimental procedure.** Each participant completed two sessions on two different days. One session consisted of 10 blocks, each composed of 10 trials. A trial lasted for 30s each. The design consisted of two conditions: in half of the blocks, including the first one, participants performed Binocular Rivalry (BR) trials, whereas on every other block they performed Physical Alternation (PA) ones. In BR trials, two Gabor patches, each encircled by a square frame (visual angle of the patch: 4 degrees, visual angle of the frame: 4.5 degrees), were shown separately to each participant’s eyes. Patches were different in color and inclination, either red or green,  $\pm 45^\circ$ , the color-inclination associations were kept constant throughout each experiment, but randomized between participants. The color and orientation of the stimulus served mainly to help identify the perceived stimulus and thereby facilitate perceptual reports from the participants, however the main experimental variable was the stimulus luminance. The luminance of the Gabor patches changed randomly over time, and this random sequence was designed to have the same spectral power at every frequency (fig.1A). Importantly, the range in the two colors luminance was carefully calibrated and equalized to avoid any perceptual biases. The physical position on the screen of the two Gabor patches was switched on each trial (i.e., either the left or the right side). The task was to report which patch was perceived by moving a joystick either to the left or the right (e.g., one participant instructions were to lean the joystick to the left when green was perceived and to the right when red was perceived). The color-side associations were pseudorandomized between participants. Importantly, participants were encouraged to account continuously for their visual perception, reporting intermediate joystick positions when the perception of both patches overlapped. Each trial started by pressing a joystick button, and participants were encouraged to rest between trials. Each BR block was followed by a PA one. In PA blocks only one Gabor patch was displayed at a time, replaying the exact sequence of Gabor patches reported in the previous BR block. The task’s instructions were the same, with the exception that participants were no longer performing a binocular rivalry task. The goal of such replays was to estimate precisely the reaction time in each trial, and correctly segment the actual perception in the BR blocks before computing the echoes. Moreover, PA blocks served as a control condition to assess PE in condition of monocular vision, without rivalry.

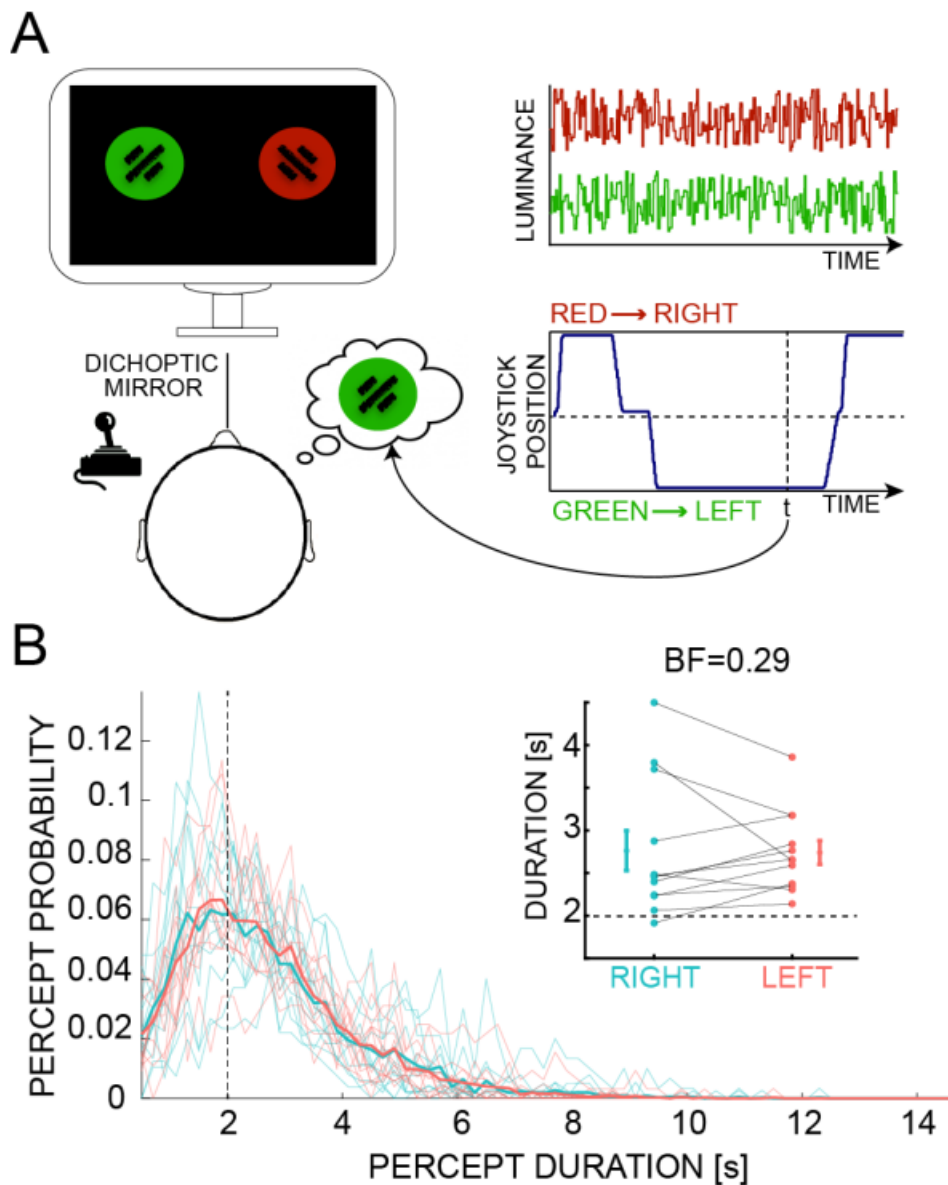


Figure 1 – Experimental design. A) Participants stared at the screen through a set of dichoptic mirrors that projected the left and right side of the screen to the left and right eye respectively. Two stimuli, placed on the two sides of the screen, were Gabor patches of different color and orientation, either red or green with a  $\pm 45^\circ$  angle. Participants reported which patch they perceived by moving a joystick to either side, each one associated to a stimulus (pseudorandomly between participants, consistent across blocks and sessions). B) Distribution of percept duration in seconds. On average, participants perceived one or the other stimulus for 2 seconds. We discarded percepts below this threshold in all analyses. Overall there was no difference in the duration of stimuli placed to the left and to the right (Bayesian t-test,  $BF_{10} = 0.29$ , error=0.021%).

EEG recording and analysis. Recording and Preprocessing. EEG signals were recorded using a 64-channel active BioSemi EEG system (1024Hz sampling rate), and 3 additional ocular electrodes were used. The preprocessing was performed in EEGLab (Delorme & Makeig, 2004) and consisted first in down-sampling the data to 160Hz followed by a high-pass (>1Hz) and a notch (47-53Hz) filter. Data were then average re-referenced and segmented from 200ms before trial beginning until its end (-200ms to 30,000ms). Each epoch was then baseline corrected by subtracting the average between -200ms and stimulus onset.

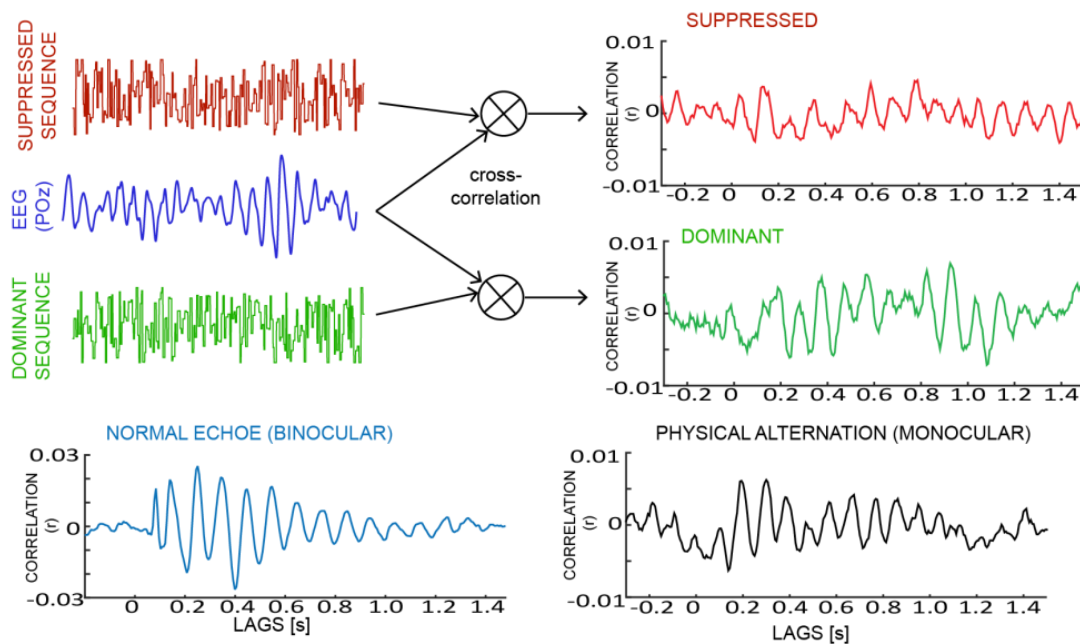


Figure 2 – Computing perceptual echoes. Two random (independent) temporal sequences of luminance were displayed on opposite sides of the screen. Given the dichoptic mirror setup, each sequence was perceived by one eye only, producing a binocular rivalry that was resolved with one perceived sequence (i.e., dominant, in green) and one non-perceived (i.e., suppressed, in red). We computed PE by cross-correlating each sequence and the corresponding EEG signal (POz electrode), revealing a reverberation in the alpha-band interval. The same procedure was used to compute the PE in the Physical Alternation condition (in black). The bottom-left panel shows for comparison a PE computed in case of binocular vision (Brüers & VanRullen, 2018). Note the difference in the y-axis.

