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Activité cérébrale reliée à la rétention des sons en mémoire à court-terme auditive

Par Sophie Nolden

Département de psychologie
Faculté des arts et des sciences

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Résumé et mots clés

Une variété d'opérations cognitives dépend de la capacité de retenir de l'information auditive pour une courte période de temps. Notamment l'information auditive prend son sens avec le temps; la rétention d'un son disparu permet donc de mieux comprendre sa signification dans le contexte auditif et mène ultimement à une interaction réussite avec l'environnement. L'objectif de cette thèse était d'étudier l'activité cérébrale reliée à la rétention des sons et, ce faisant, parvenir à une meilleure compréhension des mécanismes de bas niveau de la mémoire à court-terme auditive.

Trois études empiriques se sont penchées sur différents aspects de la rétention des sons. Le premier article avait pour but d'étudier les corrélats électrophysiologiques de la rétention des sons variant en timbre en utilisant la technique des potentiels reliés aux événements. Une composante fronto-centrale variant avec la charge mnésique a été ainsi révélée. Dans le deuxième article, le patron électro-oscillatoire de la rétention a été exploré. Cette étude a dévoilé une augmentation de l'amplitude variant avec la charge mnésique dans la bande alpha pendant la rétention des sons ainsi qu'une dissociation entre l'activité oscillatoire observée pendant la rétention et celle observée pendant la présentation des sons test. En démontrant des différentes modulations des amplitudes dans la bande alpha et la bande beta, cette étude a pu révéler des processus distincts mais interdépendants de la mémoire à court-terme auditive. Le troisième article a davantage visé à mieux connaître les structures cérébrales soutenant la rétention de sons. L'activité cérébrale a été mesurée avec la magnétoencéphalographie, et des localisations des sources ont été effectuées à partir de ces données. Les résultats ont dévoilé l'implication d'un réseau cérébral contenant des structures temporales, frontales, et pariétales qui était plus important dans l'hémisphère droit que dans l'hémisphère gauche.

Les résultats des études empiriques ont permis de souligner l'aspect sensoriel de la mémoire à court-terme auditive et de montrer des similarités dans la rétention de différentes caractéristiques tonales. Dans leur ensemble, les études ont contribué à l'identification des processus neuronaux reliés à la rétention des sons en étudiant l'activité électromagnétique et l'implication des structures cérébrales correspondantes sur une échelle temporelle fine.

Mots clés : Audition, mémoire à court-terme, mémoire de travail, hauteur tonale, timbre, électroencéphalographie, magnétoencéphalographie, potentiels reliés aux événements, oscillations cérébrales, localisations des sources

Summary and key words (Résumé et mots clés en anglais)

The capacity to retain auditory information for a short period of time is fundamental for a variety of cognitive operations. Sounds, in particular, often do not reveal their meaning before being integrated in their temporal context; the retention of tones that are no longer present in the environment is thus necessary for understanding the significance of auditory information. Retaining tones ultimately leads to a successful interaction with the environment. The goal of this thesis was to study brain activity related to the retention of tones, thereby providing a better understanding of low-level mechanisms related to auditory short-term memory.

Three empirical studies have been conducted, each of them focusing on a different aspect of the retention of tones. The first article investigated electrophysiological correlates of the retention of tones differing in timbre using the event-related potential technique. The electrophysiological results revealed a fronto-central component that varied with memory load. In the second article, the oscillatory pattern of electric brain activity was explored using electroencephalography. The results revealed that alpha band amplitudes were modulated by memory load during retention. Furthermore, a dissociation of oscillatory activity between the retention of tones and the comparison of test tones against retained tone representations was observed. This study also revealed distinct but interrelated processes taking place at the same time by showing specific amplitude modulations in the alpha and beta bands. The third article focused more on brain areas underpinning the retention of tones. Brain activity was measured with magnetoencephalography and subsequent source localisations were performed. The results suggested the implication of a network of temporal, frontal, and parietal brain areas which was more pronounced in the right hemisphere than in the left hemisphere.

The results of the empirical studies emphasized the sensory aspect of auditory short-term memory. In addition, they revealed similarities between the retention of tones differing in fundamental sound characteristics such as timbre and pitch. Considered as a whole, the studies of this thesis contributed to the identification of neural processing underlying the retention of tones by studying electromagnetic brain activity and the implication of corresponding brain areas on a fine temporal scale.

Keywords: Audition, short-term memory, working memory, pitch, timbre, electroencephalography, magnetoencephalography, event-related potentials, brain oscillations, source localisations

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Liste des sigles et des abréviations

ACN	*Auditory Cognitive Neuroscience*
AFNI	*Analysis of functional neuroimages*
ANOVA	*Analysis of variance*
ASTM	*Auditory short-term memory*
CIHR	*Canadian Institutes of Health Research*
CREATE	*Collaborative Research and Training Experience Program*
CRT	*Cathode-ray tube*
d´	Index de la sensitivité / *Sensitivity index*
DAAD	*Deutscher Akademischer Austauschdienst*
EEG	Électroencéphalographie ou Électroencéphalogramme / *Electroencephalography or Electroencephalogram*
ERP	*Event-related potential*
FDR	*False discovery rate*
Fig.	Figure / *Figure*
fMRI	*Functional magnetic resonance imaging*
FRQ-NT	Fonds de Recherche du Québec – Nature et Technologies
FRQ–S	Fonds de Recherche du Québec – Santé
GLM	*General linear model*
HEOG	*Horizontal electrooculogram*
IRM	Imagerie par résonance magnétique
IRMf	Imagerie par résonance magnétique fonctionnelle

IUGM	Institut Universitaire de Gériatrie de Montréal
K	Index de la capacité mnésique / *Memory capacity index*
M	*Mean*
MCT	Mémoire à court-terme
MCTA	Mémoire à court-terme auditive
MCTV	Mémoire à court-terme visuelle
MEG	Magnétoencéphalographie / *Magnetoencephalography*
MEM	*Maximum entropy of the mean*
MLT	Mémoire à long-terme
MNI	*Montreal Neurological Institute*
MRI	*Magnetic resonance imaging*
MSE	*Mean squared error*
NSERC	*Natural Science and Engineering Research Council of Canada*
PET	*Positron emission tomography*
PRE	Potentiel relié aux événements
RFT	*Random field theory*
RNQ	Regroupement Neuroimagerie / Québec
SAN	*Sustained Anterior Negativity*
SD	*Standard deviation*
SPCN	*Sustained Posterior Contralateral Negativity*
SPL	*Sound pressure level*
STM	*Short-term memory*
T	*Tone*

TE	*Echo time*
TR	*Repetition time*
TEP	Tomographie par émission de positrons
UNF	Unité de Neuroimagerie Fonctionnelle
VEOG	*Vertical electrooculogram*
WN	*White noise*
ß	Index du biais des réponses / *Response bias index*

Dédicace

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Partie 1 : Introduction

Chapitre 1 : Objectif

Ma thèse se penche sur les mesures de l'activité cérébrale reflétant directement les processus reliés à la mémoire à court-terme auditive (MCTA). Plus précisément, l’objectif est de parvenir à une meilleure compréhension des mécanismes de bas niveau de la rétention des items auditifs. Dans cette perspective, je vise à identifier les processus neuronaux et les régions du cerveau qui contribuent à la rétention des sons en utilisant l’électroencéphalographie (EEG) et la magnétoencéphalographie (MEG).

Chapitre 2 : Approches théoriques à la mémoire à court-terme

La capacité de retenir des informations sensorielles après qu’elles aient disparu de l’environnement est une capacité clé pour une majorité des processus cognitifs. La rétention des sons doit permettre de garder active une représentation de l'information auditive qui contient tous les aspects importants pour bien pouvoir interagir avec l'environnement. Avant de réviser les études les plus importantes en neurosciences auditives, quelques modèles influents de la mémoire à court-terme sont présentés. Ces modèles sont les modèles les plus pertinents pour cette thèse.

2.1. La mémoire à court-terme et sa relation avec la mémoire sensorielle et la mémoire à long-terme

Plusieurs approches théoriques intègrent la mémoire à court-terme dans des systèmes de mémoire qui incluent également la mémoire à long-terme (MLT) et la mémoire sensorielle. Malgré que ces termes soient souvent utilisés dans la recherche sur la mémoire, il y a des modèles bien différents concernant l'interaction de la MCT, la MLT, et la mémoire sensorielle.

Un des modèles multi-store de la mémoire ayant attiré énormément d'attention est le modèle modal d'Atkinson et Shiffrin (1968). Les auteurs proposaient trois sous-composantes de la mémoire : Le registre sensoriel, la MCT, et la MLT. Selon les auteurs, les informations de l'environnement passent d'abord par le registre sensoriel, puis celles qui sont sélectionnées sont maintenues par la MCT, et quelques unes arrivent enfin dans la MLT d'où elles peuvent être récupérées plus tard. Les trois sous-composantes sont non seulement différentes en termes de leur emplacement dans le système cognitif, mais aussi en termes de leur capacité et durée. Le registre sensoriel est caractérisé par une grande capacité et une dégradation rapide. Il est considéré comme étant spécifique à la modalité, non-intentionnel et non-sélectif. Sa fonction principale est d'absorber toute l'information avant de procéder à une sélection. La MCT a une capacité limitée et un temps de dégradation moyen. Seulement quelques items sélectionnés entrent en jeu dans cette étape, c'est donc ici où se trouve le goulot d'étranglement (*bottleneck*) du système. La MLT est caractérisée par une grande capacité et une longue durée de vie. Malgré que l'idée d'un traitement consécutif soit controversée, la distinction entre les trois sous-composantes de la mémoire proposées dans ce modèle, a été souvent reprise et a contribué à d'importants développements dans le domaine.

Une approche qui renonce au postulat d'unités distinctes pour la MCT et la MLT est représentée par le modèle de Cowan (1993, 1995, voir aussi Cowan, 1988). Ce modèle n'est pas seulement un modèle de mémoire, car il tient compte des processus attentionnels et intègre l'attention et la mémoire dans un système cognitif général. Cowan suggère que la MCT n'est que la partie de la MLT qui est momentanément activée. Parmi les représentations activées, quelques unes sont dans le faisceau de l'attention et peuvent aussi être manipulées. Cette conception excède la notion d'une activation simple. Le faisceau de l'attention peut être dirigé par un contrôle descendant (*top-down*) ou par des stimuli nouveaux qui entrent dans le registre sensoriel (facteurs ascendants, *bottom-up*), suivant ainsi la volonté de l'individu sans négliger les informations importantes venant de l'extérieur du système. Selon Cowan (2001), le nombre de représentations qui se trouvent dans le faisceau de l'attention est limité approximativement à quatre (voir aussi Miller, 1956). La supposition que la MCT est la partie de la MLT qui est momentanément activée requiert que la MLT ait une certaine structure organisationnelle. Selon le modèle, le contenu de la MLT est organisé dans un réseau géré par les expériences d'apprentissage de l'individu; chaque item a cependant un certain potentiel d'activation par rapport aux items voisins. Une représentation qui est activée mais qui ne se trouve pas présentement dans le faisceau de l'attention peut, par exemple, avoir un effet d'amorçage sur les stimuli subséquents. Ce modèle a le mérite d'intégrer la recherche sur l'attention et la mémoire et fait des suppositions simples concernant la relation entre MCT et MLT.

2.2. La mémoire à court-terme et la mémoire de travail

Un modèle qui a le mérite d'avoir mis de l'avant l'utilisation du terme « mémoire de travail » est le modèle de Baddeley et Hitch (1974; Baddeley, 1986, 2000). Le terme « mémoire de travail » met l'emphase sur le fait que les représentations ne sont pas seulement maintenues par des processus mnésiques, mais peuvent également être manipulées. Le lien entre la mémoire de travail et la MCT sera abordée plus loin. Baddeley et collaborateurs remplacent la notion d'un système unitaire de la mémoire de travail par quatre composantes. Selon ce modèle, un système exécutif central (*central excecutive*) contrôle le déploiement de l'attention sur des systèmes esclaves. Les systèmes esclaves sont la boucle phonologique (*phonological loop*), le calepin visuo-spatial (*visuospatial sketchpad*) et la mémoire tampon épisodique (*episodical buffer*). La boucle phonologique maintien et manipule l'information verbale et fait un lien avec le langage. Le calepin visuo-spatiale est responsable du maintien et de la manipulation de l'information visuelle et spatiale et fait un lien avec la modalité visuelle. Il est également possible qu'un stimulus visuel soit verbalisé puis traité par la boucle phonologique. Alors que la boucle phonologique et le calepin visuo-spatiale sont spécifiques à la modalité, la mémoire tampon épisodique (*episodical buffer*) génère un code multimodale et intègre l'information venant des différentes modalités et sert à créer une modélisation de l'environnement. Il se sert également du contenu de la mémoire à long-terme épisodique.

La boucle phonologique est, selon Baddeley (2000), la composante la plus étudiée à ce jour. Elle consiste en un registre phonologique (*phonological store*) qui stocke l'information phonologique et qui est caractérisé par une dégradation rapide. Par contre, un mécanisme de répétition de l'information (*articulatory rehearsal component*) maintien celle-ci active. Baddeley (1986) propose que la boucle phonologique maintien aussi les informations auditives non-verbales, qui entrent directement dans le mécanisme de répétition sans passer par le registre phonologique (voir aussi Williamson, Baddeley, & Hitch, 2010, pour une vue plus développée de la rétention des sons non-verbaux). Le modèle de Baddeley et collaborateurs a contribué à notre compréhension de la mémoire de travail et a également inspiré de nombreux travaux de recherche. Par contre, quelques problèmes conceptuels persistent. Il faut d'abord noter que ce modèle est surtout basé sur la mémoire verbale, donc sa validité générale peut être douteuse. Par conséquent, des modifications ont été suggérées comme la proposition d'une boucle supplémentaire qui traiterait l'information non-verbale (Berz, 1995; Pechmann & Mohr, 1992; voir aussi Williamson et al., 2010). De plus, la distinction entre la boucle phonologique et le calepin visuo-spatial est basée sur des études d'interférence sélective (par exemple Baddeley, Grant, Wight, & Thomson, 1975). Cette approche pourrait mener à un nombre indéfini de sous-composantes à chaque fois qu'une dissociation est observée. Finalement, l'idée que l'information est transférée entre les unités de la mémoire de travail qui stockent et manipulent les représentations est difficile à concilier avec les connaissances sur les propriétés du cerveau (voir par exemple D'Esposito, 2007).

La MCT et la mémoire de travail dans le sens de Baddeley et collaborateurs partagent beaucoup de propriétés, notamment le temps dégradation moyen et la capacité limitée. C'est pour cette raison que plusieurs chercheurs ont tenté de clarifier la signification de ce terme et de discuter le lien entre la MCT et la mémoire de travail. Par exemple, Cowan (1993, 1995) fait une distinction entre les termes MCT et mémoire de travail. Selon lui, le terme MCT décrit seulement le contenu activé pendant que le terme mémoire de travail décrit la MCT plus le contrôle attentionnel, faisant ainsi de la MCT une partie de la mémoire de travail. Étant inspiré par les travaux de Cowan, Engle et collaborateurs ont développé un modèle de mémoire de travail dans lequel la MCT est une sous-composante de la mémoire de travail (Engle, Kane, & Tuholski, 1999; Engle & Oransky, 1999). Dans ce cas, la mémoire de travail consiste en la MCT, c'est-à-dire la partie de la MLT activée au-dessus d'un certain seuil, les processus et capacités nécessaires pour réaliser et maintenir cette activation et finalement un système de contrôle exécutif qui régit l'attention et limite la capacité de la mémoire de travail. Les auteurs proposent que les représentations maintenues sont de nature spécifique à la modalité, similaire à la proposition de la boucle phonologique et du calepin visuo-spatiale de Baddeley et Hitch, même si Engle et collaborateurs ne spécifient pas le nombre de ces systèmes ni leurs caractéristiques. Les auteurs mettent leur modèle dans un contexte plus général et considèrent les différences interindividuelles, en faisant par exemple un lien entre l'intelligence fluide et la capacité maximale de l'attention. Le modèle résout la coexistence de concepts de la MCT et de la mémoire de travail et offre également de grandes perspectives sur d'autres processus cognitifs.

2.3. La spécificité à la modalité de la mémoire à court-terme

Les modèles résumés jusqu'ici ont déjà postulé une certaine spécificité de la modalité de la mémoire à court-terme, par exemple Baddeley et collaborateurs (Baddeley, 1986, 2000; Baddeley et Hitch, 1974) et Engle et collaborateurs (Engle, Kane, & Tuholski, 1999; Engle & Oransky, 1999). La spécificité de la modalité, au moins jusqu'à un certain degré, est aussi appuyée par les approches théoriques qui visent à réconcilier des études neuroscientifiques et des études purement comportementales, mettant ainsi les concepts de la MCT dans un autre contexte (D'Esposito, 2007; D'Esposito, Postle, & Rypma, 2000). Les résultats de quelques études neuroscientifiques suggèrent qu'un réseau de régions cérébrales contribue au maintien des représentations internes. Ce ne serait donc pas une seule structure qui maintiendrait l'information, mais plusieurs structures interconnectées (par exemple Grimault et al., 2014; pour la modalité auditive). En plus, dépendamment des caractéristiques des items, différents réseaux pourraient être impliqués. Plus précisément, les auteurs suggèrent que les structures qui contribuent à la perception et celles qui sont responsables du maintien en MCT se chevauchent. La rétention se ferait donc par une réactivation du patron généré lors de la perception. Les régions sensorielles impliquées interagissent, selon les auteurs, avec des régions du cortex associatif pour faciliter la rétention. Par exemple, le cortex préfrontal, à qui était assigné un rôle important dans l'intégration temporelle des événements, a ainsi une influence sur l'activation de certains patrons. Pendant que des caractéristiques sensorielles simples seraient retenues par les cortex sensoriels, des stimuli plus complexes pourraient être retenus par d'autres réseaux. Par exemple, des réseaux neuronaux communs pour la rétention des stimuli linguistiques présentés en modalité visuelle et auditive ont été proposés (Penney, 1989; Schumacher et al., 1996).

2.4. Résumé

En résumé, la recherche sur la MCT a suscité beaucoup d’intérêt ces dernières décennies, ce qui s’est traduit par un grand nombre d’études empiriques et également par le développement de théories influentes. Bien que la MCT verbale ait été l’intérêt principal pendant des années, la recherche s’est aussi penchée, plus récemment, sur des aspects non-verbaux de la MCT. On peut également observer une certaine direction théorique. Les modèles d’Atkinson et Shiffrin et Baddeley et Hitch, par exemple, ont encore une fois avancé le point de vue modulaire et isolé d’autres processus cognitifs, par contre les approches les plus récentes tentent de mieux intégrer la MCT dans l’appareil cognitif.

Chapitre 3 : La mémoire à court-terme dans la modalité auditive : Une perspective neuroscientifique

Les processus reliés à la MCTA se reflètent dans des patrons d'activité cérébrale qui peuvent être observés pendant qu'une personne exécute une tâche de MCTA. En mesurant ces patrons d’activité, une meilleure compréhension de la MCTA peut être atteinte.

3.1. Corrélats électrophysiologiques : Vers une meilleure compréhension des processus reliés à la rétention des sons

Étant donné que les modèles actuels, incluant ceux prenant en compte les neurosciences, mettent l’emphase sur la spécificité de la modalité de la MCT, il semble approprié d’isoler l’activité cérébrale correspondante avec du matériel qui engage une modalité sensorielle spécifique. Pour la modalité auditive, beaucoup d'études ont utilisé du matériel verbal comme des mots ou des chiffres présentés oralement à l'aide d'écouteurs (Crottaz-Herbette, Anognoson, & Menon, 2004; Pelosi, Hayward, & Blumhardt, 1998). Malgré l'importance d'étudier la MCTA verbale, les résultats obtenus ne reflètent probablement pas seulement les processus de bas niveau de la MCTA, mais également la rétention des codes verbaux. Pour accéder à la rétention des représentations des sons et à ses corrélats cérébraux, une approche avec du matériel plus simple paraît utile.

Plusieurs études ont utilisé des stimuli verbaux et non-verbaux pour dissocier l'activité cérébrale reliée aux stimuli verbaux et non-verbaux. Des stimuli visuels et auditifs étaient également utilisés pour isoler l'activité cérébrale spécifique à chaque modalité. Par exemple, dans une étude, des participants retenaient des chiffres présentés sur un écran ou via des écouteurs ou alors des sons non-verbaux. Les stimuli mémoire étaient comparé avec les stimuli test après un intervalle de rétention (Lang, Starr, Lang, Lindinger, & Deecke, 1992; voir aussi Sternberg, 1966). Les auteurs ont analysé des potentiels reliés aux événements (PRE, *event-related potential, ERP*) pendant l'intervalle de rétention. Ils se sont donc focalisés sur l'activité cérébrale reflétant la rétention et ont ainsi minimisé la probabilité de contaminer les résultats avec l'activité reliée à l'encodage, la récupération, la comparaison, la décision ou la sélection de la réponse. Les résultats montraient une composante négative frontale qui était plus prononcée pour les chiffres présentés auditivement que pour les chiffres présentés visuellement. Cette composante était encore plus négative pour les sons non-verbaux. En plus, une composante négative temporale postérieure a été observée et était plus prononcée pour les stimuli visuels que pour les stimuli auditifs. Les auteurs ont conclu que les processus cérébraux de la MCT étaient spécifiques à la modalité et au matériel verbal. L'étude a également montré qu'une composante PRE soutenue et frontale reflétait en partie la rétention des sons (Lang et al., 1992; voir aussi Pelosi et al., 1998; Ruchkin et al., 1997).

Une étude récente s'est focalisée encore plus sur les mécanismes de bas niveau de la MCT (Lefebvre et al., 2013). L'objectif était l'isolation des corrélats électrophysiologiques de la rétention des sons en MCTA. La méthodologie utilisée dans cette étude était particulièrement susceptible de minimiser tous les facteurs confondants évidents. Premièrement, les stimuli retenus en MCTA étaient des sons purs variant en hauteur tonale. Il est peu probable qu'un tel stimulus soit encodé de façon verbale, surtout si les participants ne sont pas des musiciens. Deuxièmement, les fréquences des sons ne correspondaient pas aux sons d'une échelle musicale (« sons non-musicaux »), et il est donc peu probable que ces sons soient mis en lien avec des connaissances musicales explicites ou implicites (Trehub, Schellenberg, & Kamenetsky, 1999). Troisièmement, les PRE étaient analysés pendant l'intervalle de rétention silencieux, évitant ainsi les PRE reflétaient aussi l'encodage, la récupération, la prise de décision ou le choix de réponse. Enfin, un nombre différent de sons était présenté dans chaque séquence; la charge mnésique était donc variée. Les résultats ont révélé une composante PRE aux électrodes fronto-centrales, surtout au site de l'électrode AFz, qui variait avec la charge mnésique. Plus précisément, la composante devenait plus négative quand la charge mnésique augmentait. Il y avait également une corrélation entre les données comportementales et cette composante : L'effet de charge en électrophysiologie était corrélé avec la capacité de la MCTA individuelle qui était calculée sur la base des données comportementales. Les auteurs ont nommé cette composante la négativité antérieure soutenue (*Sustained Anterior Negativity, SAN*). Dans une expérience subséquente, les participants essayaient de retenir des nombres de sons qui dépassaient systématiquement leur empan mnésique (Alunni-Menichini et al., 2014). L'empan mnésique était calculé sur la base des données comportementales. Les auteurs ont trouvé que la composante SAN devenait plus négative entre la charge la plus petite et les charges moyennes. Dès que l'empan fut atteint, cependant, l'amplitude de la SAN atteignait un plateau. Les auteurs ont conclu que la SAN était un corrélat électrophysiologique du nombre d'items en MCTA plutôt qu'un indicateur de la difficulté de la tâche.

L'étude de Lefebvre et collaborateurs (2013) a aussi fait ressortir l'aspect spécifique de la modalité des stimuli, suivant ainsi la logique de plusieurs modèles influents de la MCT. Les auteurs ont comparé la rétention d'items visuels avec la rétention de stimuli auditifs et ne démontraient la présence de la SAN que pour les stimuli auditifs. La rétention des stimuli visuels, par contre, menait à une composante latéralisée postérieure, la négativité postérieure controlatérale soutenue (*Sustained Posterior Contralateral Negativity, SPCN,* voir aussi Vogel & Machizawa, 2004). Dans l'expérience auditive de Lefebvre et collaborateurs, la charge mnésique impliquait aussi une augmentation de la difficulté de la tâche, donc il se peut que la composante SAN la reflète aussi, du moins en partie. Cette confusion possible était clarifiée avec l'expérience visuelle de Lefebvre et collaborateurs. La difficulté augmentait également dans cette expérience, mais les auteurs n'observaient pas de SAN.

Lefebvre et collaborateurs proposaient que la SAN reflète les mécanismes de rétention en MCTA, et en particulier l'activité reliée au maintien en état actif des représentations des sons. Pour éviter que les participants utilisent des stratégies mnésiques comme la répétition et le regroupement (*chunking*), des « sons non-musicaux » étaient utilisés, soit un ensemble de sons qui ne correspondent pas à la gamme tempérée. Dans une expérience qui visait à mettre en évidence plus précisément ces stratégies mnésiques, le protocole de Lefebvre et collaborateurs a été modifié (Guimond et al., 2011). Au lieu de retenir des séquences de sons, les participants retenaient un ou deux sons présentés simultanément. Ainsi, il était impossible d'utiliser un contour mélodique pour accomplir la tâche. L'utilisation de la stratégie du regroupement était aussi minimisée parce qu'un seul son test était présenté après l'intervalle de rétention, et les participants devaient donc distinguer les deux sons distincts pour accomplir la tâche. L'utilisation de la stratégie de la répétition interne était peu probable étant donné que deux sons présentés simultanément sont très difficiles ou impossibles à répéter. Pour que l'utilisation de cette stratégie soit encore plus improbable, les participants comptaient de 1 à 10 pendant la moitié des essais. Utilisant les termes de Baddeley et Hitch, leur « boucle phonologique » était engagée dans une activité autre que la MCTA et ne pouvait donc pas contribuer à la tâche de mémoire. Les résultats montraient la présence d'une SAN pour la rétention des sons présentés simultanément, avec et sans suppression de la boucle phonologique, appuyant ainsi la notion que la composante SAN reflète la rétention simple des sons plutôt que l'application d'une stratégie de répétition.

Les expériences de Lefebvre et collaborateurs et Guimond et collaborateurs ont également démontré que la rétention est un mécanisme fondamental de la MCTA qui requiert de l'activité mnésique délibérée et qui dépasse les exigences d'un registre sensoriel. Dans ces expériences, il y avait des conditions contrôles associées à des conditions de mémoire. Dans ces conditions contrôles, les participants écoutaient les mêmes sons que dans les conditions de mémoire, mais il n'était pas nécessaire de retenir les sons en MCTA pour accomplir la tâche. La tâche contrôle était d'indiquer si le dernier son test était aigu ou grave (Guimond et al., 2009) ou si le dernier son de la séquence test était plus grave ou plus aigu que l'avant-dernier son (Lefebvre et al., 2013). Ces tâches contrôle ne généraient pas de SAN. Une SAN n'a été observée que dans les conditions de mémoire, confirmant ainsi qu'un processus actif de mémoire était la source de la SAN, plutôt qu'un registre sensoriel passif. Dans les conditions de mémoire, il y avait une baisse des taux de succès quand la charge mnésique augmentait. Ces effets ne peuvent pas être expliqués par un registre sensoriel dont les caractéristiques principales sont l'automaticité et une grande capacité pour l'information en entrée. Ces études démontrent donc que la rétention est un processus actif qui requiert un effort délibéré.

Pour résumer, des études en PRE ont suggéré qu'une composante fronto-centrale est reliée à la MCTA. D'autres études qui avaient pour objectif d'isoler des corrélats électrophysiologiques de la rétention ont découvert une composante spécifique à la modalité auditive qui reflète directement le nombre de sons retenus. Cette composante est nommée la *SAN.* Elle reflète le nombre d'items en MCTA et elle est corrélée avec la capacité mnésique individuelle.

3.2. Analyses temps-fréquence : Déchiffrer le patron temporel de l'activité mnésique

L'EEG et la MEG sont des méthodes appropriées pour explorer l'activité cérébrale reliée à la MCTA parce qu'elles ont une très bonne résolution temporelle. Elles permettent donc d'enregistrer l'activité électrique du cerveau sur une fine échelle temporelle avec une précision de l'ordre de la milliseconde. Ceci rend possible l'examen de l'activité cérébrale à un moment précis pendant une tâche de MCTA. Le signal enregistré peut non seulement être analysé avec des méthodes de PRE classiques, mais aussi avec des analyses temps-fréquence. Les analyses temps-fréquence constituent un complément intéressant aux analyses PRE parce qu'elles ne sont pas affectées par l'annulation par phase qui se produit lors d'un simple moyennage du signal mesuré dans plusieurs essais (Tallon-Baudry & Bertrand, 1999). En plus, il est possible de regarder l'évolution du signal dans différentes bandes de fréquences.

Les patrons dissociatifs dans des bandes de fréquences distinctes aident à mieux comprendre comment les sons sont retenus en MCTA et aident à dévoiler des processus distincts qui se passent en même temps.

Jusqu'à date, il y a peu d'études à ma connaissance qui se sont spécifiquement focalisées sur les analyses temps-fréquence reliées à la MCTA (voir par exemple Leiberg, Lutzenberger, & Kaiser, 2006). Quelques études se sont penchées sur la mémoire verbale en utilisant des stimuli auditifs. Une séquence de quatre voyelles était présentée et les participants comparaient les voyelles mémoire à une voyelle test qui était présenté après un intervalle de rétention (Pesonen, Haarala Björnberg, Hämäläinen, & Krause, 2006; voir aussi Krause, Lang, Laine, Kuusito, & Pörn, 1996). L'EEG était analysé avec des transformations par ondelette de Morlet. Pendant la présentation du stimulus test, les auteurs ont observé que les amplitudes étaient plus grandes pour les stimuli test « différents » (pas parmi les stimuli de mémoire) que pour les stimuli test « pareils » (faisant partie des stimuli de mémoire) dans la bande alpha (~8–12 Hz) et la bande beta (~15–30 Hz).

Dans l'étude de Pesonen et al. (2006), il n'y avait pas de manipulation de la charge mnésique. Comment une manipulation de charge en MCTA affecterait l'activité oscillatoire reste donc inconnu. En plus, le signal pendant la rétention n'était pas analysé. Par contre, on a effectué une manipulation de la charge mnésique et observé l'activité oscillatoire dans quelques études en MCT visuelle (MCTV). Pendant la période de rétention de stimuli visuels, une augmentation de l'activité dans la bande alpha était observée quand la charge mnésique augmentait (Grimault, Robitaille, Grova, Lina, Dubarry, & Jolicoeur, 2009; Jensen, Gelfand, Kounios, & Lisman, 2002). En plus, l'augmentation de l'activité en bande alpha était corrélée avec la performance (Khader, Ranganath, & Rösler, 2010; Meeuwissen, Takashima, Fernández, & Jensen, 2011).

En ce moment, il y a plusieurs approches qui essayent d'interpréter l'activité oscillatoire en attribuant des fonctions générales à des bandes de fréquences spécifiques (par exemple, la paresse corticale (bande alpha), voir Pfurtscheller, Stancák Jr., & Neuper., 1996; l'inhibition (bande alpha), Jensen et al., 2002; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007, la transition à un mode de traitement interne (bande alpha), Hanslmayr, Gross, Klimesch, & Shapiro, 2011; l'activité motrice (bande beta), Stancák Jr. & Pfurtscheller, 1995). La plupart de ces approches sont basées sur des études utilisant des stimuli visuels. Il faut noter que, à date, il n'est pas clair si l'activité oscillatoire a toujours la même signification fonctionnelle pour toutes les modalités sensorielles. Le peu d'études qui existent en MCTA suggèrent plutôt qu'il y a bien des différences entre la MCTA et la MCTV concernant la modulation de l'activité oscillatoire (par exemple Pesonen et al., 2006). Étudier l'activité oscillatoire reliée à la MCTA nous permettrait donc non seulement de mieux comprendre les processus reliés à la MCTA, mais également de clarifier si des fonctions générales peuvent être attribuées à des bandes de fréquences particulières ou si une telle approche demeure injustifiée.

3.3 Études en imagerie cérébrale : Quelles sont les structures cérébrales soutenant la rétention des sons?

Les études discutées dans les sections précédentes ont traité des corrélats électrophysiologiques de la rétention des sons. L'activité cérébrale était mesurée avec l'EEG, une méthode qui a une résolution temporelle très fine, de l'ordre de la milliseconde. L'EEG est donc appropriée pour l'étude des mécanismes de rétention et permet d'isoler les corrélats électrophysiologiques dans chaque intervalle d'intérêt dans une tâche de MCTA. Par contre, la résolution spatiale de l'EEG est moins bonne que pour d'autres méthodes qui sont plus appropriées pour révéler les endroits dans le cerveau où le signal mesuré à la surface ou hors de la tête est généré. La section prochaine traite des études d'imagerie cérébrale sur la MCTA pour complémenter les études en électrophysiologie en ajoutant un aspect de localisation spatiale.

Plusieurs études ont tenté d'isoler les structures cérébrales soutenant la rétention des sons en MCTA. Malgré que les méthodes appliquées soient bien différentes, il est possible de trouver des convergences dans les résultats des études qui seront discutées dans cette section. Une étude qui visait l'isolation des régions cérébrales reliées à la rétention des sons a utilisé la tomographie par émission de positons (TEP, *positron emission tomography, PET*, Zatorre, Evans, & Meyer, 1994). Les participants écoutaient des séquences de huit sons qui différaient en hauteur tonale. Ils comparaient le premier son soit avec le deuxième son (charge « mnésique » basse), soit avec le dernier son (charge « mnésique » élevée). Dans la condition de charge « mnésique » élevée, les participants retenaient donc le premier son pour une durée d'environ trois secondes en MCTA, alors qu'ils comparaient les sons immédiatement dans la condition de la charge « mnésique » basse. Les auteurs utilisaient le terme « charge » donc pour décrire la durée de la rétention, et non pour le nombre de sons retenus (voir par exemple Lefebvre et al. 2013). En comparaison avec une condition d'écoute passive, le cortex frontal inférieur droit était activé dans la condition de charge « mnésique » basse; et dans la condition de la charge « mnésique » élevée, le cortex temporal droit et les cortex pariétal et insulaire étaient activés, entre autres. Les auteurs ont conclu que les cortex frontal et temporal droit font partie d'un réseau cérébral qui participe à la rétention des sons en MCTA.