**Perceptual Echoes.** PE are computed by cross-correlating the luminance sequences with the corresponding EEG signal. As reported in previous studies, PE are stronger in occipital and parietal regions (VanRullen, 2016; Vanrullen & MacDonald, 2012), hence we focused our analysis on signals recorded in POz (note that similar results are obtained when

using the electrodes Oz and Pz). First, the reaction time (RT) for each response was estimated from the PA condition, as we knew the exact time when the stimuli were presented to the subjects. We used these RT estimates to infer the exact timing of the perceptual switch during the BR condition, that is we shifted backward the responses in BR to account for the reaction times. Next, we segmented the EEG signals and the corresponding sequences according to participants' perceptions. In order to identify the temporal segments in which participants reported a full perception (either left or right), we normalized joystick responses between -1 (left) and 1 (right), and we included all the sequences in which the response was above a threshold set to  $\pm 0.95$  and longer than 2 seconds to ensure the sequences were long enough for the reliable estimation of PE (figure 1B). In BR blocks, for each segment we cross-correlated the EEG signal with the sequence of the perceived patch (i.e., dominant) and the non-perceived patch (i.e., suppressed). In PA blocks, we crosscorrelated the EEG signal with the one sequence shown. In both conditions, the crosscorrelation was computed on lags between -0.5 and 2 seconds. The module of the PE spectra was computed with a Fast Fourier transform over the delays between 0.25 and 1 second. From each spectra we extracted the average power in the alpha-band [8-12Hz]. To estimate a baseline for comparison, we computed the same power spectra in surrogate echoes, obtained by cross-correlating the EEG signals with the luminance sequences after having shuffled their temporal order. Lastly, we compared the amount of alpha power in the echoes between conditions (dominant, suppressed and physical alternation) by means of a Bayesian ANOVA having CONDITION as a fixed factor and subject as a random term. For dependent variable we considered the amount of alpha power computed in decibel [dB] as:

$$echoes [dB] = 10 * \log_{10} \left( \frac{\textit{alpha power}}{\textit{surrogate alpha power}} \right).$$

Regarding the time-frequency analysis we computed the power-spectra using a wavelet transformation (1-40 Hz, in log-space frequency steps with 1-20 cycles) of each IRF (i.e., the result of cross-correlating each luminance sequence and the temporally-aligned EEG signal). We applied a baseline correction by subtracting the average activity 200 ms prior to 0 lags, and we extracted the mean value in the alpha range [8-12Hz] in the time-window between 250ms and 850ms. As previously, we computed a Bayesian ANOVA to compare the alpha power spectra between each condition.

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**Travelling waves analysis.** We eventually assessed how PE propagate through cortex as a travelling wave. As in our previous studies (Alamia & VanRullen, 2019; Pang et al., 2020) we computed the echoes in seven midline electrodes (Oz, POz, Pz, CPz, Cz, FCz, Fz), and we created 2D maps by stacking signals from those electrodes (see figure 4A). From the 2D map we computed a 2D-FFT, in which the power of the upper left quadrant represents the amount of waves travelling in a forward direction (FW - from occipital to frontal electrodes) whereas the lower left quadrant quantifies the amount of waves travelling backward (BW - from frontal to occipital). Note that the same values can be found in the right quadrants, since the 2D-FFT is symmetric around the origin. Since we investigated the propagation of the alpha-band echoes, we extracted the maximum values within the alpha range [8-12Hz]. In order to quantify the amount of waves above chance level, we computed a surrogate distribution of values by shuffling the electrodes order before quantifying the 2D-FFT (obtaining FW<sub>ss</sub> and BW<sub>ss</sub> for forward and backward waves respectively). Similarly to the previous analyses, we computed the amount of waves in decibel [dB] for FW and BW waves according to the following formula:

$$FW \text{ waves [dB]} = 10 * \log_{10} \left( \frac{FW}{FW_{ss}} \right); \quad BW \text{ waves [dB]} = 10 * \log_{10} \left( \frac{BW}{BW_{ss}} \right).$$

**Statistical analyses.** All statistical tests were performed within the Bayesian framework, assessing the likelihood of a model given the data. This analysis produces a Bayes Factor (BF), which quantifies the ratio between models testing the alternative over the null hypothesis. Throughout the paper, all BFs comply with this convention – i.e., the probability of the alternative hypothesis over the null hypothesis, usually indicated as BF10. In practice, a large BF ( $\sim$ BF>3) provides evidence in favor of the alternative hypothesis, whereas low BF ( $\sim$ BF<0.3) suggests a lack of effect (Bernardo & Smith, 2009; Masson, 2011). All analyses were performed in JASP (Love et al., 2015; Team, 2018).

## 5.4 RESULTS

**Echoes.** The main goal of this study was to determine whether PE are influenced by conscious perception. First, we estimated the averaged alpha-band power of the PE generated by the dominant and suppressed stimuli, along with those measured during the physical alternation (PA) task. Each PE was obtained by crosscorrelating the EEG recording (POz electrode) with the corresponding luminance sequence (Fig 2). In order to quantify the power in the alpha range in each condition (figure 3A) we computed the corresponding surrogate values after shuffling the temporal order of the sequence, thus expressing the PE alpha amplitude as a ratio measured in dB (see Methods for details). The graph in figure 3B reveals a significant difference between conditions, as confirmed by a Bayesian ANOVA (CONDITION factor:  $BF_{10} = 9.442$ , error=0.411%). A post-hoc Bayesian t-test comparison confirms a significant difference between dominant and suppressed echoes ( $BF_{10} = 23.926$ , error < 0.001%). Moreover, echoes generated in the PA conditions were larger than the one generated by the suppressed sequence ( $BF_{10} = 3.276$ , error < 0.001%), but we observed no difference between PE generated by the dominant sequence and in the PA conditions ( $BF_{10} = 0.159$ , error < 0.001%). Interestingly though, both dominant and suppressed echoes proved to be significantly larger than zero (Bayesian one sample t-test, both dominant and suppressed  $BF_{10} \gg 100$ , error < 0.001%), suggesting that PE can be elicited also without conscious perception. Not surprisingly, we also found significant echoes in the Physical Alternation conditions, i.e. when only one Gabor was displayed ( $BF_{10} \gg 100$ , error < 0.001%), confirming the results of a recent study (Schwenk et al., 2020) showing that PE, although strongly reduced, can still be observed in conditions of monocular vision.

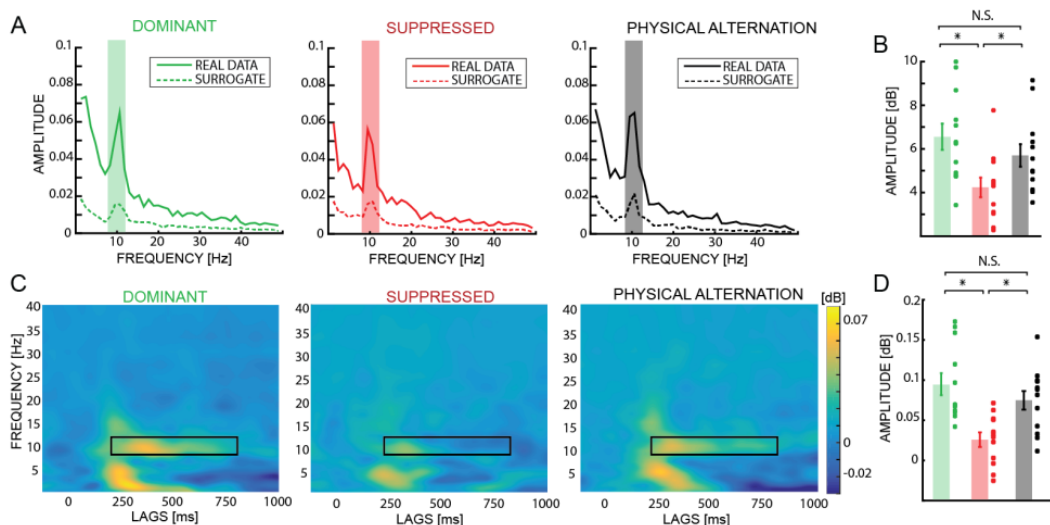




Figure 3 –Echoes and time-frequency results. A) The figure shows the power spectra of the PE obtained in the dominant (green), suppressed (red) and PA (black) condition. The dashed line is the spectra obtained in the surrogate echoes, i.e. computed after having shuffle the temporal order of the luminance sequence. We focused the analysis in the alpha range (shaded in each panel). B) The difference in the power spectra in the alpha range expressed in dB. The plot reveals a significant difference between suppressed and both dominant and PA conditions, revealing that conscious perception increases the amplitude of the PE. However, all the conditions have PE larger than chance. C) Time-frequency spectrogram for each condition (color-code as in A). Dominant and PA show a larger amplitude than in suppressed, as confirmed by the plot in D) comparing the amplitude in the time-frequency region of interest (black box) in each condition.

**Time-Frequency.** In order to assess the temporal dynamics of the PE in each condition (i.e., dominant, suppressed and physical alternation) we performed a timefrequency analysis on the echoes. In line with our previous results, figure 3C reveals a stronger effect in the alpha band in the dominant and PA conditions compared to the suppressed condition. We confirmed this result by computing per each subject the average power within the temporal window [250ms – 850ms], in the alpha range [8Hz – 12Hz]. As in the previous analysis, a Bayesian ANOVA confirmed a significant difference between the three conditions (CONDITION factor:  $BF_{10} = 54.22$ , error=0.011%), as well as the post-hoc Bayesian t-test which positively confirms a difference between dominant and suppressed ( $BF_{10} \gg 100$ , error < 0.001%) and PA and suppressed ( $BF_{10} = 13.15$ , error < 0.001%), with mild evidence in favor of no difference between dominant and PA ( $BF_{10} = 0.414$ , error = 0.022%). Moreover, all the conditions proved significantly larger than zero, even though much larger Bayes Factors were observed in the dominant and PA conditions (dominant and PA:  $BF_{10} \gg 100$ , error < 0.001%; suppressed  $BF_{10} = 5.769$ , error < 0.001%). Overall the time-frequency analysis confirmed the previous results, indicating that PE elicited in the dominant and PA conditions are larger than in the suppressed condition.

**Travelling waves.** Eventually we investigated whether PE elicited during binocular rivalry propagate through cortex as forward travelling waves (i.e., from occipital to frontal regions), as recently showed in the case of binocular vision (Alamia & VanRullen, 2019; Lozano-Soldevilla & VanRullen, 2019). We quantified the amount of forward and backward waves as shown in figure 4 obtaining for each participant a value in dB for each condition (see methods for details). Interestingly, a Bayesian ANOVA performed with factors

DIRECTION (FW and BW) and CONDITION (dominant, suppressed and PA) revealed a significant difference between FW and BW waves ( $BF_{10} = 3.963$ , error = 0.001%) but neither a difference between conditions ( $BF_{10} = 0.100$ , error = 0.007%), nor an interaction ( $BF_{10} = 0.097$ , error = 0.012%). A Bayesian t-test comparing the amount of FW waves against zero confirmed that PE propagates from occipital to frontal regions when elicited by dominant ( $BF_{10} = 6.783$ , error < 0.001%), suppressed ( $BF_{10} = 18.907$ , error < 0.001%) and monocular sequences (PA,  $BF_{10} = 3.655$ , error = 0.001%).

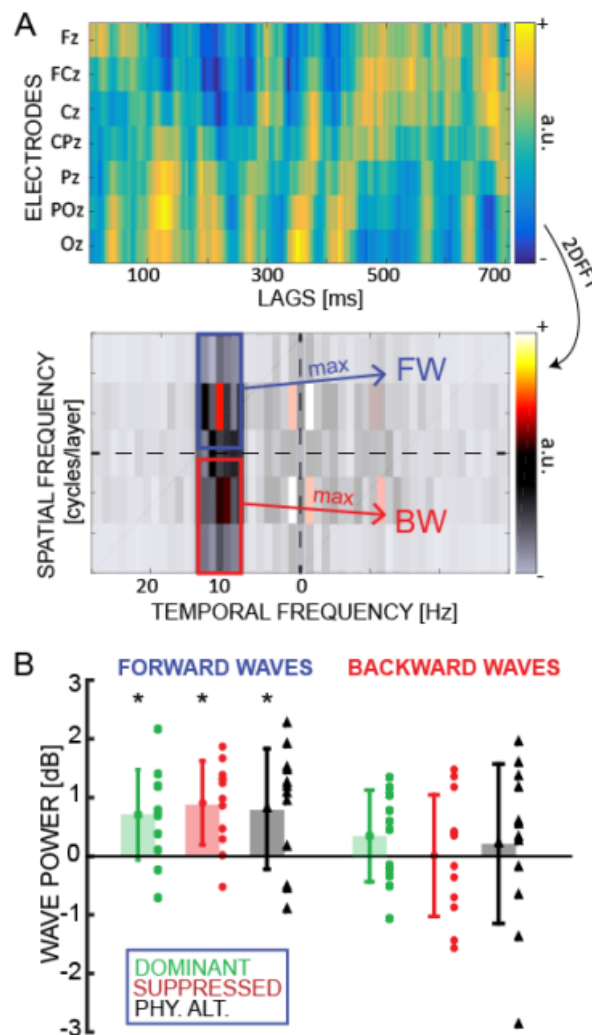


Figure 4 –Travelling waves results. A) We first obtain 2D maps stacking the PEs recorded over the 7 midline electrodes. The color code indicates the PE amplitude. From the 2DFFT we computed the amount of FW and BW waves in each condition as the maximum amplitude value in the corresponding quadrant (restricted to alpha-band frequencies). B) The results –expressed in dB, i.e. corrected using the surrogate, see methods- show that PE travel as FW waves in all conditions, irrespective of the conscious perception of the stimulus.

## 5.5 DISCUSSION

Previous studies showed that visual information reverberates in posterior brain regions in the alpha-band frequency range, as observed by cross-correlating white noise luminance sequence with EEG recordings (VanRullen, 2016; Vanrullen & MacDonald, 2012). Such reverberation, dubbed as Perceptual Echoes (PE), proved in several studies to be related to various cognitive functions, such as attention (Vanrullen & MacDonald, 2012) and statistical learning (Chang et al., 2017). In this study we investigated whether PE can be modulated by conscious visual perception using a binocular rivalry design. Our results indicate that PE can be generated by both consciously perceived and suppressed stimuli, but the former elicit larger PE than the latter, and of comparable amplitude as the PE generated during monocular vision. Moreover, we reported that the PE generated by both conscious and unconscious visual perception propagates as a travelling wave from occipital to frontal regions, possibly reflecting bottom-up processing in the visual system (Alamia & VanRullen, 2019; Lozano-Soldevilla & VanRullen, 2019; Pang et al., 2020).

Similar to the finding that PEs are enhanced by attention (Vanrullen & MacDonald, 2012), we found that PEs generated by the consciously perceived sequence (i.e., the dominant stimulus) contain larger alpha power. If on the one hand previous studies demonstrated that binocular rivalry might be modulated by attentional mechanisms (Zhang et al., 2011), on the other hand the alpha power enhancement we observed in the PE in the dominant condition is unlikely to be due to selective attentional processes, as participants were not instructed to pay attention specifically to one of the two stimuli. Yet, we can de facto assume that the attentional focus is driven to the stimulus perceived as conscious, thus increasing the PE alpha power as compared to the suppressed one. Interestingly, previous studies reported opposite effects of attention on alpha power: while attention decreases stimulus non-specific alpha power, it nonetheless increases the spectral (alpha-band) power of PE (Thut et al., 2006; VanRullen & MacDonald, 2012; Worden et al., 2000). It could be interesting then to test the hypothesis that conscious perception plays a similar role in the modulation of alpha power. One possible experimental approach would be to lateralize the suppressed and dominant stimulus, thus assessing whether conscious perception modulates the alpha power in each occipital hemisphere similarly to attention. Further experiments will shed light on this interesting hypothesis.

The enhancement of PE alpha power in the dominant condition together with the previous finding that attention enhances PE are reminiscent of the application of frequency-tagging in binocular rivalry. Previous studies revealed that both conscious perception and attention allocation increase the spectral power corresponding to the steady state visually evoked potential (SSVEP) (Ding et al., 2006; Srinivasan et al., 1999; Tononi et al., 1998). Even though SSVEP showed similar effects as PE in binocular rivalry and attention tasks, their underlying mechanisms are likely different. SSVEP is a passive brain response to a rhythmic stimulation, reflecting the spectral characteristics of the generating stimulus, whereas PEs are characterized by a clear 10 Hz oscillation without a corresponding 10Hz peak in the visual stimulus, possibly reflecting computational cortical mechanisms (Alamia & VanRullen, 2019). Despite the functional differences, it is tempting to speculate that in both SSVEP and PE, conscious perception modulates the amount of synchronized activity in brain regions: the higher alpha power in dominant PE might be associated with a larger synchronization of local neural activity, which might be akin to the increase in the power of the SSVEP related to conscious perception.

Besides their oscillatory temporal dynamics, PE elicited in conditions of binocular vision have been described in view of their spatial component, characterized as a travelling wave propagating from occipital to frontal regions (Alamia & VanRullen, 2019; Lozano-Soldevilla & VanRullen, 2019). In this study we replicate a similar pattern of results, as we observed the same amount of forward travelling waves in both dominant and suppressed conditions, as well as during the physical alternation task (i.e., monocular vision). Surprisingly, the difference in PE amplitude observed between dominant and suppressed conditions was not reflected in the waves' directional power, as waves seem to propagate from lower to higher brain regions with the same strength irrespective of conscious perception. Possibly, the relatively poor spatial resolution of EEG recordings prevents us from accurately comparing the two conditions, and different experimental techniques will be required to reveal different directional strengths in the propagation of dominant and suppressed travelling waves. However, one could speculate that PE generated by the consciously perceived sequence (i.e. dominant) propagate further in the visual hierarchy, reaching frontal regions which are supposedly involved in conscious perception (Koch et al., 2016; Miller, 2011), whereas the oscillatory waves of PE generated by the suppressed sequence vanish at an earlier stage of visual processing. Further studies will be needed to fully address this hypothesis.

Several previous studies investigated conscious perception in light of the Predictive Coding framework (Hohwy et al., 2008; Lamme, 2015; Seth et al., 2012; Weinhhammer et al., 2017). Predictive Coding (PC) is an influential scheme in cognitive neuroscience that describes the brain as a hierarchical system, in which higher regions generate predictions about the activity of lower ones, and the difference between predictions and actual activities (i.e. the prediction error) is used to update the upcoming predictions (Huang & Rao, 2011). Is it possible to combine within the same framework predictive coding, conscious perception and PE? In a previous study we demonstrated that a simple model simulating the interaction between brain regions and based on PC principles can account for the generation and propagation of PE as travelling waves (Alamia & VanRullen, 2019), under the assumption of plausible biological constraints (i.e., communication delays and time constants). Interestingly, additional experimental evidence supporting the tie between conscious perception, predictive coding and travelling waves was recently reported in another study investigating how psychedelic drugs altered travelling waves, supposedly by relaxing the weighting of top-down predictions, thereby releasing the bottom-up flow of information carried by sensory input (Alamia et al., 2020). On the other hand, other studies have characterized conscious perception within a PC framework as the consequence of prediction-error minimization (Friston, 2013; Hohwy, 2012; Hohwy et al., 2008; Strauss et al., 2015): this compelling hypothesis advocates that predictions are generated to efficiently explain and interpret the causes underlying our sensory information, thus generating our conscious perception of the world (Panichello et al., 2013). All in all, the result that PE are influenced by conscious perception –as we demonstrated in this study-, leads to the compelling speculation that Predictive Coding is pivotal in the generation of both PE and conscious experiences.

In conclusion, the current study investigated PE by employing binocular rivalry, and revealed that these are modulated by conscious perception, but consciousness is not necessary to elicit them. In addition, PE evoked by both consciously and unconsciously perceived stimuli propagate from occipital to frontal regions as a travelling wave, irrespective of the conscious modulation.

## **Communication with directionality: top-down processing in conscious perception**

We can see that there is stronger alpha power in perceptual echoes when subjects are consciously perceiving the stimuli, indicating more neurons synchronizing to allow visual sampling in conscious perception. The inter-area communication can have directions, meaning that the information is going from one location to the other. This is the main way the higher-level areas (e.g., frontal areas) and the lower-level areas (e.g., occipital areas) of the brain exchange information in complex cognitive functions such as attention (Connor et al., 2004) and consciousness (Dehaene et al., 2006). Next, we move further to discuss how the directed communication conducted by oscillations is involved in conscious perception.

## **6 CHAPTER 6. TOP-DOWN BETA AND THETA OSCILLATIONS DRIVE PERCEPTUAL SWITCHES IN BINOCULAR RIVALRY**

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This chapter contains an original manuscript in preparation: Canhuang Luo, Rufin VanRullen and Andrea Alamia. "Top-down beta and theta oscillations drive perceptual switches in binocular rivalry"

### **6.1 ABSTRACT**

The interplay between higher and lower brain areas is an essential prerequisite for conscious perception. In binocular rivalry, the resolution of ambiguous perception may occur at a particular stage in the visual pathway to the frontal cortex. Thus, the existence of a flow of information from the frontal areas to the visual areas (or vice versa) has been hypothesized. However, the mechanisms involved in the communication between frontal areas and sensory areas remained mostly unknown. Here, we investigate whether neural oscillations reflected the information flow involved in the binocular rivalry perceptual switches by performing Granger causality analysis in the EEG signals of human participants performing a binocular rivalry task. Our results revealed an increase in the top-down beta activity preceding the perceptual switches, demonstrating this frequency band's crucial role in the communication from higher to lower brain regions during conscious perception. Our study provides the first empirical evidence that oscillatory top-down processing is involved in the resolution of visual ambiguity, giving rise to conscious perception.