Dans une étude plus récente basée sur un paradigme similaire (Gaab, Gaser, Zaehle, Jancke, & Schlaug, 2003) l'activité cérébrale était mesurée avec l'imagerie par résonance magnétique fonctionnelle (IRMf, *functional magnetic resonance imaging, fMRI*). Les auteurs ont utilisé une technique d'échantillonnage clairsemé pour éviter une confusion de l'activité cérébrale reliée à la tâche mnésique avec l'activité cérébrale reliée au traitement du bruit du scanneur. Les participants écoutaient des séquences de six ou sept sons. Ils comparaient le premier son de la séquence avec un des deux derniers sons dans la condition mémoire. Une tâche motrice servait de condition contrôle. En contrastant la condition de mémoire avec la condition contrôle, les auteurs ont observé une activation du gyrus temporal supérieur, du gyrus supramarginal, des régions frontales et pariétales ainsi que du cervelet, en lien avec la MCTA. Ils ont également trouvé que le gyrus frontal inférieur gauche était impliqué dans la MCTA, la structure que Zatorre et collaborateurs (1994) avaient trouvé à droite dans leur condition de charge « mnésique » élevée. De plus, les auteurs ont corrélé l'activité cérébrale avec la performance des participants. Les résultats révélaient que l'activité dans le gyrus supramarginal, surtout à gauche, et dans le cervelet dorso-latéral étaient significativement corrélée avec la performance individuelle.

Dans une autre étude en IRMf, les participants écoutaient des syllabes chantées (Koelsch et al., 2009). Ils retenaient soit la hauteur tonale, soit les voyelles, avec ou sans chant simultané (conditions avec ou sans suppression). Les auteurs concluaient sur la base de leurs résultats qu'un réseau incluant les cortex prémoteurs, le planum temporale, le cortex pariétal inférieur, l'insula antérieure, des structures sous-corticales et le cervelet étaient impliqués dans la rétention de l'information auditive. Ils soutenaient que des réseaux très similaires sont responsables de la rétention de la hauteur tonale et des voyelles. Cependant, dans cette étude, ce que les participants faisaient dans les différentes conditions n'est pas tout à fait clair; s'ils encodaient et retenaient donc juste la hauteur tonale ou juste la voyelle, ou s'ils traitaient les sons comme une unité composée de la hauteur tonale et de la voyelle (voir aussi Schulze, Mueller, & Koelsch, 2011, et Schulze, Zysset, Mueller, Friederici, & Koelsch, 2011, pour des différences entre des musiciens et des non-musiciens).

Une étude récente a localisé des régions cérébrales qui contribuent à la rétention des sons en utilisant la MEG (Grimault et al., 2014). Dans cette étude, les auteurs ont utilisé un paradigme qui ressemble beaucoup à celui de Lefebvre et collaborateurs (2013) en PRE. Les participants retenaient des séquences des sons et les comparaient avec une séquence test après un intervalle de rétention. Les auteurs appliquaient les mêmes stratégies que Lefebvre et collaborateurs qui ont été discutées à la section précédente : des stimuli engageant le moins de systèmes cognitifs possible était utilisés, la charge mnésique était manipulée, l'analyse des données était faite pendant l'intervalle de rétention, et la capacité mnésique individuelle était tenue en compte. La MEG donne d'une bonne résolution temporelle, tout comme l'EEG. Les caractéristiques des champs magnétiques, des méthodes sophistiquées de réduction de bruit, et un nombre élevé de capteurs MEG permettent également de faire de précises localisations de source. Grimault et collaborateurs ont isolé les régions cérébrales où l'activité augmentait quand les participants retenaient plus d'items en MCT. Ils ont donc directement visé les générateurs de la SAN. Le nombre d'items retenus pendant l'intervalle de rétention, estimé avec l'index de la capacité mnésique K (Cowan, 2001, Pashler, 1988), était utilisé comme régresseur dans un modèle linéaire général. Cette approche était antérieurement utilisée dans des études visant aux régions cérébrales soutenant la rétention des items visuels (Robitaille et al., 2010; Todd & Marois, 2004). En prenant K comme régresseur, les auteurs utilisaient un index qui variait entre les participants est qui reflétait leurs capacités mnésiques. Les résultats de cette étude démontrent une implication du lobe pariétal supérieur bilatéral, du gyrus inférieur frontal / gyrus précentral bilatéral, du gyrus frontal supérieur / moyen bilatéral, du gyrus temporal moyen bilatéral, du gyrus temporal supérieur bilatéral, et du gyrus parahippocampal droit. L'activité dans ces régions augmentait quand les participants retenaient plus de sons en MCTA.

Considérés dans leur ensemble, les résultats de toutes ces études suggèrent que des régions temporales, frontales, et pariétales contribuent à la rétention des sons, plus précisément à la rétention des sons qui différent en hauteurs tonale. Premièrement, des études en TEP et en IRMf ont révélé un rôle important de ces régions et du cervelet dans la rétention de sons. Deuxièmement, une étude en MEG où l'activité cérébrale était corrélée avec le nombre d'items retenus indique également une implication des régions temporales, frontales et pariétales.

Chapitre 4 : Présentations des articles

Les études en PRE et en imagerie cérébrale présentées dans les sections précédentes ont permis des avancées de nos connaissances sur la rétention des items auditifs. Une composante PRE, la SAN, semble prometteuse comme corrélat du nombre d'items retenu, et plusieurs études en imagerie cérébrale ont visé à isoler les régions cérébrales qui contribuent à la rétention. Ma thèse vise à étendre nos connaissances sur les régions cérébrales et l'activité oscillatoire contribuant à la rétention des sons, et à approfondir nos connaissances sur les propriétés de la SAN.

Le premier article vise à étendre nos connaissances sur la SAN. La SAN est un corrélat électrophysiologique du nombre de sons retenus en MCTA avec une topographie fronto-centrale. Jusqu'à ce jour, les expériences sur la SAN étaient réalisées avec des stimuli variant en hauteur tonale. Malgré le fait que les sons simples ne variaient que dans une seule caractéristique et avaient l'avantage de pouvoir isoler des processus simples, les résultats obtenus n'étaient valide que pour la hauteur tonale. Cette étude vise donc à généraliser la SAN en variant une autre caractéristique des sons, soit le timbre. Le timbre d'un son caractérise sa qualité et est parfois identifiable à un processus physique de production, par exemple quand la même note est jouée par un violon ou un saxophone. Le timbre est une caractéristique multidimensionnelle qui corrèle surtout avec l'intensité relative des harmoniques et le décours temporel de l'attaque (Caclin et al., 2006; Caclin, McAdams, Smith, & Winsberg, 2005; Plomb, 1970). Dans la première étude, des séquences des sons variant en timbre étaient présentées et retenues pour être comparées avec une séquence test. Le but est de déterminer si une SAN est observée pendant l'intervalle de rétention, ce qui généraliserait ainsi la SAN à une autre caractéristique des sons.

Le deuxième article vise à identifier l'activité oscillatoire reliée à la MCTA. Deux expériences se concentrant sur la rétention et la récupération des sons étaient analysées afin de mieux comprendre l'interaction de la bande de fréquence alpha (8-12 Hz) et la bande de fréquence beta (18-28 Hz). Pour la première fois, à ma connaissance, les effets d'une manipulation de charge sur l'activité oscillatoire est explorés en MCTA avec des sons non-verbaux. Cette étude aide non seulement à mieux comprendre les processus fondamentaux de la MCTA, mais contribue aussi à déchiffrer le patron temporel de l'activité cérébrale reliée à la MCTA.

Dans le troisième article, je vise à localiser les régions du cerveau qui contribuent à la rétention des sons en utilisant la MEG. L'objectif est d'identifier l'activité cérébrale indispensable pour la rétention en utilisant un paradigme qui minimise la possibilité que les participants fassent autre chose que de retenir les représentations des sons présentés. Les expériences antécédentes sur les régions cérébrales contribuant à la rétention ont possiblement mesuré d'autres processus que la rétention. Plus précisément, des confusions pourraient provenir du fait que quelques études aient utilisé du matériel verbal (par exemple Koelsch et al., 2009), du matériel qui pouvait facilement être mis dans un contexte musical (par exemple Gaab et al., 2003; Zatorre et al., 1994), des sons supplémentaires présentés pendant la rétention (Gaab et al., 2003; Zatorre et al., 1994) et que les sons qui étaient retenus consistaient en séquences de sons, permettant ainsi l'application des stratégies de répétition ou de regroupement (par exemple Schulze, Mueller, & Koelsch, 2011). Pour éviter ces confusions, du matériel non-verbal était utilisé et la tâche était construite pour que les participants ne puissent pas appliquer des stratégies de répétition ou de regroupement. Des localisations de source étaient réalisées sur le signal enregistré durant l'intervalle de rétention pour révéler les régions engagées par ce processus. Étant donné que certaines théories de la MCT suggèrent que la rétention, en grande partie, consiste dans la réactivation des patrons d'activation formés lors de la perception (par exemple D'Esposito, 2007; D'Esposito, Postle, & Rypma, 2000), il est fort probable que les localisations de sources porteront sur les cortex auditifs secondaires, plus précisément sur le cortex temporal supérieur. De plus, en accord avec des études antérieures, on pourrait aussi trouver que des régions frontales inférieures et pariétales soutiennent la rétention des représentations. La comparaison de nos résultats avec des études qui utilisaient du matériel présenté séquentiellement permet de distinguer les régions qui sont impliquées dans la rétention simple de celles qui contribuent aux stratégies mnésiques (possiblement regroupement et répétition interne).

Tous les participants ont signé le formulaire de consentement informé (voir Annexe 1) et toutes les procédures sont approuvées par le comité d'éthique de la Faculté des Arts et des Sciences de l'Université de Montréal et / ou par le comité mixte d'éthique de la recherche du Regroupement Neuroimagerie / Québec.

Partie 2 : Études empiriques

Chapitre 5 : La rétention des sons variant en timbre

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Electrophysiological correlates of the retention of tones differing in timbre in auditory short-term memory

Sophie Nolden[1, 2], Patrick Bermudez[1, 2], Kristelle Alunni-Menichini [1, 2], Christine Lefebvre[1, 2], Stephan Grimault[1, 2, 3], & Pierre Jolicoeur[1, 2]

[1]CERNEC, Université de Montréal, Québec, Canada, [2]BRAMS, Montréal, Québec, Canada, [3]CNRS, Marseille, France

5.1. Abstract

We examined the electrophysiological correlates of retention in auditory short-term memory (ASTM) for sequences of one, two, or three tones differing in timbre but having the same pitch. We focused on event-related potentials (ERPs) during the retention interval and revealed a sustained fronto-central ERP component (most likely a Sustained Anterior Negativity; SAN) that became more negative as memory load increased. Our results are consistent with recent ERP studies on the retention of pitch and suggest that the SAN reflects brain activity mediating the low-level retention of basic acoustic features in ASTM. The present work shows that the retention of timbre shares common features with the retention of pitch, hence supporting the notion that the retention of basic sensory features is an active process that recruits modality-specific brain areas.

Keywords: Audition; short-term memory; working memory; timbre; electroencephalography (EEG); event-related potentials (ERP); sustained anterior negativity (SAN).

5.2. Introduction

Short-term memory, the capacity to retain information from the environment for a short period of time, is a key capacity for human cognition and behaviour. To participate in an interesting conversation or for enjoying an artful piece of music, we need to represent the information that we have just heard for a certain time after it is no longer present in the environment. In this study, we used event-related potentials (ERPs) as indices of auditory short-term memory (ASTM). More precisely, we targeted a very basic underlying mechanism — the simple retention of tones differing in timbre. We thus aimed to isolate brain activity that directly reflects representations of these tones as they are actively held in short-term memory.

Research on short-term memory has inspired the development of various theoretical models. An influential model proposed by Baddeley and colleagues emphasises that information is not only stored for a short period of time but can also be manipulated and transformed (Baddeley, 2000; Baddeley & Hitch, 1974). The authors proposed a central executive that controls several subsidiary systems that process information in various ways. According to the model, a visuo-spatial sketch pad and a phonological loop store and manipulate modality-specific information (visual and phonological, respectively) whereas an episodic buffer provides multimodal codes to represent events or episodes. Other models of short-term memory that incorporate neurological findings also propose that simple maintenance in short-term memory would be modality-specific, taking place in sensory areas responsible for the perception of the features, though more elaborate processes (e. g. monitoring and manipulation of information held in short-term memory) might engage executive functions and their subservient areas. Activity patterns arising from perception would thereby overlap with those that contribute to retention (Cowan, 2008; D'Esposito, 2007; D'Esposito et al., 2000; Goldman-Rakic, 1987; Petrides, 1991, 2005; Postle, 2006; Postle et al., 1999; Ruchkin et al., 2003).

Given that the models described above emphasise that short-term memory is at least partly modality-specific, it seems reasonable to use stimuli that target specific senses. Regarding ASTM, much of the research to date has used language-related material, usually in the form of aurally presented words (Koelsch et al, 2009; Crottaz-Herbette, Anognoson, & Menon, 2004) or digits (Pelosi, Hayward, & Blumhardt, 1998). Despite the value of this approach, the results might not uniquely reflect fundamental processes of ASTM. When we retain language-related material, it is very likely that the brain activity we observe also reflects the use our explicit and/or implicit knowledge of language and its related codes (phonological, orthographic, etc.) to accomplish the task (Penney, 1989; Schumacher et al., 1996). The use of musical stimuli is similarly problematic given our implicit and (in a minority of the population) explicit knowledge of musical syntax.

Despite a preponderance of work using verbal material, research on the electrophysiological correlates of ASTM has gone some way to dissociate language and non-language related as well as sensory-specific electrophysiological signatures of short-term memory. For example, an interesting effect of memory load has been found during probe presentation (Pratt, Michalewski, Barrett, & Starr, 1989; see also Pratt, Michalewski, Patterson, & Starr, 1989a, 1989b). Participants had to retain visually or aurally presented digits or musical notes while brain activity was measured with electroencephalography (EEG). The number of items to be retained (memory load) was varied. The authors observed a fronto-central positive component after probe presentation that was less pronounced for higher memory loads and generally larger for the visually-presented digits than for aurally-presented digits or musical notes. Furthermore, a later, parieto-central component was characterized by an interaction between stimulus type and memory load. Additionally, ERPs differed between the memory load conditions, thus reflecting different degrees of memory demand. Note, however, that the data were analyzed during a relatively long interval during and after probe presentation and may consequently have been contaminated with a variety of processes other than memory, *per se*, such as perception, decision making, and response selection. Nonetheless, the study provided useful data concerning variations in memory load and indications that short-term memory for different types of information — visual and auditory short-term memory — may rely on at least partly distinct structures that produce dissociable brain activity, consistent with theoretical notions on the modality-specificity of short-term memory.

Another study focused on brain activity during the retention interval (Lang, Starr, Lang, Lindinger, & Deecke, 1992), participants had to retain visually or aurally presented digits or musical notes. ERPs were assessed during the retention interval, thus focusing on activity related to short-term memory and not to other processes such as encoding, retrieval, comparison, decision-making, or response selection. A frontal negative shift was observed that was more pronounced for aurally-presented digits than for visually-presented digits. Furthermore, this negative shift was more pronounced for musical notes than for aurally-presented digits. Over posterior temporal regions, on the other hand, a negative shift occurred that was more pronounced for visual than auditory stimuli. The authors interpreted this to mean that short-term memory relies on modality-specific processes and processes specific for verbal material. Although no memory-load manipulation was used in this study, the results suggest that a sustained negative frontal ERP might reflect the retention of aurally presented material and be sensitive to whether or not the stimuli are linguistic in nature (see also Pelosi, Hayward, & Blumhardt, 1998; Ruchkin et al., 1997).

Other ERP studies (Alunni-Menichini et al., 2013; Guimond et al., 2011; Lefebvre et al., 2013) have introduced a paradigm that used several strategies to minimize possible confounds between brain activity related to ASTM and other cognitive processes (see also Grimault et al., 2013; Nolden et al., 2013). First, the stimuli were pure tones differing in pitch that were not very likely to be verbally encoded. Second, the relations of frequencies (pitches) between these tones did not correspond to those of known musical scales and therefore tone sequences would be less likely to match, and activate, our implicit knowledge of music (Trehub, Schellenberg, & Kamenetsky, 1999). Third, memory load was varied while other parameters of the task remained constant, thus making it possible to measure activity related to changes in short-term memory load and minimize the effect of activity related to the task. Fourth, ERPs were assessed during the retention interval (between stimulation and probe), thereby avoiding contamination of brain activity related to perception, encoding, retrieval, comparison, decision-making, or response selection. A fronto-central ERP, predominantly at electrode site AFz, was isolated during the retention interval and named sustained anterior negativity (SAN). Importantly, this ERP became more negative as memory load increased. Additionally, the growth of the SAN with memory load was larger for participants with higher memory capacity (Alunni-Menichini et al., 2013; Lefebvre et al., 2013).

Lefebvre et al. (2013) provided evidence for modality-specific electrophysiological indices of STM by comparing the correlates of the retention of tones and visual items. The SAN was only observed for the retention of tones whereas only the visual items gave rise to a sustained posterior contralateral negativity (SPCN, Klaver, Talsma, Wijers, Heinze, Mulder, 1999; Robitaille et al., 2010; Vogel & Machizawa, 2004）.

The electrophysiological studies of ASTM described above have only used tones varying in multiple tonal characteristics or pure tones varying in pitch. The first approach made difficult the isolation of low-level processes related to the retention of tones and, though the latter approach permitted to focus on the low-level retention of very simple acoustic material, the interpretation of the results of these studies was strictly speaking only valid for the retention of pitch and not for ASTM in general, including the retention of other characteristics of sounds.

Sounds have different characteristics such as pitch, duration, loudness, spatial location, and timbre. One approach to study simple tone retention is to vary one sound characteristic at a time. In this study, we chose to focus on timbre. Timbre can be described as the quality of a sound that distinguishes different musical instruments or differences in voice quality across speakers, as for example when we compare a note played on a violoncello with the same note played on a saxophone, or a Les Paul[1]. Timbre is a multidimensional characteristic that is determined by frequency and time, with attack and the relative intensity of harmonics often emphasized as having particular importance. (Caclin et al., 2006; Caclin, McAdams, Smith, & Winsberg, 2005; Grey, 1977; Marozeau, de Cheveigné, McAdams, & Winsberg, 2003; McAdams, Winsberg, Donnadieu, Soete, & Krimphoff, 1995; Plomb, 1970; Samson, Zatorre, & Ramsay, 1997). As will soon be described, we mainly made use of the variation of the relative intensity of the harmonics in the design of our stimuli.

Timbre and pitch are distinct tonal characteristics and a behavioral study has shown that timbre and pitch are dissociated in auditory short-term memory (Semal & Demany, 1991). There are nonetheless small interactions between the perception of pitch and timbre (for example Singh & Hirsh, 1992; Vurma, Raju, & Kuuda, 2010; Warrier & Zatorre, 2002). Russo and Thompson (2005) demonstrated that timbre can also influence the perceived size of a pitch interval. In their study, two tones were played consecutively with an interval of either six or seven semitones. Pitch could either be ascending or descending. The brightness of the timbre was either congruent (a dull timbre for the low pitch tone and a bright timbre for the high pitch tone), incongruent (a dull timbre for the high pitch tone and a bright timbre for the low pitch tone), or identical for both tones (both tones either dull or bright). Participants judged the size of the tone interval. Six-semitone intervals with congruent timbre were judged to be larger than seven-tone intervals with incongruent timbre, thus the smaller interval was perceived to be larger than the larger interval in certain timbre configurations. This effect occurred especially in conditions in which participants had difficulties to discriminate the two pitch intervals and was under some circumstances also found for musicians. The influence of timbre on interval perception can, however, not be caused by the influence of timbre on pitch perception, as was demonstrated in a control experiment. For investigating the retention of timbre, it is thus important to minimize the possibility that participants retain pitch differences evoked by timbre changes in addition to the timbre itself. Therefore, the tones differing in timbre that we used had identical fundamental frequencies. Furthermore, their spectral composition did not show a monotonic change in one single physical property (see method section for details).

In this study, we modified the paradigm of Lefebvre et al. (2013) to render it suitable to the investigation of the electrophysiological correlates of the retention of timbre. We aimed to show similarities to the retention of pitch in order to corroborate modality-specificity and active processing of short-term memory in the sense that brain activity arising from perception is held in active state. We also wanted to elucidate the role of simple retention in ASTM, meaning that representations of tones arising from perception are held in an active state without necessarily recruiting mnemonic strategies, especially related to melodic contour. Thus far, the SAN has only been shown in studies on the retention of pure-tones differing in pitch (Alunni-Menichini et al., 2013; Guimond et al., 2011, Lefebvre et al., 2013). If a general mechanism of retention of individual sounds in ASTM exists, we expect that related brain activity should be similar for other basic characteristics of sounds. We therefore hypothesize that a SAN will be observed when participants retain tones differing in timbre in ASTM. In previous work with sequences of sounds, memory load was manipulated by using sequences of sounds of different length, which also increased the number of pitch transitions between tones and the complexity of pitch contours across memory load conditions. Finding a SAN in response to sequences of tones of fixed pitch but different timbres would support the hypothesis that the SAN represents basic retention of individual representations of sounds.

5.3. Method

Participants

Forty-seven neurologically normal college students participated in the experiment. All subjects had normal hearing as assessed with an audiometer (MAICO M790) before the experiment. Participants gave informed consent and all procedures were approved by the ethics board of the Faculty of Arts and Sciences at Université de Montréal. Participants were compensated $20 Canadian for a test session that lasted about two hours (including the audition test and EEG installation). Data from 10 participants who had more than 50% of their trials rejected due to artifacts, blinks, or eye movements were excluded from data analysis.

The remaining 37 participants (8 male) had a mean age of 22 years (*SD* = 3 years, range: 19-34 years).

Stimuli

We used seven tones differing in timbre and one white noise stimulus. The tones differing in timbre had the same fundamental frequency (440 Hz) but the intensity of their harmonics was varied so as to produce distinctive timbres that could be distinguished one from another even by untrained observers. We used a 440 Hz sine wave as the fundamental frequency and added multiples as harmonics with varying relative intensity. Figure 1 illustrates the spectra of the acoustic stimuli. For example, the harmonic sound no. 5 that emphasizes odd harmonics was created by decreasing the intensity of the second harmonic relative to the fundamental by 24.6 dB, increasing the intensity of the third harmonic relative to the fundamental by 3.6 dB, decreasing the intensity of the fourth harmonic by 17.8 dB relative to the fundamental, increasing the fifth harmonic by 2 dB relative to the fundamental, etc. Importantly, the tones differing in pitch are not characterized by a monotonic change in one single physical property. For example, sound no. 1 shows a monotonic decrease of intensity with increasing frequency, whereas sound no. 6 shows an increase, a decrease, and another increase of intensity with increasing frequency, and sound no. 5 shows an attenuation of every second harmonic. Hence, the differences between our stimuli can be described in multiple ways (brighter, noisier, more nasal, etc) on different timbre dimensions (e.g. Plomb, 1970). This reduces the possibility that the stimuli can be easily ranked regarding their brightness, which has shown to have a small effect on pitch perception (for example Warrior & Zatorre, 2002). We chose synthetic sounds over those of musical instruments to avoid associations with long-term memory contents related to music.

Each tone and the white-noise stimulus had a duration of 200 ms, including linear onset and offset ramps of 20 ms. The subjective loudness of the sounds was adjusted according to an equal-loudness contour function (Glasberg, & Moore, 2006). After adjusting the loudness, the intensity of the tones slightly differed (mean intensity: 71.13 dB SPL, range: 69 – 77 dB SPL).

The tones were presented binaurally via Etymotic ER-1 earphones and soft plastic ear inserts.

INSERT FIGURE 1 ABOUT HERE

A white cross at the centre of a computer screen was used to facilitate fixation. A white circle was presented when a response was required and colored feedback circles (green for correct, red for incorrect, and dark red for no response within 3 s) were centrally presented on a gray background using a personal computer with a 17-inch CRT monitor.

Procedure

Participants sat in an electrically shielded room in front of an electrically shielded computer monitor. They were instructed to fix the center of the screen as soon as the fixation-cross appeared and to avoid blinking or moving their eyes during the trials.

Participants performed five memory blocks and five control blocks that alternated. Half of the participants started with a memory block and the other half with a control block. The ten experimental blocks each had 60 trials (600 experimental trials in all) and were preceded by two practice blocks of twelve trials each, one for each condition.

Figure 2 displays the trial structure. In the memory blocks, participants pressed the space bar to initiate each trial. After a mean interval of 500 ms (+/- 100 ms random jitter), a fixation cross appeared, and 500 ms later the tone sequence started. Tone sequences had 1, 2, or 3 tones differing in timbre preceded by the number of white-noise stimuli required to produce sequences of 4 sounds, as shown in Figure 2 (i.e., WN WN WN T; WN WN T T; or WN T T T, where WN represents a white-noise stimulus, and T represents a tone). The tones were chosen randomly and were never repeated within a sequence. They were separated by silent intervals of 200 ms each. The number of tones differing in timbre varied randomly from trial to trial, but the number of trials per block was the same for all load conditions. The first sequence was followed by a retention interval of 2000 ms and, then, a second (probe) sequence of tones. The second sequence had the same number of tones as the first sequence but did not have preceding white noises. The second sequence was the same as the first sequence in half of the trials and different in the other half. When the two sequences differed, two adjacent tones were presented in the opposite order for trials of conditions load 2 and 3. For condition load 1, a different tone was randomly chosen. 500 ms after the second presentation, a white circle replaced the fixation cross, indicating that participants could respond within the next 2500 ms. Participants had to judge if the two sequences were the same or different. They responded with the index fingers of the left and right hand. Half of them responded by pressing the “c” on the keyboard for identical sequences and the “m” for different sequences. This mapping was reversed for the other half of the participants. After the response, the circle turned red or green, thus giving feedback. When no response had been made within 2500 ms after the onset of the white circle, the circle turned dark red. Feedback remained on the screen until the participants started the next trial by pressing the space bar.

In the control condition, the trial structure was the same as in the memory condition. Here, participants were asked to ignore the first sequence. They had to indicate if the last tone of the second sequence was “noisy” or “clear.” Examples of “noisy” (somewhat ‘buzzy’ timbre) and “clear” (more ‘round’ and like a pure tone) sounds were given before the practice block of the control condition. In half of the trials, the tone was to be classified as “noisy,” in the other half of the trials, as “clear,” which was indicated by pressing the “c” or the “m” key. The mapping of the tone classification to the keys was counterbalanced over participants. In the control condition, the two sequences were not related to each other, so that there would be no benefit from attending the first sequence.

INSERT FIGURE 2 ABOUT HERE

Electrophysiological recording and analysis

EEG signals were recorded continuously with a BioSemi ActiveTwo system at a sampling frequency of 512 Hz. Sixty-four Ag/AgCl electrodes were placed in an elastic cap following the International 10–10 system at Fp1, Fpz, Fp2, AF7, AF3, AFz, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, POz, PO4, PO8, O1, Oz, O2, and Iz. Additional electrodes were placed at the left and right outer canthi to track horizontal eye movements, below the left eye to track vertical eye movements (in combination with the frontal electrode Fp1 that is placed above the left eye), and on the left and right mastoids.

EEG data were re-referenced offline to the average of the two mastoids. The difference between the electrodes on the left and right outer canthi was defined as the horizontal electrooculogram (HEOG), and the difference between the electrode below the left eye and Fp1 as the vertical eletrooculogram (VEOG). We applied a 0.1 Hz, 36 dB/octave high-pass and a 10 Hz, 36 dB/octave low-pass filter on HEOG and VEOG channels to facilitate artifact detection. On all other electrodes, we applied a 0.001 Hz, 36 dB/octave high-pass filter and a 40 Hz, 36 dB/octave low-pass filter. Trials containing eye movements (HEOG changes exceeding 50 μV within a time window of 300 ms) or blinks (VEOG changes exceeding 75 μV within a time window of 150 ms) were excluded from further analysis. Individual electrodes that showed artifacts (signal changes exceeding 200 μV compared to the baseline) were interpolated using the mean signal of the surrounding electrodes. Trials with more than seven electrodes needing interpolation were excluded from further analysis. The data of a participant was entirely excluded when more than half of the trials had to be rejected due to artifacts.

Continuous EEG was segmented from 1600 ms before the onset of the 'retention' interval (200 ms before the first sound of the first sequence) until 2000 ms after the onset of the 'retention' interval (end of the 'retention' interval). Trials were baseline corrected from -1600 to -1400 ms before the onset of the 'retention' interval. Trials free from artifacts were averaged for each load condition (1, 2, and 3) and each task condition (memory and control) over all subjects. Successful and unsuccessful trials were not analyzed separately in order to maintain a good signal-to-noise ratio in all conditions with a sufficient number of trials. The mean voltage at AFz was computed for a time window from 900 ms to 1900 ms after the onset of the 'retention' interval and submitted to a 2x3 ANOVA with the between subjects factors task (memory and control) and load (1, 2, and 3). The electrode site was selected based on previous studies on the SAN (Guimond et al., 2011; Lefebvre et al., 2013). Our analysis time window began after late sensory activity and ended 100 ms before the second stimulation to avoid any anticipatory activation.

5.4. Results

Behavioral data

Mean percent correct in the memory task was 93%, *SD* = 7%, for load 1, 90%, *SD* = 8%, for load 2, and 81%, *SD* = 10%, for load 3. Mean percent correct in the control task was 85%, *SD* = 9%, for load 1, and 83%, *SD* = 9%, for load 2 and load 3. A 2x3 ANOVA for repeated measures with the factors Task (memory and control) and Load (1, 2, and 3) revealed a significant main effect of Task with higher accuracy in the memory task, $F(1, 36) = 12.06$, $MSE = 0.01$, $p < .0015$, $\eta^2 = .25$, a significant main effect of Load with decreasing accuracy as load increased, $F(2, 72) = 35.29$, $MSE = 0.003$, $p < .001$, $\eta^2 = .50$, and a significant interaction between Task and Load reflecting a larger decrease in accuracy as load increased for the memory task than for the control task, $F(1.53, 55.14) = 27.42$, $MSE = 0.003$, $p < .001$, $\eta^2 = .43$, corrected according to Greenhouse-Geisser. We decomposed the interaction and found that the main effect of load was significant for memory blocks, $F(1.40, 50.23) = 47.37$, $MSE = 0.004$, $p < .001$, $\eta^2 = .57$, corrected according to Greenhouse-Geisser, but did not reach significance for control blocks, $F(2, 72) = 2.38$, $MSE = 0.002$, $p < .10$, $\eta^2 = .06$. These results show that our memory load manipulation was effective as the task was more difficult with higher memory load. Furthermore, there was no effect of memory load in the control task, which did not involve memory manipulations. See Table 1 for supplementary behavioral results.

Event-related potentials

Grand averages at AFz for all load conditions are shown in Figure 3.a for the memory task and Figure 3.b for the control task (see Figure 4 for a topographical map).The first part of the waveform before the onset of the 'retention' interval shows a similar pattern in both task conditions. An auditory N1 is clearly visible for each timbre stimulus superimposed on a general negative-going potential during the presentation of the first sequence. In addition, the

N1 responses were more pronounced for tones differing in timbre than for white noises. The experiment was not designed to elucidate differences in the processing of timbre tones or white noise stimuli, however, one could speculate that thjs is due to the fact that only the timbre tones are task-relevant.. In the first part of the 'retention' interval, the voltage became more positive until about 700 ms into the retention interval, after which levels remained relatively stable. In the memory task, there was a sustained component in the latter part of the retention interval that separated the three load conditions and was more negative with increasing memory load (mean voltage from 900 ms to 1900 ms for load 1: 1.03 µV, *SD* = 6.57 µV, for load two: 0.10 µV, *SD* = 6.93 µV, for load three: -1.10 µV, *SD* = 5.13 µV). In the control task, the voltage was positive for all load conditions in the latter part of the 'retention' interval. The voltage was slightly more positive for load 2 compared to load 1 and load 3 (mean voltage from 900 ms to 1900 ms for load 1: 1.12 µV, *SD* = 7.31 µV, for load two: 2.53 µV, *SD* = 6.28 µV, for load three: 1.11 µV, *SD* = 7.34 µV).

INSERT FIGURE 3.a and 3.b ABOUT HERE

A 2x3 ANOVA with the factors Task (memory and control) and Load (1, 2, and 3) revealed a significant main effect of Task, $F(1, 36) = 7.12$, $MSE = 19.44$, $p < .012$, $\eta^2 = .17$, reflecting the generally more negative potential in the memory task. There was a significant interaction between Task and Load, $F(2, 72) = 3.72$, $MSE = 9.42$, $p < .03$, $\eta^2 = .08$. The main effect of load did not reach significance, $F(2, 72) = 2.86$, $MSE = 12.55$, $p > .06$, $\eta^2 = .07$. We decomposed the interaction and found a significant load effect in the memory task ($F(2, 72) = 3.26$, $MSE = 12.96$, $p < .045$, $\eta^2 = .08$) but not the control task ($F(2, 72) = 2.72$, $MSE = 9.01$, $p > .07$, $\eta^2 = .07$). This means activations at AFz increased in negativity with increased loads in the memory task, but not in the control task, as expected based on previous research involving the SAN.

INSERT FIGURE 4 ABOUT HERE

5.5. Discussion

The goal of the present study was to measure electrophysiological correlates of the retention of tones differing in timbre in ASTM. We focused on the SAN component which had been observed in studies involving the retention of auditory representations of sounds differing in pitch (Alunni-Menichini et al., 2013; Guimond et al., 2011, Lefebvre et al., 2013). We used a classic memory paradigm in which stimuli with the same pitch but differing in timbre were encoded, retained for a short period, following which memory was tested with a second sequence that was the same or different as the first. Since the SAN is characterized by an increase in amplitude with increasing memory load, we manipulated memory load by presenting different numbers of tones to be encoded and retained. Importantly, participants also performed a control task during which they heard the same sequences of tones but memory of the first sequence was not required.

During memory blocks, we found a component with a maximum near electrode site AFz during the latter part of the retention interval that was characterized by an increasing negative deflection with increasing memory load. The effect sizes are consistent with preceding studies (Lefebvre et al., 2013). The absolute value of the ERP cannot easily be interpreted; however, the decrease with increasing memory load was expected. The behavioral data suggest that participants' span was not yet systematically exceeded in the highest load condition. Once span is exceeded, we would predict a plateau in the ERP, as it has been previously observed for the retention of pich (Alunni-Menichini et al., 2014). During control blocks, we observed a different pattern. Overall, the ERPs in the 'retention' interval were more positive in control blocks than in memory blocks. Memory and control blocks differed in the task but had identical stimulation, so the sustained component found in the latter part of the retention interval in memory blocks was not due to sensory persistence of the tones. We suggest that the component we found was very likely the same SAN that has been observed in memory for pitch because it occurred during the retention interval of the memory blocks only and was load-sensitive.