### **6.2 INTRODUCTION**

Several studies indicated that conscious perception arises from the communication between different brain regions (Crick & Koch, 1990; Dehaene et al., 2006; Dehaene & Changeux, 2011; Engel et al., 2001; Engel & Fries, 2016; Lamme, 2006; Newman & Baars, 1993; Tononi & Edelman, 1998; Tononi & Koch, 2008). In particular, experimental evidence suggests that conscious perception elicits neural activity involving both occipital and frontal regions, whereas unconsciously perceived visual stimuli activate only occipitotemporal areas (Dehaene et al., 2001). Similar results from a visual masking experiment (Gaillard et al.,

2009) compared masked (unconscious perceived) with unmasked (consciously perceived) stimuli, demonstrating how the latter evoked more long-range synchronization across hemispheres than the former, as well as increased feedforward activity from occipital visual areas to the frontal ones. Yet, one could ask what mechanisms support communication between different brain regions, specifically during conscious perception. Synchronization of oscillatory signals has been proposed to be responsible for this large-scale integration. Indeed, synchrony in a distributed network of neurons is affected by bottom-up and top-down influences (Engel et al., 2001; Engel & Fries, 2016). Considering that both play a crucial role in conscious perception (Dehaene et al., 2006; Grossberg, 1999; Lamme, 2006; Lamme & Roelfsema, 2000), we investigated whether we could associate each component to a different oscillatory band, contrasting ambiguous perception and unambiguous perception in a binocular rivalry design. In binocular rivalry, visual ambiguity arises when each eye views a different image. At any given moment, the two images' representations compete to gain access to visual consciousness, leading to one dominant and one suppressed percept, which alternate every a few seconds (Levelt, 1965). At which hierarchical level the brain resolves such rivalry remains debated in the literature. Some evidence shows that the lower levels of the visual pathway settle the rivalry (Blake, 1989; Polonsky et al., 2000; Wunderlich et al., 2005). In contrast, other studies point at the higher regions as responsible for determining what's consciously perceived. Lastly, some studies investigated specifically the information flow between areas, suggesting that top-down influences are responsible for settling the rivalry, supposedly influencing low-level regions (Dijkstra et al., 2016).

All in all, how different oscillatory components relate to the information flow in binocular rivalry remains unclear. Here, we aimed at investigating the oscillatory components involved in the information integration between the high-level and low-level regions in resolving visual ambiguity during binocular rivalry, under the assumption that these reflect the top-down and bottom-up communication between brain regions. We analyzed the EEG signals of human participants performing a binocular rivalry task by achieving spectral Granger causality analyses. We were able to identify top-down beta-band oscillatory components preceding the switch in perception, suggesting their crucial role in conscious perception.



## **6.3 METHODS**

### **6.3.1 Participants**

19 subjects (10 males, all right-handed, age range 20~32, mean age 25.84 ( $\pm$ SE 0.7184)) with normal or corrected-to-normal vision participated in the experiments after giving written informed consent, in accordance with the Declaration of Helsinki. Of the 19 subjects, 12 subjects attended a different set of stimuli (see below), and their data were analyzed in a separate and independent study (Luo et al., 2020), which investigated a different scientific question using other analytical methods. This study complies with the guidelines for research at the “Centre de Recherche Cerveau et Cognition,” and the protocol was approved by the committee “Comité de protection des Personnes Sud Méditerranéen” (ethics approval number N° 2016-A01937-44).

### **6.3.2 Stimuli and presentation**

Throughout the experiment, participants attended two Gabor patches. Each one was encircled in a white square frame (visual angle of the patch: 4 degrees, visual angle of the frame: 4.5 degrees) and presented on the screen’s left and right side. Each patch had a different color (either green or red) and orientations ( $\pm 45^\circ$ ). A fixation dot was presented under each frame, and the two patches were projected to each eye separately through a system of dichoptic mirrors. The luminance of the green and red colors was calibrated to have the same luminance to prevent potential perceptual bias. For 12 of the 19 participants, the stimuli’ luminance was randomized over time following white-noise sequences. The other 7 subjects performed a task in which the stimuli’ luminance was kept constant through all the experiment. Stimuli were presented using the Psychtoolbox package for Matlab (Kleiner et al., 2007).

The experiment was composed of 20 blocks of 10 trials, each one lasting 30s. Each participant performed two sessions with the same number of blocks on two different days. Half of the blocks were binocular rivalry (BR) blocks in each session, and the other half was physical alternation (PA) ones. PA blocks served as a control condition since only one patch was presented at any moment, thus preventing visual rivalry.

Each session started with a BR block in which two Gabor patches with different color-inclination associations were presented. The color-inclination associations (green/45° and red/-45°, or vice versa) were consistent throughout the experiment and randomized across subjects. Additionally, each patch's locations (e.g., green/45°) were alternated on every trial to prevent the association between one stimulus and the dominant eye.

The subjects were instructed to report which patch they perceived by leaning a joystick to the left or right. The response-patch associations (i.e., left or right position when perceiving one or the other patch) were counterbalanced across subjects. Participants were also encouraged to report their continuous perception changes and lean the joystick to intermediate positions when seeing the two patches fusing. Each BR block was followed by a PA block, in which stimuli were replayed monocularly according to subjects' behavioral responses in the preceding BR block. Importantly, given that in PA blocks we replayed the same sequences (both luminance and color/orientation) as the one reported by the participants in the past block, we were able to estimate the subject's response time (RT), since we know precisely when the stimuli were presented, and when participants initiated the joystick movement. Such an evaluation of the RT was further used to estimate the actual perceptual switch timing.

In each block, subjects pressed a joystick button to start each trial, and they were instructed to fixate the fixation dot throughout the task. Each subject completed two BR blocks as training before the beginning of the experiment to familiarize them with the task and the mirrors dichoptic system.

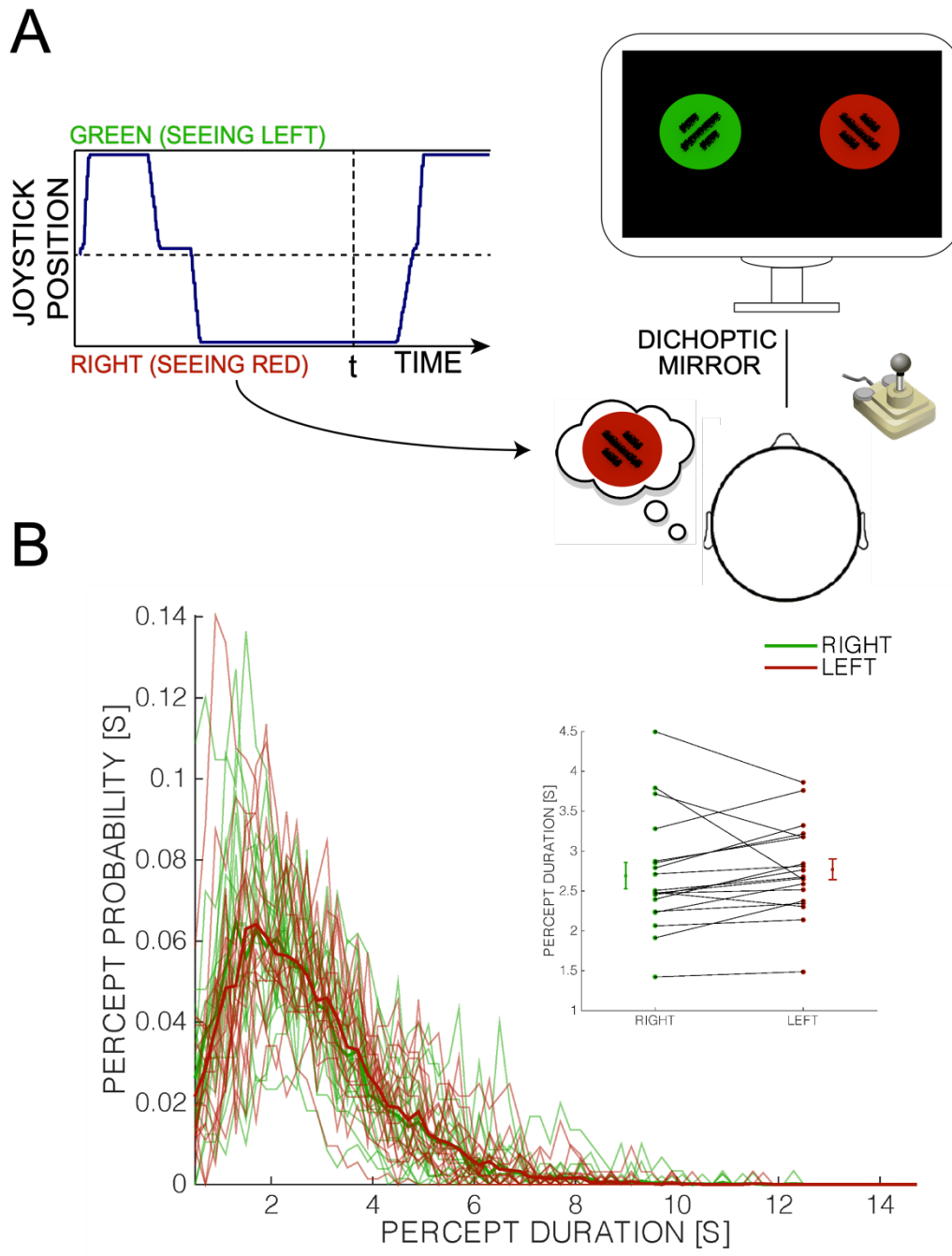


Figure 1, A) task procedure. Two Gabor patches were presented to the subjects' two eyes (on the right). Subjects used a joystick to indicate which patch he/she was perceiving. Subjects' response was recorded as time series of joystick positions (on the left). In this example, the subject was perceiving the red Gabor, and he/she leaned the joystick to the right. B) statistical description of the subjects' responses. Left, the percept probability as a function of percept duration for all the subjects. Right, the inset is the average percept duration of the left image and the right. The two durations are not significantly different.

### 6.3.3 EEG acquisition and analysis

*Acquisition and pre-processing.* Subjects were seated in a dim room while EEG signals were recorded at a sampling rate of 1024 Hz via a 64 channel Biosemi system. EOG was monitored with three extra electrodes. EEG signals were pre-processed in MATLAB (MathWorks) using EEGLab (Delorme & Makeig, 2004) and additional customized scripts. EEG data from each channel were high-pass filtered at 1 Hz before being downsampled to 160 Hz, and then notch filtered at 47~53 Hz. We then applied an average re-referenced before segmenting in epochs from -200ms to 30000ms around the stimulus onset (i.e., beginning of each trial). We finally applied a baseline correction by subtracting the mean signal between -200ms and 0ms before stimulus onset

*Time-frequency analysis.* We computed time-frequency power spectra using a Morlet wavelet decomposition, in the range from 2 to 70 Hz, increasing incrementally from 3 to 20 cycles. The spectra were further segmented into 6000ms epochs centered on the perceptual switches. The averaged alpha and beta bands' power waves were estimated in the frequency ranges 7~13 Hz and 20 ~ 30Hz.

*Spectral Granger causality.* We focused on the information flow between the frontal and the occipital areas, and we analyzed the spectral Granger causality of the EEG signals between the frontal (FC1, FCz, and FC2) and occipital electrodes (O1, O2 and Oz) using the MVGC toolbox (Barnett & Seth, 2014). Granger causality is used to estimate how much the activity of one region influence the activity of another region. The size of the influence is called granger gain or granger prediction, which is a ratio measured by comparing the error variances of a univariate autoregression in which the current value is predicted from past values of the same region (e.g., frontal predict frontal) with the error variances of a bivariate autoregression in which the current value is predicted from past values of the same region together with the other region (e.g., frontal and occipital predict frontal). Before calculating the Granger causality, the frontal and occipital electrodes' EEG signals were averaged within the frontal and occipital regions respectively to reduce noise in the signal. Similar results were obtained by using only one electrode per area. Additionally, to rule out the potential influence of volume conduction, we applied a Laplacian spatial filter (also known as density source analysis) (Srinivasan et al., 2007; Winter et al., 2007) on the EEG signal to filter out

the global signal shared by the electrodes. Furthermore, to ensure the EEG data's stationarity, we first estimated the stationarity of each trial using KPSS model of the MVGC package and discarded the trials with significant nonstationarity ( $p=0.01$ ). We used an auto-regression order equal to 16 (corresponding to 100 ms due to the 160 Hz sampling rate we used). We applied the Granger causality analysis on 6000 ms segmented EEG data using a sliding window of 1000 ms with a step size of 37.5ms (6 time points, each represents 6.25 ms due to the 160 Hz sampling rate). Each segment was de-trended and z-scored to further reduce the nonstationarity. The granger analysis generates two time-frequency maps of Granger gain (top-down: frontal to occipital electrodes, and bottom-up: occipital to frontal electrodes) for each condition (BR and PA). Next, we ran a non-parametric method to test the difference between BR and PA. First, we computed the difference between BR and PA and averaged the difference across subjects. Second, we calculated surrogates data by pooling the two conditions' trials and randomly re-distributing them into two groups. The randomized trials were used to perform the same Granger analysis on the surrogate conditions. We iterated the surrogate analysis over 5000 iterations. For each data point in the Granger gain time-frequency map, we computed the percentile (i.e., the p-value) by comparing the actual value with the surrogate distribution. Lastly, we applied FDR correction to correct for multi-comparison.

## 6.4 RESULTS

**Time-frequency analysis.** At first, we performed a time-frequency analysis to investigate the changes in the power of specific frequency bands related to the perceptual switch. The results (Figure 2A) reveal a clear pattern in two frequency bands, alpha (7~13 Hz) and beta (20~30 Hz), that is constant power during stable perception followed by a decrease after the perceptual switches. To closely assess these two frequency bands' temporal dynamics, we extracted the signals averaging within each frequency band. The resulting time course shows an apparent decrease in power following the switches in both frontal (upper row of figure 2B) and occipital electrodes (lower row). Figure 2C further confirms a significant difference between stable perception (-2000 to -1000 ms) and perceptual switches (-250 to 750 ms) in alpha and beta power, in both BR and PA conditions. All in all the time-frequency analysis reveals similar pattern of results irrespective of the frequency band and the perceptual condition (before or during the switch). We then performed a spectral Granger analysis to

investigate how the information flow propagates between the frontal and occipital regions in each frequency band.

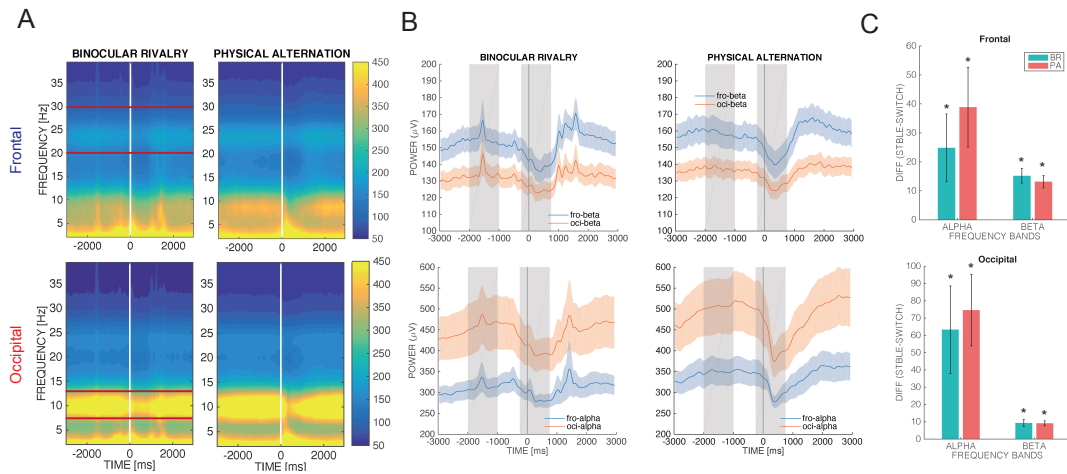


Figure 2 Time-frequency results of binocular rivalry. (A) The time frequency representation around perceptual switches (time 0) from the average of the frontal channels (FC1, FCz, and FC2) and the occipital channels (O1, O2 and Oz) for the BR and PA conditions. Red lines indicate the range of frequency used to plot the time course for figure (B). (B) The time courses of alpha (7~13 Hz) and beta (20~30 Hz) power from frontal and occipital channels for the BR and PA. The shaded areas represent the data extracted for the bar plots in figure (C). (C) Comparison between the power of alpha and beta bands during stable perception (-2000 to -1000 ms) and during perceptual switches (-250 to 750 ms). Asterisks indicate that the power is significantly higher than 0.

**Spectral Granger causality analysis.** Next, we investigated whether alpha and beta bands influence the connectivity between frontal and occipital regions using spectral Granger causality analysis. Remarkably, we found (1) large Granger gain values in both top-down and bottom-up time-frequency maps in the alpha band. (2) Apparent Granger gain in the top-down beta band. Both the alpha and the beta activities were observed in the BR and the PA conditions. (3) Considerable top-down theta activity in the BR (as shown in Figure 3 (A)). In Figure 3 (A), it appears that there are more top-down activities in the higher beta frequency band (28~33 Hz) in both conditions relative to the bottom-up activities, whereas the alpha frequency (7~13 Hz) exhibits an opposite profile.

Interestingly, the comparison between the two conditions revealed a significantly larger amount of top-down beta activity (26~29 Hz) and theta activity (3~6 Hz) in the BR condition than the PA one, at around -1.2 seconds and -2 ~ -0.8 second respectively before the perceptual switches (Figure 3, B). Additionally, our results reveal generally more bottom-up and top-down granger gain in the PA compared to the BR condition, specifically more bottom-up activity in the beta band (18~24 Hz) before the switches, and consistently more bottom-up and top-down activities before and after the switches in the alpha band, suggesting the involvement of different mechanisms in the two conditions.

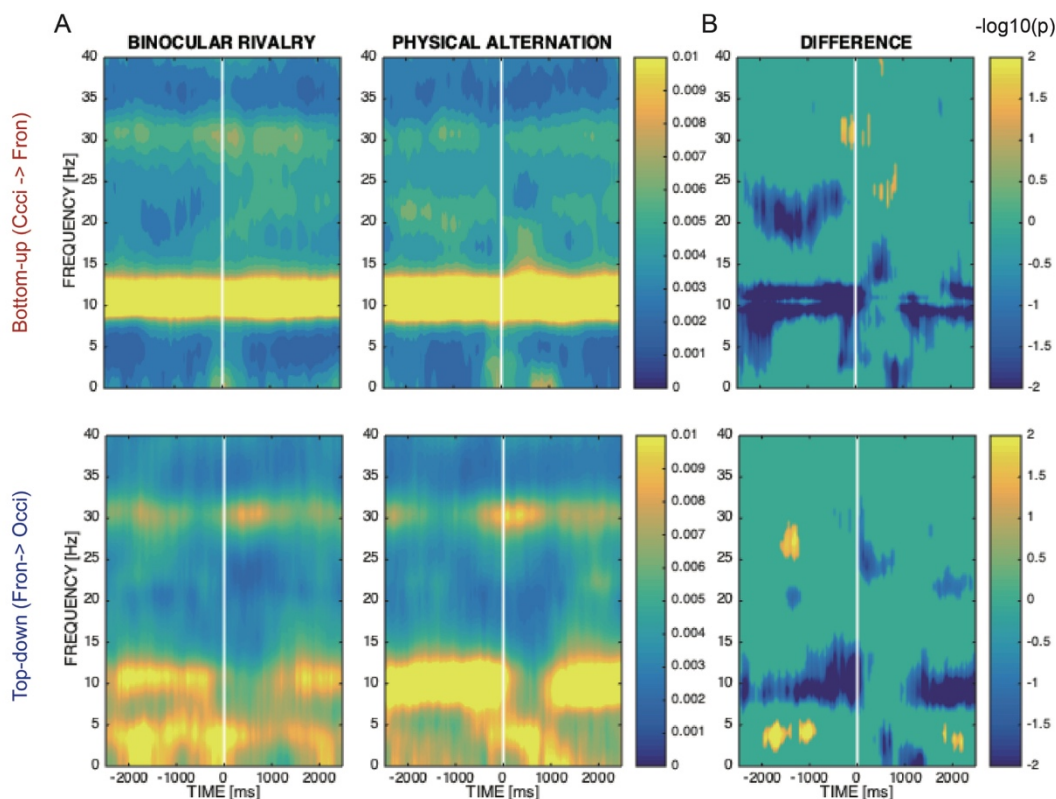


Figure 3 Granger causality results. A) The bottom-up and top-down granger gain for BR and PA conditions, respectively. B) The significant difference between BR and PA. The color bar represents  $-\log_{10}(p)$ . Multi-comparison corrected with FDR.