The data of this study provide further evidence that the SAN is an electrophysiological correlate of the retention of acoustic information in ASTM. This is the first study to demonstrate a SAN with tones differing in timbre rather than pitch, thereby extending previous studies (Alunni-Menichini et al., 2013; Guimond et al., 2011; Lefebvre et al., 2013) and suggesting that the SAN reflects the retention of basic acoustic features. Several conclusions regarding the mechanisms of ASTM follow.

First, our results allow narrowing down of the specific memory activities that support the maintenance of tones. All studies revealing a SAN used memory load manipulations but the type of acoustic material and mode of presentation differed. Alunni-Menichini et al. (2013) and Lefebvre et al. (2013) used tones differing in pitch that were presented sequentially. In these designs, participants may have relied partly on the quasi-melodic pitch contour produced by pitch transitions within sequences to retain the tones, in addition to memory representations of the individual tones. A disambiguating experiment by Guimond et al. (2011) demonstrated a load-dependent SAN even whilst using simultaneously presented tones differing in pitch despite concurrent articulatory suppression, making the use of such memory strategies very unlikely if not impossible.

In the present study, we used a sequential presentation of tones that differed in timbre but held fundamental pitch constant. The influence of timbre on pitch perception has been shown to be too small and too inconsistent to create the percept of different musical notes for timbre tones with identical fundamental (McDermott, Lehr, & Oxenham, 2008; Vurma, Raju, & Kuuda, 2010). Thus, perceived transitions in pitch that could be retained in addition to the individual tones were unlikely and overt singing to support retention was not possible as the vast majority of people cannot reproduce the subtle timbre variations that distinguished the stimuli. Nonetheless, some other form of rehearsal could still be used (e.g. looping the sequence in the mind's ear). McDermott and collaborators (2008) recently demonstrated that a pattern of brightness changes can be extracted from timbre sequences. Compared to the study by McDermott et al. (2008), the extraction of a 'timbre contour' (increase or decrease of brightness compared to the preceding stimulus) might have been more difficult here, because the differences between the stimuli were much more complex and not characterized by a monotonic change in one single physical property (see Fig. 1) and because we used gaps in between the tones differing in timbre. However, although not being as easy to extract as in the study by McDermott et al. (2008), a 'timbre contour' could have been retained in addition to the individual timbre tones.

Maintaining representations of tones in an active state is a common denominator of the mnemonic activities and strategies for all three of the aforementioned experimental approaches, and they all revealed a load-sensitive SAN. We conjecture that low-level features of pitch and timbre are preserved in a store that requires greater neural activity as memory load increases. Future research is needed to better elucidate the neural implication of this store. We further argue that this mechanism is sufficient for retaining acoustic information for a short period of time, even when tone representations are not constantly refreshed by various means as internal singing or rehearsal (Guimond et al., 2011). However, retaining a ‘timbre contour’ or using memory strategies as covert rehearsal may support retention while not being an indispensable prerequisite.

Second, we found a very similar activity pattern in the current study on the retention of timbre as in previous studies on the retention of pitch, thus replicating a finding on the retention of a different tonal characteristic. Some prominent models of short-term memory (Cowan, 2008; D’Esposito, 2007; D’Esposito et al., 2000; Goldman-Rakic, 1987; Petrides, 1991, 2005; Postle, 2006; Postle et al., 1999; Ruchkin et al., 2003) claim that short-term memory is at least partly modality-specific, for example, through divergent recruitment of brain areas when comparing visual and auditory short-term memory (see Lefebvre et al., 2013). Considering that we carefully created the stimuli to ensure that they could not be easily associated with long-term memory contents such as explicit or implicit musical or language-related knowledge, we suggest that the retention of simple material consists of sustained activation of sensory representations in the corresponding sensory cortices and their association areas amongst others. However, when memory items can be associated with long-term memory contents, additional areas may be involved. In addition, when mnemonic strategies such as rehearsal are used, so-called executive processes and the areas that subserve them may also become involved.

Third, the results of the present study confirm that our task exceeds the demands for sensory memory. The duration of the retention interval used in this study raises the question of whether our ERP results reflect short-term memory or a form of even lower-level sensory persistence. Sensory registers usually refer to modality-specific pre-attentive antecedents of short-term memory that hold items unfiltered and without conscious control (Atkinson & Shiffrin, 1968). These sensory registers, whereof the one responsible for acoustic items was called echoic memory (Neisser, 1967), are claimed to possess a large capacity but a fast decay. The lifespan of echoic memory is under debate; some studies pointed to durations as short as 250 ms (e.g., Massaro, 1970), whereas others pointed to durations as long as 10 seconds (e.g., Sams, Hari, Rif, & Knuutila, 1993; see also Massaro & Loftus, 1996). Although the longer among these estimates for echoic memory would overlap with the retention interval in our study, our data demonstrate that our memory task elicited something other than a low-level echoic memory. The most important evidence challenging a sensory-persistence interpretation of our results is that the memory load effects on ERPs differed sharply between the memory blocks and the control blocks, even though the stimulation patterns were identical. If the observed brain activity reflected an automatic form of sensory persistence, we should have observed identical patterns of ERPs across the memory and control tasks. The load-sensitive response of the SAN only in the memory task provides very strong disconfirmation of any account based on sensory-persistence. In addition, we doubt that our task could have been done effortlessly, because performance substantially decreased as memory load increased and the task became more difficult. Note that, due to the white-noise fillers, an equal number of sounds was presented in the first sequences for all load conditions. These two observations were equally true for other ERP studies on the SAN (Guimond et al., 2011; Lefebvre et al., 2013). We argue the memory task requires retention processes that are different from echoic memory, i.e. a more abstract form of ASTM that nonetheless preserves low-level acoustic properties of sound.

In conclusion, our results demonstrate that auditory short-term memory relies at least partly on active modality-specific processing, most importantly the sustained activation of sensory representations. The present work further provided additional support for the SAN as a specific index of brain activity related to the retention of acoustic features in a memory store specialized for the retention of auditory objects.

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5.7. Footnotes

1 A Les Paul is an electric guitar with a very characteristic timbre.

5.8. References

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5.9. Tables

Table 1. Behavioral data. Hits rate, false alarm rate, d', ß, and reaction times (RT) are shown for each load condition.Mean values are followed by standard deviations (in brackets).

Timbre - Table 1

	Load 1	Load 2	Load 3
Hit rate	.94 (.09)	.90 (.09)	.87 (.09)
False alarm rate	.08 (.08)	.09 (.10)	.24 (.15)
d'	3.39 (0.88)	3.00 (0.99)	2.05 (0.89)
ß	2.24 (1.79)	1.19 (1.22)	2.45 (3.21)
RT (ms)	436 (134)	411 (123)	415 (129)

5.10. Figure Captions

Figure 1. Periodogram Power Spectral Density Estimate for all acoustic stimuli. The first graph represents the white noise tone, all other graphs the harmonic tones differing in timbre.

Figure 2. Sequence of events in each trial. Sequences of 4 sounds containing 3, 2, or 1 white noises followed, respectively, by 1, 2, or 3 tones differing in timbre were presented binaurally. All stimuli are represented by grey boxes on the timeline. After a silent retention interval of 2000 ms, a second sequence containing the same number of tones differing in timbre was presented. Participants indicated if the second sequence was the same or different as the first (only 'same' sequences shown here). Sound events had a duration of 200 ms and were separated by 200 ms of silence. See text for further details.

Figure 3. Grand average event-related potentials at AFz. Time 0 refers to the onset of the retention interval, which began immediately after the presentation of the last tone in the first sequence.

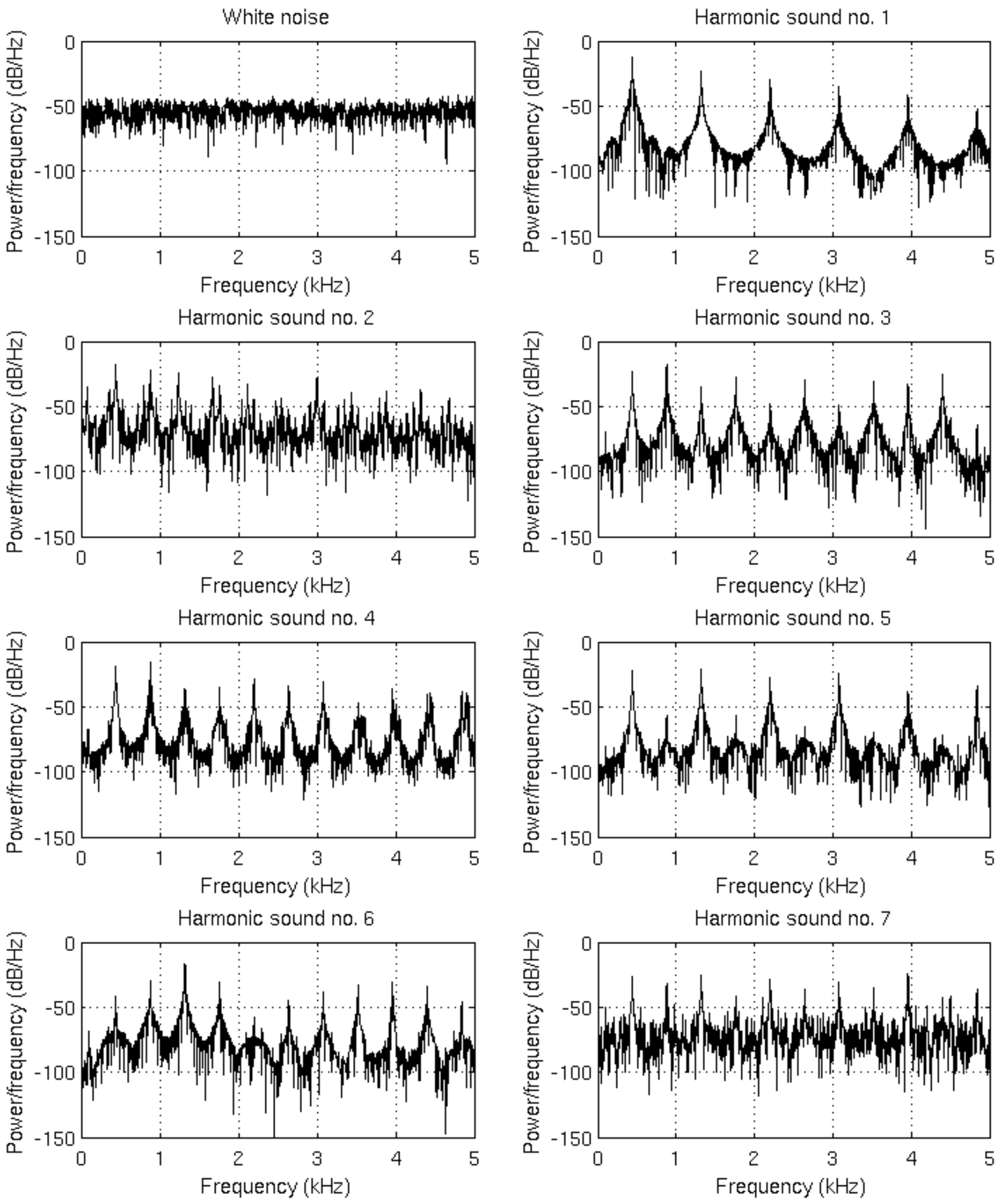
Panel a. Event-related potentials for load 1, load 2, and load 3 in the memory blocks.

Panel b. Event-related potentials for load 1, load 2, and load 3 in the control blocks.

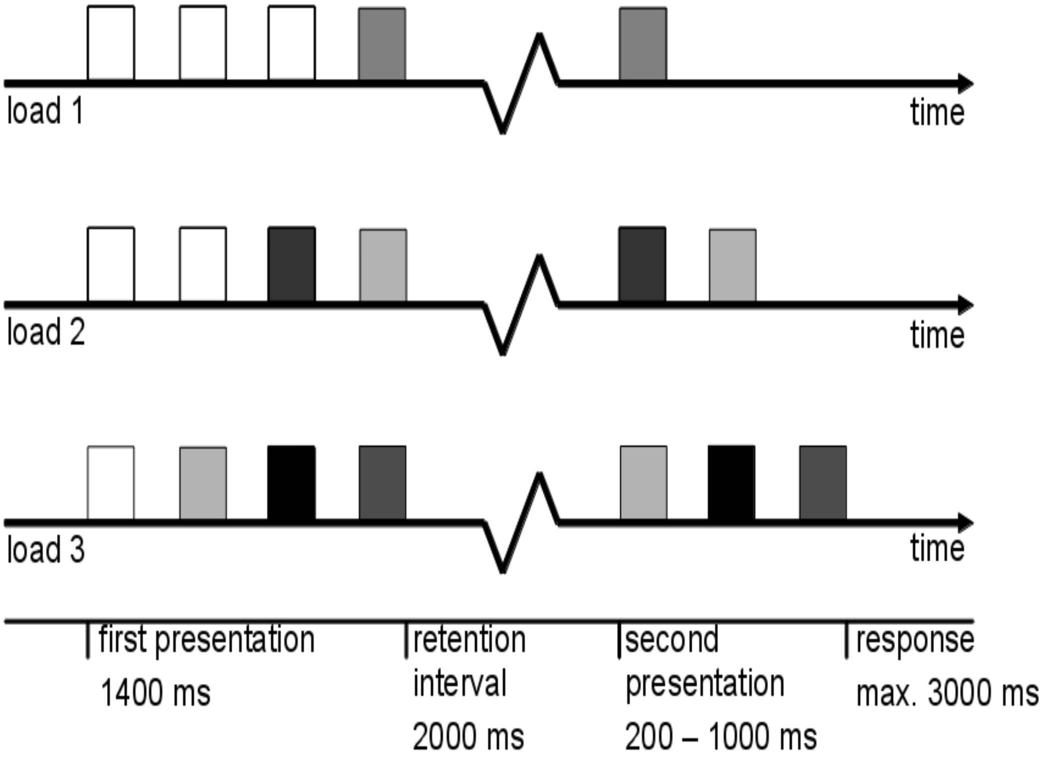
Figure 4. Topographical maps of the voltage difference between load 3 and load 1 in memory blocks, averaged during the period from 900 to 1900 ms from the beginning of the retention interval.

5.11. Figures

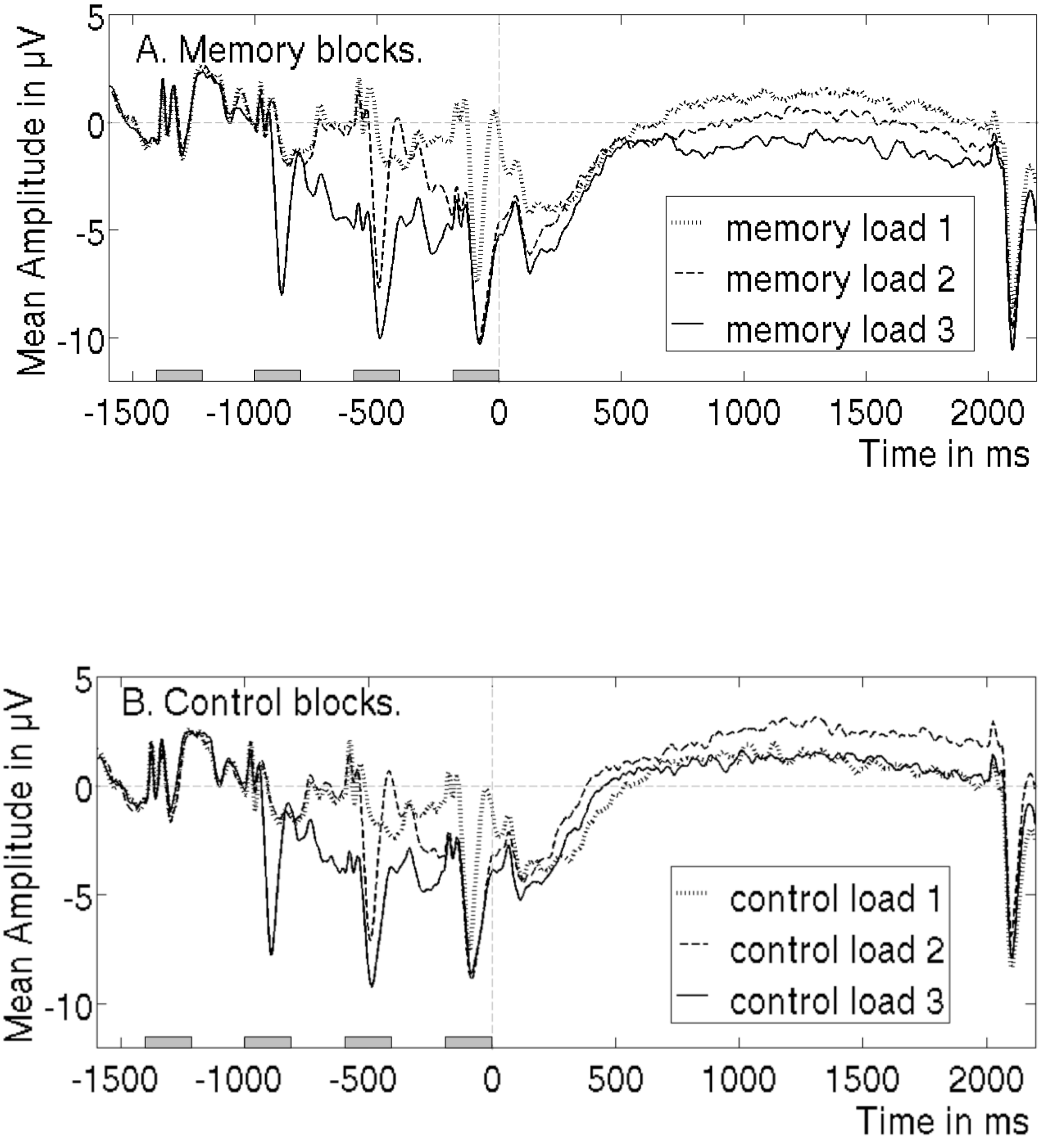
Timbre - Figure 1



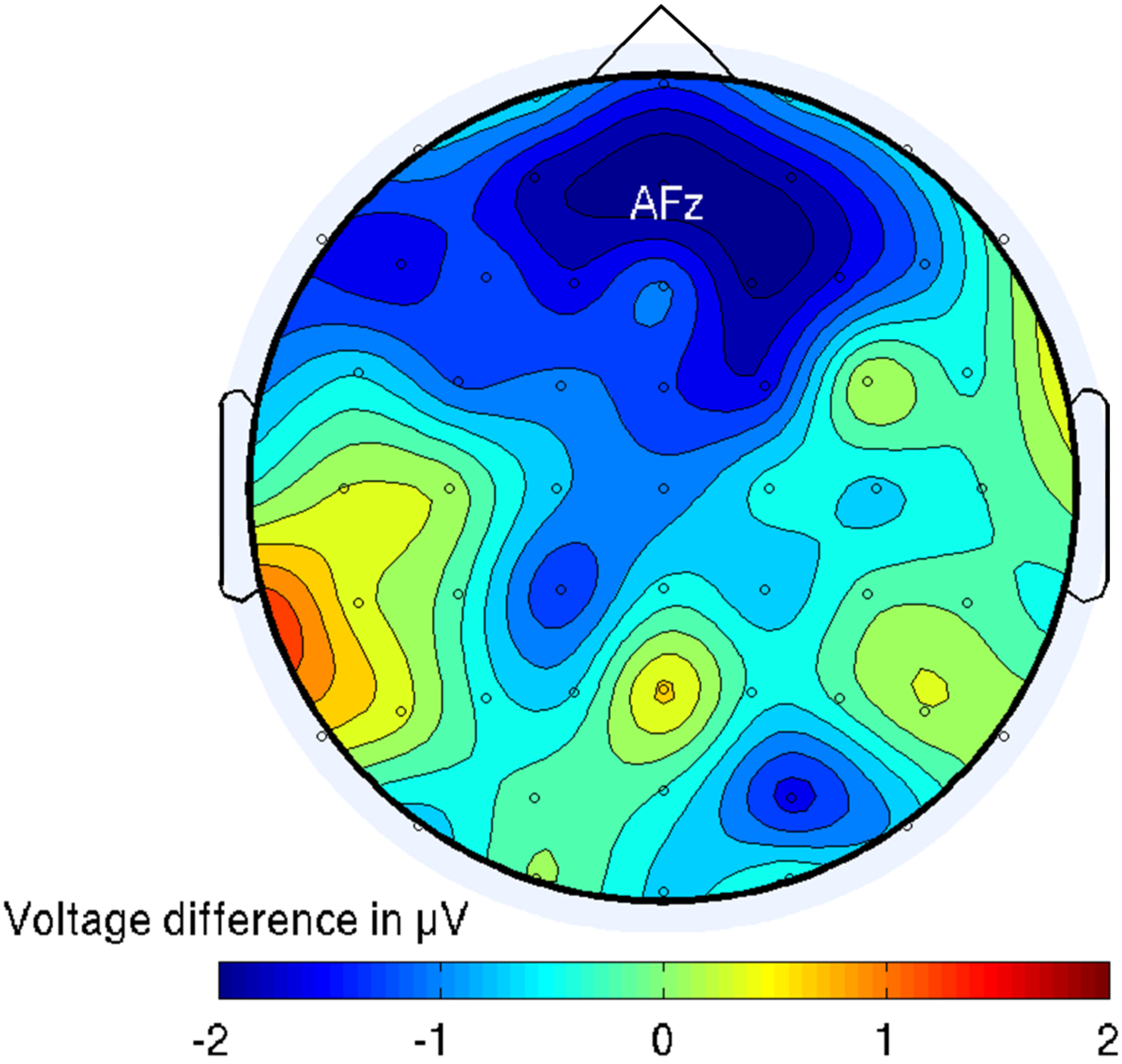
Timbre - Figure 2



Timbre - Figure 3



Timbre - Figure 4



Chapitre 6 : Analyses temps-fréquence reliées à la rétention et à la récupération des sons

Article en préparation :

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Probing auditory short-term memory: Oscillatory electric brain activity related to retrieval and comparison

Sophie Nolden[1, 2], Christine Lefebvre[1, 2, 3], Patrick Bermudez[1, 2], Stephan Grimault[1, 2, 3], &
Pierre Jolicoeur[1, 2, 3]

[1]CERNEC, Université de Montréal, Québec, Canada, [2]BRAMS, Montréal, Québec, Canada, [3]CRIUGM, Université de Montréal, Québec, Canada

6.1. Abstract

Participants encoded tones into auditory short-term memory, retained them for a short time, and were then probed with identical or different tones while we recorded ongoing brain activity using electroencephalography (EEG). We examined oscillatory brain activity related to probe processing in the ASTM tasks. Participants retained simultaneously presented tones (Experiment 1) or sequences of tones (Experiment 2) that were then compared to probe tones after a retention interval of 2000 ms. We focused on the amplitudes of oscillatory activity during the tasks. We found differences in the amplitude of alpha-band activity (8–12 Hz) for probes that matched memory versus probes that did not match memory, and differences in the amplitude of beta-band (18–28 Hz) activity depending on memory load. We argue that beta band activity reflects access to retained items whereas alpha band activity appears related to the result of the comparison process between the probe and the contents of auditory short-term memory.

Keywords: Audition; auditory short-term memory; auditory working memory; probe processing; pitch; electroencephalography (EEG); brain oscillations; alpha band; beta band.

6.2. Introduction

Auditory short-term memory (ASTM) is the capacity to retain acoustic information actively for a short period of time. When the acoustic energy is no longer present in the environment, further processing must be achieved via a corresponding representation maintained in a memory system in the brain. Representations of acoustic stimuli can then still be accessed and manipulated after a delay. In this study, we focused on brain activity during retrieval and memory-comparison operations that follow probe processing in auditory short-term memory tasks. More precisely, we measured brain activity with electroencephalography (EEG) and estimated the amplitude of oscillations in the alpha (8–12 Hz) and beta band (18–28 Hz).

When investigating neural correlates of short-term memory (STM), brain activity on a fine temporal scale is interesting because it reflects the ongoing temporal dynamics of rapid STM-related processes including encoding, retention, and retrieval mechanisms, as well as interactions between them. EEG and magnetoencephalography (MEG) methods are especially suitable for this purpose because of their millisecond-level temporal resolution. Previous research has focused on oscillatory brain activity related to STM because it is closely tied to the temporal dynamics of STM-related processes. In addition, dissociative patterns in different frequency bands shed light on how stimuli are treated in STM by revealing different, yet related, processes taking place at the same time. Modulations of oscillatory brain activity have been observed in a variety of experimental settings including studies targeting perception, attention, short-term memory, long-term memory, sleep, development, and other cognitive and physiological processes. Related to this variety of experimentation, a number of broad functional interpretations between oscillatory power in a given frequency band and general functions such as memory, or inhibition (see Klimesch, 1999, for a review). Even though this approach might be overly simple in some cases, it offers the tantalizing prospect of revealing general principles linking the structure of brain dynamics to function. For example, oscillatory brain activity was found to reflect how STM and attention interplay (for example Zanto & Gazzeley, 2009). Another approach is to focus on more specific links between mechanism and oscillations in particular brain structures (see Klimesch, 2012, for a review). Our approach lies within this latter framework, with a focus on activity taking place during retrieval from auditory short-term memory. To date, more research on oscillatory activity related to STM has been conducted with visual material. Given there is growing evidence that brain areas related to STM-processes are at least partly domain-specific (D'Esposito, 2007; D'Esposito, Postle, & Rypma, 2000, see also Lefebvre et al., 2013), more research is needed to elucidate if the functional significance of brain oscillations in certain frequency bands is equivalent for the retention of representations encoded in different sensory modalities (see also Spitzer & Blankenburg, 2012).

STM-related amplitude modulations have been revealed in the alpha frequency band (around 10 Hz), nonetheless its functional significance is still under debate. While previously being associated with 'cortical idling' (for a review see Pfurtscheller, Stancák Jr., & Neuper., 1996), alpha-band activity has been associated with inhibition more recently (e.g., Jensen, Gelfand, Kounios, & Lisman, 2002; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007). Support for this position comes from visual STM tasks showing that alpha-band activity over posterior electrodes decreases with the presentation of memory items and the amount of this decrease is correlated to performance (e.g., Klimesch et al., 1996; for converging evidence see Jokisch & Jensen, 2007; Medendorp et al., 2007; Sauseng et al., 2009, see also Khader & Rösler, 2011). Note, however, that an increase in alpha-band activity related to encoding has been found in an ASTM task (Krause, Lang, Laine, Kuusito, & Pörn, 1996; Pesonen, Haarala Björnberg, Hämäläinen, & Krause, 2006). During the retention of visual items, a load-dependent increase in alpha-band activity has been found (Grimault Robitaille, Grova, Lina, Dubarry, & Jolicoeur, 2009; Jensen et al., 2002) and has also been argued to reflect active inhibition of relevant sensory areas in order to protect sensory representations from overwriting (Jensen et al., 2002). Increases in alpha-band activity during the retention of visual items are also correlated to memory performance (Khader, Ranganath, & Rösler, 2010; Meeuwissen, Takashima, Fernández, & Jensen, 2011). Alternatively, it has been suggested that an increase in alpha-band activity reflects a transition to an internal processing mode (Hanslmayr, Gross, Klimesch, & Shapiro, 2011).

Research on beta band activity has long emphasised motor activity (e.g., Stancak & Pfurtscheller, 1995), but has more recently also been associated with other processes, including ASTM (Leiberg, Lutzenberger, & Kaiser, 2006; Pesonen et al., 2006). The functional significance of oscillations in the beta band remains unclear, although some authors recently suggested that alpha and beta activity show similar patterns in STM-tasks and that the functions they reflect probably overlap (Hanslmayr, Staudigl, & Fellner, 2012; Lundqvist, Herman, & Lasner, 2011). Some empirical studies focusing on the auditory domain, however, have found dissociations of the two frequency bands (Leiberg et al., 2006; Pesonen et al., 2006). For example, in a simple memory task with aurally presented verbal stimuli, an increase in EEG alpha band activity related to the encoding of memory items was accompanied by a decrease in beta band activity (Pesonen et al., 2006). More research is needed to elucidate the functional significance of beta band activity and to clarify the overlap and interplay with alpha band activity.

In the present study, we wanted to focus on oscillatory brain activity during probe presentation in an auditory memory task. In research on STM, there is a preponderance of studies with visual and language-related material, which have greatly influenced theoretical notions on STM as well as the functional interpretations of oscillatory brain activity in STM. These studies need to be complemented by empirical work focusing on other sensory modalities to broaden our understanding of STM. Here, we focused on simple and fundamental mechanisms of ASTM and applied three strategies to isolate related brain activity. First, we used a simple same-different memory task because it allows us — in combination with a time-sensitive measure of brain activity — to dissociate brain activity during different phases of the STM-task (encoding, delay, test). Second, we manipulated memory load, because we expected that memory mechanisms during retention and retrieval would be affected by load. Finally, we used very simple acoustic material that is difficult to associate to language or music, in order to target fundamental mechanisms of ASTM. We will present some considerations about each of these strategies in the following paragraphs.

1. The Sternberg memory task (Sternberg, 1966) has been widely used for studying short-term memory (STM). During the last decades, studies have revealed several electrophysiological correlates of STM during the different phases of STM tasks. Some have found that STM processes and their associated patterns of brain activity differ for different sensory modalities and for material related or unrelated to language (Penney, 1989; Ruchkin et al., 1997), during the presentation of memory tones (Lang, Starr, Lang, Lindinger, &

Deecke, 1992; Pratt, Michalewski, Patterson, & Starr, 1989b), delay (Lang et al., 1992; Ruchkin et al., 1997), and probe presentation (Pelosi, Hayward & Blumhardt, 1998; Pratt, Michalewski, Barrett, & Starr, 1989; Pratt, Michalewski, Patterson, & Starr, 1989a). Some researchers have proposed models in which STM is partly modality-specific, including some incorporating neurological findings (D'Esposito, 2007; D'Esposito et al., 2000; Petrides, 1991, 2005; Postle, 2006; Postle, Berger, & D'Esposito, 1999; Ruchkin, Grafman, Cameron, & Berndt, 2003). Neuronal activity underlying perception (and creating representations of the environment) has a large modality-specific component and is thought to be very similar to neuronal activity underpinning the retention of these representations, though more elaborate processes (e.g., monitoring and manipulation of information held in STM) might engage executive functions and their associated brain areas. In the present study, a same-different memory task will be used to isolate oscillatory brain activity related to probe presentation during the test phase of the task.

2. A parametric manipulation of the number of to-be-retained items has led to interesting results in previous event-related potential (ERP) studies. During probe presentation in STM-tasks with memory items, load-dependent ERPs, which were further influenced by the sensory modality of the memory items, have been observed (Pelosi et al., 1998; Pratt, Michalewski, Barrett, & Starr, 1989). In addition, for the memory load of 1 item, there was an effect of probe type ('same' or 'different') which albeit was absent for higher memory loads (Pelosi et al., 1998). To our knowledge, load-dependent oscillatory brain activity has not yet been investigated during probe presentation in ASTM. However, effects of probe type on oscillatory brain activity during and after probe presentation have been studied (Pesonen et al., 2006). Participants compared an aurally presented single probe word to four retained

words. EEG data were analysed using a Morlet wavelet transform. The authors found that signal amplitudes were greater for 'different' probes than for 'same' probes in the alpha (~8–12 Hz) and in the beta (~15–30 Hz) frequency bands during a relatively long time window during and after probe presentation. Although memory load had been held constant in this study, an effect of probe type could be demonstrated for a memory load higher than one. It is thus possible that time-frequency analyses are especially sensitive to this manipulation, which might have been missed in ERP analyses in previous studies because of phase cancellation during signal averaging (Tallon-Baudry & Bertrand, 1999). The present study will make an important contribution to the field by investigating oscillatory brain activity during probe presentation in an ASTM task using a memory load manipulation.

3. Because short-term memory for verbal material might rely on special mechanisms that differ from memory for basic perceptual features and likely engage long-term memory representations, we used very simple acoustic materials to avoid confounding verbal, semantic, and other long-term memory representations with the mechanisms required to retain simple acoustic features. Our materials consisted of pure tones differing in pitch. Furthermore, the frequencies we used did not correspond to the well-tempered scale, in order to minimize interactions with implicit musical knowledge and long-term memory of tone sequences associated with musical experience.

We wanted to discover oscillatory brain activity related to probe presentation in order to study retrieval and comparison mechanisms during the test phase of ASTM experiments. To do so we used two experiments that were designed to provide converging evidence for load-related brain activity related to memory during the retention phase of ASTM tasks. In Experiment 1, participants retained simultaneously presented tones that they compared to a single probe tone following a retention interval. An additional condition aimed to suppress covert rehearsal during retention. In Experiment 2, participants retained a sequence of tones that they compared to a later test sequence. The logic underlying each task / experiment is outlined in the introduction to each study. Following a study using language related auditory memory items (Pesonen et al., 2006), we wanted to find out if the same pattern of results with greater alpha band and beta band activity for 'different' than for 'same' probes holds when using non-verbal material. In addition, we wanted to explore load-dependent oscillatory brain activity during probe presentation in an ASTM task.

6.3. Experiment 1

Experiment 1 used a typical three-phase encode/retain/test memory design in which the stimuli to be remembered were pure tones. The special feature of this study was that the encoding phase used simultaneously-presented tones (see Guimond et al., 2011, Experiment 3, for ERPs related to the retention interval). During encoding and testing, sounds were presented simultaneously to both ears. During encoding, same tones appeared in both ears (diotic stimulation) in the load 1 condition and two different tones in the load 2 condition (dichotic stimulation), while the probe tones were always identical for both ears. A silent retention phase of 2000 ms separated the memory tones from the probe tones. The task was to decide whether that tone had been presented at the beginning of the trial, or not. In addition to the memory task, participants counted aloud from 1 to 10 in half of the blocks (suppression blocks) in order to create a condition in which internal rehearsal was minimized (Murray, 1986; Schendel & Palmer, 2007). Here, we focused on brain activity during the test phase, and in particular on differences between 'same' and 'different' probes. Moreover, we aimed to show an effect of memory load. Because a single probe tone was presented in both memory load conditions, load effects during and after probe presentation could not be due to differences in physical stimulation and thus any differences reflected an interaction of memory content with probe processing, likely reflecting retrieval, comparison, and decision processes required to perform the memory task.

Although the main focus of Experiment 1 was on brain activity related to probe presentation, we also inspected the retention interval because a series of experiments has revealed a load-sensitive event-related potential (ERP), the sustained anterior negativity (SAN), during the retention phase for non-verbal acoustic items. In these experiments, participants retained different numbers of tones varying in pitch. A sustained fronto-central component, mainly at electrode site AFz, became more negative when memory load increased (Guimond et al., 2011; Lefebvre et al., 2013; see Nolden, Bermudez et al., 2013, for tones differing in timbre; see Ruchkin et al., 1997, for load effects during the retention of verbal material; see Nolden, Grimault et al., 2013 for underlying brain areas based on companion MEG studies). For the present study, it is important to rule out that load effects are carried over from previous phases of the memory task, and therefore, the signal during the retention interval was analyzed at the same electrode sites as during probe presentation.