## 6.5 DISCUSSION

In this study, we investigated how neural activity in different regions influence each other as reflected by oscillatory synchronization in various frequency bands during a binocular rivalry

task. Our results reveal high top-down beta-band and bottom-up alpha-band activities in both conditions, as demonstrated by Granger causality analysis (Figures 3, A) and confirmed by the time-frequency analysis (Figure 2). More interestingly, we found an increase in the top-down beta and theta Granger gain preceding the perceptual switches in the BR condition, suggesting that the generation of conscious perception might rely on top-down interareal synchronization in these specific frequency bands (Figure 3, B).

Our time-frequency results confirmed the decrease in alpha and beta power following perceptual switches, consistently with previous studies of bistable perception (Nakatani & van Leeuwen, 2006; Piantoni et al., 2010, 2017; Strüber & Herrmann, 2002). A similar study involving binocular rivalry by Piantoni et al. (2010) suggests that beta oscillations correlate with the probability of perceiving rivalrous visual stimuli. Extending their findings, we found that such a pattern of alpha and beta power not only appeared in the BR condition but also in the PA condition, suggesting that high beta power is not solely present in bistable visual tasks but occurs as long as stable perception emerges.

Consistent with the time-frequency analysis, our spectral Granger causality analysis revealed the main results mostly concentrated in the alpha and beta frequency bands in both conditions, as well as theta band in the BR condition. The bottom-up alpha activity during visual stimulation is consistent with previous results investigating oscillatory traveling waves (Alamia & VanRullen, 2019; Pang et al., 2020). Interestingly, in both BR and PA conditions, the Granger analysis (Figure 3, A) reveals higher bottom-up alpha activity than the top-down one. In contrast, the beta activity showed an opposite profile. These findings agree with the hypothesis that forward sensory information is reflected in alpha-band activity (Pang et al., 2020), whereas beta-band activity may be related to top-down attention-related tasks (Bastos et al., 2015; Buschman & Miller, 2007). Altogether, these results suggest that conscious perception relies on recurrent processes implemented by beta-band top-down and alpha-band bottom-up activities.

The current study's main goal was to investigate the information flow that might be involved in resolving ambiguous visual perception. By contrasting the Granger gain in BR and PA



conditions, we found increased top-down beta and theta activity up to 1 second before perceptual switches in BR and generally less bottom-up activity at alpha and beta frequency bands in BR compared to PA. Regarding the beta activity, however, the functional role of beta oscillations is still debated. Yet, a few hypotheses have tentatively provided to account for the functional role of beta oscillations. On the one hand, Engel and Fries (2010) hypothesize that beta activity might be related to maintaining the current sensorimotor or cognitive functions, signaling the so-called “status quo.” On the same lines, Spitzer and Haegens (Spitzer & Haegens, 2017) further proposed that beta oscillations might be responsible for reactivating the endogenous representations via network dynamics, e.g., reactivate the representation of the unattended stimulus that was kept in memory. The key ingredient for these two accounts is based on the top-down role reflected by the beta activity (Bastos et al., 2015; Buschman & Miller, 2007). Additionally, experimental evidence on non-human primates confirmed this interpretation. Specifically, Buschman and Miller (2007) trained monkeys to perform a targeted search, in which the target was either very salient or confound between a few distractors. Interestingly, the authors found larger synchrony between frontal and parietal areas in the beta-band frequency in the condition involving more top-down attentional processes. In line with these results, our findings further suggest that beta-band activity might play an essential role in conveying top-down information, as well during conscious perception.

As for the theta activity, a recent binocular rivalry study (Drew et al., 2019) has found evidence regarding the role of frontal areas in resolving the rivalry. The authors found an increase in the theta activity before the perceptual switches, accompanied by a decrease in alpha activity, interpreting the results in the light of cognitive control (Cavanagh & Frank, 2014). Interestingly, we obtain similar results by normalizing the time-frequency maps. However, we analyzed un-normalized EEG power spectra in the time-frequency analysis to compare the results with those in Piantoni et al. (2010) and assess which frequencies have relatively stronger power, which can not be seen after normalization, during the task. Although the study by Drew et al. (2019) suggests that the frontal theta, which has been associated with cognitive control and conflict detection, might be related to perceptual switches, they did not discuss whether there might be information flow conveying this cognitive control signal to the lower areas. Our result of top-down theta activity further

suggests that the modulatory signal of cognitive control from the frontal areas might propagate to the visual areas, and thus partake in resolving visual ambiguity.

In contemporary theories of consciousness, such as the Global Workspace Theory (Baars, 1997) and Integrated Information Theory (Tononi, 2004), communication between brain areas is fundamental for conscious perception. Different hypotheses have been proposed to account for the communication between brain regions, including oscillatory components as in the Communication Through Coherence theory (Engel & Fries, 2016). In this framework, long-range synchronization can be mediated by top-down and bottom-up oscillatory processes (Engel et al., 2001; Engel & Fries, 2016), both supposedly involved in conscious perception (Dehaene et al., 2006; Lamme & Roelfsema, 2000). Our results provide experimental evidence in favor of this hypothesis, suggesting that binocular rivalry resolution requires top-down modulation from frontal areas (Leopold & Logothetis, 1999; Sterzer et al., 2009), a task achieved by beta and theta band activities.

## 7 CHAPTER 7. GENERAL DISCUSSION

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In chapters 3, 4, 5 and 6, I discussed neural oscillations in visual perception, attention, and consciousness, respectively, and provided answers to the questions raised in the introduction. For visual perception and attention, I focus on where (chapter 3) and how (chapter 4) the neural oscillations associated with these functions are generated. For consciousness, I study how the neural oscillations are functionally involved in conscious perception (chapters 5 and 6). Specifically, this thesis addresses the following three questions related to neural oscillations.

- 1) What's the neural basis of perceptual echoes? (Chapter 3)
- 2) What underlying mechanism gives rise to theta oscillations that modulate attentional sampling? (Chapter 4)
- 3) Are neural oscillations responsible for inter-area communication in conscious perception? (Chapters 5 and 6)

### 7.1 WHAT'S THE NEURAL BASIS OF PERCEPTUAL ECHOES?

To investigate in what regions of the brain perceptual echoes are generated, we conducted an EEG-fMRI experiment. Unlike concurrent EEG-fMRI studies, the subjects completed the same task in an EEG session and an fMRI session separately in our study. We first measured the echoes in the EEG session; then, we used the echoes as a template to reconstruct the EEG signal by doing convolution with the WN sequences in the fMRI session. We further used the reconstructed EEG to create regressors for fMRI analysis and found wide-spread activity in V1 and V2 that might be the neural basis of the echoes. In our findings, the unstimulated hemisphere was also correlated with the echoes, which could be explained by traveling waves (Alamia & VanRullen, 2019). However, it means the precise origin of the echoes might be a small part of the activated V1 and V2 even though our result could indeed serve to narrow down the location of the echoes. In the future, intracranial recordings from V1 and V2 can be used to locate where echoes are generated and moved to other locations.

Given the close relationship between ongoing alpha and the echoes, one might wonder if they share a similar neural basis. Researchers have been identifying the generator of alpha

oscillations since decades ago, yet it is still not conclusive. Previous studies have revealed that both the thalamus and visual cortex are possible sources of alpha oscillations (Clayton et al., 2018). For supporting thalamus to be the alpha generator, some studies found that alpha oscillations were diminished after lesions of the thalamus (Goldman et al., 2002; Liu et al., 2012), and some observed correlation between BOLD signal and alpha oscillations. Furthermore, electrophysiological studies in cats observed coherence of alpha activity between the thalamus and the visual cortex (Chatila et al., 1993; Lőrincz et al., 2009). On the other hand, some studies show that alpha oscillations could be generated from cortex activities. In vivo studies found pyramidal neurons in deep layers of cortex might be the pacemakers of alpha oscillations (Silva et al., 1991). Other studies reported alpha oscillations in all the layers (Bollimunta et al., 2008), possibly with stronger alpha activity in the deep layers (Buffalo et al., 2011; Van Kerkoerle et al., 2014) or the superficial layers (Haegens et al., 2015). Stronger alpha coherence between cortical areas than between cortex and thalamus indicates that cortex might be an independent generator of alpha oscillations (Silva et al., 1973). In resting-state studies, all have found a negative correlation between EEG alpha power and BOLD activity in the occipital cortex (de Munck et al., 2007; DiFrancesco et al., 2008; Goldman et al., 2002; Gonçalves et al., 2006; Laufs, Kleinschmidt, et al., 2003; Laufs, Krakow, et al., 2003; Moosmann et al., 2003) and during the task performance (Scheeringa et al., 2009, 2016; Zumer et al., 2014). In contrast, we found that the IRF envelope was positively correlated with V1 and V2 BOLD signals. The common neural basis (early visual areas) and the opposite activation profile (i.e., opposite correlation with BOLD) suggest that IRF and EEG alpha rhythms may share neural pathways, but play different functional roles in the brain.

Based on the previous results of a spatial attention task (VanRullen & MacDonald, 2012) and our findings of the echoes during binocular rivalry in Chapter 5, the echoes are not a localized function that is only restricted to V1 and V2. In the case of attentional engagement as well as conscious perception, the echoes are larger. It could be argued that while the regions that primarily generate echoes are the visual areas, higher-level regions, such as the prefrontal lobe, may influence how strong the echoes are in a top-down processing manner. It would be interesting to further investigate how top-down processing affects the echoes, for example, by analyzing how the connectivity of the frontal signal and occipital signal modulates the echoes.

In addition to helping future studies narrow down the neural origin that may produce echoes, the current study has a number of other implications. The function of the echoes is currently unclear. Now when studying the function of the echoes, we can take V1 and V2 into account. For example, a previous study linked echoes to sequence learning. Chang et al. (2017) presented subjects with repeated luminance sequences and found that the amplitude of the echoes increased with the repetition of the stimulus sequence, suggesting that echoes may carry information about such sequences. When they next presented that sequence in reverse order, the size of the echoes dropped to the same size as the echoes evoked by the new stimulus sequence. More interestingly, when they re-presented that learned sequence, the size of the echoes reverted back to the level they were at after several repetitions of the previous sequence. During this experiment, the subjects were not aware of the sequence of luminance changes, in line with the findings of another study (Turk-Browne et al., 2009), suggesting that possibly this learning only requires the involvement of the visual area and that the visual area retains the sequence information. This is supported by our finding that the echoes may have been generated in early visual areas.