6.3.1. Method

Participants. Forty-five neurologically normal college students participated in the experiment. Participants gave informed consent and all procedures were vetted by the appropriate ethics board at Université de Montréal. All participants reported normal hearing. Data from 14 participants who had an excessive number of trials rejected due to artifacts, blinks, or eye movements were excluded from data analysis. The remaining 31 participants

(23 female) had a mean age of 21 years (SD = 3 years, range: 18-30 years). All participants but one were right-handed.

Stimuli and procedure. We used 14 pure tones differing in pitch and one white noise. The tones differing in pitch were so-called non-musical tones (Trehub, Schellenberg, & Kamenetsky, 1999). They ranged from 380 Hz to 1375 Hz and were created by multiplying the starting frequency and each resulting frequency by $2^{1/7}$ and, therefore, the relation of their frequencies did not correspond to those of an equal-tempered scale. The tones had a duration of 200 ms, including onset and offset ramps of 20 ms each. All acoustic material was presented via Etymotic ER-1 earphones and soft plastic ear inserts. A white fixation cross, a white circle, and coloured feedback circles (green for the correct answer, red for the wrong answer, and dark red for no answer within the response window) were centrally presented on a gray background.

Participants sat in an electrically shielded room in front of an electrically shielded computer monitor. They were instructed to fix the fixation cross as soon as it appeared and to avoid blinking and moving their eyes during the trials. Participants performed five blocks with concurrent articulatory suppression and five blocks without suppression. Half the participants started with the five blocks without suppression and the other half with the five blocks with suppression. Each experimental block consisted of 40 trials, thus resulting in 400 trials in total. Blocks with and without suppression were each preceded by a practice block.

Participants pressed the space bar to initiate each trial. After an average interval of 500 ms (+/- 100 ms), a fixation cross appeared. Five hundred ms later, the memory tones were presented, one tone (load 1) to both ears or two different tones (load 2) presented simultaneously, one to each ear. We divided the 14 tones differing in pitch into two groups of

7 tones (a low-frequency octave and a high-frequency octave). When two different tones were presented simultaneously, they were chosen from different octaves to facilitate the distinction between them. The smallest frequency difference between two simultaneously presented tones was between 688 Hz and 759 Hz, which is still outside the range for pitch fusion (Van den Brink, Sintnicolaas, & Stam, 1976) or binaural beating (Perrot & Nelson, 1969). For any given trial, tones were not allowed to be more then 6 tones apart. For example, the third tone of the low octave could not be presented simultaneously with a tone that was higher then the second tone of the high octave.

After the presentation of the memory tones, a silent 2000 ms retention interval and a single 200 ms probe tone followed. Five hundred ms after probe presentation, a white circle replaced the fixation cross, indicating that participants had 3000 ms to judge if the probe had been the same as one of the memory tones or different (see Figure 1). They responded with the index fingers of both hands. Half responded by pressing the ‘c’ on the keyboard for a ‘same’ and ‘m’ for a ‘different’ probe tone. This mapping was reversed for the other half of participants. Five hundred ms after the response, the circle turned red or green, to provide performance feedback. When no response had been made within 3000 ms after the onset of the white circle, the circle turned dark red. Feedback remained on the screen until the participants started the next trial by pressing the space bar.

In suppression blocks, participants additionally counted overtly from 1 to 10 during the retention interval.

INSERT FIGURE 1 ABOUT HERE

EEG recording and analyses. EEG signals were sampled rate of 512 Hz using a BioSemi ActiveTwo system. Analyses were performed using EEGLAB (Delorme & Makeig, 2004), and ERPLAB (http://erpinfo.org/erplab), and custom software running under Matlab (http://www.mathworks.com/products/matlab). The location of each active Ag/AgCl electrode on the 64-electrode cap followed the 10/10 system. These were Fp1, Fpz, Fp2, AF7, AF3, AFz, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, POz, PO4, PO8, O1, Oz, O2, and Iz. External electrodes were also placed on the left and right outer canthi, below the left eye, and on the left and right mastoids. The signals were referenced to one masoid during data acquisition and then re-referenced offline to the average of the two mastoids (Keil et al., 2013). The horizontal electrooculogram (HEOG), defined as the voltage difference between the two canthi electrodes, was used to measure horizontal eye movements, while the vertical electrooculogram (VEOG), defined as the voltage difference between the electrodes placed above (Fp1) and below the left eye, was used to detect eye blinks.

For HEOG and VEOG channels only, a 0.1 Hz, 36 dB/octave, high-pass filter and a 10 Hz, 36 dB/octave, low-pass filter were applied to facilitate the artifact detection and rejection. The data from the EEG electrodes, but not the data from the VEOG and HEOG, were band-pass filtered in the alpha (8–12 Hz) or the beta (18–28 Hz) range and submitted to a Hilbert transform. The frequencies for these bands were selected to correspond to changes observed in time-frequency plots showing the differences between the conditions of interest. The amplitude envelope of oscillations in the chosen frequency band was calculated as the absolute value of the Hilbert transform and provided a continuous measure for the magnitude of oscillations. All data processing steps were performed separately for the alpha and beta bands.

Individual electrodes that showed artifacts (signal changes exceeding a certain threshold compared to baseline; threshold = 150 µV for the alpha band, threshold = 15 µV for the beta band) during a trial were interpolated using a spherical-spline interpolation based on signals of the surrounding electrodes for that trial. Different thresholds were used for the alpha band and the beta band because the data range was not identical in different frequency bands. Trials with more than seven electrodes needing interpolation were excluded from further analysis. A trial was also excluded when the HEOG signal varied by more than 45 µV over a 300-ms period, or if the VEOG signal fluctuated by more than 60 µV over a 150-ms period. Before artifact rejection, there were 50 'same' and 50 'different' trials in each load condition. In order to provide a good signal-to-noise ratio, we wanted to average at least 40 trials (80%) per condition. Therefore, the data of a participant was entirely excluded when more than 20% of the trials had to be rejected due to artifacts. This was the case for 14 participants.

For the analysis during and after probe presentation, the data were segmented from -200 ms to 600 ms relative to the onset of the probe with a baseline correction from -200 to 0 ms. Signals from trials belonging to the same condition were averaged. For statistical analyses, we focused on central electrode sites because they have shown sensitivity for differences between probe types in previous EEG studies (e.g., Pelosi et al., 1998).

We analysed data of the retention interval and probe / test phases of the experiment. For the analysis of retention, the data were segmented from -2400 to 0 ms relative to the onset of the probe with a baseline correction from -2400 to -2200 ms, which is the silent 200 ms before the onset of the memory tone presentation. The onset of the probe was chosen as a reference time point because the article mainly focuses on probe presentation. Oscillatory amplitude measures from trials belonging to the same condition with correct responses were averaged (average of the Hilbert amplitudes).

6.3.2. Results

Behavioral data. Behavioral data are shown in Table 1. In blocks without suppression, participants had on average 95% correct responses for load 1 (sensitivity index d′ = 3.92, response bias index ß = 2.80) and 83% correct responses for load 2 (d′ = 2.33, ß = 1.64). In blocks with suppression, participants had on average 93% correct responses for load 1 (d′ = 3.61, ß = 2.67) and 81% correct responses for load 2 (d′ = 2.09, ß = 0.85).

INSERT TABLE 1 AROUND HERE

A 2x2 ANOVA for repeated measures on d' with the factors suppression (with or without), and memory load (load 1 versus load 2), revealed a significant main effect suppression, $F(1, 30) = 12.82$, $MSE = 0.18$, $p < .001$, $\eta^2 = .30$, indicating that participants performance was better in blocks without suppression. The main effect of memory load was also significant, $F(1, 30) = 130.36$, $MSE = 0.58$, $p < .001$, $\eta^2 = .81$, which confirmed that participants performed better at load 1 than at load 2. The interaction was not significant, $F < 1$.

A 2x2 ANOVA for repeated measures on the response bias ß revealed a significant main effect of memory load, $F(1, 30) = 8.04$, $MSE = 8.55$, $p < .01$, $\eta^2 = .21$, which statistically confirmed that participants were more likely to indicate that a trial was 'different' in load 2 than in load 1. Neither the main effect suppression, $F(1, 30) = 2.50$, $MSE = 2.60$, $p > .12$, $\eta^2 = .08$; nor the interaction, $F < 1$; were significant. Whereas there was no a priori hypothesis regarding the response bias, the ANOVA on d' confirmed that participants' performance decreased with increasing memory load and was also impaired by suppression.

Responses were faster in load 1 than in load 2, even more so for ‘same’ trials (load 1: 407 ms, load 2: 509 ms) than for ‘different’ trials (load 1: 444 ms, load 2: 505 ms). This was supported by a significant main effect of memory load, $F(1, 30) = 43.55$, $MSE = 9368.31$, $p < .001$, $\eta^2 = .59$; and a significant interaction between memory load and probe type, $F(1, 30) = 8.47$, $MSE = 3091.10$, $p < .01$, $\eta^2 = .22$. The main effect probe type was marginally significant, $F(1, 30) = 3.99$, $MSE = 4095.63$, $p < .06$, $\eta^2 = .12$. All other effects did not reach significance, main effect suppression, $F(1, 30) = 2.58$, $MSE = 50453.85$, $p > .11$, $\eta^2 = .08$; all other $F < 1$.

EEG alpha band.

Probe presentation. Figure 2 shows the scalp distribution of oscillatory activity in the alpha band. The difference between load 2 and load 1 is shown on the right and the difference between ‘different’ probes and ‘same’ probes is shown on the left. On mid/fronto-central electrode sites, amplitudes are greater for ‘different’ probes than for ‘same’ probes (left panel). The cause for that difference could be either a greater increase of alpha activity for ‘different’ probes or a greater decrease of alpha activity for ‘same’ probes. For subsequent analyses of the signal on the electrodes, we therefore averaged the signals from electrode sites Fz, FC1, FCz, FC2, Cz.

INSERT FIGURE 2 ABOUT HERE

Figure 3 shows the grand average waveforms of alpha activity at the mid/fronto-central electrode pool during and after probe presentation. After the onset of the probe, the amplitude of the alpha band oscillations increased and reached a maximum at around 130 ms after stimulus onset. Then the amplitude decreased and reached a plateau at around 500 ms.

INSERT FIGURE 3 ABOUT HERE

A 2x2x2 ANOVA for repeated measures for the alpha amplitude averaged from 200 to 400 ms after probe onset with the factors suppression, memory load, and probe type revealed that ‘different’ probes, $M = -0.11$ µV, $SD = 0.48$ µV, led to a greater amplitude of oscillations in the alpha band than ‘same’ probes probes, $M = -0.26$ µV, $SD = 0.55$ µV, thereby yielding a main effect of probe type, $F(1, 30) = 19.20$, $MSE = 0.07$, $p < .001$, $\eta^2 = .39$. All other main effects and interactions did not reach significance, main effect suppression: $F(1, 30) = 1.02$, $MSE = 0.23$, $p > .32$, $\eta^2 = .03$; main effect memory load: $F(1, 30) = 1.75$, $MSE = 0.12$, $p > .19$, $\eta^2 = .06$; interaction between memory load and probe type: $F(1, 30) = 2.04$, $MSE = 0.15$, $p > .16$, $\eta^2 = .06$; all other $F < 1$.

In order to assess correlations between behavioural data and to rule out that the effects found in the alpha band are due to differences in response times, we correlated the amplitude difference between ‘different’ probes and ‘same’ probes with reaction times and % correct. The correlations are shown in Table 2. None of them were significant.

Retention phase. Figure 4 shows the grand average waveforms depicting the amplitude of oscillatory activity in the alpha band (8–12 Hz) at the mid/fronto-central electrode pool during the retention phase. There was a first prominent peak at about -2100 ms (100 ms after the onset of the memory tones) that likely reflected sensory processing and may be related to the N1 auditory ERP to the probe onset. Then, signal dropped around the onset of the retention interval and then increased again. At around -1100 ms, the signal reached a plateau for the remainder of the retention interval. This sustained component showed a clear memory load effect and might presumably be related to a slow ERP (Mazaheri & Jensen, 2008), the SAN (Guimond et al, 2011; Lefebvre et al., 2013; Nolden et al., 2013).

INSERT FIGURE 4 ABOUT HERE

We analysed the signal during two different time windows. To test the load effect of the sustained component, we chose the mean amplitude of the oscillations from -1100 ms to -100 ms relative to the onset of probe presentation, which is the time window used by Lefebvre et al. (2013) in their paper on the SAN (900 ms to 1900 ms relative to the onset of the retention interval). To rule out that load effects (which could be carried over after the retention interval) were present during the time window that we used as a baseline for the probe presentation analysis, we analysed the data from -200 ms to 0 ms relative to the onset of the probe.

A 2x2 ANOVA for repeated measures on the mean amplitude from -1100 to -100 ms relative to the onset of the probe with the factors suppression and memory load revealed that the amplitude of the oscillations was greater for memory load 2, $M = 0.63$ µV, $SD = 0.83$ µV, than for memory load 1, $M = 0.53$ µV , $SD = 0.79$ µV; $F(1, 30) = 6.01$, $MSE = 0.05$, $p < .03$, $\eta^2 = .17$. Neither the main effect of suppression, $F < 1$, nor the interaction , $F(1, 30) = 1.20$, $MSE = 0.04$, $p > .28$, $\eta^2 = .04$, were significant.

A 2x2 ANOVA for repeated measures on the mean amplitude from -200 to 0 ms relative to the onset of the probe (= baseline for analysis on probe presentation) with the factors suppression and memory load revealed no significant effects, mains effect suppression, $F < 1$; main effect memory load, $F(1, 30) = 1.41$, $MSE = 0.04.$, $p > .24$, $\eta^2 = .04$; interaction, $F(1, 30) = 1.85$, $MSE = 0.18$, $p > .08$, $\eta^2 = .06$).

EEG beta band.

Probe presentation. Figure 5 shows the scalp distribution of oscillatory activity in the beta band. The difference between load 2 and load 1 is shown on the right and the difference between ‘different’ probes and ‘same’ probes is shown on the left. On mid/fronto-central electrode sites, amplitudes are more negative for load 2 than for load 1 (right panel). The cause for that difference could be either a greater increase of alpha activity for load 1 or a greater decrease of alpha activity for load 2. For subsequent analyses of the signal on the sensors, we therefore used a pool of these mid/fronto-central electrode sites (average signal at electrode sites Fz, FC1, FCz, FC2, Cz).

INSERT FIGURE 5 ABOUT HERE

Figure 6 shows the grand average waveforms for the amplitude of oscillations in the beta band at the mid/fronto-central electrode pool during and after probe presentation. Soon after probe offset, the amplitude for both 'same' and 'different' probes beta-band activity decreased and reached a minimum at about 400 ms after probe onset.

INSERT FIGURE 6 ABOUT HERE

A 2x2x2 ANOVA for repeated measures with the factors suppression, memory load, and probe type on the mean amplitude from 200 to 400 ms after probe onset revealed that the amplitude in the beta decreased more in condition load 2 than in condition load 1, load 1: $M = -0.10$ µV, $SD = 0.26$ µV, load 2: $M = -0.15$ µV, $SD = 0.25$ µV, producing a main effect of memory load: $F(1, 30) = 10.50$, $MSE = 0.01$, $p < .01$, $\eta^2 = .26$. All other main effects and interactions did not reach significance, all $F < 1$.

In order to assess correlations between behavioural data and to rule out that the effects found in the beta band are simply due to differences in reaction times, we correlated the amplitude difference between load 2 and load 1 with reaction times and % correct. The correlations are shown in Table 2. None of them were significant.

INSERT TABLE 2 AROUND HERE

Retention phase. Figure 7 shows the grand average amplitude of oscillations in the beta band (18–28 Hz) at the mid/fronto-central electrode pool during the retention phase. During the presentation of the memory tones and the retention interval, the signal for all conditions followed the same pattern. There was a first peak around 100 ms after the presentation of the memory tones followed by a decrease at the beginning of the retention interval. The signal then returned to baseline and started to drop slightly before the onset of the probe.

INSERT FIGURE 7 ABOUT HERE

We analysed the beta band signal during the same time windows as the alpha band signal (see previous section). A 2x2 repeated measures ANOVA with the within factors suppression and memory load on the mean amplitude from -1100 to -100 ms relative to the onset of the probe with the factors suppression and memory load did not reveal any effects (all $F < 1$). The same was true for the ANOVA on the mean amplitude from -200 to 0 ms relative to the onset of the probe (= baseline for analysis on probe presentation).

6.3.3. Discussion

We showed an effect of probe type in the amplitude of alpha band oscillations related to probe presentation, namely that the mean amplitude was greater for 'different' trials than for 'same' trials. This effect has been observed for verbal ASTM (Pesonen et al., 2006) and may be related to the comparison between the memory items and the probe. Pesonen et al. (2006) reported a decrease of alpha band activity after the onset of the probe. In Experiment 1, a decrease in alpha band activity was preceded by an increase of short duration. Given that we did not use a wavelet approach as Pesonen et al. (2006) but Hilbert-transformed data, Experiment 1 might have a finer temporal resolution than the wavelet data where the short increase of alpha band activity might have been overlooked. There was no memory load effect in the alpha band.

In the beta band, we found that the amplitude of oscillations related to probe presentation decreased more for load 2 than for load 1 and therefore might reflect access to representations of sounds that differed in number between the two load conditions. However, comparison between representations held in memory and the probe might be reflected to a lesser extent in the beta band than in the alpha band, as we did not find an effect of probe type. The beta band data could not confirm results obtained with verbal material (Pesonen et al., 2006) that have revealed a greater amplitude of the beta-band oscillations for ‘different’ than for ‘same’ trials. Therefore, it is possible that variations in beta band oscillations are sensitive to the type of material used.

Interestingly, alpha band and beta band activity showed different patterns during retention, where there was no load effect at all in the beta band but a sustained load effect in the alpha band, especially in the latter part of the retention interval. First, this confirmed that the load effect in the beta band during and after probe presentation was not carried over from previous phases, but rather reflected a new process that is relevant in this phase. Second, the dissociation between alpha and beta band activity during retention and probe presentation led us to suggest that alpha and beta band activity did indeed reflect different brain processes and this, in turn, justified separate analyses. Third, our data revealed different patterns for each of the phases of the ASTM task. Brain activity related to retention seemed to manifest primarily on alpha band signal, as illustrated by the load effect. During and after probe presentation, both alpha and beta band activity were present but showed different effects related to probe presentation, hence likely reflected different functions. The observed effects in oscillatory brain activity were not correlated with response time. This confirmed that the patterns in oscillatory brain activity were not driven by motor preparation. There was also no correlation with percent correct, which is not surprising given the generally good performance of the participants.

There was no effect of suppression of internal rehearsal during retention and probe presentation. In a previous study, it was suggested that internal rehearsal might not have been the most important strategy in this specific task, which would explain the absence of significant suppression effects (Guimond et al., 2011).

We argue that the effect of probe type in the alpha band observed in Experiment 1 was related to mnemonic activity. However, as the probe is a repetition of the memory tones in 'same' trials, simpler explanations for this effect (such as adaptation to repeated tones) cannot be completely ruled out by this experiment. We therefore analyzed the data of another experiment with sequentially presented tones (Experiment 2).

6.4. Experiment 2

Experiment 1 revealed that the amplitude of alpha-band oscillations was greater for 'different' than for 'same' trials. We claimed that this effect was due to the comparison between memory contents and probe tone. Adaptation processes could be an alternative explanation for this result, namely that neurons responding to the frequency of one of the memory tones responded in a weaker way to a probe tone with the same frequency. We wanted to rule out this alternative explanation with Experiment 2 and provide support for the hypothesis that the probe type effect found in the alpha band reflects a memory-related process.

In Experiment 2, the tones to be memorized were presented sequentially, retained for 2000 ms (retention interval), and then followed by a test sequence that was either the same or different relative to the initial sequence. Pitch tones had a duration of 100 ms and were separated by silent intervals of 100 ms. The pitch tones of the test sequence were identical and in identical order as the pitch tones of the memory sequence in 'same' trials. In 'different' trials, the order of two adjacent tones was reversed (see Lefebvre et al., 2013, auditory task, for analyses of ERPs). The memory sequences consisted of 2, 4, or 6 tones differing in pitch. In the load 2 condition of the memory blocks, the participants could detect the type of trial ('same' or 'different') based on the first tone of the second sequence. In the higher memory load conditions, the inversion of two tones in 'different' trials could occur later in the sequence, so that a finer subdivision of the trials would have been necessary to analyze these conditions. The number of trials in these sub-conditions was too small to provide a sufficient signal-to-noise ratio. We therefore only focused on the load 2 condition and the probe type effect, while not investigating memory load.

As the same tones were used as memory tones and as probe tones in 'same' and 'different' trials, only memory-related processes can explain greater amplitude in the alpha-band oscillations in 'different' trials than in 'same' trials. If adaptation had caused the probe type effect reported in Experiment 1, the inversion of adjacent tones in 'different' trials would furthermore lead to the prediction of opposite alpha-band results in Experiment 2 compared to Experiment 1. In the load 2 condition, the second memory tone was identical to the first probe tone in 'different' trials (2100 ms from onset to onset) whereas identical tones were temporally further apart in 'same' trials (2300 ms from onset to onset), thereby providing more time for the cells tuned to a certain frequency to recover (see Figure 6 and 7). An adaptation process should therefore lead to greater amplitude in the alpha-band oscillations for 'same' trials than for 'different' trials, whereas memory related activity should be reflected in greater amplitude for 'different' trials than for 'same' trials, according to the results of Experiment 1.

Experiment 1 and Experiment 2 differed regarding the concrete task and participants needed to give consideration to different aspects of the retained tones. In Experiment 1, retaining the identity of the tones was sufficient to solve the task, whereas temporal order had to be retained as well in Experiment 2. The comparison process is thus presumably somewhat different in Experiment 2. Finding similar results in the alpha band as in Experiment 1 would therefore support a robust finding that might be more related to the outcome of the comparison between memory and probe tones, rather than being related to details of the comparison itself.

To sum up, Experiment 2 should rule out the alternative explanation that adaptation was the cause of the alpha-band results found in Experiment 1. At the same time, Experiment 2 served as a replication of Experiment 1 and helped to clarify the cognitive mechanism causing the probe type effect in the alpha band.

6.4.1. Method

Participants. Thirty-nine different neurologically normal college students participated in the experiment. Participants gave informed consent and all procedures were vetted by the appropriate ethics board at Université de Montréal. All participants reported normal hearing except one who afterwards reported suffering from tinnitus and whose data was excluded for that reason. Data from 8 participants who had an excessive number of trials rejected due to artifacts, blinks, or eye movements were excluded from data analysis. The remaining 30 participants (14 female) had a mean age of 24 years (*SD* = 4 years, range: 20-33 years). All participants were right-handed.

Stimuli. Stimuli were as in Experiment 1 (14 tones differing in pitch), except that they had a duration of 100 ms, including onset and offset ramps of 10 ms each. Visual stimuli (fixation and feedback) were identical to those used in Experiment 1.

Procedure. Figure 8 displays the procedure for memory load condition 2. Participants performed five memory blocks and five control blocks that alternated. Half of the participants started with a memory block and the other half with a control block. Each experimental block consisted of 60 trials, resulting in 600 trials in total. The ten experimental blocks were preceded by two practice blocks.

In the memory blocks, participants pressed the space bar to initiate each trial. After a mean interval of 500 ms (+/- 100 ms), the fixation cross appeared. Five hundred ms later, the first tone sequence started. It consisted of 2, 4, or 6 tones differing in pitch. The tones differing in pitch were preceded by 5, 3, or 1 white noise segments (also 100 ms in duration). The tones were chosen randomly and were never repeated within a sequence. They were separated by silent intervals of 100 ms each. The number of tones differing in pitch varied randomly from trial to trial, but the number of trials per block was the same for all load conditions. The first sequence was followed by a retention interval of 2000 ms and, then, a second sequence of tones. The second sequence had the same number of tones differing in pitch as the first sequence but they were not preceded by white noise stimuli. The second sequence was the same as the first sequence in half of the trials and different in the other half. When the two sequences differed, two adjacent tones were inversed. Five hundred ms after the second presentation, a white circle replaced the fixation cross, indicating that participants could respond within the next 3000 ms. Participants had to judge if the two sequences were the same or different. Response and feedback were given as in Experiment 1.

Control and memory conditions had the same trial structure. Here, participants were asked to ignore the first sequence. They had to indicate if the last tone of the second sequence was higher or lower in pitch than the second-to-last. In half of the trials, the last tone was 'higher' than the second-to-last tone, in the other half 'lower,' indicated by pressing the 'c' or the 'm.' The mapping of the tone classification to response keys was counterbalanced over participants. In the control condition, the tones of the two sequences were not related to each other, so that there was no benefit to remembering the identity of the tones from the first sequence.

INSERT FIGURE 8 ABOUT HERE

EEG recording and analyses. EEG data acquisition, filtering, artifact detection and rejection, and separate analyses of alpha and beta bands were as in Experiment 1. Data were segmented from -200 to 600 ms relative to the onset of the probe (the onset of the second sequence) and baseline-corrected from -200 to 0 ms relative to the onset of the probe. Trials requiring 'same' responses and 'different' responses were averaged separately for trials with correct responses. Only trials from memory blocks with a memory load of 2 were analysed. In the conditions load 4 and load 6, the inversion of the tones in 'different' trials could occur at 3, respectively 5, different positions and the data analysis would have required a finer subdivision of the trials. As we wanted to provide at least 40 trials per condition, we decided to only analyse the condition load 1 in order to have a good signal-to-noise ratio.

6.4.2. Results

Behavioral data. Behavioral data for Experiment 2 are shown in Table 1. Participants had an average of 98% correct trials (d′ = 4.10, ß = 0.86).

Response times were significantly faster for ‘different’ trials, *M* = 371 ms, than for ‘same’ trials, *M* = 412 ms, *t*(29) = 3.29, *p* < .01, *d* = 0.61.

EEG alpha band. Figure 9 shows the grand average waveforms of amplitudes in the alpha band (8–12 Hz) at the mid/fronto-central electrode pool. After the onset of the probe sequence, the amplitude of alpha-band oscillations increased and reached a maximum at around 100 ms after stimulus onset. Then the amplitude decreased, showed a second but smaller peak at around 300 ms (100 ms after the onset of the second tone) and reached a plateau at around 500 ms. The mean amplitude from 200 to 400 ms was significantly greater in ‘different’ trials, *M* = -0.04 µV, *SD* = 0.58 µV) than in ‘same’ trials *(M* = -0.25 µV, *SD* = 0.66 µV, *t*(29) = -2.18, *p* < .04, *d* = 0.40.

INSERT FIGURE 9 ABOUT HERE

In order to assess correlations between behavioural data and to rule out that the effects found in the alpha band are simply due to differences in reaction times, we correlated the amplitude difference between ‘different’ probes and ‘same’ probes with reaction times and % correct. The correlations are shown in Table 2. None of them were significant.

EEG beta band. Figure 10 shows the grand average waveforms of oscillatory amplitude in the beta band (18–28 Hz) at the mid/fronto-central electrode pool. Soon after probe offset, the amplitude for both ‘same’ and ‘different’ probes decreased and reached a minimum at about 400 ms after probe onset. The mean amplitude was -0.17 µV in ‘same’ trials, *SD* = 0.21 µV, and -0.23 µV in ‘different’ trials, *SD* = 0.22 µV, in the interval from 200 to 400 ms after probe onset. The difference between these conditions did not reach significance, *t*(29) = 1.04, *p* > .31, *d* = 0.20.

INSERT FIGURE 10 ABOUT HERE

6.4.3. Discussion

The purpose of Experiment 2 was to reveal differences in the amplitude of EEG alpha and beta band oscillatory activity for ‘same’ and ‘different’ probes and to serve as a control to Experiment 1. In the alpha band, the amplitude of the oscillations was significantly greater for ‘different’ than for ‘same’ probes, as in Experiment 1. Although the effect of probe type was similar and of the same direction, the waveforms differed slightly between the two experiments. Experiment 2 showed a second small peak at around 300 ms after the onset of the probe sequence that was absent in Experiment 1. This is likely related to differences in stimulation as two tones were presented in Experiment 2 and only one tone in Experiment 1. The peaks may be reflecting evoked activity related to the auditory N1 ERP. More importantly, the effect of probe type was present in both experiments and therefore cannot be explained by adaptation to repeated tones.

6.5. General Discussion

The goal of the present study was to isolate oscillatory brain activity related to probe presentation and processing in two ASTM experiments. In both experiments, participants retained memory tones for 2000 ms that were then compared to probes. Data were analyzed during and after the onset of the probe. Our results demonstrate an effect of probe type in the alpha band where the amplitude of the oscillations was significantly greater for ‘different’ probes than for ‘same’ probes. In the beta band, amplitude of oscillations decreased significantly more when two items had been retained (load 2) than when only one items had been retained (load 1). This load effect was found to ride on top of a general decrease in beta activity during the test phase of the experiment.

The effect of probe type we found in the alpha band reflects how memory content and the presentation of the probe item interact. The greater alpha oscillatory amplitude we found for ‘different’ probes relative to ‘same’ probes converge nicely with those from a previous EEG study on verbal ASTM that used a time-frequency approach (Pesonen et al., 2006). These findings suggest a certain robustness because we observed them in both Experiments 1 and 2, despite several differences in some critical points. First, participants retained sequences of tones in Experiment 2 rather than simultaneously-presented tones in Experiment 1. Second, a probe sequence was presented in Experiment 2 whereas a single probe tone was presented in Experiment 1. Finally, the order of tones in the probe sequence was inversed in the ‘different’ trials in Experiment 2 whereas a completely new probe tone was presented in ‘different’ trials in Experiment 1. Thus, not only did the properties of the presented tones differ between the experiments, but also the criteria that participants had to apply in order to complete the task based on the relation of memory and probe tones. We therefore argue that alpha band activity in the present context indexes a relatively abstract cognitive process assessing if retained sensory representations and incoming sensory stimulation differ based on some criterion. In this sense, modulations in the alpha band activity reflects the outcome of a comparison between two auditory representations. The results in the alpha band cannot entirely be explained by active inhibition of sensory areas (Jensen et al., 2002; Klimesch et al., 2007) because there are no a priori reasons to believe the degree of inhibition of external stimulation would depend on whether memory was probed with a ‘same’ or a ‘different’ probe. Both types of probes must be processed and compared to what is presumably actively retained in memory. It thus seems that the alpha band activity reflects a cognitive process related to the active comparison of two auditory representations.

Importantly, the effect of probe type in the alpha band cannot be explained by simple mechanisms like adaptation. In Experiment 1, a new probe tone (not heard at encoding) was presented in ‘different’ trials, which showed indeed greater amplitude of the alpha-band oscillations than the ‘same’ trials. We argue that this effect is due to memory processes, which is supported by results revealed by Experiment 2. In this experiment only the order of tones that had already been heard served as probes. Although adaptation cannot explain greater amplitude in ‘different’ than in ‘same’ trials in Experiment 2, the results in the alpha band were no different from Experiment 1. In conjunction, these two experiments provide strong evidence for an active mnemonic comparison process reflected in the alpha band oscillations as both showed greater amplitude in the alpha band for ‘different’ trials than for ‘same’ trials.

Furthermore, our data revealed an interesting load effect in the beta band. In Experiment 1, participants were always simultaneously presented one tone to each ear (the same tone for load 1, two different tones for load 2), which were then compared to a single probe tone presented to both ears at test. Given the equivalent physical stimulation in both load conditions during probe presentation, the load effect must therefore be related to mnemonic activity. We found that the amplitude of the oscillations decreased to a lesser extent in load 1 than in load 2 condition. This load effect might reflect the process of retrieval, or comparison to memory. Importantly, beta-band activity varied with load only during probe presentation, not during retention. It must therefore reflect a memory process that is relevant the probe presentation phase, presumably related to the manipulation of representations of tones, but unrelated to retention. Load effects during and after probe presentation can also be interpreted as reflecting ‘memory scanning’ in the sense originating from Sternberg (1966). This notion underscores the active access to retained memory items. Whereas the representations of the memory items might still be active during the delay between presentation of memory and probe tones, it might be necessary to access them sequentially when comparing to probes. That is an important difference to retrieval from long-term memory where representations of memory items must be reactivated. The fact that the probe type effect in the alpha band and the load effect in the beta band occur at around the same time suggests that access to memory items and comparison with probe tones — based on identity as well as chronological order criteria — are not necessarily sequential phases but might overlap in time. In this view, beta activity reflects a more complex comparison with increasing load, whereas alpha reflects the specific outcome of the comparison, as ‘same’ or ‘different,’ independently of load.

The results of this study suggest that alpha band and beta band oscillations support different cognitive processes during probe presentation. This double dissociation would not have been revealed with classical ERP analysis because of phase cancellation during signal averaging (e.g., Tallon-Baudry & Bertrand, 1999). Analyses of oscillatory brain activity in certain frequency ranges provide therefore a useful supplement to ERP analysis. Interestingly, a dissociation between alpha band and beta band activity was also present during the retention phase (Experiment 1). When participants kept the representations of memory tones in active state, alpha band activity showed a memory load effect, whereas beta band activity was the same for all conditions. In addition to indicating the functional differences between alpha and beta band activity, this result also nicely distinguishes between the different phases of our

ASTM task. Retention is mainly supported by activity in the alpha band, whereas alpha and beta band oscillations are related to different cognitive operations after probe presentation. Alpha-band activity reflects the outcome of comparison processes during the test phase. In contrast, beta activity varies with memory load during the comparison process in the test phase.

Recent contributions to the field suggest that alpha band and beta band activity reflect similar functions (Lundqvist et al., 2011; Hanslmayr et al., 2012; Zanto & Gazzaley, 2009), for example inhibition or controlled attention. Our results, on the other hand, show a clear dissociation between alpha band and beta band activity. This seeming discrepancy with the aforementioned studies might partly arise because they focused mainly on studies on the visual domain. Here, we focused on the auditory domain, and our study alongside previous ASTM studies (Leiberg et al., 2006; Pesonen et al., 2006) suggests that alpha band and beta band activity are not functionally equivalent for ASTM.

The goal of this study was to examine correlates of memory processes related to probe presentation in ASTM tasks in oscillatory brain activity. Using simple acoustic materials and paradigms that avoided interactions between short-term and long-term memory, we revealed probe type effects and memory load effects for specific frequency bands. Beta band activity may reflect access to memory items whereas alpha band activity may reflect higher cognitive processes related to the outcome of the comparison between memory and probe tones.