In the general introduction, I used the echoes as one of the demonstrations for discrete visual perception. Since we found that V1 and V2 might be the neural basis of perceptual echoes, can we consider that visual sampling or discrete visual perception might originate from V1 and V2? Before answering this question, maybe we should answer another crucial question first: Is the discrete visual perception revealed by perceptual echoes the same as that demonstrated by the other studies in section “Oscillations in visual perception”? In fact, the studies that I listed in the visual perception section of the introduction, although they are in support of the notion - discrete visual perception, have discrepancies between each other. For instance, some studies reported higher frequency (~10Hz) (e.g., Dugué et al., 2011; Romei et al., 2008), while others found relatively lower frequency (~7Hz) (e.g., Busch et al., 2009; Hanslmayr et al., 2013). This frequency difference might be due to various reasons, such as task and individual difference and so forth. To tentatively answer the questions just mentioned, we can also examine the topographic maps and fMRI results of some studies. Several studies reported that occipital areas are involved in visual sampling (Dugué et al., 2011; Romei et al., 2008; Samaha & Postle, 2015). Whereas in some studies, the effect is revealed in the frontal areas (Busch et al., 2009) and connectivity between left lateral occipital cortex and right intraparietal sulcus in a concurrent EEG-fMRI study (Hanslmayr et al., 2013). It seems that when the effect is around 10Hz, it is more likely to be found at

occipital areas, which might have the possibility of sharing the neural basis with perceptual echoes. As we cannot be certain what led to the difference of frequencies and the effect locations in the brain in the previous studies, we cannot answer the question raised at the beginning of this paragraph that whether discrete visual perception originates from V1 and V2.

## **7.2 DOES ATTENTIONAL SAMPLING ARISE FROM THE THETA RHYTHM GENERATED BY VISUAL COMPETITION?**

Chapter 5 replicated the behavioral experiment of a monkey study, which investigated whether the theta activity is generated from the neuronal competition in V4 when one object is presented in the excitatory center and one in the suppressive surrounding (Kienitz et al., 2018). Together with the monkey study, our study aims to investigate the underlying mechanism of the theta rhythm of attentional sampling. We obtained similar results with the monkey study; saccadic reaction time fluctuated at theta frequency. The phases of the RT oscillation depend on the order of an object and two flankers presented to the subjects, which were assumed to elicit theta oscillations in the brain. Our results support the hypothesis that the theta rhythm of attentional sampling may be derived from the competition of V4 neurons, hence establishing a link between the theta rhythm in neural activity and behavioral oscillations, demonstrating that the attention-related theta activity in V4 could be a general mechanism for attentional sampling across species.

In our experiment, attention sampling was modulated by the order that the stimuli were presented, meaning that this attentional sampling is a bottom-up modulation by external stimulus. It is reminiscent of the studies using phase resetting to capture subjects' attention using an external event. There are a number of experiments using phase resetting (Fiebelkorn et al., 2013; Hogendoorn, 2016; Landau et al., 2015; Landau & Fries, 2012). For example, Landau and Fries (2012) resetted subjects' ongoing attention using a flash stimulus. Attention can be a top-down process, and the attentional network is the basis of this process. Many studies of attentional oscillations have focused on top-down attention, such as sustained attention. A recent study showed that the process of sustained attention also oscillates at the theta band (Helfrich et al., 2018). They reported that multiple regions of the attentional network exhibited theta oscillations during the task and that these oscillations were correlated with behavioral oscillations, suggesting that attentional oscillations may arise from the

attentional network. How do the theta oscillations of V4 and the attentional network coordinate? There are several possibilities. One possibility is that the theta activity of the attentional network dominates when top-down processing is taking place, such that this theta rhythm modulates the behavioral response. It could be that when external stimuli attract attention, a V4 theta activity is elicited, and this theta propagates to the attentional network, thus resetting the phase of the theta oscillations in the attention-relevant areas. It could also be that in the monkey study and the current study, the theta phase was determined in the attentional network then fed back to V4. These are only speculations that remain to be tested since we cannot know where the theta activity originates from both the monkey study and our study. Regardless of which possibility is true, it would be of importance to investigate whether there is a connectivity between the attentional network and V4 in attentional sampling. Yet, so far, there is no evidence on the synchronization of attention-related theta activities between the sensory areas and the attention network during attentional sampling (Fiebelkorn & Kastner, 2019). However, in the short-term memory context, theta connectivity has been found between frontal and visual cortices (Liebe et al., 2012), implicating there is a possibility that the synchronization exists for attentional sampling.

While the current study and the monkey study can explain how the theta rhythm is elicited when two stimuli are in close spatial proximity, these two studies did not cover some other conditions, leaving several unsolved questions. For example, what if three or four stimuli are presented? What if the stimuli are presented further apart? The receptive field size of V4 neurons is shown to be a function of eccentricity in V4 (Pinon et al., 1998). The receptive field size of some V4 neurons can span more than 15 visual degrees. It is possible that the theta activity could be derived from these neurons when stimuli are further apart. When more stimuli are presented, there might be multiple theta activities evoked in V4, mutual inhibiting or mixing such that giving rise to a lower frequency attentional sampling. Nevertheless, these are only pure speculations. The questions raised here call for more investigation in the future.

Saccades may be controlled by the FEF region, which is part of the attentional network. In our experiment, the subjects were responding by saccades. It has been reported that saccades follow a theta rhythm during free viewing (Engbert & Mergenthaler, 2005; Otero-Millan et al., 2008). How does our brain coordinate saccades and covert attention via theta activity? A recent model of rhythmic attention proposed by Fiebelkorn et al. (2018, 2019) characterized two attentional states alternating at theta band based on the interaction between

FEF and LIP of the attention network. One state represents increased perceptual sensitivity, reflected by high beta and gamma activity in FEF and LIP at the “good” theta phase. This state is associated with increase of sensory processing and suppression of eye movement, since beta activity has been related to movement suppression (Gregoriou et al., 2012; Pogosyan et al., 2009; Zhang et al., 2008) and gamma activity is linked to enhanced sensory processing (Fries, 2009; Fries et al., 2001; Landau et al., 2015; Womelsdorf et al., 2006). In contrast, the other state, defined by increased alpha activity in LIP at the “poor” theta phase, is related to reduced perceptual sensitivity. This state is associated with impaired visual processing at the currently attended location, which, combined with low beta inhibition, periodically create time windows for the shift of attention. These time windows could be the moments that our subjects started to saccade if the theta activity in LIP synchronized with the theta activity in V4.

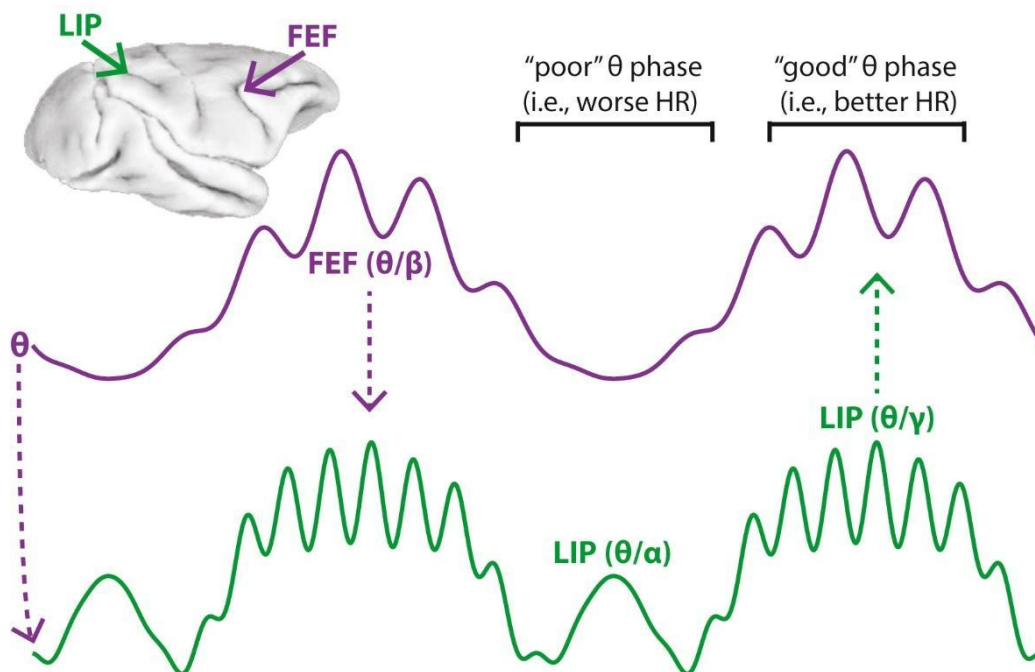


Figure 7-1 Fiebelkorn et al., (2018, 2019)’s model describes two attentional states organized by theta oscillations in FEF and LIP. One state, which occurs at the “good” phase of theta oscillations, is associated with enhancement of perceptual sensitivity. It is defined by increased gamma activity (better sensory processing) in LIP and increased beta activity (suppression of movement) in FEF. The second state, which is at the “poor” phase of theta activity, is linked to attenuation of sensory processing and higher likelihood of attention shifting. This state is characterized by increased alpha in LIP.



### **7.3 ARE NEURAL OSCILLATIONS RESPONSIBLE FOR INTER-AREA COMMUNICATION IN CONSCIOUS PERCEPTION?**

According to the CTC (communication through coherence) theory (Fries, 2005, 2015), an essential function of neural oscillations is communication, which creates optimal information transmission windows for neuronal coordination via synchronization of different regions. Communication between different brain regions is believed to be an essential component in conscious perception; hence in Chapters 5 and 6 we focused on the communication role played by neural oscillations in conscious perception.