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6.7. References

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6.8. Tables

Table 1. Behavioral data. For both experiments, d’ and ß are shown for each load condition, for the data of Experiment 1 separately for memory blocks and suppression blocks. In addition, % correct and reaction times are given for ‘same’ and ‘different’ trials of the aforementioned conditions. Mean values are followed by standard deviations (in brackets).

Oscillations - Table 1

	Experiment1								Experiment 2	
	Load 1 without suppression		Load 2 without suppression		Load 1 with suppression		Load 2 with suppression		Load 2	
d´	3.92 (0.84)		2.33 (1.11)		3.61 (1.08)		2.09 (1.02)		4.10 (0.60)	
ß	2.80 (2.98)		1.64 (2.21)		2.67 (2.93)		0.85 (0.59)		0.86 (0.64)	
	‘Same’ trials	‘Different’ trials	‘Same’ trials	‘Different’ trials	‘Same’ trials	‘Different’ trials	‘Same’ trials	‘Different’ trials	‘Same’ trials	‘Different’ trials
% correct	0.99 (0.02)	0.92 (0.15)	0.78 (0.21)	0.87 (0.09)	0.98 (0.04)	0.89 (0.16)	0.75 (0.19)	0.86 (0.11)	0.97 (0.04)	0.99 (0.03)
Reaction times (ms)	378 (113)	420 (129)	490 (180)	484 (160)	436 (174)	467 (190)	528 (191)	525 (235)	412 (137)	371 (104)

Table 2. Correlations between electrophysiological and behavioral data. For Experiment 1, the amplitude difference between ‘different’ and ‘same’ trials in the alpha band and the amplitude difference between load 2 and load 1 in the beta band are correlated with behavioral data (*n* = 31). For Experiment 2, the amplitude difference between ‘different’ and ‘same’ trials in the alpha band is correlated with behavioral data (*n* = 30). For both experiments, d’ und ß are shown for each load condition, for the data of Experiment 1 separately for Memory blocks and suppression blocks. In addition, % correct and reaction times are given for ‘same’ and ‘different’ trials of the aforementioned conditions. Mean values are followed by standard deviations (in brackets).

Oscillations - Table 2

			% correct			Response times		
			Mean	‘Different’ – ‘same’ probe	Load 2 – load 1	Mean	‘Different’ – ‘same’ probe	Load 2 – load 1
Experiment 1	Alpha amplitudes: ‘different’ – ‘same’ probe	*r*	.16	.17	-.19	-.26	-.30	.13
		p	.39	.36	.31	.15	.10	.50
	Beta amplitudes: load 2 – load 1	*r*	.04	.12	.04	.06	.09	-.04
		p	.82	.54	.83	.75	.63	.83
Experiment 2	Alpha amplitudes: ‘different’ – ‘same’ probe	*r*	.10	.07	-	.19	-.18	-
		p	.61	.72	-	.32	.34	-

6.9. Figure Captions

Figure 1. Trial procedure for Experiment 1. One tone was presented binaurally or two tones were presented simultaneously, one to each ear. After a silent retention interval of 2000 ms, a single test tone was presented. In half of the trials, the test tone had been presented before, in the other half of the trials it had not. Participants indicated if the probe was the same as any of the memory tones or different. Sound events had a duration of 200 ms. In half of the blocks, participants counted from 1 to 10 during the retention interval to suppress internal rehearsal. See text for further details.

Figure 2. Alpha band, topography. Topographical maps of the amplitude difference between load 2 and load 1 (left) and between ‘different’ probes and ‘same’ probes (right), averaged during the period from 200 to 400 ms from the onset of the probe. Data of the alpha band (8-12 Hz) in Experiment 1 is shown. The difference between ‘different’ and ‘same’ probes has a mid/fronto-central distribution, related electrode sites are named in black ink (right).

Figure 3. Alpha band, probe presentation. Grand average waveforms reflecting alpha band amplitude (8–12 Hz) at a pool of mid/fronto-central electrodes (Fz, FC1, FCz, FC2, Cz) in Experiment 1. Time 0 refers to the onset of the probe, baseline at -200 to 0 ms. The vertical dashed line marks the onset of the probe tone. The signal for ‘same’ and ‘different’ probes and for load 1 and load 2 in memory blocks, averaged over both suppression conditions, is shown.

Figure 4. Alpha band, retention phase. Grand average waveforms representing the amplitude of oscillations in the alpha band (8–12 Hz) at a pool of mid/fronto-central electrodes (Fz, FC1, FCz, FC2, Cz) from Experiment 1. Time 0 refers to the onset of the probe, which began immediately after the retention interval, baseline at -2400 to -2200 ms. The vertical dashed line marks the onset of the retention interval. The signal for each memory load condition, averaged over both suppression conditions, is shown.

Figure 5. Beta band, topography. Topographical maps of the amplitude difference between load 2 and load 1 (left) and between 'different' probes and 'same' probes (right), averaged during the period from 200 to 400 ms from the onset of the probe. Data of the beta band (18-28 Hz) in Experiment 1 is shown. The difference between load 2 and load 1 has a mid/fronto-central distribution, related electrode sites are named in black ink (left).

Figure 6. Beta band, probe presentation. Grand average waveforms for the amplitude of oscillations in the beta band (18–28 Hz) at pool of mid/fronto-central electrodes (Fz, FC1, FCz, FC2, Cz) from Experiment 1. Time 0 refers to the onset of the probe, baseline at -200 to 0 ms. The vertical dashed line marks the onset of the probe tone. The signal for 'same' and 'different' probes and for load 1 and load 2, averaged over both suppression conditions, is shown.

Figure 7. Beta band. retention phase. Grand average waveforms for signal amplitude in the beta band (18–28 Hz) at a pool of mid/fronto-central electrodes (Fz, FC1, FCz, FC2, Cz) from Experiment 1. Time 0 refers to the onset of the probe, which began immediately after the

retention interval, baseline from -2400 to -2200 ms. The vertical dashed line marks the onset of the retention interval. The signal for each memory load condition, averaged over both suppression conditions, is shown.

Figure 8. Trial procedure of Experiment 2. Sequences of two pure tones differing in pitch were presented binaurally. These tones were preceded by 5 white noise stimuli. After a silent retention interval of 2000 ms, a second sequence of two tones was presented. In half of the trials, the sequences were the same, in the other half of the trials, the order of the sounds was inversed. Participants indicated if the second sequence was the same or different as the first. Sound events had a duration of 100 ms and were separated by 100 ms of silence. See text for further details.

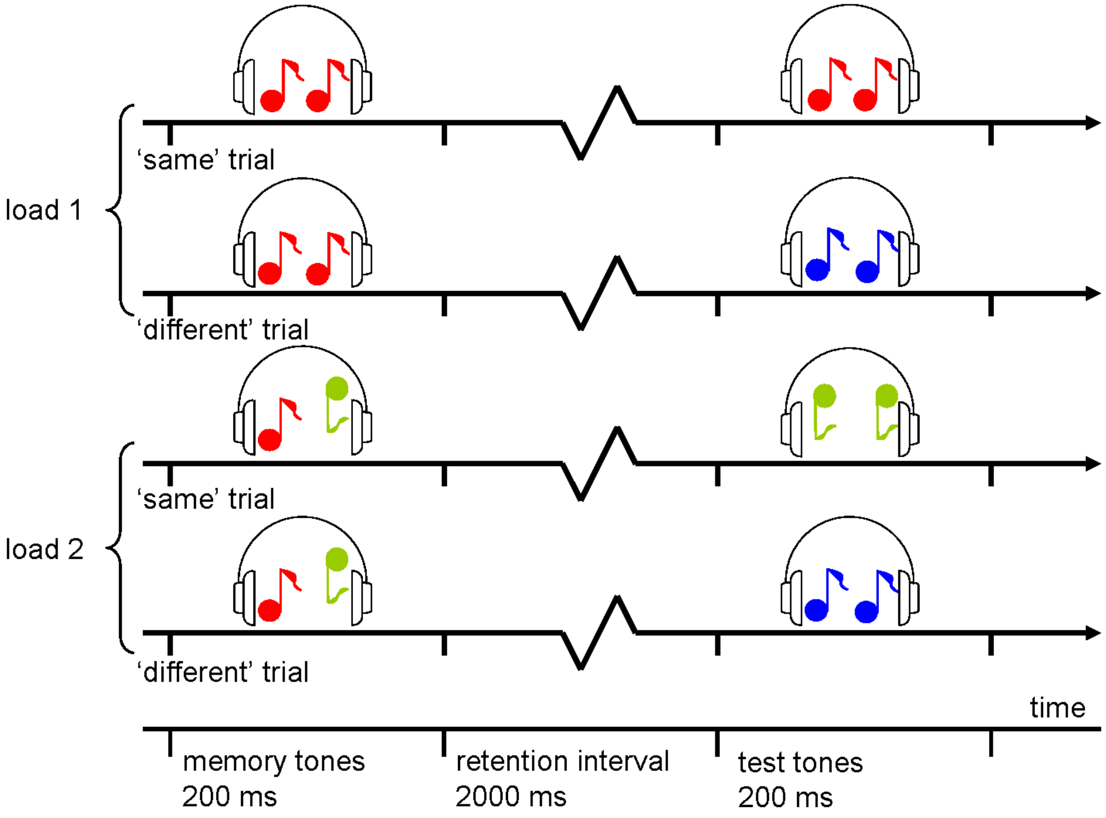
Figure 9. Alpha band, probe presentation. Grand average waveforms for the amplitude of oscillations in the alpha band (8–12 Hz) at a pool of mid/fronto-central electrodes (Fz, FC1, FCz, FC2, Cz) from Experiment 2. Time 0 refers to the onset of the probe, which began immediately after the retention interval, baseline at -200 to 0 ms. The vertical dashed line marks the onset of the probe tone. The signal for 'same' probes and 'different' probes is shown.

Figure 10. Beta band, probe presentation. Grand average waveforms for the amplitude of oscillations in the beta band (18–28 Hz) at a pool of mid/fronto-central electrodes (Fz, FC1, FCz, FC2, Cz) from Experiment 2. Time 0 refers to the onset of the probe, which began immediately after the retention interval, baseline at -200 to 0 ms. The vertical dashed line

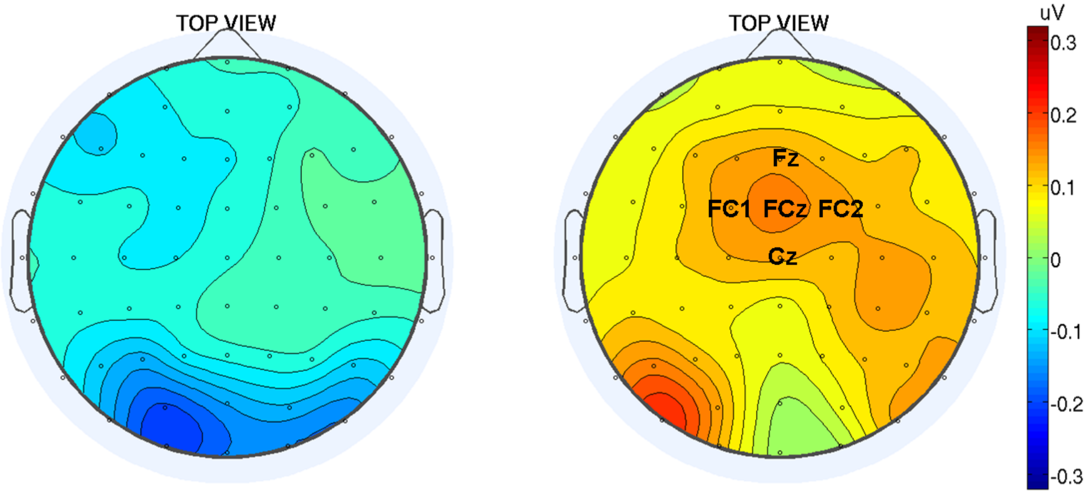
marks the onset and the offset of the probe tone. The signal for ‘same’ probes and ‘different’ probes is shown.

6.10. Figures

Oscillations - Figure 1



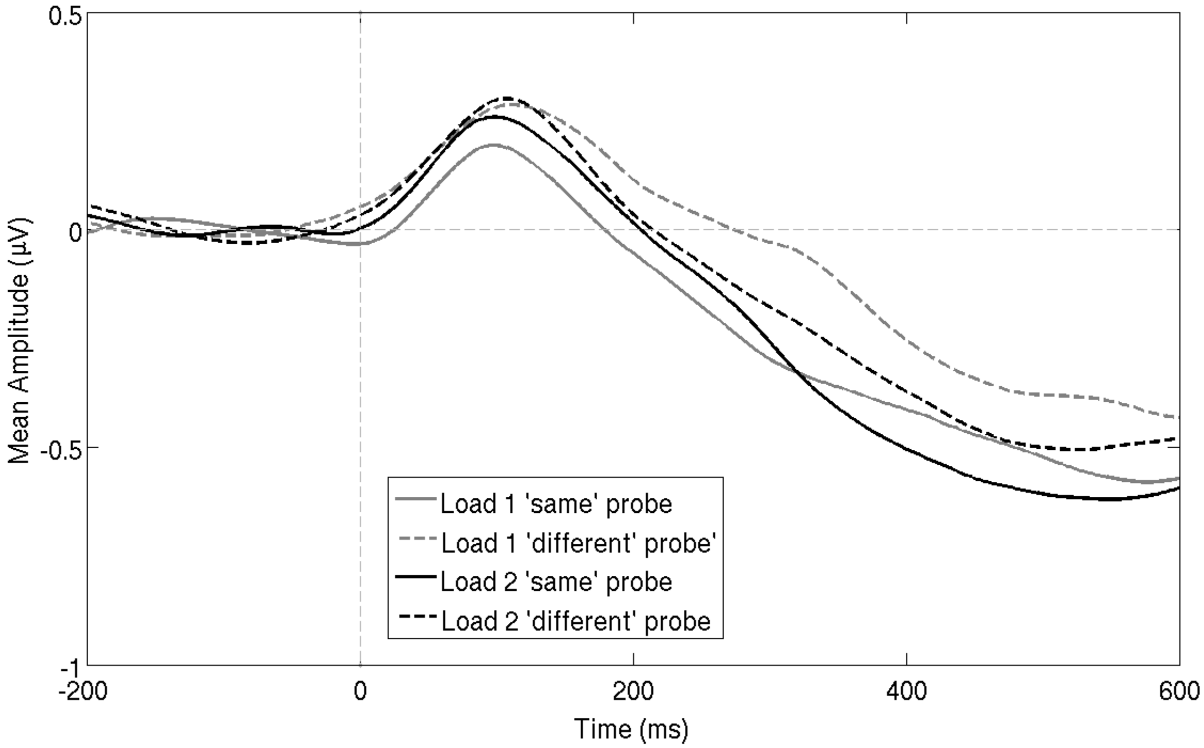
Oscillations - Figure 2



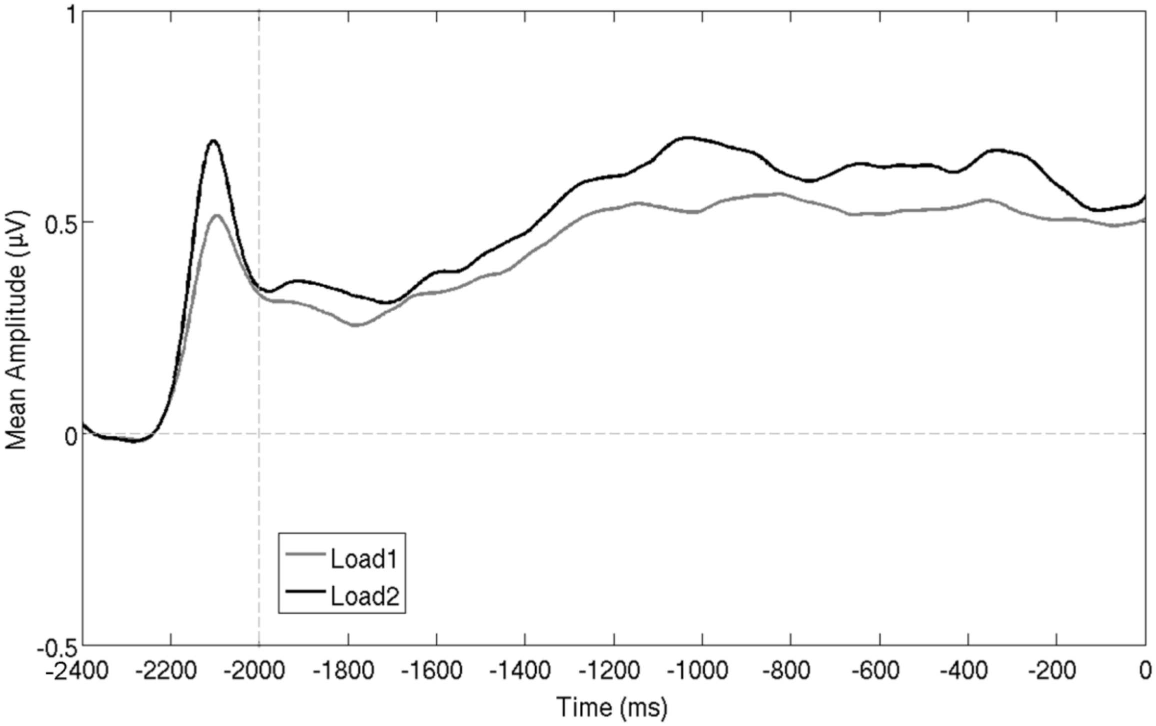
Load 2 - Load 1
200 ms to 400 ms

'Different' probes - 'same' probes
200 ms to 400 ms

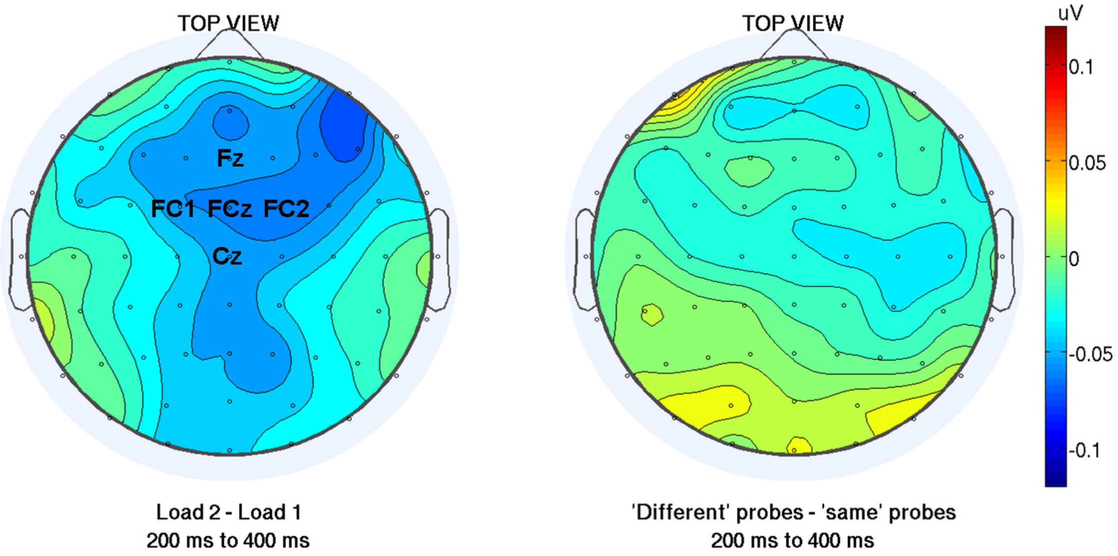
Oscillations - Figure 3



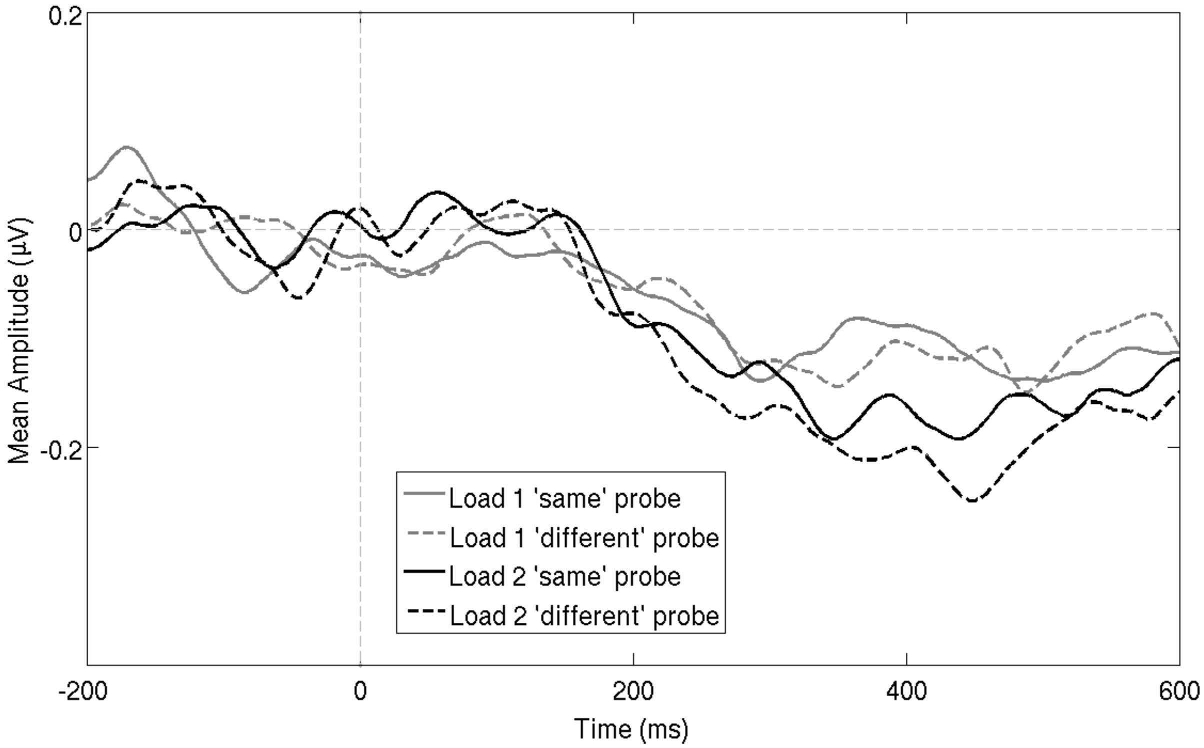
Oscillations - Figure 4



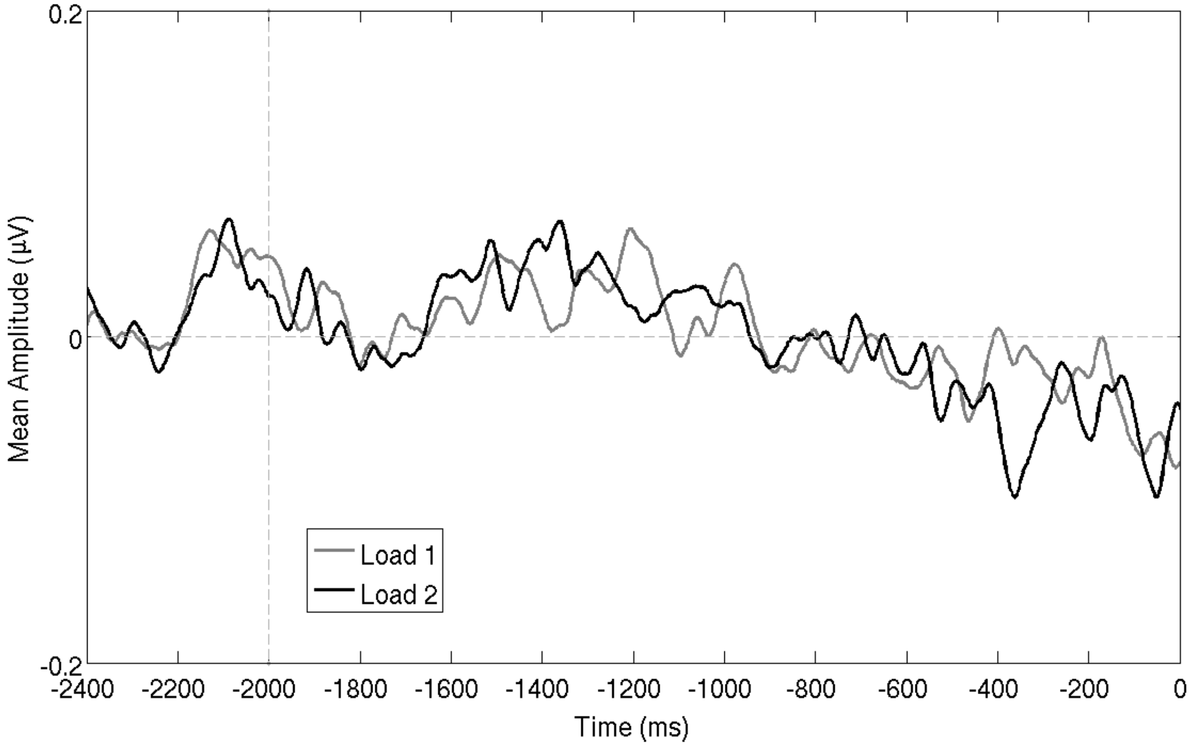
Oscillations - Figure 5



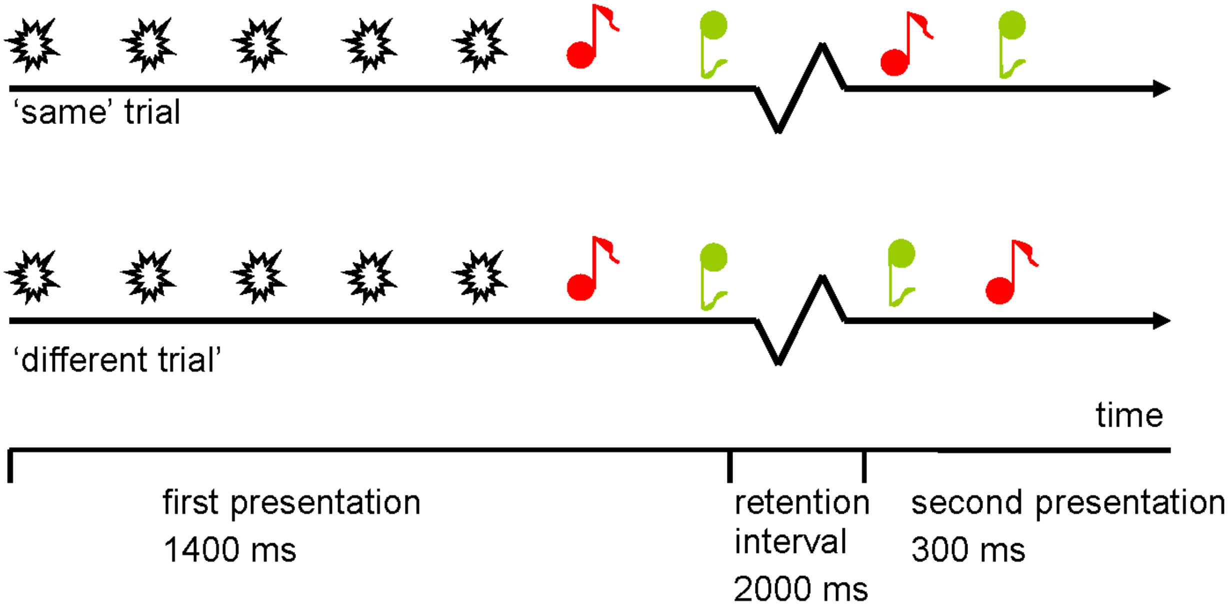
Oscillations - Figure 6



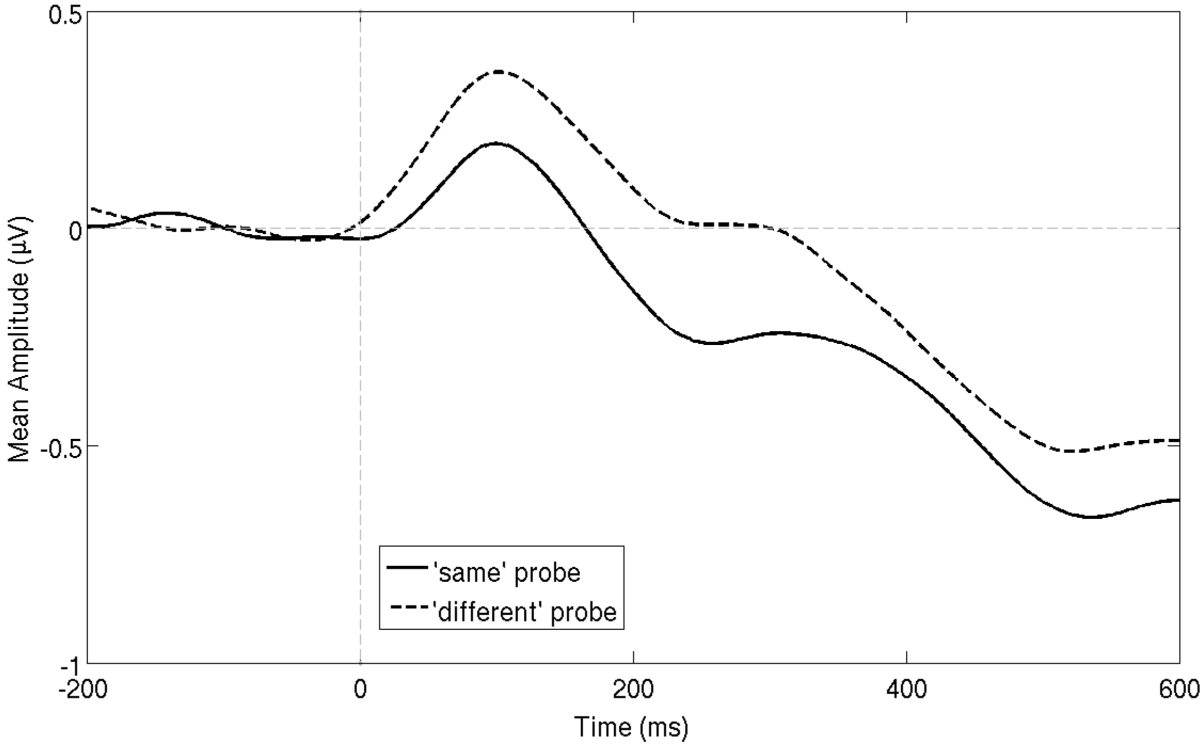
Oscillations - Figure 7



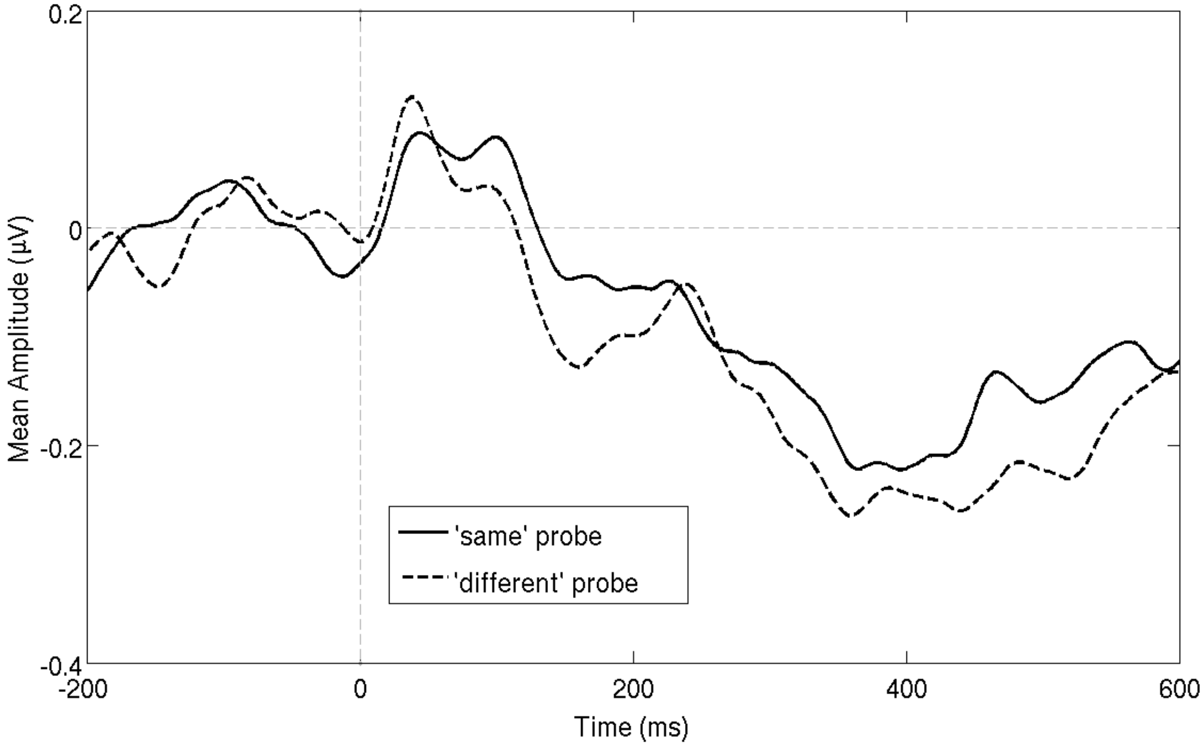
Oscillations - Figure 8



Oscillations - Figure 9



Oscillations - Figure 10



Chapitre 7 : Localisation des sources de l'activité mnésique

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The retention of simultaneous tones in auditory short-term memory: A magnetoencephalography study

Sophie Nolden[1, 2], Stephan Grimault[1, 2, 3], Synthia Guimond[1, 2], Christine Lefebvre[1, 2], Patrick Bermudez[1, 2], & Pierre Jolicoeur[1, 2]

[1]CERNEC, Université de Montréal, Québec, Canada, [2]BRAMS, Montréal, Québec, Canada, [3]CNRS, Marseille, France

7.1. Abstract

We used magnetoencephalography (MEG) to localize brain activity related to the retention of tones differing in pitch. Participants retained one or two simultaneously presented tones. After a two second interval a test tone was presented and the task was to determine if that tone was in memory. We focused on brain activity during the retention interval that increased as the number of sounds retained in auditory short-term memory (ASTM) increased. Source analyses revealed that the superior temporal gyrus in both hemispheres is involved in ASTM. In the right hemisphere, the inferior temporal gyrus, the inferior frontal gyrus, and parietal structures also play a role. Our method provides good spatial and temporal resolution for investigating neuronal correlates of ASTM and, as it is the first MEG study using a memory load manipulation without using sequences of tones, it allowed us to isolate brain regions that most likely reflect the simple retention of tones.

Keywords: Audition; short-term memory; working memory; pitch; magnetoencephalography (MEG); source localizations.

7.2. Introduction

The ability to retain acoustic items in memory for a short period of time after they are gone from the senses is a key capacity for the integration of acoustic information over time. It is crucial for participating in spoken language and equally important in the non-verbal domain, such as enjoying the aesthetic of a piece of music. In this study, we focused on the retention of non-verbal acoustic items to assess fundamental aspects of auditory short-term memory (ASTM). We aimed to isolate brain areas that are engaged in ASTM with a design that minimized the number of cognitive systems engaged and therefore targeted the retention of pure tones differing in pitch.

Previous studies have suggested that certain brain structures are related to memory processes during the retention of pitch. In a positron emission tomography study (PET) (Zatorre et al, 1994), participants listened to melodies of eight tones and had either to indicate if the first tone had a higher or lower pitch than the second (low memory load), or if the first tone had a higher or lower pitch than the last (high memory load). Thus, in the high memory load condition, participants had to maintain one tone in ASTM for about three seconds (but also to ignore intervening tones). Compared to a passive listening condition, the right inferior frontal lobe was activated in the low memory load condition and the right inferior frontal lobe, the right temporal lobe, the parietal and the insular cortex were activated in the high memory load condition. The authors concluded that the frontal and temporal cortices in the right hemisphere are part of a network that underpins the retention of pitch information in short-term memory.

A more recent study (Gaab et al., 2003) used a similar paradigm. Brain activity was assessed with functional magnetic resonance imaging (fMRI) that used sparse temporal sampling to avoid contamination by scanner noise. Participants listened to a sequence that contained six or seven tones. They compared the first tone of the sequence to the last or second-to-last tone, which was indicated by instruction after the sequence. The authors observed that the superior temporal gyrus, the supramarginal gyrus, frontal regions, parietal regions and the cerebellum were engaged in the retention of tones differing in pitch. Interestingly, they found that the left inferior frontal gyrus was activated whereas Zatorre et al. (1994) found its right hemisphere homologue active in their high memory load condition. Importantly, Gaab and collegues found that activity in the supramarginal gyrus (especially in the left hemisphere) and the dorsolateral cerebellum were most strongly correlated with individual performance in the memory task.

In another fMRI study (Koelsch et al., 2009), participants were asked to remember either the pitch or the vowel of sung syllables, with or without simultaneous singing of a well-known song (suppression conditions). The authors argue that a network of activity in premotor cortices, the planum temporale, the inferior parietal lobe, the anterior insula, sub cortical structures, and the cerebellum were involved in the retention of acoustic items. They concluded that similar structures are involved in the retention of pitch and speech information (see also Schulze et al., 2011, for differences between musicians and non-musicians). However, it is not clear whether participants encoded and retained either pitch or vowel identity rather than treating the presented sounds as a unit and encoding both dimensions simultaneously.

Another fMRI study (Schulze, Mueller, & Koelsch, 2011) addressed mnemonic strategies that could be used when retaining sequences of tones. Musicians and non-musicians retained sequences in ASTM that contained tones of the same musical scale or tones without a tonal relation to each other. Contrasting these two populations can be especially interesting because musicians might use different or additional mnemonic strategies compared to musically untrained participants. The behavioral data suggested that musicians made use of their special knowledge for sequences containing tones of the same scale as their performance was better compared to the other conditions. This sub-group of participants with high expertise showed increased brain activity in the right superior frontal gyrus, the right inferior precentral gyrus, the right premotor cortex, and the left intraparietal sulcus for the tonal sequences. The authors argue that these brain areas might be especially important for strategies that make use of the melodic structure of sound sequences.

A recent study using magnetoencephalography (MEG, Grimault et al., 2012) localized brain areas that contribute to the retention of tones with a paradigm adapted from event-related potential (ERP) experiments (Guimond et al., 2011; Lefebvre et al., 2012, Nolden et al., 2013). Participants listened to a sequence of tones that they had to compare to another sequence of tones after a retention interval of 2000 ms. To isolate brain activity that was related to the retention of acoustic material specifically, the authors used the following strategies: First, the stimuli were designed to engage auditory short-term memory with as few other cognitive systems as possible. Being pure tones differing in pitch, it is very unlikely that these stimuli would engage any verbal process. Further, to avoid memory strategies related to learned melodic contours the octave was subdivided into 7 equidistant tones and therefore did not correspond to those of any musical scales. Second, the number of tones that had to be retained, and consequently the memory load, was varied. Third, the authors focused on brain activity during the retention period, thereby avoiding activity related to perception, encoding, retrieval, comparison, decision-making, or response selection. Finally, brain activity was correlated to the individual memory capacity of the participants. Participants with a high memory capacity should show increasing brain activity as memory load increases. Participants with a lower brain activity should reach their ASTM capacity limits earlier and, from this point on, brain activity should plateau, even when the set of items to memorize increases. Grimault et al. (2012) found that activity in the left superior/middle temporal gyrus, the left pre/post central gyrus, the left middle frontal gyrus, the right inferior frontal gyrus, and the right middle frontal gyrus showed a positive correlation with individual ASTM capacity.

Taken together, there are many indications that temporal, frontal, and parietal areas are involved in the retention of pitch information. First, PET and fMRI studies found brain activity in these areas during the retention of tones. The cerebellum is also often activated, although its functional significance for ASTM remains unclear. Second, a MEG study that correlated individual memory capacity with brain activity also points to temporal and frontal areas (Grimault et al., 2012). Even though activity in some brain areas has been repeatedly shown to be a correlate of ASTM, it is still unclear whether and how the retention of pitch in ASTM is lateralized, as there are studies pointing to either hemisphere (Gaab et al., 2003; Zatorre et al., 1994).

Recent models of short-term memory (Cowan, 2008; D’Esposito, 2007; D’Esposito et al., 2000; Goldman-Rakic, 1987; Petrides, 1991, 2005; Postle, 2006; Postle et al., 1999; Ruchkin et al., 2003) propose that the active retention of items makes use of brain areas that are involved in the perception of these items. These models can adequately explain why various studies on ASTM revealed that secondary auditory cortices appear to contribute to ASTM. In these brain areas, representations of the sounds arising from perceptual processes would then be held active during retention. Studies on ASTM have also found activity in the frontal lobe, for which a variety of mnemonic functions have been ascribed. Some models propose that activity in the frontal lobes may reflect executive control over the parts of the brain where the to-be-retained items are represented (e.g., auditory cortex). Areas in the frontal cortex also seem to play a role for memory strategies. During rehearsal of verbal material, the ventrolateral frontal cortex has shown increased activity (Awh et al., 1996; Paulesu et al., 1993) and other frontal areas have been associated with rehearsal that was not exclusively verbal (Courtney et al., 1998; Postle & D'Esposito, 2000). Some authors further argue that the dorsolateral frontal cortex was involved in chunking strategies (Bor et al., 2003; Rypma et al., 2002).

The role of the parietal cortex in ASTM is still unclear and the few studies on the retention of pitch information have not been decisive. Zatorre et al. (1994) found activation in the superior parietal lobe and Koelsch et al. (2009) found activation in the inferior parietal lobe during ASTM tasks. Gaab et al. (2003) reported a correlation between individual memory performance and activation in the inferior parietal lobe, while Schulze, Mueller, and Koelsch (2011) found that the intraparietal sulcus is more active in the retention of tonal than atonal melodies in musicians. Interestingly, parietal structures have also been discussed as part of a network involved in the retention of visual items (Robitaille et al., 2009, 2010; Todd & Marois, 2004, 2005) and seem to be sensitive to increased memory load, particularly for the retention of spatial locations (Harrison et al., 2010; Sereno et al., 2001). It might thus be that the parietal lobe contributes to processes related to short-term memory in general without being modality-specific, in which case the intraparietal sulcus might have a certain role regarding the relation between the retained items. Another reason for the observation of parietal activity in studies of ASTM could be that participants had to deploy a certain amount of attention to accomplish the task, and parietal structures, in particular the right superior parietal lobe, have been discussed as part of a modality-independent network for attention (Belin et al., 1998; Farah et al., 1989; Pardo et al., 1991; Paus et al., 1997; Zatorre et al., 1999).

It seems, therefore, in the light of recent data and theories, that some of the various areas found to participate in ASTM can be connected to core processes in ASTM, while the functional meaning of other areas remains ambiguous and/or speculative. The activity of keeping sound representations activated, simple retention, is a fundamental mechanism of ASTM. We conjecture that retention requires effortful mnemonic activity and goes beyond sensory memory (Atkinson & Shiffrin, 1968, Neisser, 1967). In particular, retention-specific brain activity is postulated to increase with the number of items held memory, at least in a number of structures participating in retention, a hypothesis that has been recently confirmed in ERP studies from our laboratory (Guimond et al., 2011; Lefebvre et al., 2012; Nolden et al., 2013).

Many previous imaging studies on ASTM are still ambiguous about the neuronal correlates of retention, as other memory-related processes might have taken place in parallel and might have influenced the results. For example, the use of verbal material might have engaged brain processes related language, the retention of sequences of tones might have led to the use of chunking and rehearsal, that is to say an internal repetition of the activated representations, and the presentation of further tones that had not to be remembered during retention might have led to the observation of auditory perceptive or interference processes unrelated to ASTM.

In this study, we aimed to isolate brain areas that underpin retention by eliminating or controlling confounds that have possibly contributed to results of some previous studies. To this end, we developed a design that encouraged participants to retain acoustic items in ASTM without using strategies such as chunking or rehearsal. Our results would therefore provide insight into brain areas related to the retention of tones with little contamination by other processes and thereby help to integrate findings from the literature. We adapted the procedure used by Guimond et al. (2011) for use in MEG. Participants heard zero (white-noise stimuli), one (the same tone in both ears), or two (a different tone in each ear) tones presented simultaneously. The encoding duration was thus identical in all load conditions. Participants were to retain the information for two seconds and then compare a test tone with memory. We hypothesized that secondary auditory cortices would be active bilaterally in support of the representation of the acoustic items. Comparing this study with the results of Grimault et al. (2012) allowed us to dissociate brain areas involved in the retention of tonal sequences, presumably in the frontal cortex, compared to the retention of simultaneously-presented tones.

7.3. Method

Participants

Seventeen neurologically normal college students participated in the experiment (8 male, mean age: 22 years, range: 19–30 years). All participants reported normal hearing and gave written informed consent for procedures that were vetted by the appropriate ethics committee.

Stimuli and apparatus

We used 14 pure tones and one white noise. The tones differing in pitch were so-called non-musical tones (Trehub et al., 1999). They ranged from 380 Hz to 1375 Hz and were created by multiplying the starting frequency and each resulting frequency by $2^{1/7}$ and, therefore, the relation of their frequencies did not correspond to those of an equal-tempered scale. The tones had a duration of 200 ms, including onset and offset ramps of 20 ms each. The subjective loudness of the sounds was adjusted using the loudness function (Garner & Miller, 1944). All acoustic material was presented via Etymotic ER-1 earphones and soft plastic ear inserts. A white fixation cross, a white circle, and coloured feedback circles (green for the correct answer, red for the wrong answer, and dark red for no answer within the response window) were centrally presented on a gray background. Participants responded on LUMItouch optical response keypads.

Procedure

At the beginning of each trial, a fixation cross appeared in the middle of the screen. After a mean interval of 500 ms (+/- 100 ms) following the onset of the fixation cross, one (Load 1) or two tones (Load 2) differing in pitch, or a white noise (Load 0), were presented for 200 ms. In conditions Load 1 and Load 0, the tone or white noise was presented to both ears. In condition Load 2, two different tones were presented simultaneously, one to each ear. We divided the 14 tones differing in pitch into two groups of 7 tones (low frequency octave and high frequency octave). When two different tones were presented simultaneously, they were chosen from two different octaves to facilitate the distinction between them. The smallest frequency difference between two simultaneously presented tones was between 688 Hz and 759 Hz which is still outside the range for pitch fusion (Van den Brink et al., 1976). For a given trial, tones were not allowed to be more then 6 tones apart, for example, the third tone of the low octave could not be presented simultaneously with a tone that was higher then the second tone of the high octave.

A silent retention interval of 2000 ms was followed by a single 200 ms probe tone presented to both ears. In half of the Load 1 or Load 2 trials, this tone had already been presented before the retention interval. A white circle replaced the fixation cross at the onset of the probe tone, indicating that participants could judge if the probe tone had been presented before or not and respond within the next 2500 ms. Half the participants responded by pressing a key with the left index finger for a same response and another key with the right index finger for a different response, and this mapping was reversed for the other half. In the condition Load 0, participants were asked always to press the corresponding "different" key. The circle turned red (error) or green (correct) to provide accuracy feedback after each response. When no response had been made within 2500 ms after the onset of the test tone, the white circle at fixation turned dark red. Feedback remained on the screen for 500 ms after the end of the response time. One thousand ms later, the next trial started with the appearance of the fixation cross (see Fig. 1).

Participants were instructed to fixate at the center of the screen and not to blink during the trials. They performed ten experimental blocks consisting of 60 trials each, thus resulting in 200 trials per load condition (Load 0, Load 1, and Load 2). Memory load varied randomly from trial to trial within each block. The experimental blocks were preceded by a practice block consisting of 24 trials.

INSERT FIGURE 1 ABOUT HERE

Magnetoencephalography recording

MEG signals were recorded with a whole-head CTF-VSM 275 system in a magnetically-shielded chamber. Analyses were based on recorded signals from 271 stable sensors. The signal was acquired at a sampling rate of 1200 Hz with a 300 Hz low-pass antialiasing filter. External electrodes were placed at the left and right outer canthi to track horizontal eye movements and above and below the left eye to track vertical eye movements and detect blinks. The difference between the electrodes on the left and right outer canthi was defined as the horizontal electrooculogram (HEOG), and the difference between the electrodes above and below the left eye as the vertical eletrooculogram (VEOG). Three coils for measuring the head position between blocks were placed on the nasion and before the upper end of the tragus of the left and right ear.

Anatomical Magnetic Resonance Imaging (MRI)

To provide high quality source localizations, the MEG data of each participant was combined with an individual anatomical scan obtained with MRI. Scanning was performed on a Siemens 3T MRI Magnetom Trio Tim scanner at the Unité de Neuroimagerie fonctionelle (UNF), Montréal, Canada. A high-resolution T1-weighted anatomical scan was obtained for anatomical localization for each subject (echo time (TE) of 2.98 ms; repetition time (TR) of 23 ms; matrix size, 256 × 256; voxel size, 1 mm × 1 mm × 1 mm).

Magnetoencephalography pre-processing

After the recording, the signal of reference magnetic sensors was used to reduce noise on the MEG sensors (third-order gradient noise reduction, applied using the CTF software). MEG signals were segmented from 400 ms before the onset of the retention interval until 2000 ms after the onset of the retention interval. Relative to the onset of the memory stimulus, the segmentation window was -200 to 2200 ms because the retention interval began at the offset of the tone (which lasted 200 ms). For technical reasons, the segments from two participants were cropped and lasted from -200 ms to 2000 ms relative to the onset of the retention interval. Trials with blinks or eye movements were removed by visual inspection of the VEOG and the HEOG channels. Trials containing movements or apparent external noise were also removed from further analysis. Head position was measured between blocks with the three external coils. When the difference between blocks exceeded 15 mm or more, the whole block was removed from further analysis. This had to be done for one subject.

For each participant, the segments in each load condition were separated into odd and even trials to increase the statistical power of the GLM analysis while maintaining a good signal-to-noise ratio. Then the segments were baseline corrected and averaged for each load condition and odd and even trials. The baseline was taken from -400 ms to -200 ms relative to the onset of the retention interval except for the participants with the cropped data files, for which the baseline was from -200 ms to -150 ms.

Source localization analyses

The white-matter/grey-matter surface was segmented from the anatomical scan of each participant using BrainVISA software (Mangin et al., 1995; Rivière et al., 2002). Source localization analyses were performed with the MEG signals using the maximum entropy on the mean method (MEM, Amblard et al., 2004; Grova et al., 2006). About 4000 sources were used in distributed source localization analyses performed for the average event-related magnetic field for odd and even trials of every condition separately on every sample point of a time window from 1100 ms to 1900 ms after the onset of the retention interval, as in Grimault et al. (2012). Sources were oriented perpendicularly relative to the cortical surface, hence modeling the orientation of pyramidal cells, which are likely the cause of the magnetic fields observed by MEG (Dale & Sereno, 1993). For each participant, the localizations of every sample point in the analyzed time window were averaged for each memory load and odd and even trials, thus obtaining an average cortically constrained localization map.

Each averaged cortically constrained localization map was interpolated in the volume MRI image of each individual participant. The resulting images were smoothed using a Gaussian filter with an 8-mm full width at half maximum. Activation in the cerebellum was not assessed. The individual images were then normalized to a common template in MNI-space.

Statistical analysis

We performed multiple linear regression analyses at each voxel using a general linear model (AFNI, Cox, 1996) with the localized sources as a function of individual memory capacity. The model revealed brain areas in which intensity changes of the signal were correlated to individual behavioral data (the index K represents the average number of items held in ASTM for each condition, Cowan, 2000; Pashler, 1988). We used K as a regressor because it takes individual differences in memory capacity into account and therefore more precisely maps to brain activity that varies with presentation load. K was 0 for Load 0. Thus, our model targeted brain areas that showed increased activity when the number of items that were actually retained in ASTM increased.

We used to random field theory (RFT, Worsley et al., 2002) to determine our statistical thresholds corrected for multiple comparisons. According to RFT, a cluster of voxels with a volume of at least 605.74 mm^3 and a $t = 3.19$ was significant at $p < .05$.

7.4. Results

Behavioral data

Mean accuracy was 98%, *SD* = 4%, for Load 0, 95%, *SD* = 4% for Load 1, and 82%, *SD* = 11%, for Load 2. A one-way ANOVA revealed a significant effect of load, $F(1.14, 18.24) = 40.46$, $MSE = 0.01$, $p < .001$, $\eta^2 = .72$, adjusted with a Greenhouse-Geisser correction. Accuracy differed significantly between all load conditions, Load 0 and Load 1: $t(16) = -3.66, p < .0022, d = 1.63$; Load 0 and Load 2: $t(16) = -9.82, p < .0001, d = 2.27$; Load 1 and Load 2: $t(16) = -6.04, p < .0001, d = 1.97$.

Additionally, we estimated the memory capacity index K for the memory task. We calculated it by multiplying the number of to-be-retained tones with the difference of hits and false alarms. The maximal K is the number of to be retained tones in each load condition. K had a mean of 0.90, *SD* = 0.09 for Load 1 and 1.26 *SD* = 0.42 for Load 2 (see Fig. 2). A paired-*t* test showed that this difference was significant, $t(16) = -3.96, p < .0015, d = 1.34$.

INSERT FIGURE 2 ABOUT HERE

Signal on the sensors

Grand average event-related magnetic fields of all sensors are shown in Fig. 3 for the 15 datasets that had been segmented from -400 ms to 2000 ms relative to the onset of the retention interval. A 40 Hz lowpass filter was applied for clearer visualization only; all analyses were performed on the unfiltered data. Trials of each condition were averaged for each participant and then averaged over participants. For these grand average waveforms we did not correct for differences in individual head position during the analyses. However, participants were positioned as similarly as possible within the MEG apparatus during the recordings to ensure good signal correspondance across participants.

At approximately -100 ms, that is 100 ms after tone onset, a burst that is consistent with the ERP N1 begins to evolve. It is more pronounced for Load 1 than for Load 0 and greatest for Load 2. Later, especially in the latter part of the retention interval, a sustained load effect is visible, similar to the ERP Sustained Anterior Negativity (SAN). Once again, the signal is greater for Load 1 than for Load 0 and greatest for Load 2 (see Guimond et al., 2011; Lefebvre et al., 2013, for ERPs obtained in a similar experimental design). Figure 4A shows the difference between the grand average waveforms of Load 1 and Load 0 and Fig. 4B shows the difference between the grand average waveforms of Load 2 and Load 0 including global field power. Compared to baseline level, the signal increased as load increased in the latter part of the retention interval.

INSERT FIGURE 3 ABOUT HERE

INSERT FIGURE 4 ABOUT HERE

ANOVAs on the average signal were performed on all sensors from 1100 ms to 1900 ms relative to the onset of the retention interval, the time window that would also be used for source localizations (see Table 1). Correction for multiple comparisons was based on the false discovery rate (FDR) approach (Benjamini & Hochberg, 1995, Benjamini & Yekutieli, 2001). The Greenhouse-Geisser correction for violation of sphericity was applied. For better readability we only report integer degrees of freedom. Figure 5 shows a topographical map of the significant sensors. Significant sensors over the left hemisphere show an amplitude increase with increasing memory load whereas significant sensors over the right hemisphere show an amplitude decrease with increasing memory load.

INSERT TABLE 1 ABOUT HERE

INSERT FIGURE 5 ABOUT HERE

Source localizations

The main results of the source localization analyses are shown in Figures 6A, 6B, and 6C. The source localization analyses of brain activity and individual memory capacity revealed six significant brain areas at a corrected $p < .05$ (see Table 2) located in the right superior temporal gyrus (cluster 1, BA 21/22/41, see Fig. 6A), right inferior temporal gyrus (cluster 2, BA 20, see Fig. 6A), right superior parietal lobule (cluster 3, BA 7, see Fig. 6A and Fig. 6B), left superior temporal gyrus (cluster 4, BA 42, see Fig. 6C), right precuneus (cluster 5, BA 7, see Fig. 6B), and the right inferior frontal gyrus (cluster 6, BA 6/9, see Fig. 6A).

INSERT TABLE 2 ABOUT HERE

INSERT FIGURE 6 ABOUT HERE

7.5. Discussion

In this study, we aimed to isolate brain areas that are involved in the retention of simultaneously presented tones using MEG. The temporal resolution of MEG allowed us to focus on brain activity taking place during the retention interval in an analysis window that was well after sensory encoding, but prior to the memory test. Hence, we were able to examine retention in ASTM without confounding influences from other sensory, perceptual, or cognitive processes. In our analysis, we predicted cortical activity based on the estimated amount of information held in ASTM (Cowan’s K), on a subject-by-subject basis. To our knowledge, this is the first MEG study that measured activity related to ASTM by manipulating the number of simultaneously presented tones differing in pitch.

Participants had to retain one or two pure tones for 2000 ms. The behavioural results suggest that participants retained on average 0.9 tones in the Load 1 condition and 1.26 tones in the Load 2 condition. The poorer average performance in the Load 2 condition — compared to the possible maximum of two tones — was accompanied by increased inter-individual differences in this condition (Fig. 2). This range of performance among participants allowed us to perform a covariation analysis of brain activity and the number of items retained in ASTM. We note that it is not important if some of this performance difference reflected a difficulty in encoding the two distinct tones as opposed to a difficulty in only retaining them.

What is important is that the measure of effective capacity derived from each subject's in-scanner performance (K) was positively correlated with brain activity during the latter portion of the retention interval. This approach revealed that the bilateral superior temporal gyri were involved in ASTM. In the right hemisphere, the inferior temporal gyrus, the inferior frontal gyrus, and parietal structures were also involved.

Some earlier brain-imaging studies on ASTM for pitch found similar results. However, the explicit link we are able to draw between estimates of ASTM retention and brain activity provides a more confident view on brain areas related to ASTM than studies without memory a load manipulation. Furthermore, as this is the first MEG study that varied memory load without using sequences of tones, the results more likely reflect activity that is solely related to retention because the possibility of rehearsal and retaining information about the pitch relations of the tones (contour) is minimized.

The activity in the superior temporal gyri, consistent with previous brain-imaging studies on the retention of pitch (Gaab et al., 2003; Grimault et al., 2012; Koelsch et al., 2009; Zatorre et al., 1994), was almost symmetric and supports recent models of short-term memory that propose that active retention of auditory information takes place in brain areas involved in its perception, perhaps as a re-activation of patterns that arose during perception (Cowan, 2008; D'Esposito, 2007; D'Esposito et al., 2000; Goldman-Rakic, 1987; Petrides, 1991, 2005; Postle, 2006; Postle et al., 1999; Ruchkin et al., 2003).

The fact that activity in the right inferior frontal lobe increased with load during the retention interval suggests that this area may participate actively in the retention of tones in ASTM. This confirms results of earlier brain-imaging studies on the retention of pitch (Grimault et al., 2012; Zatorre et al.,1994). Some authors (D'Esposito et al., 2000; Postle et al., 1999) argue that the frontal cortex has an important role in memory-related processes, which would be confirmed by our results. Interestingly, we did not find a broad network of frontal activity. Only activity in the right inferior frontal lobe increased when participants retained more items in ASTM. As we minimized the probability of rehearsal and chunking strategies in our design, we suggest that the right inferior temporal lobe has a somewhat more general and less strategy-related role in ASTM.

We also found areas in the right parietal cortex that showed increased activity when the number of retained tones increased, namely the right superior parietal lobe and the right precuneus. The role of the parietal cortex for ASTM is unclear. Areas very similar to the ones we found were activated during ASTM tasks in two previous brain-imaging studies (Gaab et al., 2003; Zatorre et al., 1994). Koelsch et al. (2009) found that the inferior parietal lobe was activated during an ASTM task and Schulze et al. (2011) suggested that the intraparietal sulcus might be important when musicians encode melodic contours. Grimault et al. (2012), on the other hand, did not find any parietal areas related to variations in estimated memory load during retention despite the use of sequences of tones. Parietal structures have also been convincingly demonstrated to be involved in retention of visual representations (presumably in visual short-term memory; Harrison et al., 2010; Robitaille et al., 2009, 2010; Todd & Marois, 2004, 2005). Integrating over our results and those of these previous studies, we hypothesize that the areas in the parietal lobe that we found play a more general modality-independent role for short-term memory. Specifically, activity in the superior parietal lobe correlates strongly with the number of stored representations and may reflect activity that maintains separate links, or pointers, to individuated representations held in memory. Such pointers are required to maintain the individuation of representations for later retrieval, comparison, or manipulation. In visual short-term memory studies, activity is often found in both hemispheres. In the present study, however, load-related parietal activity was found only in the right hemisphere. It is possible that this lateralization reflects the involvement of spatial attention given that our task, in the Load 2 condition, involved the presentation of a tone in each ear, and their individuation as separate representations may have engaged spatial (by ear) selection mechanisms (Belin et al., 1998; Farah et al., 1989; Pardo et al., 1991; Paus et al., 1997; Zatorre et al., 1999). Further research will be required to elucidate the functional role of the parietal lobe activations to ASTM.

In this study, we found that the superior temporal lobule was activated bilaterally, but also additional right-hemispheric activity in the temporal, frontal, and parietal lobes. It should also be kept in mind that the cluster in the secondary auditory area on the right side was larger than on the left. Previous studies on non-verbal ASTM have been inconsistent about the laterality of activity for the retention of pitch. For instance, Zatorre et al. (1994) found an advantage of the right hemisphere whereas others (Gaab et al., 2003; Grimault et al., 2012; Koelsch et al., 2009) found various areas in the left hemisphere to be involved in the retention of pitch in addition to areas in the right hemisphere. There are some indications that the right hemisphere is more strongly activated than the left hemisphere when finer spectral processing is required (for a review see Zatorre et al., 2002). We conjecture that our task required a more elaborate spectral analysis and processing than previous brain-imaging studies because of the necessary individuation and retention of simultaneous tones, in contrast to retention of sequential tones. If this factor is relevant, it is interesting that the consequence would be observed more than 1000 ms after the initial encoding of representations, during the retention period. This would suggest that auditory memory representations would retain multiple features of the original presentation and not only the resulting individuated tone representations. Although speculative, this general notion has been strongly supported for the retention and retrieval of visual representations in visual short-term memory. For example, visual short-term memory representations preserve information about the visual field in which the memorized object was presented at encoding (Dell'Acqua et al., 2010; Fortier-Gauthier et al., 2012; see also Gratton, 1998; Gratton et al., 1997).

Grimault et al. (2012) used a design that is quite similar to the one that we used in this study. They too used a memory load manipulation and focused on brain activity during retention that increased with the number of items held in ASTM. The key difference is that they used sequences of tones and we used simultaneously-presented tones. Grimault et al. found that activity in the left superior/middle temporal gyrus, the left pre/post central gyrus, the left middle frontal gyrus, the right inferior frontal gyrus, and the right middle frontal gyrus co-varied with the number of items held in ASTM. We found similar activity patterns in the left superior temporal gyrus, which leads us to suspect that this structure is generally important for the retention of low-level features of sounds. We found fewer frontal and left-hemispheric structures than Grimault et al., for instance, no middle frontal gyri nor pre/post central gyrus in the left hemisphere. We might now speculate that those frontal structures that were not present in our study have a special importance for the retention of tone sequences, perhaps regarding the encoding of a tone contour, and/or the use of chunking, or perhaps rehearsal strategies, given that all of these possibilities were minimized in our design.

The present study investigated the neural underpinnings of the retention of pitch in short-term memory by recording brain activity that varied in relation to changes in memory load and individual differences of ASTM capacity. Because our experimental design and stimuli minimized confounds with other cognitive processes and other memory systems, we believe that the brain areas we found to be active are specifically involved in the retention of basic acoustic information in ASTM. The results suggest that secondary auditory areas contribute to ASTM, in concert with frontal and parietal structures that contribute to keeping tone representations activated. Further research will be required to clarify the functional role of some of these structures, particularly of right parietal structures.

7.6. Author Note

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7.7. References

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7.8. Tables

Table 1. Descriptive and inferential statistics of significant sensors based on ANOVAs for repeated measures with the factor memory load (Load 0, Load 1, and Load 2). The false discovery rate approach was used to correct for multiple comparisons and the Greenhouse-Geisser correction was used for violation of the sphericity assumption. For better readability, only integer degrees of freedom are reported.

Localisations - Table 1

Sensor name	Mean signal (standard deviation) in 10^{-13} T			Hemisphere	*F*(2, 15)	*p*	η^2
	Load 0	Load 1	Load 2				
MLP42	0.03 (0.51)	0.31 (0.50)	0.60 (0.62)	left	9.80	.002	.38
MLP44	0.28 (0.59)	0.57 (0.66)	0.84 (0.81)	left	7.86	.004	.33
MLP52	-0.22 (0.38)	0.03 (0.43)	0.30 (0.58)	left	9.25	.001	.37
MLP53	-0.11 (0.48)	0.21 (0.49)	0.46 (0.62)	left	11.73	.001	.42
MLP54	0.04 (0.57)	0.39 (0.61)	0.62 (0.71)	left	12.21	.001	.43
MLP55	0.20 (0.68)	0.57 (0.70)	0.80 (0.80)	left	11.47	.002	.42
MLT14	0.31 (0.73)	0.64 (0.73)	0.85 (0.74)	left	7.68	.002	.32
MLT15	0.14 (0.66)	0.46 (0.65)	0.77 (0.80)	left	12.16	.001	.43
MLT26	0.04 (0.53)	0.29 (0.51)	0.48 (0.64)	left	7.89	.007	.33
MRP56	-0.09 (0.43)	-0.38 (0.58)	-0.53 (0.47)	right	7.80	.004	.33
MRT15	-0.13 (0.47)	-0.37 (0.46)	-0.70 (0.63)	right	10.78	.003	.40
MRT16	-0.17 (0.51)	-0.38 (0.52)	-0.66 (0.87)	right	8.86	.004	.36
MRT25	-0.06 (0.40)	-0.22 (0.36)	-0.47 (0.55)	right	7.70	.008	.33

Table 2. Coordinates of the sources. Results of the covariation analyses on the source localization maps are reported for significant clusters at *p* < .05, corrected.

Localisations - Table 2

Cluster number	Brain area	Brodmann area (BA)	Hemisphere	Sterotaxic coordinates (MNI-Tal space) for the center of the cluster (mm)			Volume of the cluster (mm^3)	t-value for peak voxel of the cluster
				x	y	z		
1	Superior temporal gyrus	21/22/41	right	43	-33	-1	1032	4.21
2	Inferior temporal Gyrus	20	right	45	-13	-23	896	4.1
3	Superior parietal lobule	7	right	23	-68	45	888	4.69
4	Superior temporal gyrus	42	left	-64	-23	11	840	4.06
5	Precuneus	7	right	7	-50	59	832	4.15
6	Inferior frontal gyrus	6/9	right	37	0	36	624	3.97

7.9. Figure Captions

Figure 1. Schematic trial procedure. One tone or a white noise was presented to both ears or two tones differing in pitch were presented simultaneously, one to each ear. After a retention interval of 2000 ms, a single tone was presented to both ears. Participants were asked to indicate if the single tone had been presented before the retention interval or not.

Figure 2. Memory capacity index (K) for each participant, and the group average, for memory Load 1 and memory Load 2.

Figure 3. Grand average event-related magnetic fields on all sensors over the 15 subjects whose datasets had been segmented from -400 ms to 2000 ms relative to the onset of the retention interval. Every line represents one MEG sensor. The sounds were presented from -200 to 0 ms, as indicated by the symbols underneath the graph. A 40 Hz lowpass filter was applied for clarity of illustration.

A. Condition Load 0.

B. Condition Load 1.

C. Condition Load 2.

Figure 4. Differences of grand average event-related magnetic fields on all sensors over the 15 subjects whose datasets had been segmented from -400 ms to 2000 ms relative to the onset of the retention interval. Every black line represents one MEG sensor, the red line represents

global field power. The sounds were presented from -200 to 0 ms, as indicated by the symbols underneath the graph. A 40 Hz lowpass filter was applied for clarity of illustration.

A. Difference between Load 1 and Load 0.

B. Difference between Load 2 and Load 0.

Figure 5. Topographical map of the MEG sensors. Significant sensors are illustrated in red, non-significant sensors are illustrated in blue. See text and Table 1 for further details.

Figure 6. Results of the covariation analyses on the source localization maps are shown as *t*-statistical maps superimposed on a 3D brain anatomical image of the white-matter/gray-matter interface (Collins, Neelin, Peters, & Evans, 1994).