We employed a binocular rivalry paradigm in Chapter 5 to investigate the perceptual echoes evoked by the dominant percept and suppressed percept. The alpha power of the echoes was greater in the dominant condition compared to the suppressed, possibly reflecting the fact that more neurons were synchronized during conscious perception. It may also imply that visual sampling in conscious perception is more efficient (e.g., the processing is more exhaustive) due to the larger number of neurons involved. This result partly demonstrates the importance of neurons communicating with each other through more synchronization in conscious perceptual visual sampling. Notably, perceptual echoes did not disappear entirely in the suppressed condition, suggesting that the generation of perceptual echoes does not necessarily require the involvement of consciousness. Surprisingly, the amount of traveling waves was as large in the suppressed condition as in the dominant and control conditions. According to past research, conscious percepts should reach further to the higher-level regions such as the frontal cortex compared with the unconscious ones (Dehaene & Changeux, 2011), which did not appear in our results. Other methods could shed light on such information flow, and granger causality is a good candidate. To this end, we conducted an additional granger causality analysis between the echoes of Oz (occipital electrode) and of Fz (frontal electrode) using the same dataset as chapter 5. The analysis revealed similar forward granger gain (Oz  $\rightarrow$  Fz) between dominant and suppressed conditions and showed significantly stronger granger gain in the physical alternation (Figure 7-2b). Presumably, the echoes of the suppressed stimuli travel as far as the echoes of the dominant stimuli. Our second study on consciousness (Chapter 6) discussed more about communication across regions in conscious perception.

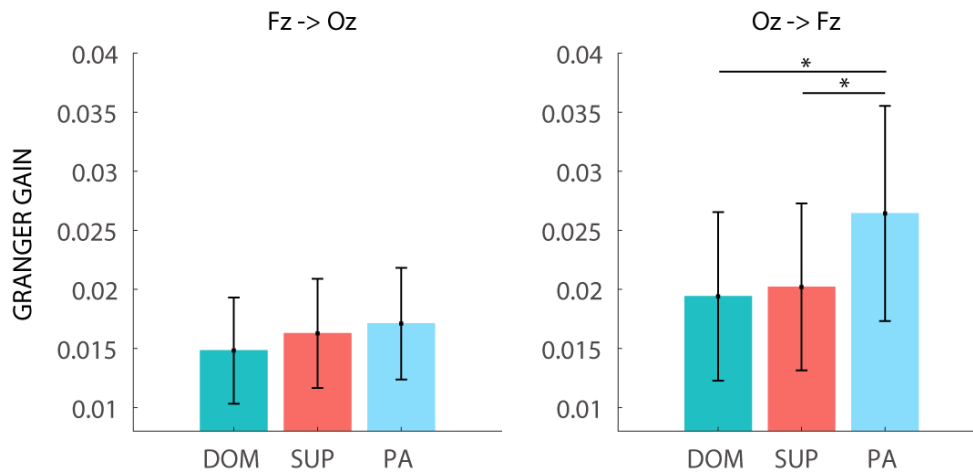


Figure 7-2 Granger causality result of the echoes between frontal and occipital electrodes. Compared with the dominant (DOM) and suppressed (SUP) condition of binocular rivalry, physical alternation (PA) shows higher bottom-up granger gain (right plot). The DOM and SUP conditions have similar top-down and bottom-up granger gain. The asterisks represent significant differences ( $p < 0.05$ ).

In Chapter 6, we investigated whether there is information flow in binocular rivalry as reflected by oscillations. First, we showed that the amplitude of alpha and beta oscillations in the binocular rivalry and the physical alternation condition follows a similar pattern, i.e., the amplitude does not reflect the unique processing that may be required to solve ambiguous perception in binocular rivalry. The increased power of these two oscillations is present as long as there is a stable or clear perception. We further applied granger causality analysis and found an increased top-down beta activity prior to perceptual switches in binocular rivalry.

In the BR condition, top-down beta and theta activities were larger, while in the PA condition, bottom-up beta and alpha activities were more considerable. Note that Granger causality is not really measuring the causal effect, but instead a prediction (Cohen, 2014). When the signal from the frontal areas predicts the signal from the occipital area, we assume that there is top-down processing. As I stated in the introduction, the specific functionality of beta oscillations is currently unclear. The beta activity we found is consistent with the findings of some previous studies, albeit not in the same task context. For example, in an attention study, the voluntary attention condition (top-down) has stronger beta synchronization than the bottom-up condition (Buschman & Miller, 2007). In another attention experiment, researchers also found top-down beta activity (Bastos et al., 2015). Our results show top-down beta activity occurs before the perceptual switches, which possibly

reflects the fact that the suppressed percept is being “activated”. Several working memory experiments have shown that content-specific beta activity (i.e., stimulus information can be decoded from the beta activity) emerges when unattended memory representations begin to be attended (Rose et al., 2016; Spitzer et al., 2014; Spitzer & Blankenburg, 2011). This suggests the possibility that beta oscillations are associated with “reactivation” of the latent representations (Spitzer & Haegens, 2017). Since top-down theta and beta activities co-occurred before the perceptual switches in our results, a question arises: do they represent two different processes, or do they coordinate to perform one cognitive task? Analyzing the correlation between them could partially answer this question. On the other hand, the widespread bottom-up processing in the PA condition may be because, in this condition, the subjects were passively receiving visual information, and the visual input was clear. Another possibility is that there may be a push-pull mechanism that leads to more bottom-up processing in the absence of top-down processing. Consistent with this result, more substantial bottom-up granger gain in PA can also be found in our additional granger causality analysis using perceptual echoes (Figure 7-2).

It is unclear in which region the resolution of binocular rivalry starts. A recent MEG study (Dijkstra et al., 2016) has revealed top-down processing prior to perceptual switches during binocular rivalry. This study decoded signals from each region and submitted the decoded results to a Granger causality analysis, and they found a flow of information from the temporal areas to the occipital areas that precedes the perceptual switches. Although also supporting top-down processing, our study differs in that 1) we found information flow from the frontal to the occipital areas and 2) our analysis is based on oscillations. For the first difference, we chose to analyze the frontal and occipital electrodes primarily because we drew on past literature. Several studies have indicated that the frontal cortex is associated with perceptual switches in bistable vision tasks (Leopold & Logothetis, 1999; Sterzer & Kleinschmidt, 2007; Weinhhammer et al., 2013), and the occipital areas are related to visual information processing in the tasks (Haynes & Rees, 2005b). Regarding the second difference, there is theoretical support for the idea that different brain regions communicate via oscillations (CTC) and that this communication can be achieved through synchronization of oscillations that are subject to top-down or bottom-up processing (Engel & Fries, 2016; Fries, 2005, 2015). According to our findings, this processing may serve as the information flow that is required for perceptual switches in binocular rivalry.

A growing number of models or theories consider that the brain is an active processor or interpreter which actively interprets, infers and predicts sensory input (Aitchison & Lengyel, 2017; Huang & Rao, 2011; Rauss et al., 2011). These models or theories highlight the importance of neural networks that include frontal, parietal and sensory areas in sensory information processing (Summerfield et al., 2006), consistent with the view positing frontoparietal networks as the hub of cognitive control (Zanto & Gazzaley, 2013). The same holds in conscious perception (Weilnhammer et al., 2017; Whyte, 2019). Several imaging studies have pointed out that the frontal and parietal areas are associated with perceptual switches during binocular rivalry or other bistable visual tasks (Britz et al., 2009; Kleinschmidt et al., 2002; Lumer et al., 1998; Sterzer et al., 2002; Sterzer & Kleinschmidt, 2007). Importantly, the connectivity between frontoparietal areas may be vital for resolving ambiguous perceptions. Enhanced synchronization has been observed between the frontal and parietal cortex prior to perceptual switches when viewing the Necker cube (Nakatani & van Leeuwen, 2006). Furthermore, an fMRI study (Weilnhammer et al., 2013) using a dynamic causal model found greater activation in frontoparietal regions during perceptual switches of seeing a rotating Lissajous figure, and this activation was associated with a top-down connectivity from the frontal to the occipital areas, implying that higher-level areas might initiate the perceptual switches. Whereas these studies are convincing, fMRI may fail to detect subtle neural activities due to its low temporal resolution. This is where our study provides more evidence for top-down on a finer temporal scale.

What information does the top-down process convey during bistable perception? And from where to where? A recent meta-analysis paper summarized all the fMRI and TMS studies of bistable perception that entail the frontoparietal regions. Of the frontoparietal regions, the inferior frontal cortex (IFC) is the most observed area that probably plays a critical role in directing perceptual switches. IFC is associated with sensory decision making (Heekeren et al., 2004) and inhibitory control (Aron et al., 2014), and it is sensitive to the fidelity of sensory information (Haynes & Rees, 2005a; Heekeren et al., 2004; Sunaert et al., 2000). From the predictive coding point of view, perceptual switches arise due to risen perceptual errors (Hohwy, 2007). This view has received evidence from an fMRI study that used the Bayesian predictive model to compute the time course of perceptual errors, which is correlated with the neural signal time-courses of IFC (Weilnhammer et al., 2017). During perceptual switches, IFC might serve to detect and send feedback information that could contribute to perceptual switches. The involvement of IFC in resolving ambiguous perception

has been further supported by a most recent study, in which the perceptual switches decreased when IFC was disrupted by TMS stimulation (Weilnhammer et al., 2020). Future studies are needed to record electrophysiology signals from IFC and visual areas to verify whether the top-down beta activity we found is sent from IFC to the visual areas.

Chapter 6 emphasizes that inter-area communication, as reflected by oscillations, is essential for conscious perception. However, this has only been found under one paradigm. More validations are needed to verify whether this result can be generalized across various conscious perceptions, for example, using a different bistable paradigm and a backward masking paradigm. More importantly, to establish the causal role of top-down activity in resolving ambiguous perception, studies using brain stimulation are required.

In short, we have demonstrated the communication role of oscillations in conscious perception through two studies. The first study mainly suggests that visual sampling in conscious perception may involve more neurons synchronizing in the alpha band. Complementarily, the second study shows that there is interareal directed communication in conscious perception.

## **7.4 CONCLUSION**

The four studies in this thesis discuss the role of oscillations in the brain from the perspective of three perceptual and cognitive functions: visual perception, attention and consciousness. Brain oscillations could act as an “exciter”, modulating visual perception and attention in such a way that our brain samples visual information rhythmically. The first two studies (chapters 3 and 4) set out to investigate the neural origin and the generation mechanism of the oscillations related to these visual and attentional samplings. We found that the perceptual echoes, the visual sampling related oscillations, might originate from early visual areas; and the theta oscillations, the underlying attentional samplings modulator, might arise from the visual competition of V4 neurons. Brain oscillations could also operate as a “communicator”, allowing exchanging information between brain areas via synchronization. The last two studies (chapters 5 and 6) demonstrate that inter-area communication and information flow reflected by oscillations might be associated with conscious perception. All in all, the brain is a dynamic system in which the oscillations flexibly facilitate various brain functions.

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