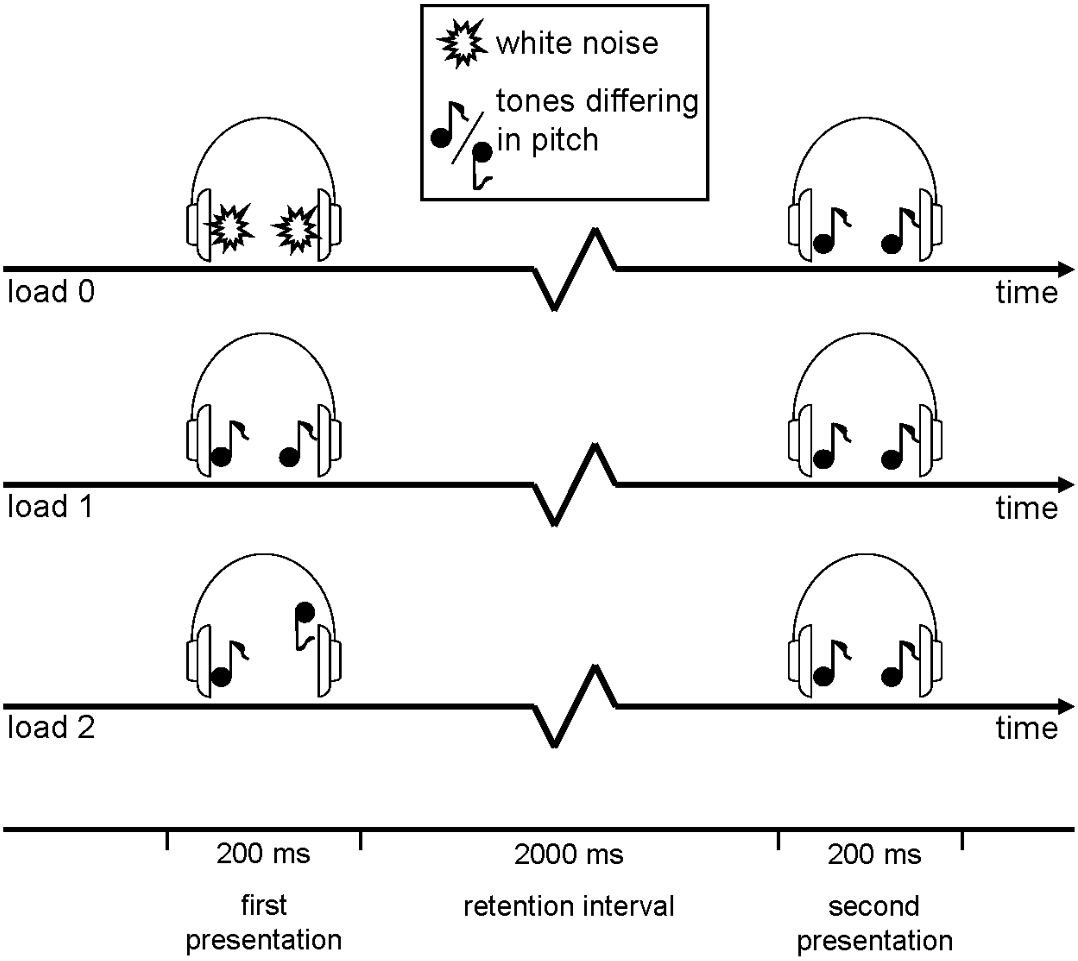
A. Right brain view, with Clusters 1, 2, 3, and 6.

B. Top brain view, with Clusters 3, and 5.

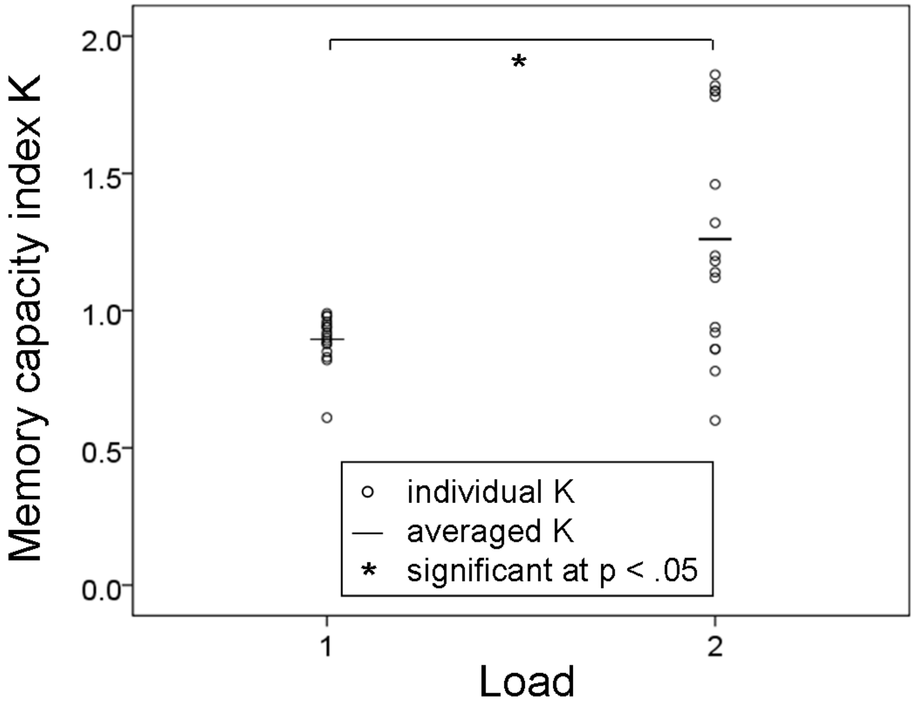
C. Left brain view, with Cluster 4.

7.10. Figures

Localisations - Figure 1

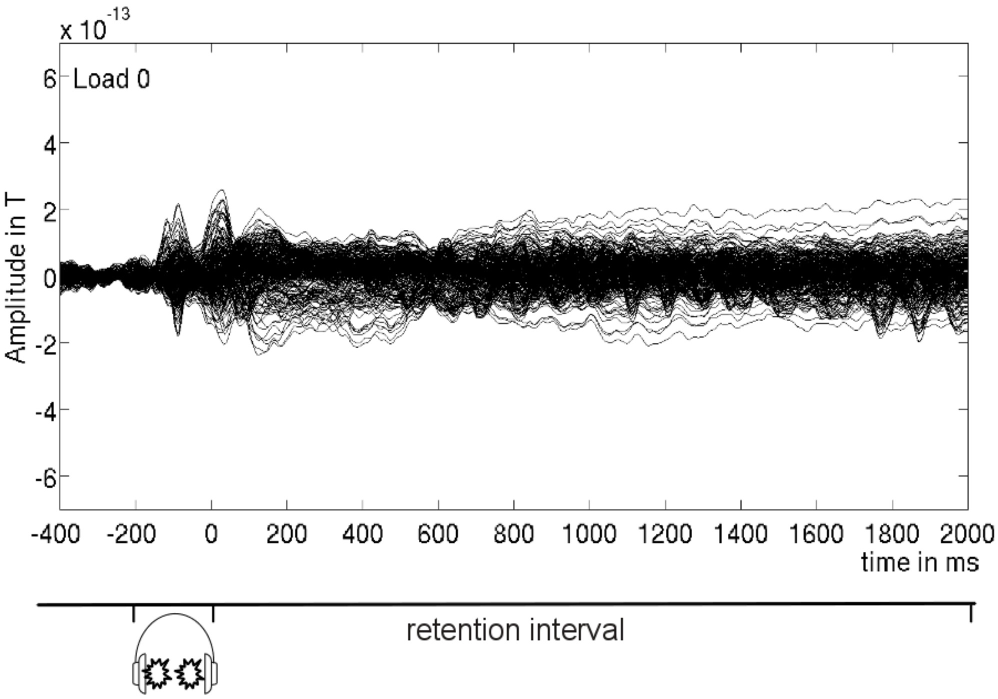


Localisations - Figure 2

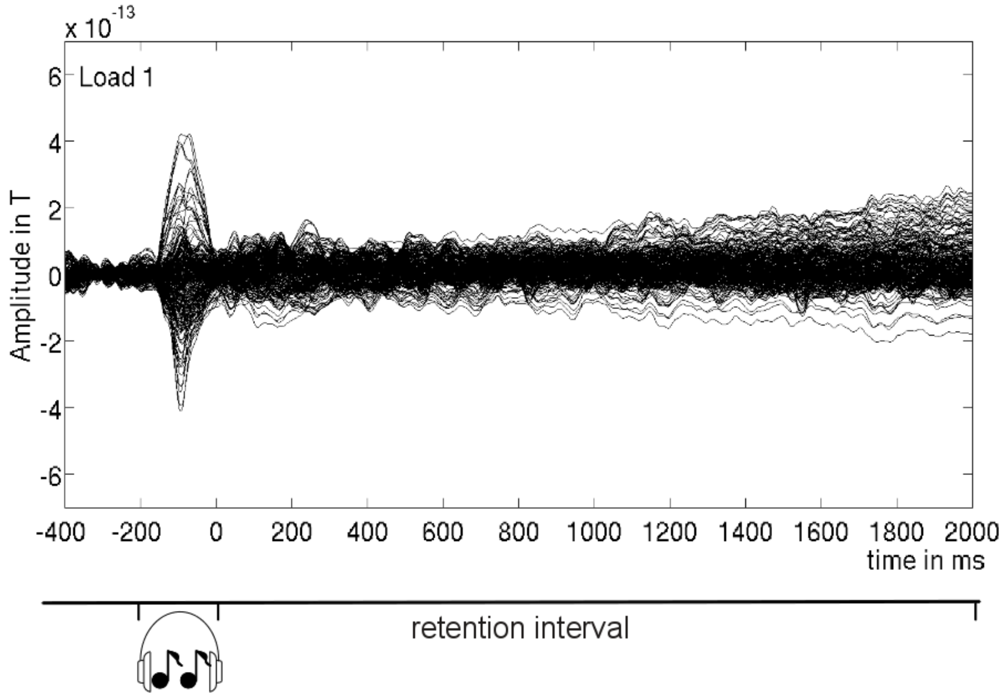


Localisations - Figure 3

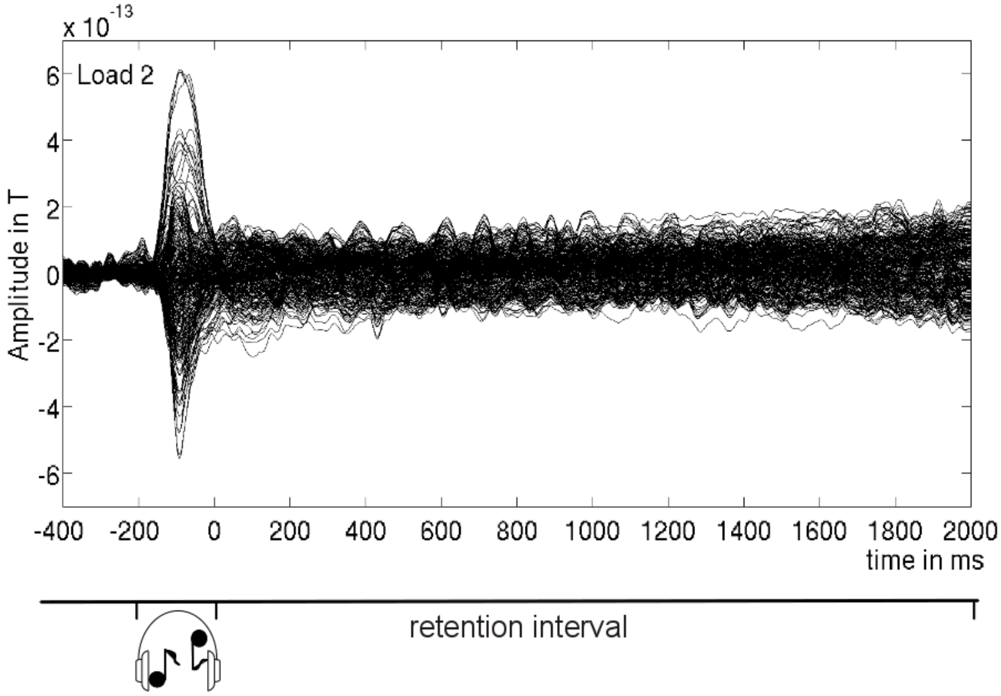
A.



B.


x 10^-13
Load 1
6
4
2
0
-2
-4
-6
Amplitude in T
-400
-200
0
200
400
600
800
1000
1200
1400
1600
1800
2000
time in ms
retention interval

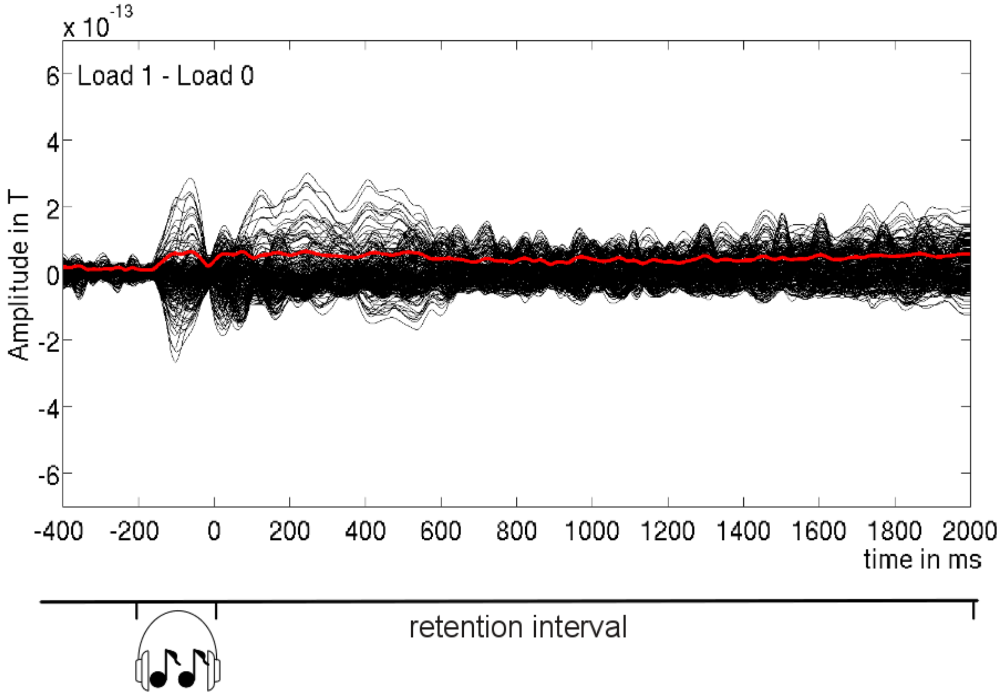
C.


x 10^-13
Load 2
Amplitude in T
6
4
2
0
-2
-4
-6
-400
-200
0
200
400
600
800
1000
1200
1400
1600
1800
2000
time in ms
retention interval

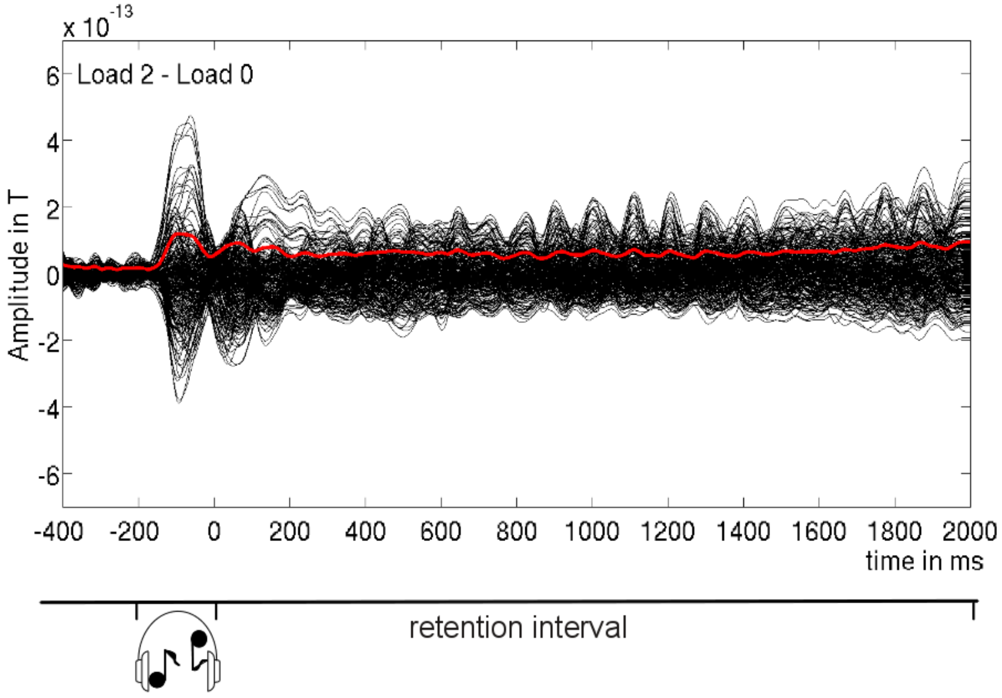
.

Localisations - Figure 4

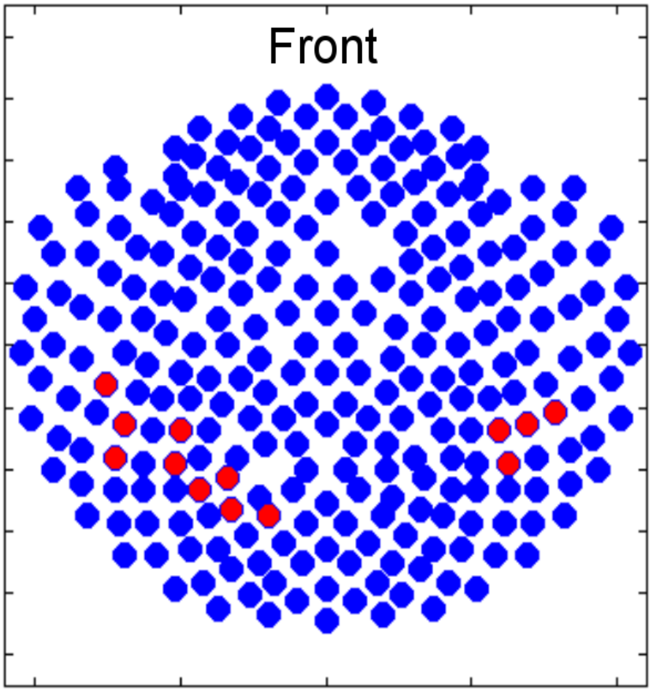
A.



B.

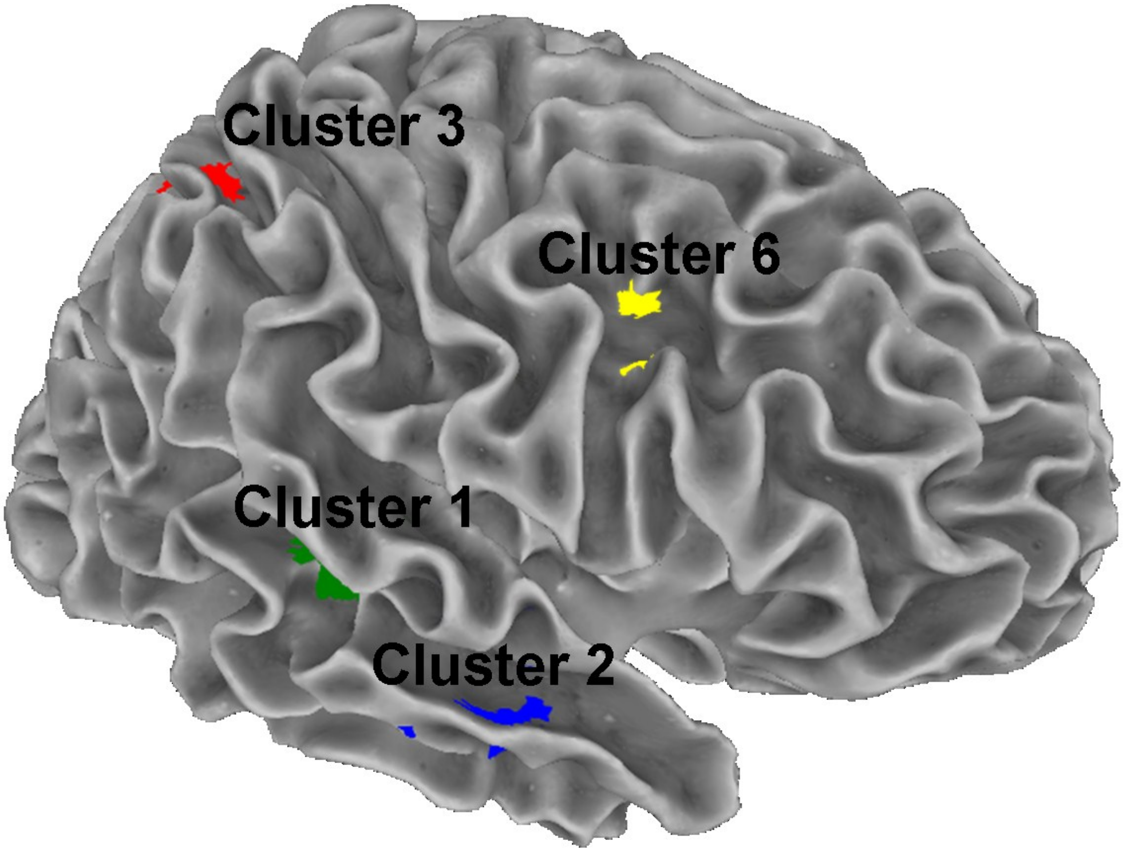

x 10^-13
Load 2 - Load 0
6
4
2
0
-2
-4
-6
Amplitude in T
-400
-200
0
200
400
600
800
1000
1200
1400
1600
1800
2000
time in ms
retention interval

Localisations - Figure 5

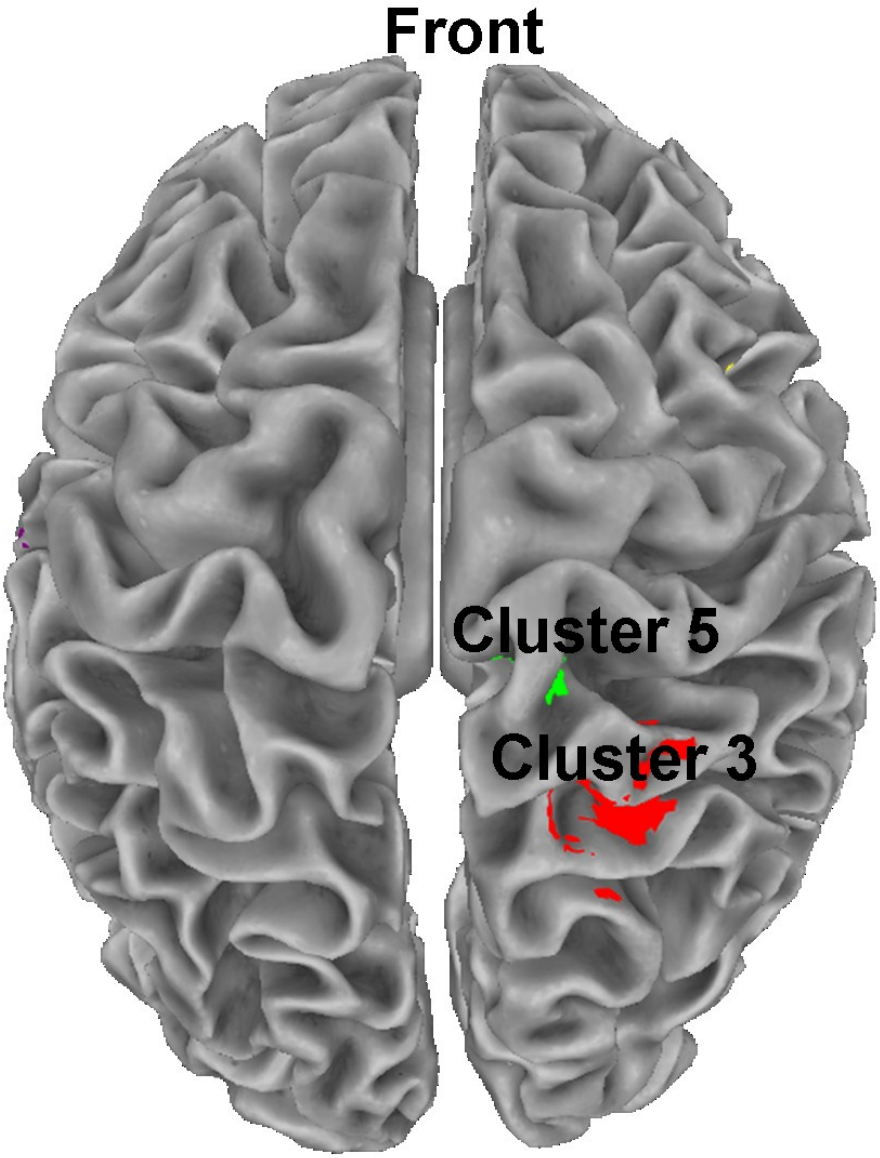


Localisations - Figure 6

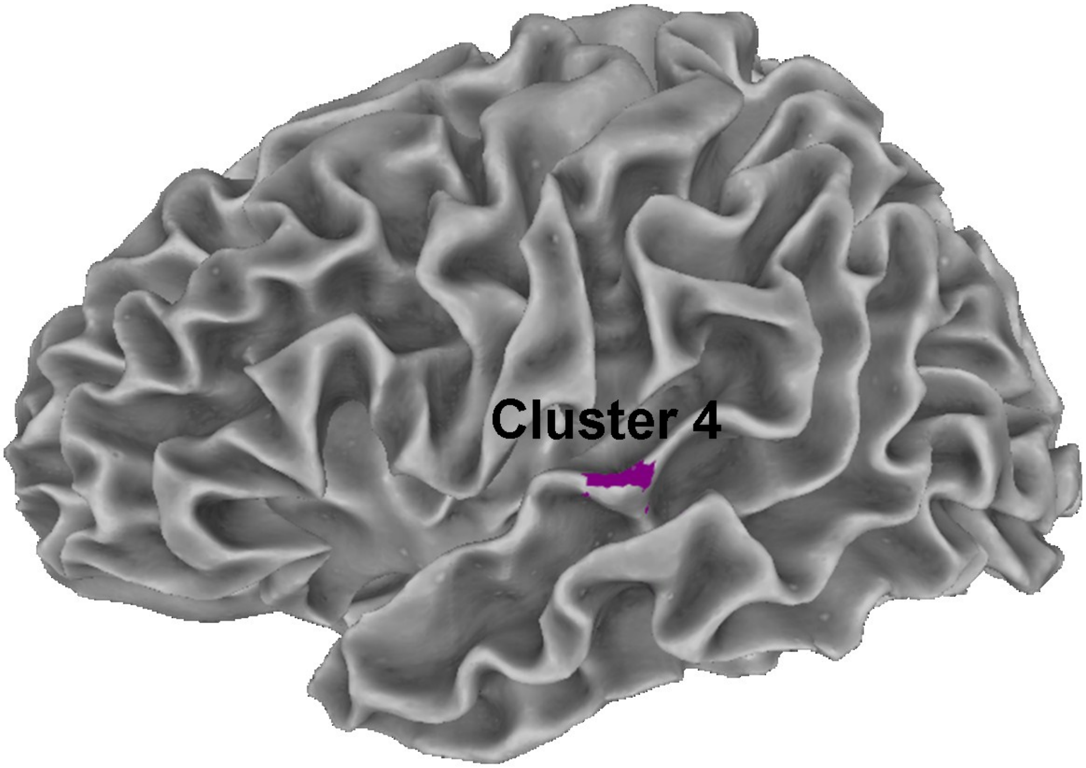
A.



B.



C.



Partie 3 : Discussion générale

Chapitre 8 : L'empreinte neuronale de la rétention des caractéristiques tonales et ce qui en peut être conclu

L'objectif de cette thèse était de contribuer à la compréhension des mécanismes de bas niveau de la rétention des sons et à la compréhension de l'activité cérébrale reliée à ces mécanismes. Trois études différentes en EEG et en MEG ont été réalisées et offrent de nouvelles perspectives sur la mémoire à court-terme auditive.

8.1. La rétention des caractéristiques acoustiques est un processus actif

Les études empiriques ont mené à une conclusion importante sur les mécanismes de la MCTA : La rétention des caractéristiques acoustiques comme montrée dans les études de cette thèse doit être un processus actif qui excède les demandes d'un registre sensoriel.

Le premier article (Chapitre 5) appuie surtout cette notion. Si on présume, comme beaucoup de modèles importants de la mémoire (Atkinson & Shiffrin, 1968; Cowan, 1988), que les stimuli distaux, c'est-à-dire des stimuli venant de l'environnement, passent d'abord un registre sensoriel sans filtre avant d'être soumis au soi-disant « goulot », on doit se demander à quelle phase correspond l'activité cérébrale observée dans les études empiriques de cette thèse. La durée de l'intervalle de rétention ne suffit pas comme indice ici parce qu'il n'y a pas de consensus sur la durée de vie du registre sensoriel dans la modalité auditive (nommé « mémoire échoïque » selon Neisser, 1967). Quelques études ont suggéré que la durée de vie de la mémoire échoïque n'excède pas 250 ms (par exemple Massaro, 1970); l'intervalle de rétention utilisé dans la première étude ne pourrait donc pas chevaucher avec la mémoire échoïque. Dans d'autres études, la conclusion est cependant que la mémoire échoïque peut avoir une durée de 10000 ms ce qui est encore dans la portée de l'intervalle de rétention utilisé dans les études empiriques de cette thèse (par exemple Sams, Hari, Rif, & Knuutila, 1993; voir aussi Massaro & Loftus, 1996).

Par contre, les différences bien prononcées entre la tâche mémoire et la tâche contrôle de la première étude élucidaient les faits. Les séquences de sons à retenir étaient construites avec soin; les bruits blancs antécédents assuraient une durée égale de toutes les séquences de mémoire. Par conséquent, seul le nombre de sons variant en timbre changeait. Les mêmes séquences de bruits blancs et sons variant en timbre étaient présentées avant le délai, dans la tâche contrôle comme dans la tâche mémoire. Dans la tâche mémoire, une composante PRE qui variait avec la charge mnésique, vraisemblablement une SAN, a été observée. Cette composante PRE n'était pas présente lors de la tâche contrôle, par contre, les amplitudes étaient en général un peu plus positives que dans la tâche mémoire. Si l'activité cérébrale variant avec la charge mnésique avait été due à la mémoire échoïque, elle aurait été observée aussi pendant la tâche contrôle ce qui n'est pas le cas. Nos résultats empiriques apportent donc des indices forts que l'activité cérébrale observée ici corresponde à un processus actif, en accord avec des modèles de la MCT (par exemple, Cowan, 1993, 1995). De plus, les résultats comportementaux démontraient une baisse de performance quand la charge mnésique augmentait. Cette observation est aussi à l'encontre d'une association avec la mémoire échoïque qui est classiquement décrite comme un mécanisme automatique ayant un grand empan mnésique.

Le patron des résultats obtenu avec les sons variant en timbre est similaire à celui de deux autres études qui visaient les corrélats électrophysiologiques de la rétention de la hauteur tonale (Guimond et al., 2011; Lefebvre et al., 2013). Considérées dans leur ensemble, les études citées précédemment et la première étude de cette thèse constituent une forte base empirique de l'aspect actif de la MCTA (voir aussi Nolden, 2014).

8.2. Similarités concernant la rétention de différentes caractéristiques acoustiques

Le premier article de cette thèse avait pour objectif, la mise en évidence des corrélats neuronaux de l'activité cérébrale reliée à la rétention du timbre (voir Chapitre 5). Les résultats principaux dévoilent un PRE fronto-central pendant l'intervalle de rétention. Ce PRE devient plus négatif avec une plus grande charge mnésique. Un PRE très similaire a déjà été observé pendant la rétention de sons variant en hauteur tonale (Alunni-Menichini et al., 2014; Guimond et al., 2011; Lefebvre et al., 2013). La rétention de ces deux caractéristiques des sons, du timbre et de la hauteur tonale, trouve donc des corrélats électrophysiologiques communs ou au moins très similaires ce qui est en accord avec certaines théories de la MCT. Plusieurs auteurs appuient la notion que la rétention des caractéristiques sensorielles simples est spécifique à la modalité et implique l'activité cérébrale reliée à la perception (D'Esposito, 2007; D'Esposito et al., 2000; Postle, 2006; Postle et al., 1999; Ruchkin, Grafman, Cameron, & Berndt, 2003). Les stimuli variant en timbre du premier article ont été créés justement, afin de ne pas pouvoir les associer avec du contenu de la MLT (avec du contenu relié à la langue ou à la musique surtout). Il est donc fort probable que les participants retenaient les aspects sensoriels au lieu du contenu sémantique (voir Chapitre 5 pour plus de détails).

Le fait d'observer des similarités entre la rétention du timbre et la rétention de la hauteur tonale permet aussi de mieux définir la signification fonctionnelle de la SAN. D'abord, elle est reliée à la rétention d'au moins deux caractéristiques tonales fondamentales, le timbre et la hauteur tonale. Dans le premier article de cette thèse il a été démontré pour la première fois que la rétention du timbre est reliée à une SAN, ce qui apporte ainsi, une généralisation à une autre caractéristique des sons. De plus, en considérant les paradigmes avec lesquelles une SAN était observée, on peut limiter les mécanismes corrélés avec la SAN. Dans une autre étude, les différentes charges des sons variant en hauteur tonale étaient réalisées avec une présentation simultanée (Guimond et al., 2011). L'objectif de cette dernière étude était de créer une tâche expérimentale qui porte les participants à n'utiliser que le maintien des sons en état actif. D'un autre côté, Lefebvre et collaborateurs (2013) et Alunni-Menichini et collaborateurs (2014) ont utilisé des séquences des sons variant en hauteur tonale. Il est possible que les participants aient constamment rafraîchi les représentations des sons dans ces études, par exemple par la répétition interne, en plus du maintien en état actif des représentations des sons. Les participants auraient pu retenir le contour mélodique en MCTA ce qui n'est pas possible avec la présentation simultanée. Dans l'étude de la rétention du timbre, une présentation séquentielle était utilisée. Il est peu probable que les participants retiennent le contour des timbres en sus des sons individuels (mais voir McDermott, Lehr, & Oxenham, 2008), le chant interne n'est pas très probable comme stratégie mnésique non plus, parce que les différences subtiles en timbre sont difficiles à imiter par les participants. Cependant, la répétition interne ne peut pas être complètement exclue comme stratégie mnésique. Toutes ces approches différentes, avec des modes de présentation distincts et avec des caractéristiques des sons distinctes, sont reliées à l'observation d'une SAN en PRE. Le mécanisme commun de ces différentes approches est le maintien des représentations des sons en état actif, reflétée par la SAN. Malgré la présence d'autres mécanismes qui peuvent également soutenir la rétention des sons, souvent induits par des stratégies mnésiques, les études résumées ici ont dévoilé un contributeur indispensable.

8.3. Plus d'activité cérébrale avec une plus grande charge mnésique

Les études empiriques de cette thèse avaient toutes comme objectif d'isoler l'activité cérébrale reliée à la MCTA. Dans ce but, plusieurs stratégies expérimentales sont reprises, dont l'emploi d'une manipulation de la charge mnésique. La manipulation de charge résulte en des nombres d'items retenus distincts, reflétés plus précisément par l'index de capacité mnésique K. La supposition sous-jacente est que, durant la rétention, l'activité cérébrale non-reliée à la rétention n'augmente pas quand le nombre d'items retenus augmente.

Dans les études EEG, une augmentation de l'activité cérébrale avec une augmentation de la charge mnésique est observée. D'abord, un PRE fronto-central, une SAN vraisemblablement, est observé pendant l'intervalle de rétention (voir Chapitre 5). Sa signification fonctionnelle est discutée dans la section précédente. De plus, on observe que l'activité oscillatoire présente un patron qui reflète les différentes charges mnésiques (Chapitre 6). Dans le deuxième article, les amplitudes des oscillations dans la bande alpha (8-12 Hz) et dans la bande beta (18-28 Hz) sont quantifiées et analysées pendant l'intervalle de rétention et pendant la présentation du son test (pour plus de détails voir Chapitre 6). Pendant l'intervalle de rétention, l'augmentation de l'amplitude avec une augmentation de charge dans la bande alpha ressemble légèrement à ce qui a été observé en PRE. Cependant, cet effet n'est pas observé dans la bande beta où il n'y a pas de différence entre les charges mnésiques. L'activité oscillatoire dans la bande alpha semble donc supporter la rétention des sons en MCTA.

Plusieurs tentatives dans la littérature essayent d'expliquer la signification fonctionnelle de l'augmentation et de la baisse de l'activité oscillatoire dans la bande alpha. L'hypothèse que l'activité oscillatoire dans une certaine bande de fréquence représente une certaine classe de processus plutôt qu'un domaine cognitif (Klimesch, 2012, p. 608) est en accord avec des approches qui proposent que l'activité dans la bande alpha représente l'inhibition contrôlée (Jensen et al., 2002; Klimesch et al., 2007). Le rôle inhibitoire de la bande alpha semble être une explication satisfaisante pendant l'intervalle de rétention dans le sens d'une protection pour que les représentations des sons ne soient pas écrasées. Un patron similaire a été trouvé également en MCTV (par exemple, Grimault et al., 2009). Par contre, quand on considère l'activité en alpha pendant la présentation du son test, on s'aperçoit que cette explication n'est pas suffisante. Pendant la présentation du son test, il y a de plus grandes amplitudes pour les sons test « différents » (pas de correspondance avec les sons mémoire) que pour des sons test « pareils » (correspondance avec les sons mémoire). Il n'y a pas d'explication plausible sous la prémisse que l'activité dans la bande alpha représente un mécanisme d'inhibition parce que chaque son test doit être traité de la même façon et comparé avec les représentations de sons en mémoire. Il faut aussi noter que l'activité dans la bande alpha varie en fonction de la modalité sensorielle (auditive versus visuelle) pendant les trois phases de la tâche (encodage, rétention, récupération). Ceci est aussi évident quand on regarde l'augmentation de l'amplitude en alpha qui est assez prononcée à environ 100 ms après la présentation des sons mémoire. Elle est en outre modulée par la charge (voir Oscillations – Figure 4, autours de -2100 ms, voir aussi Krause et al., 1996; Pesonen et al., 2006). En mémoire visuelle, de l'autre côté, l'observation typique est plutôt une baisse de l'activation alpha pendant l'encodage (par exemple Klimesch et al., 1996). À cause de ces différences entre le domaine auditif et le domaine visuel, une interprétation de la signification fonctionnelle d'une bande de fréquence doit aussi tenir compte qu'il n'est pas entièrement possible à date d'exclure que l'activité oscillatoire soutenant la MCT soit spécifique à la modalité.

Dans la deuxième étude (Chapitre 6), une dissociation du patron oscillatoire est aussi observée entre l'intervalle de rétention et la présentation du son test. Pendant l'intervalle de rétention, l'amplitude en alpha augmente avec la charge, alors que l'amplitude en beta baisse avec la charge pendant la présentation du son test. Ces effets de charge reflètent donc des processus distincts plutôt que de représenter directement les sons maintenus en mémoire (voir aussi Hanslmayr, Staudigl, & Fellner, 2012, pour la thèse que l'information est mieux codée quand l'activité en bande alpha est réduite). L'hypothèse de travail proposée dans le deuxième article (Chapitre 6) est que l'activité oscillatoire dans la bande alpha et l'activité oscillatoire dans la bande beta interagissent de différentes façons et reflètent une adaptation aux exigences de chaque phase de la tâche. Pendant l'intervalle de rétention, c'est surtout l'activité dans la bande alpha qui supporte la rétention des sons. Par contre, pendant la présentation des sons test, les bandes alpha et beta reflètent des aspects distincts reliés à la comparaison d'items retenus et les sons test. Alors que la bande beta reflète probablement l'accès aux représentations des sons mémoire et la comparaison, la bande alpha reflète plutôt le résultat de la comparaison. Les résultats de cette étude démontrent donc que l'activité oscillatoire reliée à la MCTA reflète des processus complexes qu'on ne peut pas facilement réduire à une simple classe de processus (Klimesch, 2012). Cette étude a servi en plus à dévoiler des processus distincts ayant lieu en même temps, reflétés dans deux bandes de fréquences différentes.

Pour le troisième article en MEG, une analyse de covariation a été utilisée au lieu d'une simple comparaison de différentes conditions de charge (Chapitre 7). Pour ceci, l'index de la capacité mnésique K était utilisé comme prédicteur, ainsi permettant un modèle qui inclue les structures cérébrales montrant une plus grande activité avec plus d'items retenus et qui prend en considération les différences individuelles en performance. Le modèle de covariation utilisé dans le troisième article sert à révéler les structures cérébrales qui montrent une activation variant avec le nombre estimé d'items retenus. Ceci est réalisé avec une expérimentation paramétrique et une approche de covariation statistique. Comparé avec une approche expérimentale qui vise à contraster une condition de mémoire avec une condition de contrôle (par exemple Gaab et al., 2003), les méthodes utilisées ici ne dépendent pas de la qualité de la tâche contrôle. De plus, étant donné que l'activité cérébrale non-reliée à la MCTA ne devrait pas varier avec la charge mnésique durant la 2^{e} partie de l'intervalle de rétention, l'approche utilisée dans le troisième article était optimale pour découvrir les aires cérébrales du système de la MCTA.

Les structures cérébrales révélées ainsi sont situées dans les gyri temporaux supérieurs des deux hémisphères, le gyrus temporal inférieur droite, le gyrus inférieur frontal, et dans deux structures pariétales. L'augmentation de l'activité dans une structure cérébrale avec l'augmentation du nombre d'items retenus ne veut pas nécessairement dire que les sons sont directement représentés « dans » ces structures (voir aussi Nolden, 2014). Par contre, ces structures cérébrales peuvent occuper des fonctions différentes qui aident chacune la rétention de sons. En particulier, le rôle des structures temporales et le gyrus frontal inférieur reflètent bien la relation entre la rétention et la perception des sons (pour une interprétation plus spéculative du rôle des structures pariétales voir Chapitre 7 et Nolden, 2014).

Les structures symétriques dans les lobes temporaux et la structure dans le cortex frontal inférieur ont été antérieurement associées avec la perception de la hauteur tonale (par exemple Zatorre et al., 1994). Les structures temporales chevauchent les cortex auditifs secondaires qui assument un rôle important pour la perception auditive. Les résultats de cette étude ne confirment donc pas seulement les études antérieures sur la MCTA utilisant d'autres approches expérimentales (Gaab et al., 2003; Grimault et al., 2014; Koelsch et al., 2009; Zatorre et al., 1994), mais appuient également la notion que la rétention des stimuli sensoriels se sert de la (ré-)activation du patron de l'activité cérébrale créé lors de la perception (Cowan, 2008; D'Esposito, 2007; D'Esposito et al., 2000).

La prédominance des structures révélées dans l'hémisphère droit dans le troisième article peut aussi être interprétée dans ce sens. Dans l'hémisphère droit, cinq régions étaient isolées contre une région dans l'hémisphère gauche. Les résultats de quelques études ont suggéré qu'il y avait une spécialisation relative des deux cortex auditifs (gauche et droit) pour le traitement de quelques aspects spécifiques en audition. Une spécialisation pour le traitement temporel est attribuée au cortex auditif gauche et une spécialisation pour le traitement spectral est attribuée au cortex auditif droit (voir Zatorre, Belin, & Penhune, 2002). Étant donné que le traitement des sons présentés simultanément a probablement eu besoin d'un traitement plus précis de l'information spectrale que de l'information temporelle, il est bien possible d'interpréter l'activité latéralisée observée ici selon ce modèle. Les deux cortex auditifs secondaires sont activés pendant la rétention, mais c'est plus évident dans l'hémisphère droit. Par conséquent, l'activation du cortex auditif secondaire droit peut impliquer un réseau avec d'autres structures à droite (frontale, pariétale). Ceci est aussi intéressant parce que les études antécédentes sur les structures reliées à la rétention des sons ne sont pas concluantes sur la latéralisation (voir Gaab et al., 2003, pour une prépondérance de l'hémisphère gauche). Si les différences de latéralisation constituent réellement un résidu du traitement spécialisé pendant la perception, l'ensemble des articles antérieurs et la troisième étude de cette thèse fourniront un indice important de l'aspect sensoriel de la MCTA (voir aussi Dell'Acqua, Sessa, Toffanin, Luria, & Jolicœur, 2010; Fortier-Gauthier, Moffat, Dell'Acqua, McDonald, & Jolicoeur, 2012, pour voir de l'évidence convergente en MCTV).

En résumé, les trois articles de cette thèse ont fourni des données qui démontrent une variation de l'activité cérébrale avec la charge mnésique, ou, plus précisément, le nombre d'items retenus. Ce faisant, les études se sont penchées sur les PREs, l'activité oscillatoire et les structures cérébrales qui reflètent la rétention des sons d'une façon ou d'une autre. Les patrons d'activité cérébrale dévoilés reflètent bien les mécanismes complexes de la MCTA et contribueront à une meilleure compréhension de leurs fonctions dans l'architecture cognitive.

8.4. L'activation des représentations des sons – Corrélats cérébraux

L'ensemble des études antérieures et les études réalisées lors de cette thèse a d'abord mené à des résultats semblables concernant l'empreinte neuronale de la rétention des caractéristiques tonales. Cependant, des nuances entre différentes méthodologies utilisées dans ces études, suggèrent que les réseaux soutenant la rétention des sons s'adaptent dynamiquement au contexte et aux exigences de la tâche (voir Chapitre 7). Ceci se manifeste par exemple dans les différences entre la rétention des séquences de sons et des sons présentés simultanément. Ces différences dans la stimulation pourraient en effet mener à une accentuation de certaines mécanismes ou stratégies mnésiques, par exemple la répétition interne.

Dans deux des expériences de cette thèse, des sons présentés simultanément étaient utilisés afin de maximiser la probabilité d'utilisation d'une stratégie principale de maintien des sons en état actif ce qui correspondant à la métaphore d'un « store » mnésique (deuxième article, première expérience ; troisième article). Le paradigme expérimental avait pour but de réduire ou d'éliminer l'utilisation du chant interne, de la répétition interne, ou de la rétention des caractéristiques mélodiques. Par conséquent, l'activité cérébrale observée dans ces études reflète avec une forte probabilité principalement le maintien en état actif des représentations des sons.

L'expérience en EEG (Chapitre 6, première article) a montré une activité oscillatoire dans la bande alpha localisée aux sites fronto-centraux. L'article en MEG (Chapitre 7) qui cherchait d'autres structures cérébrales a mis en évidence une implication des structures temporales, frontales, et pariétales avec une légère tendance de plus grande activation à droite. Dans cette étude, l'implication réduite du cortex frontal est intéressante, surtout en comparaison avec une autre étude qui utilisait des séquences de sons au lieu des sons présentés simultanément (Grimault et al., 2014). Il est donc possible que la rétention simple qui n'excède pas trop la notion du « store » ne recrute pas autant les structures frontales que les mécanismes plus complexes intégrant les stratégies mnésiques.

Les cortex auditifs secondaires, par contre, sont suggérés comme d'importantes structures impliquées dans la rétention des sons selon de nombreux autres auteurs (pour ne citer que Zatorre et al., 1994, Grimault et al., 2014). Une implication des cortex sensoriels semble être relativement importante pour la rétention réussie des caractéristiques tonales de bas niveau, pendant que l'implication d'autres structures cérébrales peut encore varier selon le contexte et les détails du matériel retenu.

Chapitre 9 : Perspectives

Les trois études empiriques de cette thèse se sont penchées sur l'activité cérébrale reliée à la rétention des sons en MCTA et les conclusions tirées fournissent la base de futures études. Il y a souvent plus d'idées pour des études futures que de ressources pour les réaliser; pour cette raison quelques idées seulement seront présentées dans cette section.

Tout d'abord, une partie de cette thèse abordait la rétention du timbre. Le timbre est une des principales caractéristiques tonales, souvent mentionnée avec la hauteur tonale, l'intensité, et la position spatiale des sons. Les résultats du premier article suggèrent une certaine similarité entre la rétention de la hauteur tonale et la rétention du timbre, et il serait intéressant de savoir si c'est aussi le cas pour d'autres caractéristiques tonales. Comme discuté plus tôt, plusieurs résultats d'études empiriques ont souligné l'aspect sensoriel de la MCT. D'ailleurs, des différences des voies perceptives ont été suggérées entre les différentes caractéristiques tonales, considérées comme l'équivalent de la voie dorsale et la voie ventrale en vision qui traitent le « où » et le « quoi » (Kaas & Hackett, 1999; Romanski et al., 1999). Alors que les expériences en hauteur tonale et en timbre touchent l'aspect « quoi », la position spatiale vise l'aspect du « où ». Une tâche mnésique de position spatiale pourrait donc mener à l'utilisation de la voie du « où ». L'hypothèse est donc que l'activation cérébrale reliée à la rétention de la position spatiale pourrait ressembler à ce qui a été observé lors de la perception. En EEG, cela peut se traduire par un déplacement de la *SAN* aux électrodes centrales et pariétales postérieures au lieu des électrodes fronto-centrales (Diaconescu, Alain, & McIntosh, 2011). Une étude en MEG pourrait apporter une clarification à l'implication des structures cérébrales et mener à l'observation d'une activation plutôt postérieure dans les cortex auditifs et une activation plus prononcée dans le cortex pariétal supérieur et inférieur. Ces aires ont été isolées lors de la perception spatiale auditive (par exemple, Alain, Arnott, Hevenor, Graham, & Grady, 2001). Une confirmation de ce patron dans une tâche mnésique pourrait constituer une accentuation forte de l'aspect sensoriel de l'MCTA.

De plus, il serait intéressant de travailler avec des stimuli multimodaux, par exemple auditifs et visuels, ou même auditifs et tactiles. Une tâche de rétention pourrait envisager soit la rétention du stimulus au complet, soit l'information d'une modalité seulement en ignorant l'autre. Ce genre de paradigme expérimental aiderait à mieux comprendre les similarités et différences entre les modalités autant que l'intégration d'information venant de deux modalités. La rétention des stimuli multimodaux pourrait être explorée avec les principes qui ont été également appliqués dans les études empiriques de cette thèse afin de non seulement cibler les processus de bas niveau, mais aussi de fournir plus de validité écologique. Dans cette perspective, il serait aussi intéressant d'intensifier les approches temps-fréquence déjà utilisées dans le deuxième article (voir Chapitre 6). Quelques questions, comme la spécificité à la modalité, pourraient très bien être abordées avec les nouveaux paradigmes décrits dans le cadre de ce travail. De plus, les analyses pourraient aussi se concentrer sur la phase et non seulement sur les modulations d'amplitude dans certaines fréquences. Pour mieux comprendre les dépendances réciproques entre certaines bandes de fréquences, des analyses de couplages phase-amplitude pourraient être effectuées. Ceci aiderait à dépiauter les différents processus reliés à la MCTA qui ont lieu au même moment. Ce faisant, la nature des représentations des sons pourrait être mieux comprise ainsi que la façon selon laquelle l'information sensorielle est retenue et récupérée.

Chapitre 10 : Conclusions

Dans cette thèse, la rétention des caractéristiques acoustiques de bas niveau étaient abordées selon trois perspectives différentes : D'abord, un PRE révélé lors de la rétention de la hauteur tonale était observé pendant la rétention du timbre, généralisant ainsi des résultats antérieurs à une autre caractéristique tonale. Deuxièmement, l'activité oscillatoire reliée à la rétention et à la récupération des sons en MCTA a été explorée dans deux expériences afin de contribuer à une meilleure compréhension des mécanismes de bas niveau et de l'empreinte oscillatoire de la MCTA. Finalement, des localisations de sources effectuées sur le signal MEG ont pu mettre en évidence les régions cérébrales qui montrent une augmentation de l'activité allant de pair avec une augmentation du nombre de sons retenus.

Les études présentées dans cette thèse apportent des connaissances importantes sur les mécanismes de bas niveau de la rétention des sons. De plus, elles reflètent le patron de l'activité cérébrale représenté par les PREs, l'activité oscillatoire, et les structures cérébrales. Enfin, c'est l'ensemble des résultats qui nous éclaire d'une bonne compréhension fonctionnelle et de l'activité cérébrale correspondante qui contribue significativement aux connaissances dans le domaine.

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Annexes

Annexe 1. Formulaire d′information et de consentement

FORMULAIRE D'INFORMATION ET DE CONSENTEMENT

Titre du projet de recherche:	Mémoire à court-terme auditive.
Chercheur responsable du projet :	Pierre Jolicoeur, Ph.D., Département de Psychologie Université de Montréal.
Organismes subventionnaires :	Fonds de recherche du Québec - Nature et technologies. Programme des Chaires de recherche du Canada.

Préambule

Nous vous invitons à participer à un projet de recherche en neuroimagerie. Cependant, avant d'accepter de participer à ce projet et de signer ce formulaire d'information et de consentement, veuillez prendre le temps de lire, de comprendre et de considérer attentivement les renseignements qui suivent.

Ce formulaire peut contenir des mots que vous ne comprenez pas. Nous vous invitons à poser toutes les questions que vous jugerez utiles au chercheur responsable du projet ou à un membre de son équipe de recherche et à leur demander de vous expliquer tout mot ou renseignement qui n'est pas clair.

Nature et objectifs du projet de recherche

Ce projet a pour but d'identifier les aires du cerveau impliquées dans la mémoire à court-terme auditive. Plus particulièrement, il vise à établir des liens entre les résultats obtenus par diverses techniques d'imagerie cérébrale, soit l'imagerie par résonnance magnétique, la magnétoencéphalographie et l'électroencéphalographie.

Pour la réalisation de ce projet de recherche, nous comptons recruter 100 participants, hommes et femmes, âgés de 18 à 35 ans.

Pour l'IRM : **Qu'est-ce qu'une imagerie par résonance magnétique (IRM)?**

L'imagerie par résonance magnétique réalisée en recherche, donne des images du corps, du

cerveau ainsi que de leur fonctionnement.
Pour la réalisation de l'IRM, aucune substance ne sera injectée. Vous serez allongé sur un matelas qui sera lentement glissé dans un grand tube. Le tube est ouvert aux deux extrémités. Un système d'interphone vous permet de communiquer avec le technicien au besoin. Pour votre confort, nous vous demanderons de porter soit un casque d'écoute, soit des bouchons protecteurs qui seront installés dans vos oreilles, et ce, afin de diminuer les bruits importants qui sont émis par l'appareil. Pendant que l'appareil fonctionne, il est important de demeurer immobile. Pour ce faire, un coussinet sera placé autour de votre tête afin d'assurer votre immobilité.

Déroulement du projet de recherche

Pour l'EEG et la MEG : Si vous acceptez de participer à l'étude, on vous demandera de passer 2 heures au laboratoire du Centre de Recherche en Neuropsychologie et Cognition de l'Université de Montréal à la date et à l'heure préalablement déterminées. À chaque essai, vous entendrez une séquence sonore composée de différents nombre de sons. Écoutez bien cette séquence puisque vous devez la garder en mémoire jusqu'à la fin de l'essai. Après un intervalle de temps plus ou moins long, vous entendrez une deuxième séquence sonore comprenant le même nombre de sons que la séquence mémorisée. Votre tâche consiste à indiquer si la deuxième séquence est identique ou non à la séquence mémorisée en appuyant sur un bouton si les séquences sont pareilles et sur un autre bouton si elles sont différentes.

Pour l'EEG : De plus, l'activité électrique de votre cerveau sera enregistrée pendant le déroulement de l'expérience. Pour ce faire, cinq capteurs électriques seront collés sur votre peau (autour des yeux et derrière les oreilles) et un bonnet contenant des capteurs vous sera installé sur la tête. Durant toute la durée de la séance, il vous sera possible de communiquer par interphone avec la personne qui sera en fonction. La pose et le retrait des capteurs de même que les enregistrements seront effectués sous la supervision d'un(e) technicien(ne) en électrophysiologie et/ou du chercheur étudiant (qui aura reçu une formation à cet effet).
Afin d'assurer une bonne qualité d'enregistrement, vous devrez remplir un questionnaire de renseignements personnels. Certains troubles neurologiques, psychologiques ou de la vision,

des traumatismes crâniens passés ainsi que la prise de certains médicaments agissant sur le système nerveux peuvent entraîner l'exclusion de la recherche, car ces facteurs peuvent fausser les données enregistrées pendant l'expérimentation.

Pour la MEG : De plus, l'activité magnétique de votre cerveau sera enregistrée pendant le déroulement de l'expérience. Pour ce faire, vous porterez un casque contenant des capteurs MEG. L'emploi d'électrodes de type EEG est également nécessaire, d'une part pour surveiller les mouvements des yeux pendant l'expérience et, d'autre part, pour établir des liens entre l'activité électrophysiologique et l'activité magnétique du cerveau pendant la tâche.
L'application d'un gel conducteur précédée au préalable d'un nettoyage du cuir chevelu sera faite. Ce nettoyage consiste en un léger grattage du cuir chevelu à l'emplacement de chacune des électrodes. Ce nettoyage sera fait avec un tampon d'alcool isopropylique et une pâte abrasive.
Afin d'assurer une bonne qualité d'enregistrement, vous devrez remplir un questionnaire de dépistage d'éléments électromagnétiques et un questionnaire de renseignements personnels. Certains troubles neurologiques, psychologiques ou de la vision, des traumatismes crâniens passés, la prise de certains médicaments agissant sur le système nerveux ainsi que la présence d'objets métalliques dans le corps peuvent entraîner l'exclusion de la recherche, car ces facteurs peuvent fausser les données enregistrées pendant l'expérimentation.
Afin que nos analyses soient les plus précises possibles, nous devons connaître l'emplacement exact des bobines de repérage qui seront installées sur votre tête. Pour bien retrouver la position de ces bobines, nous voudrions prendre une photo de chacune d'elles. Le chercheur principal sera le seul à pouvoir accéder à ces photos, qui seront utilisées seulement pour bien localiser les bobines durant les analyses des données. Notez que ces photos seront conservées en format numérique sur un serveur sécurisé.
Nous donnez-vous la permission de prendre ces photos dans le but exprimé ci-haut? (Encerclez)
Oui / Non Signature: ____

Pour l'IRM : Cette portion du projet de recherche se déroulera à l'Unité de neuroimagerie fonctionnelle de l'Institut universitaire de gériatrie de Montréal.

Votre participation à ce projet de recherche consistera à passer une imagerie par résonance magnétique décrite précédemment. Ainsi, vous devrez rester immobile pendant qu'une image de votre cerveau est enregistrée. La durée de votre participation à cet enregistrement sera de 30 minutes à l'Unité de neuroimagerie fonctionnelle.

Avantages associés au projet de recherche

Vous ne retirerez aucun bénéfice personnel de votre participation à ce projet de recherche. Cependant, les connaissances acquises permettront de préciser les régions du cerveau responsables de la mémoire auditive.

Risques et inconvénients associés au projet de recherche

Pour l'EEG : Les enregistrements électrophysiologiques et les tâches comportementales ne comportent aucun risque. Cependant, l'installation d'électrodes requiert l'application d'un gel conducteur sur le cuir chevelu, ainsi qu'un nettoyage des régions du visage où des électrodes sont appliquées. Ce nettoyage sera fait avec un tampon d'alcool isopropylique et une pâte abrasive. Ces procédures peuvent créer un léger inconfort. De plus, pour obtenir un enregistrement électrophysiologique valide, plusieurs présentations des stimuli sont nécessaires. Des mesures seront prises afin de pallier d'éventuels inconvénients qui peuvent être entraînés par la répétition de stimuli soit la fatigue, l'inconfort relié à l'immobilité et à l'attention soutenue. En effet, la présentation des stimuli sera régulièrement interrompue, vous permettant ainsi de relaxer entre les périodes de travail à la tâche expérimentale. Vous serez informé de tout nouveau renseignement ou de toute modification aux conditions expérimentales susceptibles de remettre en cause la continuation de votre participation.

Pour la MEG : Cette étude ne comporte aucun risque ou inconvénient significatif pour votre santé physique ou psychologique. Afin d'éviter d'enregistrer du bruit environnemental, l'appareil d'enregistrement est placé dans une petite pièce fermée permettant de dévier les champs magnétiques ambiants. Vous serez seul dans cette pièce fermée, mais vous serez en tout temps en communication par interphone avec la technicienne. Comme cet appareil

fonctionne en état de supraconductivité, c’est-à-dire à très basse température, il est possible que vous ressentiez une légère froideur sur votre cuir chevelu.
Des mesures seront prises afin de pallier d’éventuels inconvénients qui peuvent être entraînés par la répétition de stimuli soit la fatigue, l’inconfort relié à l’immobilité et à l’attention soutenue. En effet, la présentation des stimuli sera régulièrement interrompue, vous permettant ainsi de relaxer légèrement. Vous serez informé de tout nouveau renseignement ou de toute modification aux conditions expérimentales susceptibles de remettre en cause la continuation de votre participation.

Pour l’IRM : Selon les connaissances actuelles, votre participation à une imagerie par résonance magnétique réalisée en recherche ne vous fera courir aucun risque, sur le plan médical, si vous ne présentez aucune contre-indication.

À cause de la puissance du champ magnétique émis par l'appareil, il est nécessaire de prendre certaines précautions. C'est pourquoi vous devez obligatoirement remplir un questionnaire détaillé afin de détecter toute contre-indication, par exemple, la présence d’un stimulateur cardiaque, d’un clip d’anévrisme, de prothèse métallique, de prothèse ou clip valvulaire cardiaque, de présence de métal dans l’œil ou sur le corps, de tatouage, de piercing, de broches dentaires ou si vous souffrez de claustrophobie. La vérification rigoureuse de la présence de contre-indication sera assumée par le technologue en fonction à l’UNF.

Les conditions imposées par l'utilisation de l'imagerie par résonance magnétique réalisée en recherche peuvent entraîner un inconfort du fait de devoir rester immobile et un inconfort pourrait également être associé au bruit qui est généré par le fonctionnement de l'appareil. Vous pourriez aussi ressentir un certain stress ou une sensation de claustrophobie.

Pour l’IRM : **Risques associés à la grossesse**
La participation à ce projet de recherche peut comporter des risques, connus ou non, pour les femmes enceintes, les enfants à naître ou encore les nourrissons allaités au sein. C’est pourquoi les femmes enceintes ou qui allaitent ne peuvent pas participer à ce projet.
Les femmes susceptibles de devenir enceintes devront se prêter à un test de grossesse avant la

réalisation de l'imagerie par résonance magnétique et elles ne pourront participer à ce projet que si le résultat du test de grossesse est négatif.

Pour l'IRM : **Découverte fortuite**

Les images acquises lors de l'imagerie par résonance magnétique réalisée en recherche ne font pas l'objet d'un examen médical par un médecin ni d'un examen radiologique par un radiologiste. Cependant, elles peuvent mettre en évidence des problèmes jusque-là ignorés, c'est ce que l'on appelle une découverte fortuite. C'est pourquoi, en présence d'une particularité, la procédure en cas de découverte fortuite sera appliquée.

Participation volontaire et possibilité de retrait

Votre participation à ce projet de recherche est volontaire. Vous êtes donc libre de refuser d'y participer. Vous pouvez également vous retirer de ce projet à n'importe quel moment, sans avoir à donner de raisons, en faisant connaître votre décision au chercheur responsable du projet ou à l'un des membres de l'équipe de recherche.

Le chercheur responsable du projet de recherche, le Comité mixte d'éthique de la recherche du RNQ, l'Université de Montréal ou les organismes subventionnaires peuvent mettre fin à votre participation, sans votre consentement, si de nouvelles découvertes ou informations indiquent que votre participation au projet n'est plus dans votre intérêt, si vous ne respectez pas les consignes du projet de recherche ou s'il existe des raisons administratives d'abandonner le projet.

Si vous vous retirez ou êtes retiré du projet, l'information déjà obtenue dans le cadre de ce projet sera conservée aussi longtemps que nécessaire pour rencontrer les exigences réglementaires.

Toute nouvelle connaissance acquise durant le déroulement du projet qui pourrait affecter votre décision de continuer d'y participer vous sera communiquée sans délai verbalement et par écrit.

Confidentialité

Durant votre participation à ce projet, le chercheur responsable ainsi que son personnel recueilleront et consigneront dans un dossier de recherche les renseignements vous concernant. Seuls les renseignements nécessaires pour répondre aux objectifs scientifiques de ce projet seront recueillis.

Ces renseignements peuvent comprendre les informations concernant votre état de santé passé et présent, vos habitudes de vie ainsi que les résultats de tous les tests, que vous aurez à faire durant ce projet. Votre dossier peut aussi comprendre d'autres renseignements tels que votre nom, votre sexe et votre date de naissance.

Tous les renseignements recueillis demeureront confidentiels dans les limites prévues par la loi. Afin de préserver votre identité et la confidentialité des renseignements, vous ne serez identifié que par un numéro de code. La clé du code reliant votre nom à votre dossier de recherche sera conservée par le chercheur responsable.

Le chercheur responsable du projet utilisera les données de recherche dans le but de répondre aux objectifs scientifiques du projet décrits dans le formulaire d'information et de consentement.

Les données de recherche pourront être publiées dans des revues scientifiques ou faire l'objet de discussions scientifiques, mais il ne sera pas possible de vous identifier. Également, les données de recherche pourraient servir pour d'autres analyses de données reliées au projet ou pour l'élaboration de projets de recherches futurs. Par ailleurs, vos renseignements personnels, tels que votre nom et vos coordonnées, seront conservés pendant 5 ans après la fin du projet par le chercheur responsable et seront détruits par la suite.

À des fins de surveillance et de contrôle, votre dossier de recherche pourra être consulté par une personne mandatée par le Comité mixte d'éthique de la recherche du RNQ, par l'établissement, par l'Université de Montréal ou par une personne mandatée par des organismes publics autorisés. Toutes ces personnes et ces organismes adhèrent à une politique de confidentialité.

À des fins de protection, notamment afin de pouvoir communiquer avec vous rapidement, vos noms et prénoms, vos coordonnées et la date de début et de fin de votre participation au projet seront conservés pendant un an après la fin du projet dans un répertoire à part maintenu par le chercheur responsable.

En conformité avec la loi sur l'accès à l'information, vous avez le droit de consulter votre dossier de recherche pour vérifier les renseignements recueillis et les faire rectifier au besoin, et ce, aussi longtemps que le chercheur responsable du projet détient ces informations.

Études ultérieures

Acceptez-vous que le chercheur responsable du projet ou un membre de son équipe de recherche reprenne contact avec vous pour vous proposer de participer à d'autres projets de recherche? Bien sûr, lors de cet appel, vous serez libre d'accepter ou de refuser de participer aux projets de recherche proposés. ☐ Oui ☐ Non

Financement du projet de recherche

Le chercheur responsable du projet a reçu un financement des organismes subventionnaires pour mener à bien ce projet de recherche.

Compensation

Vous recevrez un montant de 20 *(EEG)* / 40 *(MEG) /* 30 *(IRM)* dollars en guise de compensation pour votre déplacement et votre participation au projet de recherche. Par ailleurs, si vous vous retirez ou si vous êtes retiré du projet avant qu'il ne soit complété, vous recevrez un montant proportionnel à votre participation.

Indemnisation en cas de préjudice et droits du sujet de recherche

Si vous deviez subir quelque préjudice que ce soit dû à votre participation au projet de recherche, vous recevrez tous les soins et services requis par votre état de santé, sans frais de votre part.

En acceptant de participer à ce projet, vous ne renoncez à aucun de vos droits ni ne libérez les chercheurs, les organismes subventionnaires, l'établissement et l'Université de Montréal de leur responsabilité civile et professionnelle.

Procédures en cas d'urgence médicale

Veuillez noter que l'Institut universitaire de gériatrie de Montréal n'est pas un centre hospitalier de soins de courte durée qui offre des services d'urgence et qui compte sur la présence sur place d'un médecin 24 heures sur 24. Par conséquent, advenant une condition médicale qui nécessiterait des soins immédiats, les premiers soins vous seront dispensés par le personnel en place et des dispositions seront prises afin de vous transférer, si nécessaire, aux urgences d'un hôpital avoisinant.

Identification des personnes-ressources

Si vous avez des questions concernant le projet de recherche ou si vous éprouvez un problème que vous croyez relié à votre participation au projet de recherche, vous pouvez communiquer avec le chercheur responsable du projet de recherche, Pierre Jolicoeur, au.

Pour toute question concernant vos droits en tant que sujet participant à ce projet de recherche ou si vous avez des plaintes ou des commentaires à formuler, vous pouvez communiquer avec le commissaire local aux plaintes et à la qualité des services de l'IUGM au (514) 340.2109.

Surveillance des aspects éthiques du projet de recherche

Le Comité mixte d'éthique de la recherche du RNQ a approuvé ce projet de recherche et en assure le suivi. De plus, il approuvera au préalable toute révision et toute modification apportée au protocole de recherche et au formulaire d'information et de consentement. Pour toute information, vous pouvez joindre le secrétariat du Comité, par téléphone au (514) 340.2800, poste 3250 ou par courriel à l'adresse suivante:

Consentement

Titre du projet de recherche : Mémoire à court-terme auditive

I. Consentement du sujet

J'ai pris connaissance du formulaire d'information et de consentement. Je reconnais qu'on m'a expliqué le projet, qu'on a répondu à mes questions et qu'on m'a laissé le temps voulu pour prendre une décision.

Je consens à participer à ce projet de recherche aux conditions qui y sont énoncées. Une copie signée et datée du présent formulaire d'information et de consentement m'a été remise.

Nom et signature du sujet de recherche Date

II. Signature de la personne qui a obtenu le consentement si différent du chercheur responsable du projet de recherche.

J'ai expliqué au sujet de recherche les termes du présent formulaire d'information et de consentement et j'ai répondu aux questions qu'il m'a posées.

Nom et signature de la personne qui obtient le consentement Date

III. Signature et engagement du chercheur responsable du projet

Je certifie qu'on a expliqué au sujet de recherche les termes du présent formulaire d'information et de consentement, que l'on a répondu aux questions que le sujet de recherche avait à cet égard et qu'on lui a clairement indiqué qu'il demeure libre de mettre un terme à sa participation, et ce, sans préjudice.

Je m'engage, avec l'équipe de recherche, à respecter ce qui a été convenu au formulaire d'information et de consentement et à en remettre une copie signée au sujet de recherche.

Nom et signature du chercheur responsable du projet de recherche Date